



## Research article

Crossability and inheritance of seed coat colour in cowpea at F<sub>1</sub> generation

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## Abstract

A study on crossability and inheritance of seed coat colour in cowpea was conducted between October, 2017 and August, 2018. Two accessions of cowpea: IT98K-205-8 (white seeded) and IT98K-555-1 (brown seeded) were used for the study. Plants were raised in plastic pots in the screen house, and as flowers mature, crosses were performed manually, early in the morning between 7.00 and 9:30 AM. Significant level of differences were detected between the crosses for all traits observed except for number of seeds per pod. Overall, 19 successful pods were generated from 67 crosses representing 28.36% success rate, and indicating a low level of compatibility between accessions. All seeds of F<sub>1</sub> plants were black, contradicting the model that maternal parents determine the phenotypes of F<sub>1</sub>s. However, the two parents bred true for seed coat colour indicating their pure line status. It was shown that maternal effect played significant role regarding crossability, but did not influence the seed coat colour inheritance of the crop. These results indicated epistasis, and it is suggested that the inheritance of seed coat colour in cowpea is polygenic.

**Keywords:** Cowpea; epistasis; maternal effect; polygenic; seed coat color

## 1. Introduction

Cowpea (*Vigna unguiculata* L. Walp) is crop of significant importance in Africa; it serves as a source of proteins in the tropical and subtropical countries (Lelou et al., 2011; Stoilova and Pereira, 2013), where Nigeria is ranked the highest in terms of production (FAOSTAT, 2020). It is a source of income for the people of Africa where it is widely cultivated for different purposes (Ogunkanmi and Adekoya, 2013; Rangkhom and Khanna, 2018). Despite the good attributes of cowpea, one of the major constraints hampering its productivity in Nigeria is drought (Fatokun et al., 2009). Breeding of genotypes with high level of tolerance to drought stress for all stages of growth and development are desirable to sustain yield. Nevertheless, breeding for drought must be done with consumer acceptability considerations to prevent drawbacks that might arise from rejection of improved varieties; as utilization of the crop in Africa is heavily dependent on consumer preference (Egbadzor et al., 2014).

One of the most important attributes of cowpea influencing its acceptability and its introduction to markets is the seed coat colour which has been a subject of study for ages, with the genetic factors underlying their expression elucidated (Herniter et al., 2019). There are various patterns of seed coat displayed by cowpea seeds and the preferred colours and pigmentations are region specific (Herniter et al., 2019). According to Egbadzor et al. (2014), the seed coat colour and pigmentation in crop plants are influenced by anthocyanin syntheses and controlled by some anthocyanin genes (like *pac 1* gene) which are abundant in plants and important to plants in signaling abiotic stress such as drought (Carvalho et al., 2019). Seed coat colour and pigmentation inheritance in cowpea has been reported to be quantitative in nature involving several genes (Oluwatosin, 2000; Mustapha, 2009), contrary to the findings of Yilwa (2012). These number of genes involved have been attributed to the seed coat colour combinations of the parental lines involved in specific crosses (Egbadzor et al., 2014).

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Development of improved cultivars for any constraint requires combination of genotypes of diverse origins as parental stocks. Adapted individuals in terms of specific constraints in a particular ecology are normally the best sources of genes for breeding improved varieties. A larger genetic variability in existence in the tropics among cowpea genotypes serves as source of information for developing hybrids for specific constraints. However, proper choice of parents is critical to a successful breeding program of cowpea because of limitations resulting from hybridization for inheritance of polygenic traits (Aremu et al., 2007). Therefore, information on genetic compatibility and inheritance of seed coat colour and their relationship with drought tolerance in cowpea would contribute positively to the improvement of the crop through hybridization.

This research aimed at studying the level of crossability between two cowpea accessions and inheritance of seed coat colour in  $F_1$  generation.

