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Heterosis and Combining Ability for Yield Traits in Cowpea Diallel Crosses from Northern Côte d'Ivoire

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Abstract This study investigated the hybrid vigor and combinability of five elite cowpea accessions in northern Côte d'Ivoire. A complete diallel cross (without self-pollination) between the varieties NTE015, NKO08, NFE011, NKO03 and NBO04 produced 20 F1 hybrids, which were evaluated on the basis of sixteen quantitative traits. The hybrids outperformed their parents for 64 % of the traits, with genotypes NTE015 and NBO04 standing out as the best general combiners (GCA), capable of favorably transmitting advantageous traits to their offspring. The NTE015 × NBO04 and NBO04 × NTE015 crosses outperformed their parents for 64.3 % of the traits, whilst NTE015 × NFE011 and NBO04 × NKO08 demonstrated strong specific combining ability (SCA). Maternal effects proved negligible, influencing only 14.3 % of traits, suggesting that the direction of the cross is not a determining factor for hybrid performance. All hybrids also reached maturity more quickly than their parents, offering a strategic advantage against environmental stresses such as late-season drought. These results highlight promising genetic diversity and justify the inclusion of these hybrids in recurrent breeding programmers aimed at developing high-yielding, early-maturing cowpea varieties adapted to local agroecological conditions.

Keywords: *Cowpea, heterosis, genotypes, maternal effects, Côte d'Ivoire*

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1. Introduction

Originally from Africa, cowpea (*Vigna unguiculata* (L.) Walp), also known as *black-eyed pea*, is a multipurpose legume – used as a vegetable, fodder plant, and staple crop – widely cultivated across the globe [1,2,3,4]. It is among the most important food legumes worldwide.

This species is mainly grown in the tropical and subtropical regions of Africa, Asia, Central America, and South America. Highly valued for its fresh leaves, green pods, and seeds, cowpea is a rich source of both macronutrients and micronutrients, including carbohydrates, proteins, vitamins, and minerals. In the absence of animal-based proteins, it provides a reliable plant-based alternative [5,6,7]. In developing countries, where nutritional deficiencies remain a major public health concern, cowpea plays a key role in the fight against malnutrition [8]. In several of these countries, it accounts for more than half of total protein intake, thus significantly contributing to food and nutritional security. It is widely consumed in various traditional forms across many African regions. Young leaves, either fresh or dried, as well as immature pods, are also highly prized dietary components [9].

In Côte d'Ivoire, although cowpea is widely consumed, it remains a marginal crop. National production, estimated at approximately 36.310 tones, accounts for less than 2 % of total African production [10].

Despite its many advantages, local production remains insufficient to meet national demand. The main barrier to large-scale sustainable production lies in the lack of improved varieties adapted to local conditions. Nonetheless, ongoing research into agronomic practices including planting density [11], floral phenology [12], plant growth habits [13], and quality seed production [14] provides a solid foundation for breeding programmers.

The present study aims to assess the effect of heterosis on certain yield-related agronomic traits in five elite cowpea accessions (*Vigna unguiculata (L.)* Walp), with the goal of contributing to the development of improved varieties.

2. Material and Methods

2.1. The Study Area

The study was carried out on experimental plots of the vegetable garden of the botanical garden of the University Peleforo GON COULIBALY (UPGC) in the municipality of Korhogo. The climate of the department of Korhogo belongs to the tropical dry climate regime, of soudano-sahelian type characterized by a dry season (November to June) and a rainy season (July to September) with an average annual rainfall of about 1200 mm [15].

2.2. Material

The plant material used in this study consisted of seeds from five elite cowpea accessions (NTE015, NKO08, NFE011, NKO03, and NBO04), obtained from the gene bank of Peleforo GON COULIBALY University (UPGC) [12]. The morphological and agronomic characteristics of these five accessions have been previously described by [16]. A complete diallel cross, excluding self-pollination, was performed among these five accessions, resulting in 20 hybrids. In total, 25 genotypes (the 5 parents and the 20 hybrids) were used for this study (Table 1).

Table 1. Crossing plan (complete diallel without self-fertilization)

♀ / ♂	NBO04	NKO03	NFE011	NKO08	NTE015
NBO 04	**X**	NKO03*NBO04	NFE011*NBO04	NKO08*NBO04	NTE015*NBO04
NKO 03	NBO04*NKO03	**X**	NFE011*NKO03	NKO08*NKO03	NTE015*NKO03
NFE 011	NBO04*NFE011	NKO03*NFE011	**X**	NKO08*NFE011	NTE015*NFE011
NKO 08	NBO04*NKO08	NKO03*NKO08	NFE011*NKO08	**X**	NTE015*NKO08
NTE 015	NBO04*NTE015	NKO03*NTE015	NFE011*NTE015	NKO08*NTE015	**X**

2.3. Methods

Experimental Setups

A randomised complete block experimental design with three replicates was set up on a plot measuring 318.75 m² (25.5 m long and 12.75 m wide). The design comprised three blocks, each consisting of 15 furrows. Each furrow contained 15 sowing points. The spacing between furrows was 0.75 m, whilst the distance between two successive planting holes within the same furrow was also 0.75 m. The blocks and the borders were separated by 2-metre-wide paths.

