

Diallel Analysis of Certain Yield Traits Related to Cowpea Seed (*Vigna unguiculata* (L.) Walp)

Marie Pierre Alimata Wentoin Daramcoum^{1,2,3*}, Saraka Didier Martial Yao^{1,2,3},
Eric-Blanchard Zadjehi Koffi^{1,2}, Jean-Simon Assouman^{1,2}, Adama Ballo¹, Nafan Diarrassouba^{1,2,3}

¹Genetics Research Unit, Department of Genetics and Biochemistry, Peleforo GON COULIBALY University, Korhogo, Cote d'Ivoire

²Biotechnology and Agro-Food Valorization Laboratory (BiVA), Peleforo GON COULIBALY University, Korhogo, Cote d'Ivoire

³African Center for Research and Applications on Shea (CRAK), Peleforo GON COULIBALY University (UPGC), Korhogo, Côte d'Ivoire

Email: *mariepierrekiss@yahoo.fr

How to cite this paper: Daramcoum, M.P.A.W., Yao, S.D.M., Koffi, E.-B.Z., Assouman, J.-S., Ballo, A. and Diarrassouba, N. (2026) Diallel Analysis of Certain Yield Traits Related to Cowpea Seed (*Vigna unguiculata* (L.) Walp). *American Journal of Plant Sciences*, 17, 701-717.
<https://doi.org/10.4236/ajps.2026.177043>

Received: March 13, 2026

Accepted: July 26, 2026

Published: July 29, 2026

Copyright © 2026 by author(s) and Scientific Research Publishing Inc.
This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).
<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

Cowpea is a major food legume in West Africa, but its yields remain low in Côte d'Ivoire despite its recognized nutritional value and agronomic importance. This study aims to evaluate the agronomic performance of F1 hybrids from diallel crosses and to determine the genetic parameters of interest. To do this, three parental accessions (NBO04, NKO03, and NFE011) showing the best agro-morphological and nutritional characteristics were selected and crossed according to a 3 × 3 diallel design. The traits studied were the number of seeds per pod, seed length, 100-seed weight, and seed yield. These parameters were analyzed using an ANOVA test. The determination of genetic diversity parameters (heterosis, potency ratio) as well as the diallel analysis (General combining ability, specific combining ability, and the General combining ability/specific combining ability variance ratio) were then carried out. The results showed that the three parental genotypes NBO04, NKO03, and NFE011 are phenotypically divergent from each other for the traits number of seeds per pod, 100-seed weight, and seed yield. Heterosis (%) and the hybrid vigor ratio of F1 hybrids indicate that only the NBO04 × NFE011 hybrid (9.12%) compared to the mid-parent and reciprocal cross, NFE011 × NBO04 hybrid (11.58%) compared to the better parent show positive heterosis for yield. General combining ability (GCA) and specific combining ability (SCA) are significant for all traits. The GCA/SCA variance ratio confirms the predominance of additive effects over non-additive gene effects in the inheritance of quantitative traits. The results obtained provide breeders with indications on the mechanisms of trait transmission, with the main objective of better guiding the selection of the best parents when establishing a hybridization program.

Keywords

Vigna unguiculata (L.) Walp, Quantitative Traits, Combining Ability, Diallel, Heterosis, Ivory Coast

1. Introduction

Commonly known as cowpeas, the species *Vigna unguiculata* (L.) Walp is mainly cultivated in West Africa [1]-[4]. Its global production is estimated at 6.4 million hectares on an area of about 12.7 million hectares [5]. In West Africa, cowpea accounts for 85% of the area under pulses and 10% of the total cultivated land [6]. In Côte d'Ivoire, although widely consumed, cowpea is grown in the north and remains a marginal crop [7]. Cowpea production is around 36,310 tons/year, which represents less than 2% of African production [5]. It plays an important role in cropping systems by restoring soil fertility through atmospheric nitrogen fixation but also in terms of food because it is rich in dietary protein (20% - 25%) and secondarily in vitamins and mineral elements [8].

Despite the agronomic importance and nutritional value of this legume, yields remain very low. In addition, there is the phenomenon of genetic erosion, which threatens the survival of cowpea genetic resources. This low yield could be due to abiotic and biotic conditions and especially to the lack of knowledge of the genetic potential of the cultivars available in a given region [9]. Recent studies on cowpea genetic improvement have highlighted the importance of diallel analysis, heterosis, and combining ability in identifying superior parental genotypes and promising crosses for improving yield and agronomic traits. Studies by [10]-[12] demonstrated the involvement of additive and non-additive gene effects in the genetic control of yield-related traits in cowpea. These approaches provide better insight into genetic interactions among parental genotypes and help guide breeding strategies aimed at exploiting heterosis and combining ability effects. The objective of this study is to evaluate the performance of F1 hybrids and to determine the genetic parameters associated with cowpea yield traits in northern Côte d'Ivoire.

2. Materials and Methods

2.1. Experimental Site

The study was carried out in the vegetable garden of the botanical garden of the Université Peleforo GON COULIBALY (UPGC) in Korhogo, northern Côte d'Ivoire. It is an area with a Sudano-Guinean tropical climate, characterized by two main seasons: a rainy season, which lasts from May to October, and a dry season, which lasts from November to April [13]. The average annual temperature in this region is 27°C, while the average annual precipitation is around 1200 mm.

2.2. Plant Material

The study focused on three cowpea self-fertilization lines coded NBO04, NFE011

and NKO03 (**Figure 1**). These elite cowpea lineages are present in the cowpea seed bank of the Peleforo GON COULIBALY University (UPGC) in Korhogo. This seed bank is composed of local cowpea cultivar collected in seed form and coded according to origin and introduced under accession numbers. The three (3) parental accessions selected have the best agro-morphological and nutritional characteristics [14].

NBO04 has a seed that has a wrinkled appearance. The shape is kidney-shaped and the color is white. Its flower maturation time is 59 to 63 days. Its germination time is 3 days with white flowers. The maturity period varies from 80 to 84 days and the grain yield varies from 2000 to 4000.

