Combining ability and genetic components for pod and seed traits in cowpea lines

Monininuola Adefolake Ayo-Vaughan, Omolayo Johnson Ariyo, Christopher Olusanya Alake

Department of Plant Breeding and Seed Technology, Federal University of Agriculture, Abeokuta, Nigeria

Abstract

The identification of suitable parental genotypes potentially generating superior lines with traits contributing to the overall yield of cowpea is an important step in the development of improved varieties. Eight parents and their 28 hybrids obtained through diallel crossing design were evaluated in a randomized complete block design with three replications. Highly significant differences among the parents and their hybrids for different traits were observed. General combining ability (GCA) mean squares were larger than the specific combining ability mean squares for all the traits analysed. The ratio h^2/H_2 revealed different number of genes controlling the traits, pointing out their polygenic inherited control. The estimated low narrow sense heritability recorded in this study indicated that recurrent selection procedure could be effective to improve the analysed traits in the genotypes included in this study. *Kananado* with large, positive and significant GCA effects was identified as the parent with desirable genes for the genetic improvement of the considered yield component in cowpea. In addition, IT03K-316-1 × Cowpea-2 and IT99K-316-2 × Kananado seemed to be the best hybrids for number of pods/plant and 100-seed weight, respectively.

Correspondence: Monininuola Adefolake Ayo-Vaughan, Department of Plant Breeding and Seed Technology, Federal University of Agriculture, P.M.B. 2240 Abeokuta, Nigeria. Tel: +234.08033432804.
E-mail: folakevaughan@gmail.com

Key words: *Vigna unguiculata*, parents, hybrids, additive gene, transgressive segregation, yield traits.

Acknowledgements: the authors thank the International Institute of Tropical Agriculture (IITA), the Institute for Agricultural Research and Training (IAR&T) and the National Centre for Genetic Resources and Biotechnology (NACGRAB), all in Ibadan, Nigeria for providing the seeds of parental lines for this study. Mr. Tayo Oyelakin of IITA, Ibadan, Nigeria is also appreciated for his assistance in the computer analysis of the collected data. This article forms part of a Ph.D thesis of Monininuola A. Ayo-Vaughan.

Received for publication: 6 July 2012.
Revision received: 7 February 2013.
Accepted for publication: 8 February 2013.

Italian Journal of Agronomy 2013; 8:e10
doi:10.4081/ija.2013.e10

Introduction

Cowpea, *Vigna unguiculata* (L) Walp, is an important legume crop in tropical African countries, particularly in Nigeria. It is a staple food crop widely cultivated and consumed by many people, both in the Northern and Southern parts of Nigeria and is part of the farming system of people in these ecologies. All the plant parts that are used for food are nutritious, providing proteins, vitamins and minerals. Mature dry seeds of cowpea contain proteins, ranging from 23-30% depending on the cultivar (Bliss, 1975), and 50-67% starch (Quin, 1997).

Despite the increasing importance of cowpea in the diet of many Nigerians, yield per hectare remains low. Although yields of 2500 kg/ha are achievable, several constraints have kept farmers' yields constantly low at levels between 350 and 700 kg/ha. If the yield barrier is to be overcome, a new strategy to improve the genetic potential of cowpea plants by introducing new genes is required. For this to be achievable, genotypes with a potential for better quality traits are needed as parent stocks to develop improved varieties (Aremu, 2005). Accurate selection of parents is normally difficult because yields of potential parents rarely provide an effective basis for identifying those genotypes with the greatest potential for generating superior lines once crossed (Moalafi *et al*., 2010). It is usually necessary to evaluate various traits contributing to the overall yield of the genotype in crossbred populations prior to making any decision regarding parental combinations. Pod and seed traits are examples of such yield components in cowpea. Yield per hectare is the product of population density, number of pods per plant, number of seeds per pod and mean seed weight. Hence, seed yield is a complex trait that includes various components and finally results in a highly plastic yield structure (Amiri-Oghan *et al*., 2009; Diepenbrock, 2000).

