IOSR Journal of Agriculture and Veterinary Science (IOSR-JAVS)
e-ISSN: 2319-2380, p-ISSN: 2319-2372. Volume 14, Issue 7 Ser. I (July 2021), PP 22-34
www.iosrjournals.org

Inheritance of Fodder and Seed Yield in Dual-purpose Cowpea

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Abstract
Genetic studies of dual-purpose traits in cowpea was carried out at Teaching and Research Farm of Joseph Saawuan Tarka University, Makurdi, Nigeria. The objectives of the study were to determine the type and magnitude of gene action controlling dual-purpose traits and to determine heritability and genetic advance for the traits under study. Six generations viz: P_1, P_2, F_1, F_2, BC_1 and BC_2 constituted the experimental material. They were grown in a Randomized Complete Block Design with three replications. Data were obtained on 100-seed weight, seed yield, stem weight, pod weight, pod length. number of pods per plant, number of branches, number of seeds per plant, leaf weight, leaf-stem ratio, dual trait and fodder yield. Statistical analyses conducted included analysis of variance, scaling tests and gene effects, heritability and genetic advance under selection. Significant variation existed among the generations in the two crosses for all the traits indicating sufficient diversity for those traits. Non-allelic interactions along with additive and dominant components played pertinent role in the determination of various characters in cowpea. Inheritance of all traits studied in both crosses were governed by duplicate gene action. Selection in later generation for duplicate gene action is recommended. Moderate to high heritability and genetic advance exhibited by most of the traits indicated that heritability was due to additive gene effect. The presence of both additive and non-additive gene effects, moderate to high heritability coupled with moderate/high expected genetic advance in inheritance of most of the traits, suggest that pureline method of breeding could be employed. Breeding methods involving crossing like biparental, pureline breeding, mass selection, that take care of both additive and non-additive gene action should be adopted for improvement of various characters studied.

Key Words*: dual-purpose, heritability, genetic advance, generation mean analysis, duplicate gene action, biparental, pureline.*

Date of Submission: 28-06-2021 Date of Acceptance: 12-07-2021

I. Introduction

Cowpea, (*Vigna unguiculata* (L.) Walp. (2n=22) belongs to the family Fabaceae (Ibrahim *et al*., 2017; OECD, 2016). It is one of the most important legume crops in the world and it is a major food crop in Africa. The bulk of cowpea production and consumption is in sub-Saharan Africa (SSA) particularly West and Central Africa. Nigeria produces the most quantity of cowpea grains annually at approximately 2.14 million metric tonnes (FAOStat, 2017) and consumes more than 3.0 million metric tonnes.

The crop is of vital importance to the livelihood of millions of people in West and Central Africa. From its production, rural families derive food, animal feed and cash income. It provides nutritious grain and an inexpensive source of protein for both rural poor and urban consumers. Cowpea grain contains about 25% protein and 64% carbohydrate (Bressani, 1985) and therefore has a tremendous potential to contribute to the alleviation of malnutrition among resource-poor farmers. The cowpea haulm is used to feed the livestock, whereas the latter provides manure (Tarawali *et al*., 1997). Cowpea fodder is as important as the grains, especially in the dry savannas, where, in the driest months of the year, cost of fodder per kg is as much as that of the grain (Langyintuo *et al*., 2003). Considering the importance of cowpea for both humans and animals, there is need to develop a variety with both good grain and fodder productivity, otherwise known as dual-purposeness.

Understanding the genetic control of these traits will facilitate development of a viable breeding strategy for improved dual-purpose cowpea varieties with high grain and fodder yield. However, being a cleistogamous plant, production of hybrid cowpea remains economically nonviable for now. Therefore, a more detailed genetic study involving not only the F_1 generation but also advanced generations (F_2 and backcross) will be useful for a breeding programme. Hence the use of generation mean analysis (GMA). Therefore, this study was carried out to: (i) determine the type and magnitude of gene action controlling dual-purpose traits in cowpea and (ii) to determine heritability and genetic advance for the traits under study.

II. Materials and Methods

Geographic and Edaphic Details of the Experimental Area

The experiment was conducted at the Teaching and Research Farm of Joseph Saawuan Tarka University, Makurdi, (Latitude 7.41^0N and Longitude 8.37^0E at an elevation of 97 m above the sea level). Makurdi falls within the Southern Guinea Savannah Agro-ecological zone of Nigeria. The climatic environment of the study area was characterized by an annual rainfall of about 1330.20 mm and a mean annual temperature of about 27.80°C. The soil was classified as Typic Paleustalfs i.e. associated with moderately deep, well drained, fine loamy soils.

Experimental materials

Six generations *viz*: P_1, P_2, F_1, F_2, BC_1 and BC_2 of two crosses involving four varieties of cowpea constituted the experimental material. Details of the experimental material used are given below.