Prior to sowing, the plot was cleared and then ploughed to a depth of 30 cm, in accordance with the recommendations [17]. Sowing was carried out manually at a rate of two to three seeds per hole, at a depth of between 3 and 5 cm.

Two weeks after sowing, thinning was carried out, leaving a single plant per pot.

Weeding was carried out manually using a hoe, depending on the level of weed growth observed onthe plots. No fertilizer was applied throughout the entire experimental period.

Data collection

Data collection focused on five plants per genotype, selected at random from each block, making a total of 375 plants measured for the entire trial. Sixteen quantitative variables were used to evaluate the twenty-five genotypes in this study. Measurements were carried out in accordance with the cowpea descriptors established by the International Board for Plant Genetic Resources [17] (Table 2).

Table 2. Parameters used to assess heterosis effects and their measurement methods in cowpea

Variable	Abbreviation	Explanation
Plant height	HtP	measured 6 weeks after sowing; from the collar to the last apical bud
Plant width	LaP	Plant width (cm) measured 6 weeks after sowing; distance between the two outermost leaflets of two consecutive internodes
Number of nodes	NNo	Count of nodes on the main stem from the 6th week after sowing
Leaflet width	LaFo	Average measurement (cm) taken on three terminal folioles of the plant at the 6th week after sowing
Leaflet length	LoFo	Average measurement (cm) taken from three terminal cotilions of the plant at the 6th week after sowing
Time to first flower appearance	TFl	Number of days elapsed from sowing to the day the first flower opened
Time to first mature pod identification	TPGoM	Number of days elapsed from the appearance of 50% of the flowers to the appearance of the first mature pod
Number of pods	NGo	Count of pods per plant after harvest
Pod length	Lo Go	Average measurement taken using a measuring tape on 5 pods per plant after harvest(cm)
Pod width	LaGo	Average measurement taken using a digital caliper on 5 pods per plant after harvest (mm)
Pod weight	PGo	Average measurement taken using a digital scale on 5 pods per plant after harvest (g)
Number of chambers	NLo	Count of locules in the pod after harvest on 5 pods per plant
Number of seeds per pod	NG/Go	Count of seeds in the pod after harvest on 5 pods per plant
Seed length	LoG	Average measurement taken using a digital caliper on 5 seeds per plant after harvest (mm)
Weight of 100 seeds	P100G	Measure the weight of 100 seeds from the pods of the same plant; dried after harvest (g)
Yield	Rend (kg/ha)	Estimated in kg/ha based on the average yield per plant with a sowing density of 26,667.67 plants/ha ((P100 seeds / 100) x No. of seeds per pod x No. of pods x sowing density) / 1,000

Statistical Analysis of Data

We began by checking the normality of the data, followed by a multivariate analysis of variance (MANOVA). This method enabled us to perform several analyses of variance simultaneously, generate descriptive statistics for the variables, and compare the performance of individuals according to different traits. These analyses were carried out using IMB software, Statistical Package of Social Science (SPSS) version 22.0 (IBM corp. New York, USA.

The percentages of heterosis, calculated in relation to both the mean of the parents (MPH) and the best parent (BPH), were then determined using the following formulae (Mather and Jinks, 1971).

$$\text{MPH \%} = \frac{(F1 - Vm)\, X\, 100}{Vm}$$

$$\text{BPH \%} = \frac{(F1 - P2)\, X\, 100}{P2}$$

With F1= mean value of F1 hybrids, P1= mean value of weak parent, P2= mean value of best parent,

Vm= (P1+P2) /2 = value of mean parent.

The critical difference (CD) is used to determine the significance of heterosis using the formulae [19]

t = (F1-Vm)/ $\sqrt{\left(\left(\frac{3}{2}\right) * Mse\right)}$, to test the significance of heterosis relative to the mid-parent value, and;

t'= (F1-Vm)/ $\sqrt{\left(\left(\frac{1}{2}\right) * Mse\right)}$, to test the significance of heterosis relative to the better parent.

Where is the mean square error from the experimental data, and **t** is the critical value from the t-distribution table at the 5 % or 1 % significance level, corresponding to the degrees of freedom associated with the mean square error.

Finally, general combining ability (GCA), specific combining ability (SCA), and their effects were tested against their standard errors using Student's *t*-test. The formulas for GCA and SCA are shown below:

GCA P1 = (Mean of P1 (row) + Mean of P1 (column)) / 2 – Overall mean

SCA (P1 × P2) = Observed value – Expected value, where Expected value = Overall mean + GCA P1 + GCA P

3. Results

3.1. Agronomic Performance of F1 Hybrids and Parental Lines

For average performance, all the probability values are below the P = 0.05 probability threshold. Also, the coefficients of variation per trait recorded were below 30 %, except for leaflet length (LoFo) and yield (Rend (kg/ha)) (Table 3).

Comparing the average performance of the parents with that of the hybrids for each trait, the hybrids were superior to the parents for 9/14 or 64 % of the traits.