Information on the general and specific combining abilities (GCA and SCA, respectively) of parents will be helpful in the analysis and interpretation of the genetic basis of important traits (Rajani *et al.*, 2001). Ogunbodede *et al.* (2000) also implied in their work on maize that the best performing progeny may be produced by crossing two parents having the highest estimates of general combining ability. Diallel crossing technique is commonly adopted to evaluate the parentals in terms of their performance and to obtain a rapid, overall picture of the genetic control of a trait in a number of inbred lines (Jinks, 1954). This mating system has also been identified by Adeniji and Kehinde (2003) as a tool for evaluating genetic components underlying inheritance of metric traits. The model presented by Griffings (1956) shows that genotypic variation is partitioned into the general and specific combining abilities, while Hayman (1954) analysis of combining ability further explains the combining ability and the genetic components underlying inheritance of traits. The present study, therefore, seeks to understand the gene actions and combining abilities of cowpea genotypes for pod and seed traits with the aim of developing a strategy for improving such yield traits.

Materials and methods

The experiment under consideration was carried out in two phases. Phase 1 was aimed to generate the F_1 seeds in a greenhouse at International Institute of Tropical Agriculture (IITA) (Ibadan) in February-May 2008, while Phase 2 was carried out at the Teaching and Research Farm of the Federal University of Agriculture (Abeokuta, South-Western Nigeria) (FUNAAB) during the second planting season (September-December 2008) to evaluate the diallel crosses and combining ability under field conditions. Abeokuta is generally located within the forest-savannah transitional zone; the experimental field was located at latitude 7.53°N, 3.38°E with elevation of 450 m asl. The soil type around the experimental site was composed of loamy sand and was classified as Arenic Plinthic Kandindalf (Busari, 2011) with a pH range of 6.8 to 7.8. Climate conditions during the crop cycle were hot and humid with an average rainfall of 7.99 mm (Table 1).

Eight genetically-divergent genotypes were selected as the parents for the diallel crosses (Table 2) on the basis of the classification in a molecular dendrogram (results not included). The seeds of the parents were sown in 12-cm-diameter plastic pots filled with garden soil. The soil was kept moist by watering and hand-weeded when necessary. At anthesis, plant to plant pollination of all possible crosses except reciprocals was made in twenty-eight cross combinations following the 8×8 diallel crossing pattern in the greenhouse. Each cross was tagged for easy identification, and, at maturity, the F_1 seeds were harvested separately. The experimental field was thoroughly prepared by ploughing and harrowing, and weed stubbles and crop residues were removed to make the land clean. The 8 parents and their 28 F_1 genotypes were then evaluated on the field. Their seeds were sown in 10.80-m-long single row plots and spaced 0.60 m apart. Intra-row spacing was 0.45 m and seeding rate was one seed/hole. The experiment was laid out in a randomized complete block design with three replications. Field pests were controlled using cypermethrin + dimethoate (Sherpaplus®, University of Nottingham, UK) at a rate of 40 mL/s in 15 L of water and weeding was done manually when necessary. During the course of the study, data were collected on the following 4 agronomic traits: number of pods per plant, pod length (cm), number of seeds per pod and 100-seed weight (g). For each parent, the mean of twenty plants per plot was obtained, while for the 28 hybrids for each evaluated trait, the means of ten plants per plot were obtained due to the smaller number of seeds. Means per plot were analyzed for combining ability in the parents and F_1s (excluding reciprocals) following Griffings's model I (fixed effects) - method II (1956). Genetic parameters for estimating the gene effects and parameter ratios in the parents and F_1s of the diallel cross were obtained according to Hayman's method (1954) using Ukai's DIAL statistical package (1998). Mean squares from the analysis of variance showing the effects of additive and dominance components were obtained according to Walter and Morton (1978). The dominance component b_1 measuring directional dominance; b_2 examining the difference between selfs and crosses among parents, and b_3 measuring residual dominance variation, *i.e.* variation not yet accounted for by b_1 and b_2, were calculated. Heritability was estimated for each trait differently. Narrow-sense heritability, which measures the proportion of additive variance in the overall variance, was estimated as follows:

$$(h^2_n) = \delta^2A/(\delta^2_A + \delta^2_D + \delta^2_E) \quad (1)$$

While, broad-sense heritability, which measures the proportion of both additive and dominance variances in the overall variance, was estimated as follows:

$$(h^2_b) = (\delta^2_A + \delta^2_D)/(\delta^2_A + \delta^2_D + \delta^2_E) \quad (2)$$

where: δ^2_A, additive variance;
δ^2_D, dominance variance;
δ^2_E, environmental or error variance;

Students *t-test* was used to test the hypothesis GCA or SCA=0.