Cross	Generation	Features
I	IT89KD-288 x UAM10 2021-1	
	P_1	IT89KD-288, white seeded, fodder type
	P_2	UAM10 2021-1, brown seeded , seed type
	F_1	IT89KD-288 x UAM10 2021-1
	F_2	(IT89KD-288 x UAM10 2021-1) F_1 self
	BC_1	(IT89KD-288 x UAM10 2021-1) x IT89KD-288
	BC_2	(IT89KD-288 x UAM10 2021-1) x UAM10 2021-1
II	UAM09 1055-6 x UAM09 1051-1	
	P_1	UAM09 1055-6, white seeded, fodder type
	P_2	UAM09 1051-1, brown seeded, seed type
	F_1	UAM09 1055-6 x UAM09 1051-1
	F_2	(UAM09 1055-6 x UAM09 1051-1) self
	BC_1	(UAM09 1055-6 x UAM09 1051-1) x UAM09 1055-6
	BC_2	(UAM09 1055-6 x UAM09 1051-1) x UAM09 1051-1

Crossing Technique

The F_1 hybrids were generated from the above two single crosses between August, 2017 and April, 2018. Selfing of the F_1 to produce F_2 as well as backcrossing of the F_1 were done between August, 2018 and April, 2019. The crosses were carried out in the green house of Joseph Saawuan Tarka University, Makurdi, Nigeria. The crossing work was done by emasculation of the flower in the evening followed by artificial pollination next day morning. The seeds of individual parental lines, F_2 seeds from selfed F_1 plants seeds including backcrosses were harvested separately and labelled accordingly.

Experimental Design, Evaluation and Agronomic Practices

The six generations (P_1, P_2, F_1, F_2, BC_1, and BC_2) of each cross were grown in a Randomized Complete-Block Design with three replications in Teaching and Research Farm, Joseph Saawuan Tarka University, Makurdi. Parental lines and the F_1s were grown in two-row plots while the F_2 families and the BC_1 and BC_2 were grown in four-row plots, each of 4m length. The planting was be done in 25th August, 2019. Recommended agronomic practices were followed throughout the cropping season.

Data Collection

In each replication, 5 plants from the P_1, P_2 and F_1 generations (the non-segregating generations), and 100 from F_2 plants, 18 plants from the BC_1 plants and 17 plants from BC_2 plants (F_2, BC_1 and BC_2 being the segregating generations) were randomly selected and observations were recorded on per plant basis for the following characters:

i. 100-seed weight: weight (g) of 100 seeds.
ii. Seed yield: Total dry grain weight in grams per plant.
iii. Dry stem weight: Weight in grams of the dry shoot at maturity excluding leaves of each plant.
iv. Pod weight: Weight in grams of all dry pods per plant.
v. Pod length at maturity.
vi. Number of pods per plant at maturity.
vii. Number of branches: total number of primary branches per plant.
viii. Dry leaf weight at maturity**:** Weight in grams of all the leaves per plant.
ix. Number of seeds per plant.
x. Leaf-stem ratio: Ratio of dried leaves to dried stems for each plant.
xi. Dual trait**:** Ratio of dried pods weight to total biomass.
xii. Fodder yield: Weight in grams of dried leaves, chaff, and dried stem per plant.

Statistical analysis

Data collected was subjected to analysis of variance (ANOVA) to test for the significant difference between generations in a cross for various characters with a fixed effect model. Crosses showing significant differences among entries (progenies) for the character were subjected to generation mean analysis for estimation of gene effects using six parameter model as suggested by Hayman (1958) and Jinks and Jones (1958).

Scaling tests as described by Hayman and Mather (1955) were used to check the adequacy or otherwise of the additive-dominance model for different characters in each cross. The adequacy of scale must satisfy two conditions *viz*: additivity of gene effects and independence of heritable component from non-heritable ones. The test of first condition provides information regarding the absence or presence of gene interaction. If one of four scaling tests was found significant, it indicated presence of epistasis and inadequacy of additive-dominance model. The A, B, C and D tests were made using the following equations for their scales and variances.

(a) Estimates of scales

$A = 2\,\overline{BC_1} - \overline{P_1} - \overline{F_1}$

$B = 2\,\overline{BC_2} - \overline{P_2} - \overline{F_1}$

$C = 4\overline{F_2} - 2\overline{F_1} - \overline{P_1} - \overline{P_2}$

$D = 2\overline{F_2} - \overline{BC_1} - \overline{BC_2}$

(b) Estimates of variances

$V_A = 4V(\overline{BC_1}) + V(\overline{P_1}) + V(\overline{F_1})$

$V_B = 4V(\overline{BC_2}) + V(\overline{P_2}) + V(\overline{F_1})$

$V_C = 16V(\overline{F_2}) + 4V(\overline{F_1}) + V(\overline{P_1}) + V(\overline{P_2})$

$V_D = 4V(\overline{F_2}) + V(BC_1) + V(BC_2)$

Where,

A, B, C and D are the scales and $\overline{P_1}$, $\overline{P_2}$, $\overline{F_1}$, $\overline{F_2}$, $\overline{BC_1}$ and $\overline{BC_2}$ are generated mean of a character, while V_A, V_B, V_C, and V_D are the corresponding variances of the scales and $V(P_1)$, $V(P_2)$, $V(F_1)$, $V(F_2)$, $V(BC_1)$ and $V(BC_2)$ are the variance of the sample means of the respective generation.

In the absence of non-allelic interactions as indicated by non-significance of scaling test, three parameter model suggested by Jinks and Jones (1958) was used for estimation of genetic components.