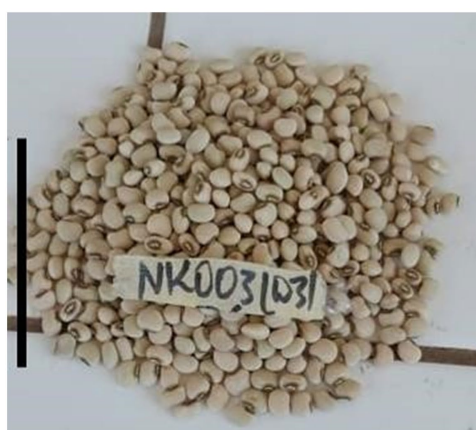
NKO03 has a seed that has a smooth appearance. The shape is ovoid. The color is white. Its flower maturation time is 41 to 42 days. Its germination time is 3 days with white flowers. The maturity period varies from 57 to 58 days and the grain yield varies from 3000 to 5000.

NFE011 has a smooth-looking seed. The shape is ovoid. The color is light red. Its flower maturation time is 40 to 42 days. Its germination time is 3 days with white flowers. The maturity period varies from 56 to 58 days and the grain yield varies from 2000 to 5000.



Scale: one bar measures 2.5 cm

(a) Accession NBO04



(b) Accession NKO03



(c) Accession NFE011

Scale: each bar measures 2.5 cm

Figure 1. Plant material used in the experiment.

3. Method

3.1. Experimental Seeding Device

The trial was conducted on a single 100 m² plot (10 m long × 10 m wide). The plot was subdivided into two sub-plots called as follows: the parental plot and the F1 hybrid plot. The parental plot included a Fisher block device with three (3) replicates consisting of three (3) blocks (block A; block B; block C) in which the parental accessions NBO04, NKO03 and NFE011 were arranged. The spacing between two neighboring blocks was 2 m. Each block consisted of three seeding rows separated by 1 m on each row. The spacing between the ten (10) seeding points was 0.75 m. One seed was used per pocket, a total of 10 seeds for one parental accession, 90 seeds for the three (3) accessions. The Fisher block device with three (3) replicates, consisting of three (3) blocks (block A, block B and block C) was used on the plot of the F1 hybrids. The distance between the two neighboring blocks was 2 m. Six (6) seeding lines separated by 1 m on each row with a spacing of 0.75 m between the ten (10) seeding points in each block. Sowing was carried out in July 2022, due to one seed per pocket. A total of 10 seeds were used for one F1 hybrid and 180 seeds for all 6 F1 hybrids. The crossing plan used to obtain F1 hybrids is a 3 × 3 diallel without self-fertilization, for crosses between the parents at least 6 have been carried out (**Table 1**). Each seeding line corresponding to a genotype in a block was considered an experimental unit. Fifteen days after planting, for morpho-agronomic measurements, observations were made of five (5) plants in each experimental unit and the individual values obtained were averaged to produce a single value per experimental unit used in statistical analyses. Five (5) plants were selected from the viable plants present in each row. A total of 135 parental plants and 180 for F1 hybrids were measured. During the trial, weeding and hoeing were carried out by hand and with hoe according to the rate of weed invasion on the plot.

Table 1. 3 × 3 diallel crossing design without self-fertilization used to obtain the F1 hybrid progeny of cowpeas studied.

♂ \ ♀	NBO04	NKO03	NFE011
NBO04	—	NBO04 × NK003	NBO04 × NFE011
NKO03	NKO03 × NBO04	—	NKO03 × NFE011
NFE011	NFE011 × NBO04	NFE011 × NK003	—

♀ = Female parent; ♂ = Male parent; × = Direct or reciprocal crossing.

3.2. Data Collection

The quantitative characteristics measured on the fruit are the number of seeds (Nu. Se/Pod), the length of the seeds (Leng Se), the weight of 100 seeds (Weight 100 Se) and the grain yield. These traits were observed after fruit harvest day after day after seed was planted. The grain yield was estimated at harvest. For each acces-

sion, all pods from the productive plot were shelled, and the mass of the resulting seeds was determined by weighing. Yield was then calculated per plot and extrapolated to a hectare based on the harvested area (**Table 2**).

Table 2. Measured traits and their measurement methods.

Variables	Code	Measurement method
Number of seeds per pod	Nu. Se/pod	Seed count in the pod after harvest on 5 pods per plant
Seed length	Leng Se (cm)	Average measurement with a digital caliper on 5 seeds per plant after harvest
Weight of 100 seeds	Weight 100 Se (g)	Enumeration and weighing of 100 dried seeds after harvest
Yield	Yield (kg/ha)	The return was calculated using the following formula: $\text{Yield (kg/ha)} = \frac{\text{Production (kg)}}{\text{Aera (m}^2\text{)}} \times 10000$

3.3. Statistical Analysis

The SPSS version 20 and XLSTAT version 19 software were used for the statistical processing. The mean and standard deviation values of each trait were determined for the F1 broodstock and descendants. The normality of the data has been checked beforehand using the Shapiro-Wilk test, when the data does follow the normal distribution, a one-factor analysis of variance (genotypes) was performed to better assess the performance of the broodstock and their F1 progeny. For quantitative traits, their variability was assessed through a Principal Component Analysis (PCA) using the XLSTAT software version 2019, to identify the agromorphological quantitative variables that contribute to the dispersion of cowpea accessions.

3.4. Calculation of Heterosis

The percentage of heterosis according to the average value of the average parents (HPM) on the one hand and that relating to the best parent (HMP) on the other hand, for the different traits studied, was calculated using the formula proposed by Mather and Jinks (1971) [15]:

$$\text{HPM} = \frac{(F1 - V_m)}{V_m} \times 100$$

$$\text{HMP} = \frac{(F1 - P_2)}{P_2} \times 100$$

where **F1** = mean value of hybrids F1, **P₁** = mean value of the worse parent, **P₂** = mean value of the best parent, **V_m** = $(P_1 + P_2)/2$ = value of the average parent.

Critical difference (**DC**) is used to test the significance of heterosis. The significance of this **CD** was assessed through the values of the t-statistic according to the formulas proposed by Wynne *et al.* (1970) [16] and Heydari *et al.* (2012) [17]:

$$t = \frac{(F1 - V_m)}{\sqrt{\left(\left(\frac{3}{8}\right) \times \text{MCE}\right)}}$$
, to test the significance of heterosis relative to the average parent and $t' = \frac{(F1 - P_2)}{\sqrt{\left(\left(\frac{1}{2}\right) \times \text{MCE}\right)}}$, to test the significance of heterosis relative to the best parent.