Results

Mean squares for general and specific combining abilities among genotypes and their crosses for the traits analyzed are presented in Table 3. Larger and highly significant mean squares were observed for GCA in comparison to SCA for number of pods per plant, number of seeds per pod and 100-seed weight. For instance, mean squares for GCA were between two and eight times greater than the SCA estimates for all the four traits. Also, mean square ratios 2GCA/(2GCA+SCA) were very close to unity for the traits analyzed. Mean squares for SCA were also significant for all the traits except pod length.

Table 4 shows how all the traits except pod length had significant effects for GCA but in different directions. Only Kananado showed positive GCA effect for all the four traits, while others had positive GCA for some traits and negative GCA for others. However, Cowpea-2 and Kananado had relatively large and positive GCA values for number of pods per plant and 100-seed weight, respectively, while IT97K-1042-3 and Erubu had negative GCA for both traits.

Estimates of SCA effects for the 28 F_1 hybrids for the traits evaluated are provided in Table 5. Positive and significant SCA effects were observed for number of pods per plant and 100-seed weight in nine hybrids, namely IT99K-316-2 × IT97K-1042-3, IT99K-316-2 × IT03K-316-

Table 1. Mean monthly temperature, rainfall and relative humidity for cowpea crop cycle in the Federal University of Agriculture (Abeokuta) in the cropping season of September-December 2008 (Department of Agro-metrology and Water Resources Management, Federal University of Agriculture, Abeokuta, Nigeria).

Months	Mean temperature (°C)	Relative humidity (%)	Rainfall (mm)
September	26.1	86.7	11.4
October	28.2	84.5	7.04
November	30.1	80.9	0.00
December	28.3	75.9	13.5

Table 2. Code names and sources of the eight cowpea genotypes used as parents in the diallel crosses.

Source no.	Genotype code names	Source
1	IT99K-306-2	IITA
2	IT97K-1042-3	IITA
3	IT98K-131-2	IITA
4	IT03K-316-1	IITA
5	Ife-BPC	IAR&T
6	Cowpea-2	NACGRAB
7	Erubu	NACGRAB
8	Kananado	NACGRAB

IITA, International Institute for Tropical Agriculture; IAR&T, Institute of Agricultural Research and Training; NACGRAB, National Centre for Genetic Resources and Biotechnology.

Table 3. Mean squares for general and specific combining abilities for four traits of cowpea in an 8×8 diallel crosses.

Source of variation	df	Number of pods/plant	Pod length (cm)	Number of seeds/pod	100-seed weight (g)
Replication	2	33.05	25.46	0.65	13.51
GCA	7	160.47**	20.22	13.32**	150.53**
SCA	28	75.43*	14.28	5.99**	57.29**
Error	46	42.71	26.88	1.69	12.30
Ratio 2GCA/(2GCA + SCA)	-	0.81	0.74	0.82	0.84

df, degree of freedom; GCA, general combining ability; SCA, specific combining ability. *, ** significant at 0.05 and 0.01 probability levels respectively.

Table 4. Estimates of general combining ability effects for pod and seed traits among eight cowpea genotypes.

Parents	Number of pods/plant	Pod length (cm)	Number of seeds/pod	100 seed weight (g)
IT99K-316-2(P1)	-2.70**	1.65	-1.41**	1.91**
IT97K-1042-3(P2)	-4.25**	-0.94	-1.17**	-3.58**
IT98K-131-2(P3)	0.56**	-0.11	0.03**	-0.14**
IT03K-316-1(P4)	2.11**	0.04	1.03**	-0.81**
Ife-BPC (P5)	0.15**	1.25	0.29**	-1.42**
Cowpea-2(P6)	5.02**	-0.65	0.31**	1.20**
Erubu (P7)	-2.27**	-1.48	0.18**	-2.70**
Kananado (P8)	1.39**	0.24	0.74**	5.54**

*, ** significantly different at 0.05 and 0.01 probability levels respectively.