Heritability in broad sense

Broad sense heritability in percentage was calculated by using formula suggested by Warner (1952) as follows:

$h^2(b)\ (\%) = \frac{VF2 - VF1}{VF2} \times 100$

Where,

h^2b = Heritability in broad sense

VF_2 = Variance of F_2 generation (Phenotypic variance)

VF_1 = Variance of F_1 generation

VF_2-VF_1 = Genotypic variance

Heritability in narrow sense

Narrow sense heritability, as suggested by Warner (1952) was calculated as follows:

$h^2_{(n)}\ (\%) = (\frac{1}{2}\ D/VF_2) \times 100$

$h^2_{(n)}$ = Heritability in narrow sense

D = additive genotypic variance

VF_2 = phenotypic variance

Heritability percentage was categorized as demonstrated by Robinson *et al* (1949).

0-30% - low

31-60% - moderate

61% and above – high

Estimation of expected genetic advance (E.G.A.) under selection

The expected genetic advance at 5 percent level of selection intensity was estimated by using the following formula:

$E.G.A = K.h^2(b).\ \sigma p$

Where;

h^2 (b) = heritability in broad sense

σp = phenotypic standard deviation

K = selection differential = 2.06 at 5% selection pressure)
Expected genetic advance as percent of mean was estimated by the following formula:
E.G.A (% of mean) = $\frac{G.A}{\bar{X}}$ x 100
Where;
G.A = Genetic advance
$\bar{X}$ = mean of the character under study
Genetic advance as percent of mean was categorized as suggested by Johnson *et al.* (1995).
0-10% - low
11-20% - moderate
above20% – high.

III. Results

Analysis of Variance

Analysis of variance for individual character was carried out for each of the two crosses and the results are presented in Tables 1 and 2. The mean squares indicated significant differences among the generations of all the two crosses for each of the traits. Variation due to generation mean was highly significant (P≤0.01) for all the traits in cross I (IT89KD-288 X UAM10 2021-1) except for pod length which was significant at 5% probability level (Table 2). In Cross II, highly significant variation due to generation mean was recorded for all the traits (Table 2).

Table 1: Mean squares from analysis of variance for 100-seed weight, seed yield, stem weight, pod weight, pod length, number of pods per plant in six crosses in two crosses of cowpea

Source	Df	100-seed weight	Seed yield	Stem weight	Pod weight	Pod length	Number of pods
Cross I (IT89KD-288 X UAM10 2021-1)							
Generation	5	3.771**	4356.13**	3979..06**	1595.06**	1.023*	914.409**
Replication	2	0.157	57.83	22.04	69.08	0.0223	5.077
Error	10	0.128	57.27	41.12	62.37	0.232	84.446
Cross II (UAM09 1055-6 X UAM09 1051-1)							
Generation	5	9.373	2976.54**	2225.91**	3704.7**	4.168**	658.72**
Replication	2	0.792	86.01	30.86	340.7	0.090	13.6
Error	10	1.193	251.41	52.84	326.4	0.328	38.15

*,** = significant difference at 5% and 1% level of probability respectively
Df = degree of freedom

Table 2: Mean squares from analysis of variance for number of branches, number of seeds per plant, leaf weight, leaf to stem ratio dual trait and fodder weight in six crosses in two crosses of cowpea

Source	Df	Number of branches	Number of seeds	Leaf weight	Leaf to stem ratio	Dual trait	Fodder yield
Cross I (IT89KD-288 X UAM10 2021-1)							
Generation	5	5.0169**	1.51130**	411.33**	0.052406**	0.012836**	5931.38**
Replication	2	0.00889	0.03922	37.81	0.002006	0.002006	83.42
Error	10	0.00889	0.11051	11.12	0.00612	0.000686	327.46
Cross II (UAM09 1055-6 X UAM09 1051-1)							
Generation	5	3.00189**	1.8810**	350.04**	0.098877**	0.020659**	2059.25**
Replication	2	0.29556	0.2575	12.04	0.003617	0.001939	34.37
Error	10	0.07356	0.3435	13.03	0.006383	0.002352	304.35

*,** = significant difference at 5% and 1% level of probability respectively
Df = degree of freedom

Scaling Test and Estimation of Gene Effects

The mean values of all the six generations *viz*; P_1, P_2, F_1, F_2, BC_1, and BC_2 for twelve different characters of all the two crosses were first subjected to genetic analysis. The test of adequacy of scale is important because in most of the cases the estimation of additive and dominance components of variations is made assuming the absence of gene interaction. This also provides information about the type of epistasis, which depends on the sign of the two components only, *viz*; h and l. Those crosses in which h and l have similar sign (either positive or negative) indicate presence of complementary epistasis and those in which h and l have opposite sign reveal duplicate epistasis. When the scale is adequate, the values of A, B, C and D should be zero within the limits of their respective standard errors. The significance of any one of these scales (A, B, C and D) indicate the presence of non-allelic interaction. Individual sample scaling tests (A, B, C and D) of Hayman and Matter (1995) were employed to detect the presence of epistasis. For the families and characters, wherein only of the simple scaling test was significant, six parameter (m, d, h, i, j and l) model as suggested by Hayman

(1958) and Jinks and Jones (1958) was applied for the partitioning of gene effects into epistatic components including principal gene effects.
The character and cross-wise results are presented in Tables 3 and 4. "m" parameter was significant for all the traits hence this component was not been explained individually.