Where **MCE** is the mean square of the experimental error, and **t** is the value on the 5% or 1% significance table for the degree of freedom of the mean squares error.

3.5. Power Ratio Calculation

The power ratio was calculated according to Smith (1952) [18] to determine the degree of dominance as follows:

$$P = \frac{(F1 - V_m)}{0.5 \times (P_2 - P_1)}$$

where **P** = Relative power of all genes, **F1** = mean value of F1 hybrids, **P₁** = mean value of the worse parent, **P₂** = mean value of the best parent, and **V_m** = $(P_1 + P_2)/2$ = value of the average parent. Thus,

- If **P** = +1 or -1, there are additive and non-additive effects,
- If $-1 < P < 1$, there is predominance of non-additive effects,
- If **P** = 0, there are non-additive effects,
- If **P** > 1, there is predominance of additive effects.

Positive and negative signs indicate the additive or non-additive effects in relation to one of the parents.

3.6. Diallel Analysis

The diallel analysis (3 × 3) was performed according to Model 1 and Method 1 of Griffing (1956) [19]. It measures the general (GCA) and specific (SCA) abilities of the combination and provides information on the reciprocal effects (maternal effects). An initial analysis made it possible to compare the 9 genotypes. A second analysis was performed to test for effects attributable to GCA, SCA and reciprocal differences (RCTs). These effects make it possible to choose an improvement strategy. The magnitude of the reciprocal effects in relation to GCA and SCA will indicate whether maternal inheritance should be taken into account in the selection of a trait. The statistical model for the mean value of a cross (*i* × *j*) in Griffing's (1956) [19] analysis is as follows:

$$Y_{ij} = M + \text{GCA}_i + \text{GCA}_j + \text{CSA}_{ij} + R_{ij} + E_{ijkl}$$

Y_{ij} = mean value of each cell of the diallel,

M = general average of the population,

GCA_i = effect of parent *i*'s AGC,

GCA_j = effect of parent *j*'s AGC,

CSA_{ij} = effect of the specific suitability for the combination of the hybrid of the parents i and j . R_{ij} is the reciprocal effect, implying the reciprocal relations between the two parents.

E_{ijkl} is the effect of the environment associated with the observation of the individual $ijkl$

$$GCA_j = (\text{Average } P_j(\text{row}) + \text{Average } P_j(\text{column}))/2 - \text{Mean}$$

Specific Suitability for Combination (SCA) is the deviation between the observed value of a hybrid and its foreseeable value based on the general suitability for combination of the parental lines. It is essentially based on the gene actions of dominance and epistasis (effects of non-fixable genes). It is therefore recommended to delay selection until gene effects are fixed in subsequent generations [20].

The SCA between two sires (P_i and P_j) is given by the formula:

$$SCA (P_i \times P_j) = \text{Observed value} - \text{Predicted value}$$

$$\text{With Predicted value} = \text{Mean Genu} + AGC P_i + AGC P_j$$

4. Results and Discussion

4.1. Results

4.1.1. Agronomic Performance of the Parental Lines and Their F1 Descendants

Analysis of the results shown in **Table 3** shows that the parents NKO03 (18.80 seeds per pod) and NFE011 (18.20 seeds per pod) showed the highest values for the number of seeds per pod trait. Of the three parents, only parent NBO04 recorded the longest seed (10.57 mm). In terms of the 100-seed weight trait, the parental line NBO04 (17.76 g) recorded the highest values. It should be noted that the parent NFE011 (4025.24 kg/ha) had the highest yield.

Hybrids resulting from crosses NBO04 $\times$ NKO03 (16.20 seeds per pod), NFE011 $\times$ NKO03 (16.20 seeds per pod) and crosses (NKO03 $\times$ NFE011 (16.80 seeds per pod) and NKO03 $\times$ NBO04 (15.80 seeds per pod)) involving the NKO03 genotype produced a large number of seeds per pod. The analysis carried out on the seed length trait showed that the hybrids resulting from the crosses NFE011 $\times$ NBO04 (8.50 mm), NBO04 $\times$ NKO03 (8.89 mm), NBO04 $\times$ NFE011 (8.43 mm) and NKO03 $\times$ NBO04 (8.74 mm) recorded the highest values. With regard to the two traits, weight of 100 seeds and yield, two hybrids from crosses NFE011 $\times$ NBO04 and NBO04 $\times$ NFE011 involving genotypes NFE011 and NBO04 yielded the heaviest seeds (17.40 g; 15.28 g) with good yields (4491.24 kg/ha; 3933.45 kg/ha) (**Table 3**).

The comparison showed that the parents NKO03, NFE011 performed better than their F1 descendants in terms of number of seeds per pod (**Nu. Se/Pod**). In terms of seed length (**Leng Se (mm)**), only the NBO04 parent showed a better performance (10.58 mm). The NFE011 $\times$ NBO04 hybrid (17.4 g) performed statistically identical to the parent NBO04 (17.76 g). The latter had a higher weight of 100 seeds (**Weight 100 Se**). For grain yield (**Yield (kg/ha)**), hybrid perfor-

mance was statistically close (NBO04 × NKO03 (2341.68 kg/ha); NBO04 × NFE011 (3933.45 kg/ha); NKO03 × NFE011 (2923.99 kg/ha); NFE011 × NKO03 (3216.23 kg/ha)) or higher (NFE011 × NBO04 (4491.22 kg/ha)) than that of the parents (Table 3).

Table 3. Mean performance of the three parental lines and their F1 hybrids.