Table 5. Estimates of specific combining ability effects among F_1 hybrids for four cowpea traits.

Crosses	Number of pods/plant	Pod length (cm)	Number of seeds/pod	100 seed weight (g)
$P_1 \times P_2$	10.53*	-0.60	-4.10**	-9.89**
$P_1 \times P_3$	-2.53*	-3.40	1.09**	2.53**
$P_1 \times P_4$	6.75*	-0.12	2.97**	-2.59**
$P_1 \times P_5$	-7.95*	9.02	-1.10**	-8.12**
$P_1 \times P_6$	3.26*	-1.58	-1.17**	6.40**
$P_1 \times P_7$	1.02*	-1.71	1.12**	1.82**
$P_1 \times P_8$	-11.09*	-1.61	1.18**	9.85**
$P_2 \times P_3$	1.55*	1.39	0.83**	4.52**
$P_2 \times P_4$	-1.83*	1.40	1.59**	4.75**
$P_2 \times P_5$	-1.19*	-1.75	1.27**	6.70**
$P_2 \times P_6$	-8.44*	-0.44	0.67**	0.33
$P_2 \times P_7$	-3.31*	-0.39	-0.91**	-7.11**
$P_2 \times P_8$	2.69*	0.39	0.64**	0.70**
$P_3 \times P_4$	-6.12*	-0.57	-2.44**	-0.35
$P_3 \times P_5$	3.79	-0.54	1.12**	0.94**
$P_3 \times P_6$	-0.24*	0.74	-0.48**	-2.62**
$P_3 \times P_7$	-2.51*	0.19	-0.75**	-0.08
$P_3 \times P_8$	6.05*	2.19	0.62**	-3.07**
$P_4 \times P_5$	-1.49*	-1.30	0.36	-0.51**
$P_4 \times P_6$	7.29*	0.06	-0.13	-1.68**
$P_4 \times P_7$	0.49*	0.19	-1.47**	0.31
$P_4 \times P_8$	-5.10*	0.35	-0.87**	0.07
$P_5 \times P_6$	0.08	-1.71	0.19	-0.44**
$P_5 \times P_7$	-0.21	-1.40	0.14	6.02**
$P_5 \times P_8$	6.96*	-2.31	-1.70**	-2.71**
$P_6 \times P_7$	1.04*	2.44	1.47**	0.95**
$P_6 \times P_8$	-2.99*	0.55	-0.55**	-2.94**
$P_7 \times P_8$	3.48*	0.59	0.68**	-1.91**

P_1, IT99K-316-2; P_2, IT97K-1042-3; P_3, IT98K-131-2; P_4, IT03K-316-1; P_5, Ife-BPC; P_6, Cowpea-2; P_7, Erubu; P_8, Kananado. *, ** significant at 0.05 and 0.01 probability levels respectively.

1, IT98K-131-2 × Kananado, IT03K-316-1 × Cowpea-2, Ife-BPC × Kananado, IT99K-316-2 × Cowpea-2, IT99K-316-2 × Kananado, IT97K-1042-3 × Ife-BPC and Ife-BPC × Erubu, with the largest and positive SCA effect recorded in the cross IT99K-316-2 × IT97K-1042-3 for number of pods per plant. Large and negative SCA values were observed for number of pods per plant and 100-seed weight in the crosses IT99K-316-2 × Kananado and IT99K-316-2 × IT97K-1042-3, respectively. Hybrid IT99K-316-2 × Ife-BPC also recorded relatively large and negative SCA values for both number of pods per plant and 100-seed weight.

Table 6 presents the mean squares from the analysis of variance for additive (a) and dominance (b) effects and dominance components (b_1, b_2 and b_3) for the four traits evaluated. Highly significant gene effects were observed for additive (a), dominance (b) and dominance components b_1, b_2 and b_3 for all traits studied except pod length.