The average performance of the parents was better than that of the hybrids for traits such as plant height (HtP), with a value of 12.4 cm for the parents compared with 10.91 cm for the hybrids. The same applies to pod length (LoGo), with an average of 17.70 mm in the parents compared with 17.38 mm in the hybrids. Finally, the average number of seeds per pod (NGGo) in the parents was 16.72 compared with 15.34 in the hybrids. However, for all three traits, only the average number of seeds per pod (NG/Go) was lower in hybrids than in parents, with a wide distribution of values in parents than in hybrids.

3.2. Heterosis Observed in F1 Hybrids

Heterosis effects were calculated for each cross and each trait. They were either positive and significant, or positive but not significant. Only significant heterosis values were taken into account in the analysis (see Table 4 and Table 5).

All the characteristics studied recorded at least one hybrid with heterosis values, with the exception of the number of seeds per pod (NGGo).

The traits flowering time (TFl), maturity time (TPGoM), pod width (LaGo), seed length (Long graine) and weight of 100 seeds (P100G) were those for which at least 50 % of the hybrids expressed heterosis effects.

Finally, a summary of Tables 4 and 5 showed that hybrids NTE015NBO04 and NBO04NTE015 performed best, with significant heterosis effects in 64.29 % of the traits studied. Four other hybrids (NFE011NKO03, NTE015NFE011, NTE014NKO08 and NKO08NTE015) showed heterosis effects for 50% of the traits.

Tabe 3. Means, Margins, and Coefficients of Variation (CV) of the Average Performances of Parents and Hybrids by Trait

Generation	Parents		Hybrids		CV (%)	F	P
Trait	Mean	Range	Mean	Range			
HtP (cm)	12.4	10.94 – 14.20	10.91	7.70 – 14.64	14.70	6.41	>0.01
LaP (cm)	36.45	32.64 – 40.38	34.71	26.74 – 40.80	11.57	4.46	>0.01
NNo	9.24	8.60 – 10.40	9.50	8.00 – 11.40	9.13	3.77	>0.01
LoFo (cm)	12.19	10.12 – 15.38	14.63	8.60 – 38.60	53.69	1.28	0.02
LaFo (cm)	7.11	6.62 – 7.94	7.47	15.56 – 18.22	13.41	1.28	0.02
TFl (days)	45.52	40.80 – 60.80	42.23	39.00 – 49.00	9.58	25.97	>0.01
TPGoM (days)	63.84	50.20 – 82.00	60.26	54.00 – 65.20	8.61	3.76	>0.01
NGo	60.12	33.00 – 78.60	60.13	25.20 – 101.80	3.07	2.09	0.01
LoGo (cm)	17.70	16.80 – 18.40	17.38	15.58 – 19.10	5.93	4.35	>0.01
LaGo (mm)	7.73	6.99 – 9.01	7.92	6.70 – 8.87	8.27	10.66	>0.01
NGGo	16.72	13.60 – 18.80	15.34	13.20 – 16.80	8.82	4.77	>0.01
LoG (mm)	7.70	6.71 – 10.65	8.05	6.73 – 9.67	12.01	19.38	>0.01
P100G (g)	12.54	10.28 – 17.76	14.45	10.52 – 19.78	19.89	23.32	>0.01
Rend (kg/ha)	3273.14	1596.99 – 4025.23	3617.85	1292.30 – 7290.58	42.36	2.76	>0.01

CV = coefficient of variation; HtP = plant height; LaP = plant width; NNo = number of nodes; LoFo = leaflet length; LaFo = leaflet width; TFl = time to first flower appearance; TPGoM = time to first mature pod identification; NGo = number of pods per plant; LoGo = pod length; LaGo = pod width; NGGo = number of seeds per pod; LoG = seed length; P100G = weight of 100 seeds; Rend (kg/ha) = yield in kilograms per hectare.

Table 4. Heterosis effects of the top ten hybrids

F1 Hybrids	HtP (cm)		LaP (cm)		NNo		LoFo (cm)		LaFo (cm)		TFl (days)		TPGoM (days)	
	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH
NKO03*NBO04	-	-	0.12	-	-	-	-	-	2.37	2.8	**-11.89**	-	**-13.47**	-
NFE011*NBO04	-	-	-	-	-	-	-	-	-	-	**-15.75**	-	**-13.79**	-
NKO08*NBO04	-	-	2.87	0.11	**15.79**	**5.77**	0.75	-	0.93	-	**-10.51**	-	**-26.03**	**-15.66**
NTE015*NBO04	-	-	**12.48**	**8.89**	**8.33**	-	6.38	-	-	-	**-20**	**-2.37**	**-10.26**	-
NFE011*NKO03	-	-	**11.75**	**1.04**	6.52	**2.08**	7.37	1.26	7.56	3.64	**-2.18**	**-0.98**	-0.7	-0.35
NKO08*NKO03	-	-	-	-	-	-	-	-	-	-	-	-	-1.32	-
NTE015*NKO03	-	-	2.89	-	2.17	-	5.08	-	9.43	5.6	**-7.14**	**-6.7**	-1.38	-0.69
NKO08*NFE011	-	-	-	-	-	-	3.19	-	-	-	-	-	-	-
NTE015*NFE011	-	-	-	-	**9.09**	**9.09**	**202.75**	**150.98**	7.39	7.23	**-4.1**	**-2.45**	-1.04	-
NTE015*NKO08	**8.96**	**5.86**	-	-	-	-	10.01	-	-	-	**-1.66**	**-1.43**	**-6.86**	**-2.4**