Genotypes	Nu. Se/Pod	Leng Se (mm)	Weight 100 Se (g)	Yield (kg/ha)
NBO04	13.60 ± 1c	10.58 ± 0.49a	17.76 ± 2a	3184.31 ± 174ab
NFE011	18.20 ± 1a	6.82 ± 45c	10.60 ± 1d	4025.24 ± 255ab
NKO03	18.80 ± 1a	6.71 ± 55c	10.28 ± 0d	3718.86 ± 270ab
NBO04 × NKO03	16.20 ± 1.30ab	8.89 ± 0.52b	14.98 ± 1.01bc	2341.68 ± 207.51ab
NBO04 × NFE011	13.80 ± 2.28bc	8.44 ± 0.52b	15.28 ± 1.89ab	3933.45 ± 225.58ab
NKO03 × NFE011	16.80 ± 0.84ab	7.11 ± 0.47c	11.07 ± 0.18d	2923.99 ± 165.79ab
NKO03 × NBO04	15.80 ± 1.30abc	8.74 ± 0.70b	14.04 ± 1.94c	1786.18 ± 279.99b
NFE011 × NBO04	14.40 ± 2.41bc	8.50 ± 0.71b	17.40 ± 1.35a	4491.22 ± 290.11a
NFE011 × NKO03	16.20 ± 1.30ab	7.31 ± 0.38c	11.30 ± 0.94d	3216.23 ± 158.76ab
F	7.48	31.73	28.569	2.538
Pr > F	<0.0001	<0.0001	<0.0001	0.027

Values that do not share the same letter (a, b, c, ab, bc, and abc) on the same column differ significantly at $p < 0.01$ or $p < 0.05$. **F** = Test statistic F; **Pr** = calculated probability; **Nu. Se/Pod** = Number of seeds per pod; **Leng Se** = Seed length; **Weight 100 Se** = Weight of 100 seeds; **Yield** = Yield.

4.1.2. Variability Factors Identified within Cowpea Accessions

Table 4 gives an estimate of the variability represented by each axis. Two axes or factors (F1 and F2) with an eigenvalue greater than 1 have been retained. These two axes explain 95.30% of the variability present between cowpea accessions.

The first axis expresses 68.71% of the total variability. This axis was strongly correlated with the variables number of seeds per pod (Nu. Se/Pod), seed length (Leng Se) and weight of 100 seeds (Weight 100 Se), which reflects the degree of fertility. The second axis explains 26.60% of the total variability and reflects the grain yield (Yield) (Figure 2).

Table 4. Eigenvalues and percentage change expressed by the first four axes according to the PCA.

Axe	Eigenvalue	Variability (%)	Cumulative %
1	2.748	68.709	68.709
2	1.064	26.596	95.304
Correlation axes characters			
Characters	Axis 1	Axis 2	
Nu. Se/Pod	0.880	0.027	
Leng Se	0.916	0.035	
Weight 100 Se	0.940	0.021	
Yield	0.013	0.981	

Nu. Se/Pod = Number of seeds per pod; **Leng Se** = Seed length; **Weight 100 Se** = Weight of 100 seeds; **Yield** = Yield.

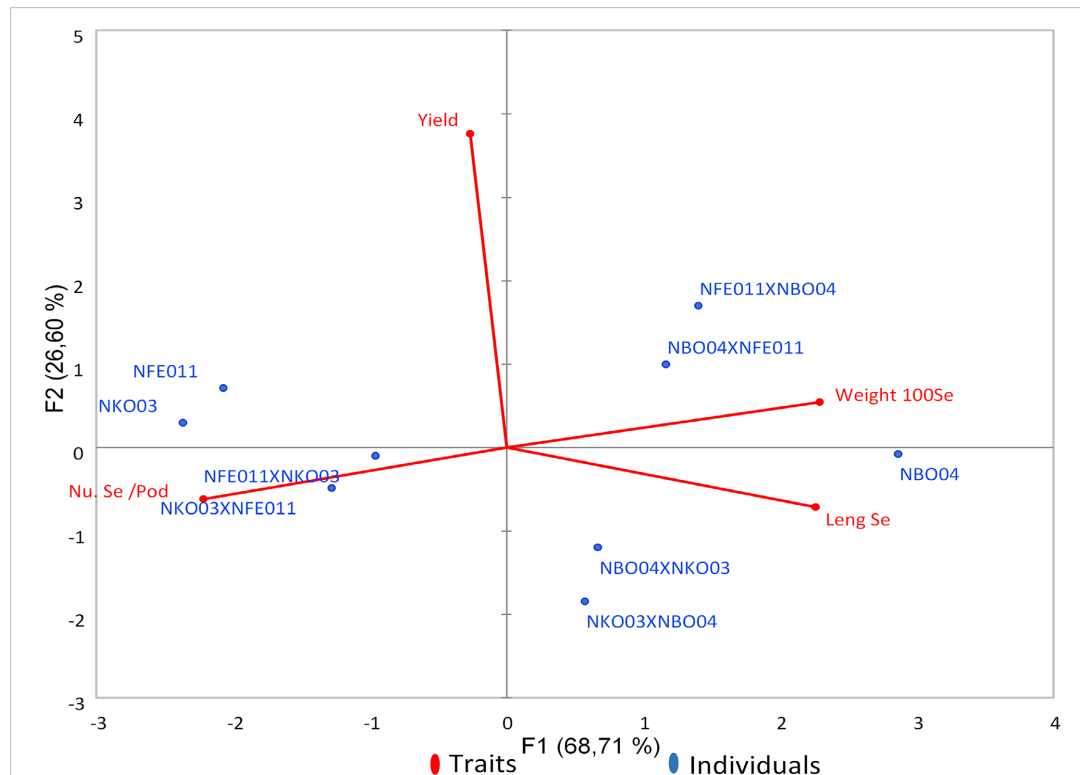


Figure 2. Projection of traits, parental accessions and F1 hybrids.

4.1.3. Heterosis and Suitability for Cowpea Self-Fertilization Lines

1) Heterosis

- Compared to the average parent

There is an absence of heterosis for the number of seeds per pod (Nu. Se/Pod) compared to the average parent at the level of the NBO04 × NKO03 hybrid.

For the other traits, no heterosis effect with respect to the average parent was recorded. Only the NBO04 × NFE011 hybrid (9.12%) showed a high heterosis value relative to the mean parent for the grain yield (Yield) trait (**Table 5**).

- Compared to the best parent

The heterosis effect with respect to the best parent was not recorded in the hybrids regarding the number of seeds per pod (Nu. Se/Pod), seed length (Leng Se), and weight of 100 seeds (Weight 100 Se). Except for the grain yield trait (Rend), only NFE011 × NBO04 (11.58%) had a high heterosis value compared to the best parent (**Table 5**).

2) Power Ratio

Values for the gene power ratio are reported in **Table 6**. In terms of the number of seeds per pod trait (Nu. Se/Pod), the potency ratio values were less than -1 without 0 for all hybrids. The potency ratio values of the hybrids NKO03 × NBO04, NKO03 × NFE011 and NFE011 × NKO03 were less than 1 while those of the hybrids NBO04 × NFE011 and NFE011 × NBO04 ranged from -1 to 1 for the seed length trait (Leng Se), except for the hybrid NBO04 × NKO03, which had a value greater than 1.