The estimates of genetic parameters and their ratios for the four traits evaluated in F_1 population of the diallel crosses are presented in Table 7. Additive (D) and non-additive (H_1 and H_2) components were greater than zero and therefore were found significant for all the characters studied. However, dominance (H_1 and H_2) effects were larger than the additive (D) and environmental (E) components in all cases. Estimates of average direction of dominance (h) were positive for all traits, while the estimates of the frequency (F) were negative for all traits. The ratio h^2/H_2, *i.e.* the number of effective factors, had a minimum value of 3.89 for number of pods per plant and a maximum of 5.72 for pod length. Estimated values of ratio ($H_2/4H_1$) ranged between 0.24 for number of pods per plant to 0.26 for pod length. Broad-sense heritability (H_B) estimates were never below 94.0% for any of the characters evaluated, but narrow-sense heritability (H_N) estimates ranged between 1.01% for 100-seed weight and 5.14% for pod length.

Discussion

The significant mean squares for GCA and SCA obtained for number of pods per plant, number of seeds per pod and 100-seed weight suggest that the parents and their hybrids in the diallel crosses were highly variable for these traits. In addition, a large portion of total variability among F_1 hybrids in the current study was a result of gene actions with predominantly additive effects. This is a desirable phenomenon necessary for better crop improvement, especially when quantitative traits are concerned. This corroborates Ojo's findings (2003) on soybean cultivars and Kumar *et al.*'s (2007) on genetic study of earliness in cowpea. Therefore, the crosses under investigation will result into effective selection in early generations of segregating materials due to small environmental effects (Karademir *et al.*, 2007). However, non-additive gene action due to dominance and/or epistasis, as revealed by significant SCA mean squares, must have contributed to the total genetic variability observed in these three traits. Gupta *et al.* (1993), however, assumed that the presence of non-additive gene effects could reduce

Table 6. Mean squares from analysis of variance for additive and dominance effects and dominance components for four traits of cowpea.

Source of variation	df	Number of pods/plant	Pod length (cm)	Number of seeds/pod	100 seed weight (g)
Replication	2	25.71	19.80	0.50	10.50
Additive effect (a)	7	96.28**	12.13	7.99**	90.32**
Dominance effect (b)	28	331.62**	165.54**	48.20**	352.15**
(b_1)	1	6049.92**	4093.68**	1088.51**	7202.38**
(b_2)	7	64.19*	8.09	5.33**	60.21**
(b_3)	20	139.30**	24.23	11.19**	111.82**
Error	70	28.28	17.82	1.11	8.17

df, degree of freedom; *,**significant at 0.05 and 0.01 probability levels respectively.

Table 7. Estimates of genetic parameters and ratios between them in the F_1 population of a half diallel cross observed for four cowpea traits (Hayman, 1954).

Parents	Number of pods/plant	Pod length (cm)	Number of seeds/pod	100 seed weight (g)
D	-10.44	-6.58	-0.41	-3.01
H_1	267.35	114.82	38.79	292.38
H_2	255.45	117.43	37.45	275.92
h	31.51	25.92	13.36	34.38
F	-15.66	-9.86	-0.62	-4.52
E	10.44	6.58	0.41	3.01
$(H_1/D)½$	5.06	4.18	9.73	9.86
h^2/H_2	3.89	5.72	4.77	4.28
$H_2/4H_1$ (±UV)	0.24	0.26	0.24	0.24
Narrow-sense (HN) (%)	3.62	5.14	1.04	1.01
Broad-sense (HB) (%)	96.38	94.86	98.96	98.99

D, additive variance; H_1, H_2, dominance variances; h, average direction of dominance; F, frequency of dominance; E, environmental variance; $(H_1/D)½$, average degree of dominance; h^2/H^2, number of effective factors; $H_2/4H_1$ (±UV), balance of positive and negative alleles.

the progress expected from early generation selection. Kang (1994) suggested the use of the ratio of GCA to SCA sums of square to determine their relative importance in genetic control of traits and thus the breeding value of genotypes. The value of approximately one obtained for all the traits in this study shows that the traits are highly heritable, and that the additive gene effects were more important than non-additive gene effects for these traits (Amiri-Oghan *et al*., 2009). Since the additive gene effects are fixable through direct selection, the predominance of additive genetic variance for the analyzed traits indicated that mass selection on the F_1 generation of the crosses would be worthwhile in the development of cowpea genotypes with increased number of pods per plant, seeds per pod and higher seed weight.