Hundred seed weight

The scaling tests, B, C and D were highly significant in Cross I (IT89KD-288 x UAM10 2021-1) indicating the presence of epistasis. Estimated genetic factors such as additive (0.29) was significant. Similarly, dominance (-7.47), additive x additive (-6.85), additive x dominance (0.69) and dominance x dominance (8.05) were highly significant. Duplicate type of gene action was responsible for this trait. In cross II (UAM09 1055-6 x UAM09 1051-1), scaling test A was significant while scales B and D were highly significant indicating the presence of epistasis. Estimation of genetic parameters i.e. additive (0.73), additive x dominance (-2.70) and dominance x dominance (4.95) were all highly significant. The character was governed by duplicate gene action.

Seed yield

In cross I (IT89KD x UAM10 2021-1), highly significant scaling tests were recorded in A, C and D indicating the presence of non-allelic interaction. All the genetic factors namely additive (74.90), dominance (162.30) additive x additive (212.32), additive x dominance (91.31) and dominance x dominance (-284.46) were highly significant. This trait was governed by duplicate type of gene action. In cross II (UAM09 1055-6 x UAM09 1051-1), scaling test C and D showed highly significant difference which indicate inadequacy of additive–dominance model and presence of epistasis. Estimates of genetic parameters revealed that dominance (135.09) and additive x additive (80.36) recorded highly significant difference. Similarly, additive (22.61), additive x dominance (-0.57) and dominance x dominance (-47.91) were not significantly different. Duplicate type of gene action was responsible for inheritance of this trait.

Stem weight

Scaling tests A and D were highly significant in Cross I indicating the presence of non-allelic interaction. Estimate of genetic parameters show that additive (41.56), dominance (151.41), additive x additive (128.34), additive x dominance (32.49) and dominance x dominance gene interactions were all highly significant in this cross. Inheritance of stem weight was governed by duplicate epistasis. In Cross II (UAM09 1055-6 x UAM09 1051-1), scale A was significant while scale D was highly significant indicating the presence of epistasis. Estimates of genetic parameters revealed that only two interactions, additive x additive (-35.92) and additive x dominance (-25.88) were highly significant. Inheritance of this trait in this cross is also governed by duplicate gene action.

Pod weight (g)

In cross I (IT89KD-288 x UAM10 2021-1), epistasis was found to be present as scaling test D was found to be highly significant. Additive (22.34) genetic effect was highly significant while dominance (103.63) was significantly higher in value. The interaction additive x additive (103.23) also had higher significant value. The other interactions additive x dominance (-19.22) and dominance x dominance (-19.49) were not significant. In cross II (UAM09 1055-6 x UAM09 1051-1) non-allelic interaction was found as scaling tests B and D were respectively significant and highly significant. Dominance (-90.59) was significant while additive (60.87) was highly significant. Results of the interactions indicate that additive x dominance (70.05) was significant while additive x additive (-155.02) and dominance x dominance (298.00) were highly significant. Duplicate gene action played a role in the inheritance of this trait.

Table 3: Scaling and gene effects in two crosses of cowpea for 100-seed weight, seed yield, stem weight, pod weight, pod length and number of pods per plant

Cross	A	B	C	D	M	d	h	I	j	l	Gene effect
100-seed weight											
I	0.08	-1.29**	5.64**	3.42**	18.09**	0.29*	-7.47**	-6.85**	0.69**	8.05**	D
II	-3.39*	2.01**	2.19	1.79**	17.74**	0.73**	-4.33**	-3.57**	-2.70**	4.95**	D
Seed yield											
I	127.38**	-55.25	-140.19**	-106.16**	58.31**	74.90**	162.30**	212.32**	91.31**	-284.46**	D
II	-16.80	-15.65	-112.81**	-40.18**	80.65**	22.61	135.09**	80.36**	-0.57	-47.91	D
Stem weight											
I	82.30**	17.31	-28.73	-64.17**	67.62**	41.56**	151.41**	128.34**	32.49**	-227.95**	D
II	-28.54*	23.22	30.60	17.96**	89.38**	-2.22	-15.39	-35.92**	-25.88**	41.25	D
Pod weight											
I	-22.59	15.85	-109.97	-51.62**	104.67**	22.34**	103.63*	103.23**	-19.22	-96.49	D
II	-1.44	-141.54*	12.04	77.51**	156.95**	60.87**	-90.59*	-155.02**	70.05*	298.00**	D
Pod length											
I	0.22	0.87	1.01	-0.04	13.11	0.68	1.71				
II	-1.86*	51.24**	-0.81	-25.09*	14.49**	-26.69**	50.85**	50.19**	-26.55**	-99.56**	D
Number of pods per plant											
I	12.66	-20.45*	-88.73**	-88.47**	49.32**	22.56**	80.08**	80.95**	16.56**	-73.16**	D
II	-32.16**	-15.76	55.68**	51.80**	66.80**	-4.43**	-73.51**	-103.61**	-8.20	151.53**	D

*,** = significant difference at 5% and 1% level of probability respectively
D = Duplicate gene effect

Table 4: Scaling and gene effects in two crosses of cowpea for number of branches, number of seeds per plant, leaf weight, leaf to stem ratio dual trait and fodder weight