Regarding the weight of 100 seeds (Weight 100 Se), the potency ratio values of the hybrids NBO04 × NKO03, NBO04 × NFE011 and NFE011 × NBO04 were greater than 1 while the other hybrids NKO03 × NBO04, NKO03 × NFE011 and NFE011 × NKO03 recorded values below 1. As for grain yields, only the two hybrids NFE011 × NBO04 and NBO04 × NFE011 recorded power ratio values greater than 1 and less than 1 respectively, while the other hybrids had power ratio values below −1.

Table 5. Percentage of average parent (MPH) and best parent (HMP) heterosis.

F1 Hybrids	Nu. Se/Pod		Leng Se (mm)		Weight 100 Se (g)		Yield (kg/ha)	
	HPM	HMP	HPM	HMP	HPM	HMP	HPM	HMP
NBO04 × NKO03	0*	−13.83**	2.89ns	−15.92ns	6.85ns	−15.65ns	−32.16**	−37.03**
t cal.	0	−2.47	0.82	5.49	1.28	4.32	−1.50	−0.31
t ob.	0.05	0.01	0.05	0.05	0.05	0.05	0.01	0.01
NBO04 × NFE011	−13.21**	−24.18**	−3.01**	−20.22ns	7.76ns	−13.96ns	9.12*	−2.28**
t cal.	−2.30	−2.18	−0.86	5.33	1.47	4.14	0.45	−0.49
t ob.	0.01	0.01	0.01	0.05	0.05	0.05	0.05	0.01
NKO03 × NBO04	−2.47*	−15.96ns	1.13ns	−17.36**	0.17*	−20.92**	−48.25**	−51.97ns
t cal.	−0.44	2.47	0.32	−5.49	0.03	−4.32	−2.26	0.31
t ob.	0.01	0.05	0.05	0.01	0.05	0.01	0.01	0.05
NKO03 × NFE011	−9.19**	−10.64ns	5.05ns	4.16**	6.05ns	4.45**	−24.48**	−27.36**
t cal.	−1.86	0.28	1.12	−0.16	0.84	−0.18	−1.29	−0.18
t ob.	0.01	0.05	0.05	0.01	0.05	0.01	0.01	0.01
NFE011 × NBO04	−9.43**	−20.88ns	−2.30**	−19.63**	22.71ns	−2.03**	24.59ns	11.58*
t cal.	−1.64	2.18	−0.66	−5.33	4.30	−4.14	1.20	0.49
t ob.	0.01	0.05	0.01	0.01	0.05	0.01	0.05	0.05
NFE011 × NKO03	−12.43**	−13.83**	8.01ns	7.09ns	8.24ns	6.60ns	−16.94**	−20.10ns
t cal.	−2.52	−0.28	1.78	0.16	1.15	0.18	−0.89	0.18
t ob.	0.01	0.01	0.05	0.05	0.05	0.05	0.01	0.05

Nu. Se/Pod = Number of seeds per pod; **Leng Se** = Seed length; **Weight 100 Se** = Weight of 100 seeds; **Yield** = Percentage of heterosis relative to the average parent; **HMP** = Percentage of heterosis relative to the best parent; **t cal** = Calculated t; **t ob** = t observed at 1% and 5%. *Significant, **Highly significant, ns: not significant.

Table 6. Power ratio value.

F1 Hybrids	Nu. Se/Pod	Leng Se (mm)	Weight 100 Se (g)	Yield (kg/ha)
NBO04 × NKO03	0	1.93	14.36	−4.15
NBO04 × NFE011	−19.32	−1.97	15.75	0.78
NKO03 × NFE011	−4.16	0.76	0.01	−6.19
NKO03 × NBO04	−2.04	0.08	0.4	−6.23
NFE011 × NBO04	−13.8	−1.5	46.11	2.11
NFE011 × NKO03	−2.76	0.13	0.55	−4.28

Nu. Se/Pod = Number of seeds per pod; **Leng Se** = Seed length; **Weight 100 Se** = Weight of 100 seeds; **Yield** = Yield.

4.1.4. General Combination Skills (GCA) and Specific Combination Skills (SCA)

• General Combination Skills Study (GCA)

The three parental genotypes NBO04, NKO03 and NFE011 showed negative general suitability for combination (GCA) values for seed-per-pod counts, seed length and 100-seed weight. The ranking of the parental accessions in descending order of their general suitability for combination (GCA) values for grain yield showed NFE011 in first place (1408.85), second place NKO03 (1370.58) and third place NBO04 (1304.53) (**Table 7**).

• Study of specific suiting skills (SCA)

High specific suitability (SCA) values for number of seeds per pod (number of Se/Pod), seed length (Leng Se (mm)) and weight of 100 seeds (weight100 Se (g)) were recorded in the hybrids NBO04 × NKO03 (11.24; 11.39; 115.16) and NKO03 × NBO04 (11.20; 11.37; 114.23), respectively. While high SCAs were noted in hybrids from crosses NFE011 × NBO04 (923.20), NBO04 × NKO03 (403.71) and NBO04 × NFE011 (365.43) for grain yield (Yield) (**Table 8**).

4.1.5. Study of the Report $\sigma^2\text{GCA}/\sigma^2\text{SCA}$

The ratio of the variance of general ability ($2\sigma^2$ g) to that of specific ability (σ^2 s). This ratio is low for grain yield (**Table 9**). The analysis of the $\sigma^2\text{GCA}/\sigma^2\text{SCA}$ ratio was high for the number of seeds per pod traits, seed length and 100 seed weight.

Table 7. Cowpea broodstock traits assessed.

Genotypes	Nu. Se/Pod	Leng Se (mm)	Weight 100 Se (g)	Yield (kg/ha)
NBO04	-508.43b	-512.83b	-510.42b	1304.53c
NKO03	-442.38a	-446.79a	-444.38a	1370.58b
NFE011	-404.11a	-408.51a	-406.10a	1408.85a
Tests Statistics	$\chi^2 = 0.667$	$\chi^2 = 0.000$	$\chi^2 = 0.667$	$\chi^2 = 0.000$
P cal	0.031	0.068	0.08	0.036

Values that do not share the same letter (a, b, and c) in the same column differ significantly at $p < 0.05$. χ^2 = Chi-two; **F** = Test statistic F; **P cal** = Calculated probability; **Nu. Se/Pod** = Number of seeds per pod; **Leng Se** = Seed length; **Weight 100 Se** = Weight of 100 seeds; **Yield** = Yield.