Cowpea-2 and Kananado with relatively large and positive GCA values could be used as parents in hybridization programs for genetic improvement of number of pods per plant and 100-seed weight. This is in line with Baker's report (1978) assuming that large and positive GCA estimates with significant additive gene effects could provide desirable genes for the improvement of the traits under consideration. Kananado, in particular, appears to be the most desirable genotype for the genetic improvement of nearly all the traits evaluated and therefore recommended for further use. IT99K-316-2, IT97K-1042-3, and Erubu were poor general combiners for number of pods per plant, number of seeds per pod and 100-seed weight because of the negative GCA values associated with them and thus undesirable parents in the genetic improvement of these traits (Daniel *et al.,* 2006). The preponderance of additive genetic variance in almost all traits among the genotypes evaluated could be exploited to an advantage by using the conventional breeding methods, such as pedigree or pure line selections. Rupela and Johnansen (1995) used pure line selection to improve nodulation in pigeon pea as a result of large GCA effects.

Positive and significant SCA effects observed for number of pods per plant and 100-seed weight in nine of the 28 crosses studied suggest that these crosses (*i.e.* IT99K-316-2 × IT97K-1042-3, IT99K-316-2 × IT03K-316-1, IT98K-131-2 × Kananado, IT03K-316-1 × Cowpea-2, Ife-BPC × Kananado, IT99K-316-2 × Cowpea-2, IT99K-316-2 × Kananado, IT97K-1042-3 × Ife-BPC, and Ife-BPC × Erubu) were the best specific combiners for these two traits. Hybridization between two good general combiners may be governed by additive × additive gene actions which might elicit transgressive segregants in the advanced generations for the traits, thus producing hybrids with good specific combining ability (Daniel *et al.* 2006). On the other hand, the crosses exhibiting good SCA effect - though deriving from parents that are poor general combiners as was observed in the crosses IT99K-316-2 × IT97K-1042-3 and IT99K-316-2 × IT03K-316-1 for number of pods per plant, and IT97K-1042-3 × Ife-BPC and Ife-BPC × Erubu for 100-seed weight - suggest the presence of dominance or epistatic gene actions and an indication of genetic interaction between favorable alleles contributed by both parents (Adeniji and Kehinde, 2003). Large and positive SCA effects for a trait have also been reported by Ojo (2003) to suggest the possibility for transgressive segregation for the trait in later generation of selfing. The negative estimate of SCA values recorded in this study is indicative of a partial dominance situation across loci (Adeniji and Kehinde, 2007). However, highly significant SCA effects do suggest that non-additive gene action (dominance and additive × dominance gene effects) could play a vital role in the improvement of cowpea for the traits of concern (Ojo, 2003).

Highly significant gene effects observed for additive (a), dominance (b) and dominance components b_1, b_2 and b_3 for all traits analyzed except pod length confirmed the presence of both additivity and dominance in the expression of these yield component traits. Among the components of dominance, the significance of b_1 indicates that dominance was unidirectional, towards the better or higher parent in this study. The highly significant variance of the b_2 also suggests that the eight cowpea genotypes probably have different number of genes (Paul *et al*., 1995). The significant residual dominance effect of b_3 is assumed to result from additive x dominance or dominance x dominance effects specific to each cross (Ayo-Vaughan, 2010).

Additive and non-additive variances were significantly different from zero for all the traits and this indicated that the two effects were important components of genetic variation for these traits. Similar results were recorded by Romanus *et al*. (2008), who reported both additive and non-additive components in the inheritance of some yield traits in cowpea. The study reported by the authors was carried out at the University of Nsukka, in the South-Eastern Nigeria. Nsukka has a sub-humid agro-ecology with sandy loam Oxisol (Ndubizu, 1981). From this study, cowpea turns out to be well adapted to a wide range of ecological conditions and soil types in Nigeria.