Cross	A	B	C	D	m	d	h	i	j	l	Gene effect
Number of branches											
I	1.52**	0.54	-0.61	-1.33**	4.33**	0.85**	3.04**	2.67**	0.49	-4.73**	D
II	-0.24	-0.22	2.24**	1.35**	4.58**	0.16	-2.21**	-2.70**	-0.01	3.16**	D
Number of seeds per plant											
I	0.26	1.19	-0.05	-0.75**	13.57**	0.01	1.94**	1.50**	-0.42	-2.95**	D
II	0.48	0.19	0.42	-0.12	13.59**	-0.48*	2.42				
Leaf weight											
I	21.84*	20.60**	-27.34**	-34.89**	25.98	6.85	73.47**	69.77**	0.62	-112.21**	D
II	-22.21**	-5.44	-8.78	9.44**	32.81**	-5.59**	-16.88**	-18.88**	-8.39**	46.53**	D
Leaf to stem ratio											
I	-0.21	0.11	-0.47*	-0.19**	0.43**	-0.13*	0.22	0.37**	-0.16	-0.27	D
II	-0.13	-0.40**	-0.34	0.09*	0.46**	-0.06*	-0.38**	-0.18**	0.14*	0.71**	D
Dual trait											
I	-0.08	-0.04	0.05	0.08**	0.53**	-0.05*	-0.15*	-0.16**	-0.02	0.28	D
II	0.17**	-0.24**	0.10	0.08**	0.55**	0.18**	-0.06	-0.17**	0.20**	0.23*	D
Fodder weight											
I	114.14**	29.99	-21.65	-82.89**	137.64**	50.30**	205.13**	165.78**	42.08**	-309.91**	D
II	-57.69	228.56	24.62**	-73.13*	141.50*	-125.75**	207.55**	146.25*	-143.13**	-317.12*	D

*,** = significant difference at 5% and 1% level of probability respectively
D = Duplicate gene effect

Pod length (cm)

In cross I (IT89KD-288 x UAM10 2021-1), none of the scaling tests A, B, C and D was significant indicating the presence of additive – dominance model. Hence the three parameter model was used. Estimates of genetic parameters revealed that both additive (0.68) and dominance (1.91) were not significant. In Cross II (UAM09 1055-6 x UAM09 1051-1), epistasis was significant since scaling tests A, B and D were significant. The results of the estimates of genetic factors revealed that additive (-26.69) and dominance (50.19) were present. All the interactions namely additive x additive (50.19), additive x dominance (-26.55) and dominance x dominance (-99.56) were highly significant. Duplicate gene action was responsible for inheritance of this trait.

Number of pods per plant

Epistasis was found present in Cross I (IT89KD-288 x UAM10 2021-1) as scaling tests B, C and D were significant. Estimates of genetic parameters revealed that additive (22.56) and dominance (80.08) were significant. In a similar vein the interactions additive x additive (80.95), additive x dominance (16.56) and dominance x dominance (-73.16) were all highly significant. In cross II (UAM09 1055-6 x UAM09 1051-1), scaling tests A, C and D were highly significant indicating the presence of epistasis. In the estimates of genetic parameters dominance (-73.51) was highly significant while additive (-4.43) was not significant. Likewise, the interactions additive x additive (-103.61) and dominance x dominance (151.53) were significant while additive x dominance (-8.20) was not significant. Inheritance of this character was governed by duplicate gene action.

Number of branches

Non allelic interaction was found in this cross I (IT89KD-288 x UAM10 2021-1) since scaling tests C and D were highly significant. The results obtained from the six parameter model indicated highly significant values of additive (0.85), dominance (3.04), additive x additive (2.67) and dominance x dominance (-4.73). Duplicate type of gene action was found responsible for this character. In cross II (UAM09 1055-6 x UAM09 1051-1), highly significant scaling tests C and D indicated the presence of epistasis. Dominance (-2.21), additive x additive (-2.70) and dominance x dominance estimates were found to be significant. Contrary, additive (0.16) and additive x dominance interaction were not significant. Duplicate type of gene action was responsible for inheritance of this trait.

Number of seeds per plant

In Cross I (IT89KD-288 x UAM10 2021-1), scaling test D was highly significant which indicated the presence of non-allelic interaction. Highly significant value was recorded for dominance (1.94), additive x additive (1.50), additive x dominance (-0.42) and dominance x dominance (-0.42) and dominance x dominance (-2.95). For inheritance of this trait, duplicate type of gene action was implicated. The non-significance of any of the scaling tests (A, B, C and D) indicated the presence of additive-dominance model. Hence the three parameter model was used in estimation of genetic parameters, additive (0.48) estimate was found significant.

Leaf weight

Scaling tests A, B, C and D were all significant in cross I (IT89KD-288 x UAM10 2021-1), indicating the presence of inter-allelic interaction. Results of the estimates of genetic parameters revealed that additive (6.85), dominance (73.47), additive x additive (60.77) and dominance x dominance (-112.21) were highly significant while additive x dominance (0.62) interaction was not significant. Inheritance of this trait was governed by duplicate gene action. In cross II (UAM09 1055-6 x UAM09 1051-1), the scaling tests A and D were highly significant indicating the presence of epistasis. Additive (-5.59) and dominance (-16.58) were highly significant. Also the interactions *viz*; additive x additive (-18.88), additive x dominance (-8.39) and dominance x dominance (45.53) were highly significant. Duplicate gene action was responsible for inheritance of this trait.