## 2. Materials and methods

The experiment was carried out at the screen house of the Department of Plant Science and Biotechnology (PSB), Adekunle Ajasin University, Akungba-Akoko (AAUA), Nigeria between October, 2017 and January, 2018 for the crosses, while evaluation of  $F_1$  was done in the Plant Breeding Field, PSB, AAUA between April and August, 2018. Two accessions of cowpea: IT98K-205-8 and IT98K-555-1 received from the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria were used for this experiment and were tagged A and B respectively. These accessions were chosen based on the following attributes: Both accessions were erect types and of Nigerian origin, while A is early maturing and moderate yielding, B is high yielding (Ajayi and Gbadamosi, 2020). Accession A had sub-hastate leaflet shape, straight pods, dark green leaves, dark green immature flowers, yellow-white mature flowers, dark green immature pod colour and white seed coat colour. Accession B on the other hand had hastate leaflet shape, slightly curved pods, pale green leaves, pale green immature flowers, purple-white mature flowers, pale green immature pods and brown seed coat colour. Accession A was drought tolerant, while B was drought susceptible and these attributes have been confirmed at seedling (Ajayi et al., 2018), vegetative (Ajayi et al., 2020) and flowering stages (data yet to be published). In addition, accession A combines *Striga* and *Alectra* resistance with early maturity and high yield (Singh et al., 2006; Ajeigbe et al., 2008; Noubissie Tchiagam et al., 2010; Hayatu et al., 2016).

Seeds were planted in plastic pots filled with 7.5 kg sandy loam soil without fertilizer application. Five seeds were planted

per pot per accession and later thinned to one plant per pot after two weeks of emergence.

Eight pots were used for each accession arranged in two rows for direct crosses and their reciprocals. Four pots from each cross held the plants which served as the pollen receptors, while the remaining four held the pollen donors. As the flowers begin to mature, crosses between accessions were performed manually very early in the morning between 7 AM and 9:30 AM (Singh et al., 1999) (with modifications). After the pollinations have been done, all pollinated flowers were tagged. The date of pollination and the type (direct/reciprocal) were written on the tags and harvesting of pods was done as they mature. Twenty seeds from each of the parents and crosses were grown in the field in non-replicated plots to produce seeds by natural self-pollination to observe the inheritance patterns of seed coat colour among individuals at pod maturity. Spacing of plants in the field was maintained at 30 cm intra row and 50 cm inter row spacing. Visual observation of seed coat colour was done and recorded for each plant at pod maturity.

The following data were collected for pollinated flowers: number of flowers pollinated, number of pods set, percentage of pods set, average pod length, average number of seeds per pod and average number of days to pod maturity. Percentage of plants emerged, percentage of plants survived, and percentage of plants expressing certain seed coat colours were also recorded for parents and the  $F_1$  hybrids at pod maturity. Data were subjected to one way analysis of variance (ANOVA) with the cross regarded as fixed factor in SPSS program version 20.

## 3. Results and discussion

The results of the crosses are presented in Table 1. Significant level of differences were detected between the crosses for all traits observed except for number of seeds per pod. Differences in number of flowers pollinated resulted from the high number of flowers produced by accession B which resulted in several of its flowers receiving pollens from one flower of accession A in the direct crosses (AxB). However, the reciprocal crosses (BxA) had lower number of flowers crossed due to fewer flower production by accession A. Number of flowers crossed per plant ranged between 10 and 14 in AxB; it had the highest number of pods set per plant (ranging between 2 and 4), highest pod length (ranging between 10.20 cm and 13.50 cm) and the least number of days to pod maturity (19.00 and 20.00 days). However, number of seeds per pod was highest in BxA, ranging between 3 and 8 seeds per pod per plant and the highest percentage pod set per plant (ranging between 25 and 50 percent). Lower number of seeds per pod observed in AxB despite its