In addition, the dominance (H_1 and H_2) effects were larger than the additive (D) components in all cases, thus suggesting that non-additive gene action played a predominant role in the inheritance of these traits. The presence of dominance was also confirmed by the estimated values of the average degree of dominance $(H_1/D)^{½}$ which ranged between 4.18 and 9.86. Among the dominance components (H_1 and H_2), a condition where H_1 was greater than H_2 ($H_1>H_2$), as observed in this study, indicated that the positive and negative alleles at the loci for these traits were not equal in proportion (Adeniji and Kehinde, 2007).

The positive estimates of average direction of dominance (h) for all the analyzed traits also confirmed that dominance was unidirectional and in the direction of the parent with higher expression of the traits (Ayo-Vaughan, 2010). On the other hand, the negative estimates of the frequency of dominance (F) for all four traits indicated a high frequency of dominant decreasing alleles than dominant increasing alleles in the parental genotypes. The ratio h^2/H_2 revealed different number of genes controlling the four traits. This study indicated a minimum of three genes involved in the inheritance of number of pods per plant and a maximum of six genes in the inheritance of pod length, revealing their polygenic inheritance as is characteristic of quantitative traits. The observed estimates of $H_2/4H_1$ were close to 0.25 (the theoretical maximum), indicative of fairly equal distribution of dominant and recessive alleles among the parents. Therefore, the loci exhibiting positive and negative genes were equally distributed in the parents for these traits (Adeniji and Kehinde, 2007; Amiri-Oghan *et al*., 2009).

Narrow-sense heritability (H_N) was low (<20%) while broad-sense heritability (H_B) was high (>30%). This shows that the dominance proportion was too high for it to affect the overall value of heritability (H_B). These hybrids, therefore, cannot be used for a direct breeding program. This is obvious from the values of the dominance components compared with those of the additive ($D<H_1$ and H_2), in addition to the high values of the dominance ratio (average degree of dominance).

Conclusions

The four cowpea traits analyzed in this study were under additive and dominance gene effects, with the additive effects being more important. The additive effects for these traits would enhance pure-line or pedigree breeding and effective selection in early generations of segregating materials. Kananado with relatively large, positive and significant GCA effects could be used as parent with desirable genes for genetic improvement of the considered yield components in cowpea. Also, from the *per se* performance (GCA values) of parents and the SCA values of the hybrids, IT03K-316-1 × Cowpea-2 and IT99K-316-2 × Kananado appeared to be the best specific combiners for number of pods/plant and 100-seed weight, respectively, and are governed by additive × additive gene actions.

Though, broad-sense heritability (H_B) estimates were very high (>94%) for all the traits evaluated, narrow-sense heritability (H_N) values were very low (<20%). Since narrow-sense heritability shows the proportion of a trait that is transmitted from parents to their progenies, all the four traits investigated cannot be used for any direct breeding program. Improvement for these traits will therefore require a recurrent selection procedure to allow for favorable gene recombination in later generations before a final selection is made.

References

Adeniji OT, Kehinde OB, 2003. Diallel analysis of pod yield in West African Okra (Abelmoschus caillei (A. Chev) Stevels). J. Genetics Breed. 57: 291-4.

Adeniji OT, Kehinde OB, 2007. Combining ability and genetic components for length and width of pods in West African Okra (Abelmoschus caillei (A. Chev) Stevels). J. Agron. 6:131-6.

Amiri-Oghan H, Fatokian MH, Javidfar F, Alizadeh B, 2009. Genetic analysis of grain yield, days to flowering and maturity in oilseed rape (Brassica napus L.) using diallel crosses. Int. J. Plant Prod. 3:19-26.

Aremu CO, 2005. Diversity, selection and genotype x environment interaction in cowpea (Vigna unguniculata (L.) Walp). Degree Diss., University of Agriculture, Abeokuta, Nigeria.

Ayo-Vaughan MA, 2010. Studies on genetics and yield stability in cowpea, Vigna unguiculata (L.) Walp. Degree Diss., University of Agriculture, Abeokuta, Nigeria.

Baker RJ, 1978. Issues in diallel analysis. Crop. Sci. 18:533-6.