Table 8. SCA values of different traits in cowpeas assessed.

Genotypes	No. Se/Pod	Leng Se (mm)	Weight 100 Se (g)	Yield (kg/ha)
NBO04 × NFE011	7.17c	7.51b	77.19d	365.43c
NBO04 × NKO03	11.24a	11.39a	115.16a	403.71b
NFE011 × NKO03	8.08b	7.99b	71.69e	-417.82d
NFE011 × NBO04	7.23c	7.52b	79.31d	923.20a
NKO03 × NFE011	8.68b	7.79b	69.41e	-710.05e
NKO03 × NBO04	11.20a	11.37a	114.23a	-1743.55f
Statistical Tests ²	$\chi^2 = 0.667$	$\chi^2 = 0.000$	$\chi^2 = 0.667$	$\chi^2 = 0.000$
P cal	0.0416	0.0316	0.016	0.006

Values that do not share the same letter (a, b, c, d, e, and f) in the same column differ significantly at $p < 0.05$. χ^2 = Chi-two; **F** = Test statistic F; **P cal** = Calculated probability; **Nu. Se/Pod** = Number of seeds per pod; **Leng Se** = Seed length; **Weight 100 Se** = Weight of 100 seeds; **Yield** = Yield.

Table 9. Component values of the variation in amplitude at combination.

Source of variation	Nu. Se/Pod	Leng Se (mm)	Weight 100 Se (g)	Yield (kg/ha)
p^2 CGA	7.84	6.84	84.85	2784.85
σ^2 CSA	6.15	5.61	73.01	927178.41
S^2 CGA/ σ^2 CSA	1.27	1.21	1.16	0.003

Nu. Se/Pod = Number of seeds per pod; **Leng Se** = Seed length; **Weight 100 Se** = Weight of 100 seeds; **Yield** = Yield.

4.2. Discussion

The results of the agronomic performance of the parental lines and their F1 progeny for the traits studied revealed that the three parental genotypes NBO04, NKO03 and NFE011 are phenotypically divergent from each other for the number of seeds per pod, 100 seed weight and seed yield traits. The principal component analysis (PCA) attests to this variability at 95.30%. This variability between the three genotypes was observed in the work of [14], who showed the existence of an important agro-morphological and nutrient diversity within cowpea cultivars collected in northern Côte d'Ivoire, which made it possible to identify among the accessions collected genotypes that are candidates for selection for the creation of interesting cowpea ideotypes. Also, [21] has shown that phenotypically divergent parental lines produce better offspring.

A heterosis effect was obtained only for the NBO04 × NFE011 hybrid compared to the average parent and the NFE011 × NBO04 hybrid compared to the best parent. This result is similar to those of the authors, [22] and [23], who showed that the expression of heterosis in a crop implies the possibility of producing superior cultivars through selection in segregated populations. This manifestation of heterosis can also be explained by the non-additive action (dominance and epistasis) of genes in trait expression [23] [24]. With the NBO04 × NKO03 hybrid, we noted a lack of heterosis for the number of seeds per pod compared to the average parent. For the other traits, no heterosis effect with respect to the average parent was recorded. Only the NBO04 × NFE011 hybrid (9.12%) showed a high heterosis value relative to the average parent for the grain yield trait (Rend). The heterosis effect with respect to the best parent was not recorded in the hybrids with regard to the number of seeds per pod, seed length, weight of 100 seeds. Except for the grain yield trait, only the NFE011 × NBO04 hybrid (11.58 %) exhibited a high heterosis value compared to the best parent. In this study, the heterosis effect was expressed by hybrids resulting from the direct cross NBO04 × NFE011 and the reciprocal NFE011 × NBO04 cross, thus indicating hybrid vigor. It should also be noted that in previous studies, only crosses involving the NBO04 genotype for yield trait expressed a heterosis effect. Similar results for heterosis of yield trait have also been reported by several authors [12] [25]-[27]. These results are consistent with those of [28], who showed that the additive effect is the main cause of the heterosis response in a diallel cross of diploid species. In this study, hybrids that showed negative or positive heterosis effects for traits 100-seed weight and seed yield could be proposed as candidate genotypes in breeding programs [14].

The values of the power ratio (the dominance effect) reflect varying degrees of gene dominance. Thus, traits with power ratio values between 0 and 1 or greater than 1 are under the effect of partial or superdominance of genes, respectively. On the contrary, those for which the negative values are between -1 and 0 or less than -1 are under the effect of partial recessivity or super recessivity of genes respectively. These varying degrees of gene dominance are consistent with the partial dominance or super-dominance proposed by [29] to explain hybrid vigor. Hybrids that showed positive heterosis effects relative to the average parent for a given trait had potency ratio values between 0 and 1 or greater than 1, while those that showed negative heterosis effects had potency ratio values between 0 and -1 or less than -1 [23] [30].

CGAs provide information on the ability of accessions to transmit their traits to their descendants, however for some traits, genotypes with high CGAs (transmission of tardiness) or genotypes with low CGAs (transmission of precocity) may be preferred. The three parental genotypes NBO04, NKO03 and NFE011 showed negative general suitability for combination (CGA) values for seed-per-pod counts, seed length and 100-seed weight. The ranking of the parental accessions in descending order of their general suitability for combination (CGA) numerical values for grain yield showed NFE011 in first place (1408.85), NKO03 second (1370.58) and NBO04 in third place (1304.53). The relatively high numerical GCA values observed for NFE011, NKO03 and NBO04 could suggest that these genotypes may represent favorable parents and potentially best combinator for yield trait. GCA that is significant for the traits we studied indicates a significant predominance of additive effect. These results are not in consistent with the work of [10] [31], who found that the mostly additive gene control of traits suggests the possibility of exploiting hybrid vigor.