Leaf to stem ratio

In cross I (IT89KD-288 x UAM10 2021-1), scaling test C was significant while D was highly significant. This indicated the presence of epistasis. Further genetic analysis revealed that additive (-0.13) was significant while additive x additive interaction was highly significant. Duplicate gene action was found responsible for inheritance of this trait. Scaling test B was highly significant while D was significant in cross II (UAM09 1055-6 x UAM09 1051-1). This indicated the inadequacy of additive x dominance model and the presence of epistasis. Significant values were recorded for additive (-0.06) and additive x dominance (0.14) while dominance (-0.38), additive x additive (-0.18) and dominance x dominance (0.71) were highly significant. Duplicate gene action was responsible for inheritance in this trait.

Dual trait

Highly significant scaling test D indicated the presence of non-allelic interaction in cross I (IT89KD-288 x UAM10 2021-1). Analysis of genetic parameters revealed that additive (-0.05), dominance (-0.15) and dominance x dominance were significant while additive x additive interaction (-0.16) was highly significant. Inheritance of this trait is governed by duplicate gene action. In cross II (UAM09 1055-6 x UAM09 1051-1), scaling test A, B and D were highly significant which indicated the presence of epistasis. From the analysis of six parameter model, additive (0.18), additive x additive (-0.17) and additive x dominance (0.20) were highly significant while dominance x dominance (0.23) was significant. Duplicate gene action was responsible for inheritance of this trait.

Fodder yield

Highly significant scaling tests were recorded in scales A and D indicting the presence of non-allelic interaction. All the genetic parameters namely additive (50.30), dominance (205.13), additive x additive (165.78), additive x dominance (42.08) and dominance x dominance (309.91) were highly significant. The trait was governed by duplicate epistasis. In Cross II (UAM09 1055-6 x UAM09 1051-1), scaling tests A and D were significant while scale B was highly significant indicating the presence of epistasis. Genetic estimates revealed that additive (-125.75), dominance (207.55) and additive x dominance (-143.13) were found to be highly significant while additive x additive (146.25) and dominance x dominance (-137.12) were found to be significant. This trait was governed by duplicate gene action.

Heritability and Genetic Advance

Heritability is a measure of the efficiency of a selection system in segregating genotypes. Quantitative traits are largely influenced by the environment, therefore, they are not highly heritable. High, moderate and low heritability are not rigidly defined as it varies from one character to another character, but the following classification as suggested by Robinson *et al*. (1949) are widely accepted.

The value of expected genetic advance for various characters is demarcated into three categories *viz*; low, moderate and high as follows (Robinson *et al*, 1955). Both broad and narrow sense heritability as well as genetic advance estimates obtained are presented in Tables 5 and 6.

One hundred seed weight

For this trait, narrow sense heritability ranged from 54.65% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 21.68% (low) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 78.85% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 45.45% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Genetic advance ranged from 15.19% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 12.56% (medium) in Cross II (UAM 09 1055-6 x UAM09 1051-1).

Table 5: Estimates of narrow sense heritability, (H_2 (n), broad sense heritability (H_2 (b) and genetic advance (GA) in two crosses of cowpea for 100-seed weight, seed yield, stem weight, pod weight, pod length, number of pods per plant

Estimate (%)	100-seed weight	Seed yield	Stem weight	Pod weight	Pod length	Number of pods per plant
H_2 (n)	54.65	43.66	42.45	41.37	26.62	41.75
H_2 (b)	78.85	87.92	82.79	60.68	43.41	70.73
GA	15.19	38.85	78.67	36.89	21.95	51.81
H_2 (n)	21.68	40.96	21.91	41.96	11.96	31.82
H_2 (b)	45.45	71.00	70.98	56.80	30.80	89.00
GA	12.56	11.10	39.87	26.54	26.54	39.24

Table 6: Estimates of narrow sense heritability, (H_2 (n), broad sense heritability (H_2 (b) and genetic advance (GA) in two crosses of cowpea for number of branches, number of seeds per plant, leaf weight, leaf to stem ratio dual trait and fodder yield

Estimate (%)	Number of branches	Number of seeds per plant	Leaf weight	Leaf to stem ratio	Dual trait	Fodder yield
H_2 (n)	41.13	11.63	34.45	47.45	33.52	46.57
H_2 (b)	70.43	43.33	76.84	65.60	57.33	78.18
GA	12.08	21.45	58.77	40.68	10.10	64.26
H_2 (n)	28.93	37.76	11.49	50.85	33.67	32.00
H_2 (b)	88.94	60.32	60.71	79.99	52.44	51.00
GA	49.63	28.02	25.39	33.77	18.41	21.81

Seed yield

Narrow sense heritability for this trait ranged from 43.66% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 40.96% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 87.92% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 40.96% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 87.92% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 71% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1). Meanwhile, genetic advance ranged from 38.85% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 11.10% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Stem weight

For this trait, narrow sense heritability ranged from 42.45% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 21.91% (low) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 82.79% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 70.98% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1). Genetic advance ranged from 78.67% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 39.87% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Pod weight

For this trait, narrow sense heritability ranged from 41.37% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 41.96% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). The broad sense heritability ranged from 60.68% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 56.80% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1) while genetic advance ranged from 36.89% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 26.54% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Pod length

For this trait, narrow sense heritability ranged from 26.62% (low) in Cross I (IT89KD-288 x UAM10 2021-1) to 11.96% (low) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 43.41% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 30.80% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Expected genetic advance ranged from 21.95% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 26.54% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Number of pods per plant