Bliss FA, 1975. Cowpea in Nigeria. In: M. Milner (ed.) Proc. Symposium on Nutritional Improvement of Food Legumes by Breeding, 3-5 July, 1972. United Nations Protein Advisory, New York, NY, USA, pp 151-156.

Busari MA, 2011. Soil physical quality and isotopic fractionation after tillage, application of poultry manure and fertilizers in Abeokuta, South-Western Nigeria. Degree Diss., University of Agriculture, Abeokuta, Nigeria.

Daniel IO, Oloyede HT, Adeniji OT, Ojo DK, Adegbite AE, 2006. Genetic analysis of earliness and yield in elite parental lines and hybrids of tropical maize (Zea mays L.). J. Genet. Breed. 60:289-96.

Diepenbrock W, 2000. Yield analysis of winter oil seed rape (Brassica napus L.): a review. Field Crop Res. 67:35-49.

Griffings B, 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Austr. J. Biol. Sci. 9:463-93.

Gupta VP, Kapila RK, Sood VK, Rana ND, 1993. Predicting transgression on the basis of combining ability and heterosis in soybean. Crop Improv. 20:143-50.

Hayman BL, 1954. The theory and analysis of diallel crosses. Genetics 39:789-809.

Jinks JL, 1954. The analysis of continuous variation in a diallel cross of Nicotiana rustica varieties. Genetics 39:767-88.

Kang MS, 1994. Applied quantitative genetics. M. S. Kang Publ., Baton Rouge, LA, USA.

Karademir C, Gencer O, Karademir E, 2007. Heterosis and combining ability for yield and fiber properties in cotton (Gossypium hirsutum L.) under drought stress conditions. Asian J. Plant Sci. 6:667-72.

Kumar PA, Sanjay K., Maurya A.N., 2007. Genetic study of earliness in cowpea (Vigna unguiculata L. Walp). Indian J. Hort. 64:63-6.

Moalafi AI, Asiwe JAN, Funnah SM, 2010. Germplasm evaluation and enhancement for the development of cowpea (Vigna unguiculata (L.) Walp dual-purpose F_2 genotypes. Afr. J. Agric. Res. 5:573-9.

Ndubizu TOC, 1981. Effect of split fertilizer application on growth and yield of falsehorn plantain (Musa spp.) in the rain forest belt of Nigeria. Tropenlandwirth Z Land-wirtsch Tropen Subtropen 82:153-61.

Ogunbodede BA, Ajibade SR, Olakojo SA, 2000. Heterosis and combining ability for yield and yield related characters in some Nigerian local varieties of maize (Zea mays). Moor J. Agric. Res. 1:37-43.

Ojo DK, 2003. Heritability and combining ability of seedling emergence, grain yield and related characteristics in six tropical Soyabean (Glycine max (L.) Merr.) cultivars. Nigerian J. Genet. 18:22-8.

Paul CP, Ng NQ, Ladeinde TA, 1995. Diallel analysis of resistance to rice yellow mottle virus in African rice. J. Genet. Breed. 49:217-22.

Quin FM, 1997. Introduction. In: B.B. Singh et al. (eds.) Advances in cowpea research. Co - publication of International Institute of Tropical Agriculture (IITA) and Japan International Research Centre for Agricultural Sciences (JIRCAS). IITA, Ibadan, Nigeria, pp 11-15.

Rajani B, Manju P, Nair PM, Saraswathy P, 2001. Combining ability in Okra (Abelmoschus esculentus (L.) Moench). J. Trop. Agric. 39:98-101.

Romanus KG, Hussein S, Mashela WP, 2008. Combining ability analysis and association of yield and yield components among selected cowpea lines. Euphytica 162:205-10.

Rupela OP, Johansen C, 1995. Identification of non-nodulating and low and high nodulating plants in pigeon pea. Soil Biol. Biochem. 27:539-44.

Ukai Y, 1998. DIAL, a new 2.0 version of half diallel statistical package. Jpn. J. Breed. 39:107-9.

Walter DE, Morton JR, 1978. On the analysis of variance of a half diallel table. Biometrics 34:91-4.