The results at the SCA level show that for all traits, the best crosses involve parents with various types of CGA (strong $\times$ strong, strong $\times$ weak and weak $\times$ weak). High specific suitability (CSA) values for number of seeds per pod, seed length and weight of 100 seeds were recorded in the hybrids NBO04 $\times$ NKO03 (11.24; 11.39; 115.16) and NKO03 $\times$ NBO04 (11.20; 11.37; 114.23), respectively. While high SCAs were noted in hybrids from the cross NFE011 $\times$ NBO04 (923.20), NBO04 $\times$ NKO03 (403.71) and NBO04 $\times$ NFE011 (365.43) for grain yield (Yield). According to [32], the genetic interaction responsible for high SCA values can be of the additivity $\times$ additivity type or additivity $\times$ dominance. The first is fixable and therefore usable in selection, but the second is non-fixable [33]. We found that direct and reciprocal crosses were equivalent, except for grain yield. We therefore do not have to worry about a maternal effect to improve these traits, as the direction of crossing has no effect on the performance of the hybrids.

The ratio of the variance of general fitness ($2\sigma^2$ CGA) to that of specific ability (σ^2 SCA) is an estimate of additive effects compared to non-additive effects. This ratio was low for the seed yield trait, suggesting non-additive effects, mainly dominance or overdominance effects, in the genetic control of this trait. The analysis of the ratio of CGA to SCA was high for seed-per-pod traits, with seed length and

100-seed weight indicating predominance of additive effects. This result confirms the preponderance of additive effects over non-additive effects of genes in the inheritance of these traits. Our results are similar to those of [34]-[36].

5. Conclusions

The objective of the work was to identify candidate genotypes in the UPGC collection to improve cowpea productivity. The results obtained showed that:

- Only hybrids resulting from the direct cross NBO04 × NFE011 and the reciprocal cross NFE011 × NBO04 showed a heterosis effect for the seed yield trait.
- General combination skills (GCA) revealed that parental accessions (NBO04, NKO03 and NFE011) could be favorable sire and potentially best combinator for seed yield.
- The combination specific suitability (SCA) presented the hybrids (NFE011 × NBO04, NBO04 × NKO03 and NBO04 × NFE01) as being good crosses for seed yield trait. We found that direct and reciprocal crosses were equivalent, except for grain yield. We therefore do not have to worry about a maternal effect to improve these traits, as the direction of crossing has no effect on the performance of the hybrids.

Funding

The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Marie Pierre Alimata Wentoin Daramcoum, Saraka Didier Martial Yao and Eric-Blanchard Zadjéhi Koffi. The first draft of the manuscript was written by Marie Pierre Alimata Wentoin Daramcoum and Jean-Simon Assouman, Adama Ballo, Nafan Diarrassouba commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

- [1] Sarr, B., Diouf, O., Diouf, M., Roy-Macauley, H. and Brou, C. (2001) Use of Agronomic Parameters as Drought Resistance Criteria in Three Cowpea Varieties Grown in Senegal and Niger. *Drought*, **12**, 259-266.

- [2] Baudoin, J.P. (2001) Contribution of Plant Genetic Resources to the Varietal Selection of Tropical Food Legumes. *Biotechnology Agronomy Society Environment*, **5**, 221-230.
- [3] Coulibaly, S., Pasquet, R.S., Papa, R. and Gepts, P. (2002) AFLP Analysis of the Phenetic Organization and Genetic Diversity of *Vigna unguiculata* L. Walp. Reveals Extensive Gene Flow between Wild and Domesticated Types. *Theoretical and Applied Genetics*, **104**, 358-366. <https://doi.org/10.1007/s001220100740>
- [4] Wamalwa, E.N., Muoma, J. and Wekesa, C. (2016) Genetic Diversity of Cowpea (*Vigna unguiculata* (L.) Walp.) Accession in Kenya Gene Bank Based on Simple Sequence Repeat Markers. *International Journal of Genomics*, **2016**, 1-5. <https://doi.org/10.1155/2016/8956412>
- [5] FAOSTAT (2016/2022) Food and Agriculture Organization Corporate Statistical Database. FAO. <https://www.fao.org/faostat/>
- [6] Alene, A.D., Coulibaly, O. and Abdoulaye, T. (2012) The World Cowpea and Soybean Economies: Facts, Trends, and Outlook. International Institute of Agriculture, 44 p.
- [7] N'Gbesso, F., Fondio, L., Dibi, B., Djidji, H. and Kouame, C. (2013) Étude des composantes du rendement de six variétés améliorées de niébé [*Vigna unguiculata* (L.) Walp]. *Journal of Applied Biosciences*, **63**, 4754-4762. <https://doi.org/10.4314/jab.v63i1.87249>
- [8] Haro, H., Sanon, K.B., Le Roux, C., Duponnois, R. and Traoré, A.S. (2017) Improvement of Cowpea Productivity by Rhizobial and Mycorrhizal Inoculation in Burkina Faso. *Symbiosis*, **74**, 107-120. <https://doi.org/10.1007/s13199-017-0478-3>
- [9] Nadjiam, D., Doyam, A.N. and Bedingam, L.D. (2015) Étude de la variabilité agromorphologique de quarante-cinq cultivars locaux de niébé (*Vigna unguiculata*, (L.) Walp.) de la zone soudanienne du Tchad. *Afrique Science. Revue Internationale des Sciences et Technologie*, **11**, 138-151. <https://www.ajol.info/index.php/afsci>
- [10] Das, R.R., Das, G., Talukdar, P. and Neog, S.B. (2021) Genetic Analysis for Yield and Yield Attributing Traits in Cowpea (*Vigna unguiculata* L. Walp.). *Legume Research*, **44**, 900-905. <https://indianjournals.com/article/lr-44-8-006>
- [11] Jou-Nteufa, C. and Ceyhan, E. (2022) Determination of Combining Ability and Heredity through Diallel Analysis Method in F2 Populations of Cowpea. *Selcuk Journal of Agricultural and Food Sciences*, **36**, 299-311. <https://doi.org/10.15316/sjafs.2022.039>
- [12] Ezin, V., Tossou, T.A.W., Chabi, I.B. and Ahanchede, A. (2023) Diallel Analysis of Cowpea (*Vigna unguiculata* (L.) Walp.) Genotypes under Water Deficit Stress. *BMC Plant Biology*, **23**, Article No. 539. <https://doi.org/10.1186/s12870-023-04508-0>
- [13] Nadège, B.A.N., Cissé, G., Koné, B. and Séri, D. (2016) Variabilité Climatique et Changements dans l'environnement à Korhogo en Côte d'Ivoire: Mythes ou Réalité? *European Scientific Journal, ESJ*, **12**, 158-176. <https://doi.org/10.19044/esj.2016.v12n5p158>
- [14] Jean Simon Konan, A., Nafan, D. and Saraka Didier Martial, Y. (2021) Preliminary Study on Morphological Diversity of Cowpea Accessions [*Vigna unguiculata* (L.) Walp.] Collected in the North of Côte d'Ivoire. *International Journal of Current Research in Biosciences and Plant Biology*, **8**, 1-12. <https://doi.org/10.20546/ijcrbp.2021.809.001>
- [15] Mather, K. and Jinks, J.L. (1971) Biometrical Genetics: The Study of Continuous Variation. Cornell University Press, 382 p.
- [16] Wynne, J.C., Emery, D.A. and Rice, P.W. (1970) Combining Ability Estimates in *Arachis hypogaea* L. II. Field Performance of F₁ Hybrids. *Crop Science*, **10**, 713-715. <https://doi.org/10.2135/cropsci1970.0011183x001000060036x>