F1 Hybrids	NGo		LoGo(cm)		LaGo (mm)		NGGo		LoG (mm)		P100G (g))		Rend (kg/ha)	
	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH
NKO03*NBO04	-	-	-	-	-	-	-	-	0.73	-	0.17	-	-	-
NFE011*NBO04	4.82	-	-	-	-	-	-	-	-	-	**22.71**	-	**24.59**	**11.58**
NKO08*NBO04	-	-	**7.73**	**6.78**	-	-	-	-	-	-	-	-	-	-
NTE015*NBO04	**64.38**	**43.71**	**5.6**	**2.46**	0.84	-	-	-	**7.61**	-	**21.7**	**6.42**	**107.57**	**89.84**
NFE011*NKO03	-	-	1.36	1.53	**10.16**	**9.95**	-	-	**8.01**	**7.09**	**8.24**	**6.61**	-	-
NKO08*NKO03	-	-	-	-	**7.46**	**7.31**	-	-	-	-	-	-	-	-
NTE015*NKO03	-	-	-	-	**2.44**	-	-	-	**8.62**	**3.98**	**16.54**	**3.31**	-	-
NKO08*NFE011	5.38	-	-	-	**10.68**	**10.32**	-	-	**9.77**	**8.33**	**3.8**	2.37	-	-
NTE015*NFE011	-	-	**4.03**	**2.5**	**4.24**	-	-	-	**10.13**	**6.3**	24.35	**11.73**	7.3	4.84
NTE015*NKO08	8.22	-	**9.27**	**6.94**	**4.37**	-	-	-	**13.82**	**11.29**	**21.32**	**10.38**	23.33	-

Bold values = significant values; Htp = plant height; LaP = plant width; NNo = number of nodes; LoFo = leaflet length; LaFo = leaflet width; TFl = time of appearance of the first flower; TPGoM = time of identification of the first mature pod; NGo = number of pods per plant; LoGo = pod length; LaGo = pod width; NGGo = number of seeds per pod; LoG = seed length; P100G = weight of 100 seeds; Rend (kg/ha) = yield in kilograms per hectare MPH : hybrid vigour of the average parent ; BPH : hybrid vigour from the superior parent

Table 5. Heterosis effects of the ten other hybrids (for the ten reciprocal crosses)

F1 Hybrids	HtP (cm)		LaP (cm)		NNo		LoFo (cm)		LaFo (cm)		TFl (days)		TPGoM (days)	
	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH
NBO04*NKO03	-	-	-	-	-	-	-	-	4.88	5.32	**-15.01**	-	**-8.6**	-
NBO04*NFE011	**7.89**	**3.1**	3.37	-	-	-	-	-	6.51	2.22	**-17.72**	-	**-8.91**	-
NBO04*NKO08	-	-	-	-	-	-	-	-	-	-	**-14.4**	-	**-10.68**	-
NBO04*NTE015	**4.38**	-	**4.73**	**1.39**	**18.75**	**9.62**	12.06	2.73	-	-	**-20**	**-2.37**	**-15.1**	-
NKO03*NFE011	-	-	-	-	2.17	-	0.65	-	164.83	155.18	-	-	-	-
NKO03*NKO08	-	-	-	-	**9.89**	**4.17**	-	-	-	-	-	-	-	-
NKO03*NTE015	3.74	3.46	-	-	**13.04**	**8.33**	-	-	-	-	**-2.86**	**-2.39**	-	-
NFE011*NKO08	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NFE011*NTE015	-	-	-	-	**13.64**	**13.64**	**202.75**	**150.98**	7.39	7.23	**-4.1**	**-2.45**	-1.04	-
NKO08*NTE015	-	-	1.08	0.54	**8.05**	**6.82**	2.94	-	-	-	**-3.09**	**-2.86**	-1.31	-