For this trait, narrow sense heritability ranged from 41.75% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 31.82% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 70.73% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 89% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1). The expected genetic advance ranged from 51.81% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 39.24% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Number of branches

The narrow sense heritability for this trait ranged from 41.13% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 28.93% (low) in Cross II (UAM09 1055-6 x UAM09 1051-1). The broad sense heritability range from 70.43% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 88.94% (high) in Cross II (UAM091055-6 x UAM09 1051-1). Expected genetic advance ranged from 12.08% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 46.93% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Number of seeds per plant

For this trait, narrow sense heritability ranged from 11.63% (low) in Cross I (IT89KD-288 x UAM10 2021-1) to 37.76% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 43.33% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 60.22% (high) in Cross II (UAM09 1055-6 x 1051-1). Expected genetic advance for this trait ranged from 21.45% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 28.02% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Leaf weight

For this trait, the narrow sense heritability ranged from 34.45% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 11.49% (low) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 76.84% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 60.71% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1). The genetic advance ranged from 58.77% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 25.39% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Leaf to stem ratio

Narrow sense heritability for this trait ranged from 47.45% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 50.85% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 57.33% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 79.99% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1). Expected genetic advance ranged from 40.68% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 33.77% (high) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Dual trait

Narrow sense heritability for this trait ranged from 33.52% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 33.67% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 57.33% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 52.44% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Expected genetic advance for this trait ranged from 10.10% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 18.41% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1).

Fodder weight

For this trait, narrow sense heritability ranged from 46.57% (medium) in Cross I (IT89KD-288 x UAM10 2021-1) to 32% (medium) in Cross II (UAM09 1055-6 x UAM09 1051-1). Broad sense heritability ranged from 78.18% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 51% (medium) in Cross II (UAM09 1055-6 x UAM 09 1051-1). Genetic advance ranged from 64.26% (high) in Cross I (IT89KD-288 x UAM10 2021-1) to 21.81% (high) in Cross II (UAM09 1055-6xUAM09 1051-1).

IV. Discussion

Analysis of Variance

The analysis of variance for individual characters was carried out in each of the two crosses for the twelve traits. Mean sum of squares revealed significant differences among the generations in all the crosses for all the traits studied indicating considerable variability in the experimental materials. Significant variation for all the characters under study might be due to more diversity between the parents which resulted in high variability among the various generations and less environmental influence for the expression of these traits. Pathak (2015) obtained similar results on cowpea.

Scaling tests and estimation of gene effects

Before any model is fitted to estimate the gene actions involved, scaling test was performed as outlined by Hayman and Mather (1955) to ascertain the adequacy or otherwise of the additive-dominance model. The significance of A, B, C and D scaling test for the characters indicated the presence of appreciable amount of epistasis and inadequacy of additive-dominance model. To calculate various non allelic gene effects in all the two crosses therefore, six parameter model was used for estimation of genetic components except in Cross II (UAM09 1055-6 x UAM09 1051-1) for number of seeds per plant where the absence of non-allelic interaction indicated by non-significance of scaling test suggested the use of three parameters model given by Jinks and Jones (1958) for estimation of genetic components. Presence of epistasis for seed yield per plant and its components have also been reported by Singh *et al*. (2006), Khan *et al*. (2007), Sarode *et al.* (2009), Kumar and Prakash (2010), Rashwan (2010), Tchiagam *et al*. (2011), Adeyanju *et al.* (2012), Haque e*t al.* (2013), Kumar *et al*. (2013), Sharma *et al.* (2013), Akhshi *et al.* (2014), Iqbal 2015), Nautiyal *et al.* (2015) and Pathak (2015).

For traits where scaling test A, B, C and D were significant indicated the inadequacy of additive-dominance model and the presence of epistasis. Additive and dominance gene effects were highly significant in all the crosses. The magnitude of dominance gene effect was higher than the additive gene effect for all the traits in Cross I and dual trait in Cross II. Among the interactions, additive x additive gene interaction was significant for all the traits. Dominance x dominance interaction contributed significantly in almost all the traits except for pod weight, and leaf to stem ratio in Cross I and, seed yield, and stem weight in Cross II. Duplicate epistasis was implicated in both crosses. The findings indicated that both additive and dominance gene effects contributed to the inheritance of the traits in both crosses. Similar results were also reported by Singh *et al*. (2006), Khan *et al.* (2007), Sarode *et al.* (2009), Kumar and Prakash (2010), Rashwan (2010), Tchiagam *et al.* (2011), Adeyanju *et al*. (2012), Haque *et al*. (2013), Kumar *et al.* (2013), Sharma *et al*. (2013), Akhshi *et al.* (2014), Iqbal (2015), Nautiyal *et al.* (2015) and Pathak (2015).

Additive x dominance gene interactions were significant for almost all the traits except seed yield and leaf weight in Cross II as well as pod weight in Cross I. Duplicate epistasis governed inheritance of all the traits in both crosses. Similar results of duplicate epistasis governing inheritance of such traits were also reported by Singh *et al*. (2006), Khan *et al.* (2007), Sarode *et al.* (2009), Kumar and Prakash (2010), Rashwan (2010), Tchiagam *et al*. (2011), Adeyanju *et al.* (2012), Haque *et al.* (2013), Kumar *et al.* (2013), Sharma *et al.* (2013), Akhshi *et al.* (2014), Igbal (2015), Nautiyal *et al.* (2015) and Pathak (2015).