- [17] Heydari, F., Ramezanpour, S. S., Soltanloo, H., Kalate, M. and Shaban, K. (2012) Estimation of Genetic Parameters and Effective Factors in Resistance to Septoria Leaf Blotch of Wheat under Field Condition. *International Journal of Agriculture and Crop Sciences (IJACS)*, **4**, 1376-1384. <https://independent.academia.edu/kalate>
- [18] Smith, H.H. (1952) Fixing Transgressive Vigor in *Nicotiana Rustica*. Iowa State University Press, 161-174.
- [19] Griffing, B. (1956) Concept of General and Specific Combining Ability in Relation to Diallel Crossing Systems. *Australian Journal of Biological Sciences*, **9**, 463-493. <https://doi.org/10.1071/bi9560463>
- [20] Falconer, D.S. and Mackay, T.F.C. (1996) Introduction to Quantitative Genetics. Longman Technical, 433 p.
- [21] Diers, B.W., McVetty, P.B.E. and Osborn, T.C. (1996) Relationship between Heterosis and Genetic Distance Based on Restriction Fragment Length Polymorphism Markers in Oilseed Rape (*Brassica napus* L.). *Crop Science*, **36**, 79-83. <https://doi.org/10.2135/cropsci1996.0011183x003600010014x>
- [22] Mohammadi, A.A., Saeidi, G. and Arzani, A. (2010) Genetic Analysis of Some Agronomic Traits in Flax (*Linum usitatissimum* L.). *Australian Journal of Crop Science*, **4**, 343-352.
- [23] Wannows, A.A., Sabbouh, M.Y. and Al-Ahmad, S.A. (2015) Generation Mean Analysis Technique for Determining Genetic Parameters for Some Quantitative Traits in Two Maize Hybrids (*Zea mays* L.). *Jordan Journal of Agricultural Sciences*, **11**, 59-73. <https://doi.org/10.12816/0030075>
- [24] Ahsan, M.Z., Wrigh, D. and Virk, D.S. (1996) Genetic Analysis of Salt Tolerance in Spring Wheat (*Triticum aestivum* L.). *Cereal Research Communications*, **24**, 353-360.
- [25] Bhushana, H.O., Viswanatha, K.P., Arunachalam, P. and Halesh, G.K. (2000) Heterosis in Cowpea (*Vigna unguiculata* (L.) Walp.) for Seed Yield and Its Attributes. *Crop Research*, **19**, 277-280.
- [26] Pal, A.K., Ram, D., Morya, A.N. and Rajput, C.B.S. (2002) Heterosis over Mid and Better Parents under Line $\times$ Tester Design in Cowpea. *Indian Journal of Horticulture*, **59**, 279-287. <https://indianjournals.com/article/ijh-59-3-013>
- [27] Verma, A.K., Mehta, A.K., Singh, R.P., Singh, P.P. and Sharma, D. (2020) Studies on Hybrid Vigor for Yield and Contributing Traits in Cowpea (*Vigna unguiculata* L. Walp). *Research Journal of Biotechnology*, **15**, 72-79.
- [28] Bailey, T.B., Qualset, C.O. and Cox, D.F. (1980) Predicting Heterosis in Wheat. *Crop Science*, **20**, 339-342. <https://doi.org/10.2135/cropsci1980.0011183x002000030012x>
- [29] Moll, R.H. and Stuber, C.W. (1974) Quantitative Genetics—Empirical Results Relevant to Plant Breeding. *Advances in Agronomy*, **26**, 277-313. [https://doi.org/10.1016/s0065-2113\(08\)60874-3](https://doi.org/10.1016/s0065-2113(08)60874-3)
- [30] Kamer, A., Yousry, M.M. and El-Gamal, A.M. (2015) Heterosis and Heritability Studies for Fruit Characters and Yield in Melon (*Cucumis melo*, L.). *Middle East Journal of Applied Sciences*, **5**, 262-273. <https://www.curreweb.com/mejas/mejas/2015/262-273.pdf>
- [31] Hasanuzzaman, M., Hakim, M.A., Farsdous, J., Islam, M.M. and Rahman, L. (2012) Combining Ability and Heritability Analysis for Yield and Yield Contributing Characters in Chilli (*Capsicum annuum*) Landraces. *Plant Omics*, **5**, 337-344.
- [32] Ahmad, Z., Kumar, P., Katyar, R.P. and Gupta, R.R. (1979) Heterosis in Macaroni Wheat. *Indian Journal of Genetics and Plant Breeding*, **39**, 279-284.

- [33] Falconner, D.S. (1974) Introduction à la génétique quantitative. Traduit par Masson, 284 p.
- [34] Meena, R., Pithia, M.S., Savaliya, J.J. and Pansuriya, A.G. (2010) Combining Ability Studies in Vegetable Cowpea [*Vigna unguiculata* (L.) Walp]. *Research on Crops*, **11**, 441-445.
- [35] Uma, M.S. and Kalubowila, I. (2010) Line × Tester Analysis for Yield and Rust Resistance in Cowpea (*Vigna unguiculata* L. Walp). *Electronic Journal of Plant Breeding*, **1**, 254-267.
- [36] Chaudhari, S.B., Naik, M.R., Patil, S.S. and Patel, J.D. (2013) Combining Ability for Pod Yield and Seed Protein in Cowpea [*Vigna unguiculata* (L.) Walp] over Environments. *Trends in Biosciences Research*, **6**, 395-398.
<https://indianjournals.com/article/tbs-6-4-019>