F1 Hybrids	NGo		LoGo(cm)		LaGo (mm)		NGGo		LoG (mm)		P00G (g)		Rend (kg/ha)	
	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH
NBO04*NKO03	-	-	0.06	-	**2.65**	-	-	-	**2.48**	-	**6.85**	-	-	-
NBO04*NFE011	7.93	-	-	-	1.56	-	-	-	-	-	**7.76**	-	9.12	-
NBO04*NKO08	**112.53**	**76.40**	-	-	**1.65**	-	-	-	**3.75**	-	**18.63**	-	**121.84**	**66.55**
NBO04*NTE015	**74.32**	**52.40**	**3.87**	**0.78**	-	-	-	-	-	-	**27.37**	**11.37**	**99.44**	**82.41**
NKO03*NFE011	-	-	1.91	2.07	**12.75**	**12.54**	-	-	**5.06**	**4.16**	**6.05**	**4.45**	-	-
NKO03*NKO08	-	-	-	-	**6.55**	**6.40**	-	-	**10.00**	**7.65**	**19.74**	**16.33**	-	-
NKO03*NTE015	-	-	0.22	-	**5.70**	-	-	-	**12.78**	**7.96**	**27.91**	**13.38**	7.29	5.59
NFE011*NKO08	-	-	-	-	-	-	-	-	**2.43**	1.08	1.58	0.18	-	-
NFE011*NTE015	-	-	-	-	**3.60**	-	-	-	**14.68**	**10.69**	**27.36**	**14.44**	-	-
NKO08*NTE015	**34.67**	**0.60**	1.49	-	**4.40**	-	-	-	**8.97**	**6.55**	**37.36**	**24.96**	**80.41**	**27.72**

Bold values = significant values; Htp = plant height; LaP = plant width; NNo = number of nodes; LoFo = leaflet length; LaFo = leaflet width; TFl = time of appearance of the first flower; TPGoM = time of identification of the first mature pod; NGo = number of pods per plant; LoGo = pod length; LaGo = pod width; NGGo = number of seeds per pod; LoG = seed length; P100G = weight of 100 seeds; Rend (kg/ha) = yield in kilograms per hectare; MPH : hybrid vigour of the average parent ; BPH : hybrid vigour from the superior parent

3.3. General Combining Ability (GCA) and Specific Combining Ability (SCA)

• General Combining Ability (GCA) values

For GCA values (Table 6), some traits show similar results. A synthesis of this table reveals that the parents NBO04 and NTE015, located at the bottom of Table 8, exhibit the best GCA performance, with positive and statistically reliable values for 64.29 % of the traits. These two genotypes thus demonstrate good combining ability with others. In contrast, the genotypes NKO03, NKO08, and NFE011, although also showing positive GCA values, did so for less than 30 % of the traits, which limits their potential as good combiners.

• Specific Combining Ability (SCA) values

In the various crosses, the values of Specific Combining Ability (SCA) were mostly either negative or positive, but generally not statistically significant (Table 7). Only the cross NTE015 × NFE011 stood out by showing positive and significant SCA values for more than 50 % of the traits. The other two crosses, NTE015 × NBO04 and NBO04 × NKO08, displayed positive and significant SCA values, but only for less than 50 % of the traits.

These results suggest that genotypes with high and reliable GCA (General Combining Ability) values tend to combine better with each other particularly when NTE015 is used as the female parent and NBO04 as the male parent. However, these genotypes can also form good combinations with other genotypes, as seen in the crosses NBO04 × NKO08 and NTE015 × NFE011, which exhibited positive and significant SCA values for 42.86 % and 57.14 % of the traits, respectively.

Moreover, it appears that certain parents perform better when crossed with specific genotypes. For example, the female parent NFE011 performs well when crossed with the male parent NKO03, and vice versa. Similarly, the female parent NKO08 produces good hybrids when crossed with NBO04 as the male parent (Table 7).

Table 6. General Combining Ability (GCA) values of the five genotypes

Génotypes	NBO04	NKO03	NFE011	NKO08	NTE015	ESii
HtP (cm)	**1.18**	**-1**	**-0.21**	**-0.79**	**0.82**	0.63
LaP (cm)	**1.14**	**-2.37**	**0.59**	**-1.83**	**2.46**	1.47
NNo	**0.38**	**-0.13**	**-0.25**	**-0.4**	**0.4**	0.36
LoFo (cm)	**-2.64**	**-3.11**	**3.25**	**-3.28**	**5.77**	3.01
LaFo (cm)	**1**	**0.15**	**-0.36**	**0.95**	**-1.73**	0.51
TFl (days)	**1**	**0.15**	**-0.36**	**0.95**	**-1.73**	0.51
TPGoM (days)	**0.92**	0.14	-0.01	**0.37**	**-1.41**	0.31
NGo	4.2	-9.56	0.72	-6.81	**11.45**	6.97
LoGo (cm)	**-0.2**	**-0.26**	**0.08**	**-0.51**	**0.53**	0.42
LaGo (mm)	**0.15**	**-0.12**	**-0.12**	**-0.24**	**0.33**	0.14
NGGo	**-0.69**	**0.54**	**0.09**	**0.09**	-0.01	0.35
LoG (mm)	**0.72**	**-0.31**	**-0.3**	**-0.24**	**0.14**	0.17
P100G (g)	**1.95**	**-1.53**	**-1.05**	**-1.03**	**1.66**	0.6
Rend (kg/ha)	561.36	-836.49	-229.41	-631.26	1135.8	506.59

Bold values = significant values; ESij = standard errors of the GCA; Htp = plant height; LaP = plant width; NNo = number of nodes; LoFo = leaflet length; LaFo = leaflet width; TFl = time to first flower appearance; TPGoM = time to first mature pod; NGo = number of pods per plant; LoGo = pod length; LaGo = pod width; NGGo = number of seeds per pod; LoG = seed length; P100G = weight of 100 seeds; Rend (kg/ha) = yield in kilograms per hectare.