**Table 1**  
Analysis of the reciprocal crosses of two accessions (A and B) of cowpea.

Trait	Cross	Mean	SE	Min	Max	MS (Df=1)	MSE (Df=6)
Number of flowers pollinated/plant	AxB	11.50	0.96	10.00	14.00	78.13**	4.29
	BxA	5.25	1.11	3.00	8.00		
Number of pods set/plant	AxB	3.00	0.41	2.00	4.00	3.13**	0.79
	BxA	1.75	0.48	1.00	3.00		
Percentage pod set/plant	AxB	26.19	3.25	20.00	33.33	102.03**	90.52
	BxA	33.33	5.89	25.00	50.00		
Pod length	AxB	11.49	0.79	10.20	13.50	17.94**	4.38
	BxA	8.50	1.25	7.10	12.23		
Number of seeds/pod	AxB	3.50	0.50	2.00	4.00	1.13 <sup>ns</sup>	3.63
	BxA	4.25	1.25	3.00	8.00		
Number of days to pod maturity	AxB	10.50	0.29	19.00	20.00	0.50**	0.17
	BxA	20.00	0.00	20.00	20.00		

\*\* : Significant. SE: Standard error; MS: Mean square value; MSE: Mean square error; DF: Degree of freedom.

longer pod length must have been as a result of bigger seeds obtained from the cross compared to the seed size of the reciprocal.

Overall 19 successful pods were generated from a total of 67 crosses representing 28.36% success rate indicating a low level of cross-compatibility between the accessions. Generally, percentage pod set of both direct (26.19%) and reciprocals (33.33%) were low, indicating a considerable level of incompatibility between the parents. Similar findings were reported (Lelou and Van Damme, 2006; Lelou et al., 2011) in intraspecific crosses of cultivated and wild accessions of cowpea. Different success rates of direct and reciprocal crosses have been reported in crosses of cowpea (Ogunkanmi and Adekoya, 2013), interspecific crosses between cowpea and mung bean (Win et al., 2015) and sesame (Laurentin and Benitez, 2014), an attribute linked to maternal influence. Failure of majority of the crosses may be attributed to lack of fertilisation as described by Lelou and Van Damme (2006), genetic variation, environmental factor, fertilisation barriers, embryo abortion and hybrid failure could have also contributed to the low success rate (Ogunkanmi and Adekoya, 2013). However, contrary findings were reported by Mohammed et al. (2010) and Rangkhram and Khanna (2018). In crosses between cultivated cowpea and wild relatives, successful crosses ranging between 54 and 63.9% were observed (Mohammed et al., 2010), while the range fell between 60 and 76.19% in crosses among accessions of cowpea of different locations of India (Rangkhram and Khanna, 2018).

The results for seed coat colour inheritance among the parents and the F<sub>1</sub> direct and reciprocal crosses are presented in Table 2.