Results from the study revealed that for most traits, both additive and dominance gene actions were significant except in Cross II for seed yield, number of pods per plant and number of branches and in Cross I for leaf weight, pod length and number of seed per plant. This indicate the need for pedigree selection for further improvement. Similar results of the contributions of both additive and non-additive gene actions controlling inheritance of such characters were reported by Singh *et al*. (2006), Khan *et al*. (2007), Sarode *et al.* (2009), Kumar and Prakash (2010), Rashwan (2010), Tchiagam *et al*. (2011), Adeyanju *et al.* (2012), Haque *et al.* (2013), Kumar *et al*. (2013), Sharma *et al.* (2013), Akhshi *et al.* (2014), Igbal (2015), Nautiyal *et al.* (2015) and Pathak (2015).

Higher magnitude of dominance components indicates that heterosis breeding could be employed for improvement of such characters but type of epistasis should also be taken into consideration in deciding breeding procedure as duplicate epistasis will result in mutual cancellation effects of such genes and there would be no heterosis for such case. Since breeders are looking towards varietal improvement programme and to take advantage of both additive and dominance component as well as inter allelic interactions, biparent mating could be effective to break undesirable linkages.

Additive gene action if present in self-pollinating crops like cowpea, it implies that the breeder can effectively select at various level of inbreeding because additive gene effects are readily transmittable from one generation to another (Gravois and McNew, 1993). Anbumalarmathi (2005) reported additive gene effect for days to first flowering in rice. The parents could be utilized as potential donors in the hybridization programme which might result in the identification of superior segregant through transgressive breeding. Significance of dominance gene effect depicts the importance of dominance gene action. The current results are in agreement with the earlier reports of Rogbell and Subbaraman (1997), Deepasankar *et al.* (2008) and Verma *et al.* (2010) in rice.

Both additive and dominance gene actions play major role in several characters. In such cases biparental mating design or reciprocal recurrent selection can be followed for further recombination of alleles to produce desirable segregants. These methods can also be well adopted in order to harness the epistatic interactions by way of breaking the undesirable linkages (Muthuvijayaragavan and Murugan, 2017).

Heritability and Genetic Advance

In crop improvement, only genetic component of variation is important being the component that is transmitted to the next generation. Heritability indicates the effectiveness with which the selection of genotypes could be based on phenotypic performance. This could be achieved through determining heritability and genetic advance under selection.

Moderate narrow sense heritability was recorded for 100 seed weight, seed yield, stem weight, fodder weight, leaf weight, pod weight, number of pods per plant, number of branches, leaf to stem ratio and dual trait in Cross I (IT89KD-288 x UAM10 2021-1). In Cross II (UAM09 1055-6 x UAM09 1051-1), moderate narrow sense heritability was recorded for seed yield, fodder weight, pod weight, number of pods per plant, number of seeds per plant, leaf to stem ratio, and dual trait.

Moderate to high broad sense heritability was recorded in all the traits in both crosses. The high estimates of heritability indicates that these traits were comparatively less affected by environment and their phenotype is good reflection of genotype and this possess paramount importance in making selection of superior genotype on the basis of phenotypic performance of the metric traits. In case of lower heritability, pedigree, sib or progeny test can be employed for genetic improvement. In the present investigation, high to moderate genetic advance was recorded for all the traits in both crosses.

Shift in the gene frequency caused by selection pressure is termed as genetic advance. Johnson *et al.* (1955) found it more useful to estimate heritability values together with genetic advance in predicting the ultimate choice of best individuals for selection. High heritability coupled with high genetic advance obtained in Cross I and Cross II for stem weight, fodder yield, leaf weight, number of pods per plant and leaf to stem ratio. Seed yield and pod weight have high heritability coupled with high genetic advance in Cross I only while number of branches and number of seeds per plant recorded high heritability coupled with high genetic advance in Cross II only.

Moderate heritability coupled with high genetic advance were recorded in Cross I (IT89KD-288 x UAM10 2021-1) for pod length, and number of seeds per plant while in Cross II (UAM09 1055-6 x UAM09 1051-1), they were recorded for pod weight and pod length. This indicated that heritability was due to additive gene effects and selection would be effective. High heritability coupled with moderate genetic advance were obtained in Cross I for 100-seed weight and number of branches while they were obtained in Cross II seed yield. This indicated the presence of additive genetic effects and that selection would be effective for these traits. Those results are similar to those of Rehman *et al.* (2009), Aremu and Adewale (2010), Kyu *et al.* (2011), Tchiagam *et al.* (2009), Noubissie *et al.* (2011), Adeyanju *et al.* (2012), Santos *et al.* (2012), Ayo-Vaughan *et al.* (2013), Akhshi *et al.* (2014), Iqbal (2015) and Pathak (2015).

V. Conclusion

Inheritance of the traits studied in both crosses were governed by duplicate gene action. Moderate to high heritability and genetic advance exhibited by most of the traits indicated that heritability was due to additive gene effect. Since both additive and non-additive gene effects, moderate to high heritability coupled with moderate/high expected genetic advance were involved for inheritance of most of the traits, pureline method of breeding could be employed. This involves conventional approach of selection of superior

recombinants and their intermating for development of elite homozygous recombinants having high performance.

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