Table 7. Specific Combining Ability values of the twenty crosses

Génotypes	HtP (cm)	LaP (cm)	NNo	LoFo (cm)	LaFo (cm)	TFl (days)	TPGoM (days)
NKO03* NBO04	-0.16	0.36	**-0.95**	2.35	**1.83**	**1.83**	-0.92
NFE011* NBO04	-0.75	0.5	-0.43	-4.49	-0.07	-0.07	-1.17
NKO08* NBO04	0.74	2.95	**1.53**	3.39	**1.83**	**1.83**	**-7.54**
NTE015* NBO04	**2.39**	2.34	0.13	-2.76	-0.3	-0.3	**3.24**
NFE011* NKO03	1.85	7.87	**0.68**	-3.2	**-1.62**	**-1.62**	**-3.39**
NKO08* NKO03	-0.92	-3.78	**-0.97**	1.36	-0.72	-0.72	-0.77
NTE015* NKO03	-0.14	1.2	-0.38	-3.21	**-1.65**	**-1.65**	-1.79
NKO08*NFE011	0.59	-0.25	-0.45	-3.6	-0.02	-0.02	1.79
NTE015*NFE011	**-3.14**	-7.23	**-2.1**	**23.79**	**-2.64**	**-2.64**	**7.87**
NTE015* NKO08	1.14	0.41	-0.9	-2.52	-0.05	-0.06	**-2.22**
NBO04* NKO03	**-2.35**	-6.03	-0.55	2.36	0.23	0.23	**2.49**
NBO04* NFE011	**2.56**	2.5	-0.03	-4.04	**-1.07**	**-1.07**	**2.24**
NBO04* NKO08	-0.06	0.11	-0.08	-0.11	-0.17	-0.17	**3.66**
NBO04* NTE015	0.01	-0.46	**1.13**	-1.96	-0.3	-0.3	-0.17
NKO03* NFE011	-0.23	-3.87	0.28	-3.92	**1.58**	**1.58**	1.81
NKO03* NKO08	-0.48	-0.14	**1.03**	2.5	0.48	0.48	**2.64**
NKO03* NTE015	0.44	-0.35	**0.63**	-4.47	0.16	0.16	0.21
NFE011* NKO08	**-2.41**	-5.15	**-0.85**	-4.14	**1.18**	**1.18**	1.99
NFE011* NTE015	-0.86	-0.96	0.35	**14.95**	-0.36	-0.35	-1.64
NKO08* NTE015	-0.18	2.19	-0.1	-3.44	-0.65	-0.65	1.19
ESij	0.31	0.74	0.18	1.5	0.26	0.26	0.65

Bold values = significant values; ESij = standard errors of the SCA; Htp = plant height; LaP = plant width; NNo = number of nodes; LoFo = leaflet length; LaFo = leaflet width; TFl = time to first flower appearance; TPGoM = time to first mature pod.

Table 7. Specific Combining Ability values of the twenty crosses (continued)

Génotypes	NGo	LoGo (cm)	LaGo(mm)	NG/Go	LoG(mm)	Poids 100G(g)	Rend (kg/ha)
NKO03* NBO04	**-24.57**	**-1.34**	**-0.66**	**0.62**	**0.29**	-0.83	**-1556.55**
NFE011* NBO04	2.35	-0.64	**-0.05**	-0.34	0.04	**2.05**	541.41
NKO08* NBO04	**-32.32**	**1.23**	**-0.23**	0.07	**-0.2**	**-1.54**	**-2265.65**
NTE015* NBO04	**20.23**	0.58	**0.48**	0.37	**0.76**	0.84	**1975.56**
NFE011* NKO03	**11.31**	**1.42**	**0.06**	0.24	**-0.12**	-0.57	664.28
NKO08* NKO03	-1.97	**-1.01**	**-0.04**	-0.16	**-0.76**	**-1.38**	-267.39
NTE015* NKO03	2.38	**-1.91**	**-0.14**	**-1.66**	**-0.25**	-0.84	-524.78
NKO08*NFE011	4.76	**-0.94**	**0.2**	**-1.51**	**0.1**	-1.22	-265.33
NTE015*NFE011	**26.69**	**-1.17**	**0.39**	**0.56**	**0.06**	**2.52**	**2203.4**
NTE015* NKO08	**-10.77**	**1.34**	**0.12**	**0.59**	**0.22**	-0.4	-769.56
NBO04* NKO03	**-18.37**	0.66	**0.28**	**1.02**	**0.44**	0.1	**-1001.05**
NBO04* NFE011	4.36	**-1.06**	**0.2**	**-0.94**	-0.03	-0.07	-16.36
NBO04* NKO08	**30.68**	-0.09	**0.3**	**-0.74**	**0.64**	**1.62**	**1755.41**
NBO04* NTE015	**26.03**	0.28	-0.02	**-1.45**	**-0.5**	**1.72**	**1689.95**
NKO03* NFE011	7.31	**1.52**	**0.24**	**0.84**	**-0.32**	-0.8	372.04
NKO03* NKO08	5.03	-0.33	**-0.1**	0.04	**0.06**	0.78	502.57
NKO03* NTE015	-0.22	0.49	**0.12**	0.14	0.04	0.5	137.89
NFE011* NKO08	**-11.45**	-0.45	**-0.86**	**0.89**	**-0.41**	**-1.45**	-734.98
NFE011* NTE015	**-10.7**	-0.55	-0.04	0.19	**0.23**	0.16	-715.52
NKO08* NTE015	2.43	-0.02	**0.12**	**0.99**	**-0.13**	**1.54**	782.4
ESij	3.49	0.21	0.07	0.18	0.09	0.3	253.3