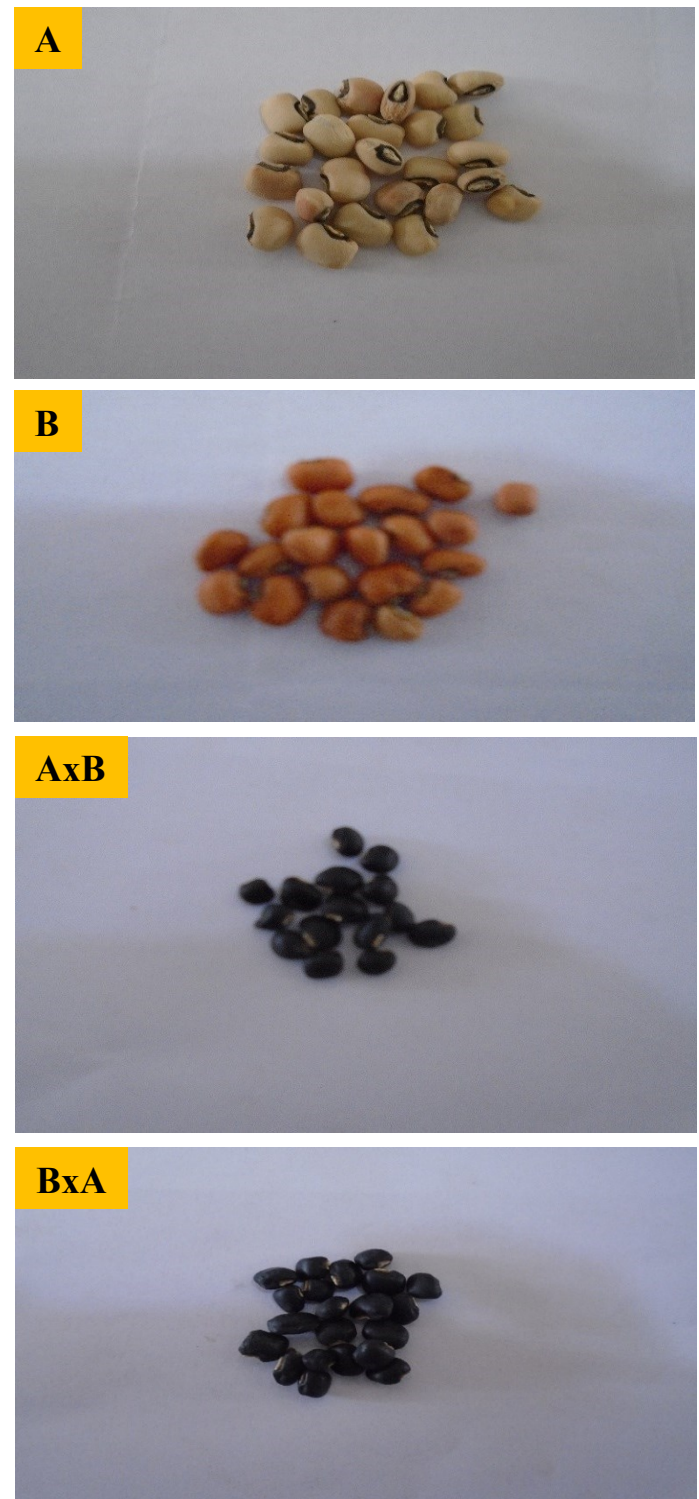
**Table 2**  
Inheritance of seed coat colours in parents and F<sub>1</sub> hybrids of cowpea.

Genotype	NSP	EM (%)	SU (%)	WS (%)	BRS (%)	BLS (%)
A	20	50	100	100	0	0
B	20	80	100	0	100	0
AxB	20	90	100	0	0	100
BxA	20	50	100	0	0	100

**NSP:** Number of seeds planted; **EM:** Percentage emerged; **SU:** Percentage survived; **WS:** Percentage of plants with white seed coat colour; **BRS:** Percentage of plants with brown seed coat colour; **BLS:** Percentage of plants with black seed coat colour.

Germination was good for F<sub>1</sub> hybrids just as for the parental lines and the plants were vigorous in growth till maturity producing viable seeds. A sufficient level of reproductive potential was indicated in the crosses by the successful advancement of the seeds of the crosses to F<sub>1</sub> generation. The parents were true breeders for seed coat colours, however, what was observed among the F<sub>1</sub> was different from what was expected. Despite the fact that both parents had white (accession A) and brown seeds (accession B), all F<sub>1</sub>s had black seeds (Figure). When crosses between white and brown seeded parents result in black F<sub>1</sub>s, it implies heterosis of seed coat colour (Egbadzor et al., 2014). Black colour is found to be dominant over brown colour, and also, black eye region of white is dominant over the brown, therefore the crosses resulted in the solid black seed coat colour. It would be important if the pattern of inheritance of the seed coat colour is studied in F<sub>2</sub> and subsequent generation to observe if the black seeds would segregate into different groups of seed coat colour. The findings of the present study are similar to what was reported by Egbadzor et al. (2014) among crosses of white and brown seeded cowpea. In their own case, the F<sub>2</sub> segregated

into three and ten seed coat groups suggesting involvement of many genes as described by Drabo et al. (1988) in cowpea and by Chandler et al. (1989) in maize. The complex nature of these crosses could be linked to epistasis or quantitative inheritance in which heterosis was involved in inheritance of seed coat colour as suggested by Mustapha (2009) and Egbadzor et al. (2014).