Bold values = significant values; ESij = standard errors of the SCA; NGo = number of pods per plant; LoGo = pod length; LaGo = pod width; NG/Go = number of seeds per pod; LoG = seed length; P100G= weight of 100 seeds; Rend (kg/ha) = yield in kilograms per hectare.

Table 8. Differences between crosses and their reciprocal crosses, and percentages of significance of these differences

Génotypes	HtP (cm)	LaP(cm)	NbNd	LoFo (cm)	LaFo (cm)	TFl (days)	TPGoM(days)
NKO03*NBO04-NBO04*NKO03	**5.8**	**8.56**	-0.4	0.46	-0.06	-2	1.78
NFE011*NBO04-NBO04*NFE011	0.16	3.72	1.2	4.25	0.08	-1.6	3
NKO08*NBO04-NBO04*NKO08	0.38	**6.34**	0.6	-1.26	1.48	-0.4	-2.2
NTE015*NBO04-NBO04*NTE015	-0.8	-2.1	-2.8	-1.18	0.86	0.2	-2.6
NFE011*NKO03-NKO03*NFE011	**2.3**	**6.48**	0.4	1.4	1.1	0.2	2.4
NKO08*NKO03-NKO03*NKO08	0.58	-4.46	-0.8	**-27.37**	0.22	**5.4**	3.2
NTE015*NKO03-NKO03*NTE015	1.41	**8.37**	-0.35	2.45	**-14.57**	**-3.2**	-2.85
NKO08*NFE011-NFE011*NKO08	1.24	-0.86	1.2	0.78	1.08	-0.4	1.2
NTE015*NFE011-NFE011*NTE015	-0.58	2.6	0.4	5.95	0.94	**-6**	**-9.3**
NTE015*NKO08-NKO08*NTE015	1.38	0.18	1	**-26.5**	0.52	**6.2**	-3.2
%V.Sing	20	40	0	20	10	40	10

Bold values = significant values; %V. Sig = percentage of significant values; Htp = plant height; LaP = plant width; NNo = number of nodes; LoFo = leaflet length; LaFo = leaflet width; TFl = time to first flower appearance; TPGoM = time to first mature pod.

Table 8. Differences between crosses and their reciprocal crosses, and percentages of significance of these differences (continued)

Génotypes	NGo	LoGo (cm)	LaGo (mm)	NG/Go	LoG (mm)	P100G (g)	Rend(kg/ha)
NKO03*NBO04- NBO04*NKO03	20.6	-0.44	**0.69**	**-2.2**	**0.89**	**2.6**	1280.77
NFE011*NBO04- NBO04*NFE011	28.6	**1.68**	**0.97**	0.6	**1.17**	1.5	2799.36
NKO08*NBO04- NBO04*NKO08	0.8	0.48	-0.5	0.2	-0.61	**-3.78**	-838.82
NTE015*NBO04- NBO04*NTE015	**-47.8**	1.1	-0.25	**2.8**	-0.24	**-5.1**	**-3652.13**
NFE011*NKO03- NKO03*NFE011	17	0.4	0.24	-1.8	**0.86**	0.64	609.14
NKO08*NKO03- NKO03*NKO08	-35.6	**-3.28**	**-0.86**	-0.4	**0.94**	-0.82	-2433.71
NTE015*NKO03- NKO03*NTE015	9.2	-0.89	0.34	-0.6	**0.98**	**5.47**	1949.9
NKO08*NFE011- NFE011*NKO08	-6.2	0.72	**1.53**	-0.2	**1.8**	**4.06**	319.48
NTE015*NFE011-NFE011*NTE015	-26.35	-1.14	-0.18	0.2	**-1.52**	**-3.49**	-2064.75
NTE015*NKO08- NKO08*NTE015	-36.4	0.82	-0.49	-0.8	0.2	**-1.38**	-2526.42
%V.Sing	10	20	40	20	70	70	10

Bold values = significant values; %V. Sig = percentage of significant values; NGo= number of pods per plant; LoGo = pod length; LaGo = pod width; NG/Go = number of seeds per pod; LoG = seed length; P100G= weight of 100 seeds; Rend (kg/ha) = yield in kilograms per hectare.

4. Discussion

The results regarding the average performance of individual plants indicate that, in general, the hybrids exhibited significantly higher average agronomic performance than the parental lines for the majority of the traits studied. These results corroborate several studies showing that hybrids often exhibit superior agronomic performance to parental lines due to heterosis, a phenomenon widely exploited in modern crop breeding programmers [20,21,22].

Thus, this improvement in performance observed in the hybrids could result from greater physiological efficiency and increased biomass accumulation, characteristics often associated with heterosis in hybrid crops [23,24]. Similar results have also been reported in sorghum and cowpea, where hybridization has significantly improved the agronomic performance of the progeny [25,26].

In contrast, the number of seeds per pod (NG/Go) did not follow the same trend as the other yield traits. This result could be explained by the fact that this trait is generally strongly genotype-controlled and exhibits relatively low variability in response to heterosis effects. A study in Cameroon showed that hybrid vigor improves certain yield components, but not the number of seeds per pod, which is more closely linked to the genetic effects of the parents [27].

Studies in West Africa indicate that certain seed and pod traits of cowpea are mainly governed by additive effects and gene interactions, limiting the expression of the hybrid advantage [26].

For traits such as plant height and seed length, the relative inferiority of hybrids can be attributed to higher variability in hybrids (14.97 % and 6.20 % respectively) compared to the parents (11.59 % and 4.09 %). This increased variability reflects more intense genetic recombination in F1 populations, producing a wider range of phenotypes, some of which perform below the parental average.

All the traits measured showed significant differences between the parental lines and the F1 hybrids, indicating that these traits are under significant genetic control and that there is a solid basis for future breeding. The observation of variable heterosis across traits is consistent with several recent studies on legumes and cereals, indicating that hybrid superiority is not uniform and that phenotypic variability is often higher in F1s [25,26,28,29,30].

These results also indicate that there is sufficient variability between parental genotypes and F1 hybrids for the traits studied, thus offering potential for genetic improvement. Furthermore, in this study, 42 % of the traits have a coefficient of variation of less than 20 %, suggesting that targeted crosses may be considered for the improvement of the most stable traits.

Analysis of heterosis revealed that positive values indicate that the hybrids outperform their parents, with high levels observed for certain traits, confirming that F1 performance is a reliable indicator for crop improvement [30].

For maturity time, all hybrids showed significant negative heterosis, maturing more rapidly than their parents—an advantageous trait in tropical or semi-arid areas for avoiding environmental stresses such as terminal drought.

Comparable results were observed in sorghum, where negative heterosis values for days to flowering and maturity indicate increased earliness in the hybrids, a favorable trait in water-deficient environments or those with short growing seasons [31].

Combining ability values showed high variability across traits, reflecting the differential contribution of the parental genotypes. This variability, observed for both general and combination-specific combining ability, confirms the importance of non-additive effects and heterosis in cowpea breeding [28,32,33].

Analysis of combinability also showed that genotypes NTE015 and NBO04 exhibited the highest values of general combinability (AGC) for the majority of the traits studied. This suggests that these genotypes possess a strong ability to favourably transmit these traits to their offspring, reflecting the predominance of additive genetic effects in the control of these traits.

Conversely, certain specific crosses, such as NTE015 × NFE011 and NBO04 × NKO08, exhibited high specific combining ability (SCA), highlighting the importance of non-additive effects and parental interaction in the expression of high heterosis for these traits.

Generally speaking, several studies have shown that yield-related traits in cowpea are controlled by both additive and non-additive effects, confirming the value of identifying both good general combiners and high-performing specific crosses in plant breeding programmers [34,35,36].

The majority of the traits studied (85.72%) are not affected by the direction of crossing, indicating that the maternal effect on hybrid performance remains limited, consistent with recent observations on cowpea and other legumes [26,37,38].

5. Conclusion

This study aimed to contribute to the development of improved cowpea (*Vigna unguiculata*) varieties adapted to the agroecological conditions of Côte d'Ivoire by evaluating heterosis, combining abilities (GCA and SCA), and maternal effects.

The results revealed 14 discriminant agronomic traits, most of which showed significant improvement in F_1 hybrids compared to their parental lines, consistent with positive heterosis effects. Hybrids derived from the crosses NTE015 × NBO04 and NBO04 × NTE015 stood out by outperforming their respective parents for approximately 64.29% of the traits assessed, thus identifying NTE015 and NBO04 as the most promising general combiners.

In addition, the crosses NTE015 × NFE011, NTE015 × NBO04, and NBO04 × NKO08 produced high-performing hybrids for over half of the evaluated traits, highlighting the value of these specific combinations in breeding programs focused on yield potential and adaptability.

Analysis of maternal effects revealed that only 14.28% of the traits were significantly influenced by the direction of the cross, suggesting a minimal impact of cytoplasmic inheritance or maternal origin on hybrid performance. Therefore, the choice of cross direction can be considered non-essential in cowpea hybrid breeding strategies.

In conclusion, this study underscores the relevance of integrating combining ability analysis and heterosis evaluation in cowpea improvement programs to optimize parent and cross selection. This approach enables the development of high-yielding, early-maturing hybrids well adapted to the climatic constraints of cowpea-growing regions.

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