**Fig.** Inheritance of seed coat colour in parents (A and B) and F<sub>1</sub> hybrids (AxB and BxA) of cowpea.

The fact that black seeded F<sub>1</sub>s were produced from crosses between white seeded and brown seeded parents proved that dominance of black over brown and other colours might not be

universal, therefore, epistasis may be responsible for the expression of the black colour at  $F_1$  and it could not have been simple dominance and recessive. Similar epistasis interactions in seed coat colour of cowpea have also been reported by other workers (Lachyan and Dalvi, 2015; Amusa et al., 2019). While the results of the present study correspond to that of Egbadzor et al. (2014) and agrees with Mustapha (2009), they contradict that of Yilwa (2012) in which similar crosses between white seeded and brown seeded cowpea gave brown in  $F_1$ . Although, the presence of white and brown in  $F_2$  and their ratios suggested involvement of two genes governing the seed coat colour trait. The present findings also contradict the ones reported in cowpea crosses (Nwofia, 2014; Lachyan et al., 2016) and sesame (Laurentin and Benitez, 2014). However, in the study done by Amusa et al. (2019), maternal effect was observed for seed coat colour in  $F_1$  generation, while the presence of intermediary seed coat colour in  $F_2$  which completely deviated from the Mendelian patterns of monogenic inheritance suggested the involvement of multiple genes in control of the trait.

Seed coat colours and patterns in cowpea have been successfully mapped into three loci namely  $C$ ,  $W$  and  $H$ , respectively linked to genes *Vigun07g110700*, *Vigun09g139900* and *Vigun10g163900* involved in flavonoid biosynthesis pathway. Segregation ratios and dominance data of another tested populations were found to be consistent with the three loci ( $C$ ,  $W$  and  $H$ ). The primary locus controlling the seed coat pattern is the  $C$  locus,  $W$  (Watson) and  $H$  (Holstein) majorly controlling the distribution of pigment throughout the seeds (Herniter et al., 2019). When pigmentation is invisible, restricted to the eye and or distributed across the seed coat (full coat), it is tagged no colour ( $C_0$ ), Eye1 ( $C_1$ ) and Eye2 ( $C_2$ ), respectively. Individual with Holstein ( $H_1$ ) which lacks Watson ( $W_1$ ) genotype expresses Holstein; conversely individual without Holstein but having Watson genotype expresses Watson.

However, individual combining the two (Holstein and Watson) expresses the full coat phenotype. Hence, individual having  $C_0C_0$  will express no colour phenotype regardless of the status at  $W$  and  $H$  loci,  $C_1C_1$  genotype will express the Eye1 regardless of  $W$  and  $H$  loci. However,  $C_2-W_0W_0H_1$  and  $C_2-W_1H_0H_0$ , respectively will express the Holstein and Watson pattern. In the

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present study, the crossing of the parent A with the Eye 2 genotype ( $C_2C_2W_0W_0H_0H_0$ ) with parent B with full coat ( $C_2C_2W_1W_1H_1H_1$ ) brown resulted in  $F_1$  full coat ( $C_2C_2W_1W_0H_1H_0$ ) black, which agrees with the findings of Herniter et al. (2019). Examples of flavonoids in plants are anthocyanins which determine seed coat colour and pigmentation in plants (Herniter et al., 2018). They perform the key role of stress signaling and tolerance in plants and have been found to be affected by environmental factors just as it occurs for quantitative traits, hence, suggesting that seed coat colour in cowpea may be under the influence of environment making it a quantitative trait (Egbadzor et al., 2014). The black seed coat colour in cowpea has been successfully mapped to the  $B1$  genes controlling enzymes in the pathway of anthocyanin biosynthesis, and a PCR marker developed for trait based on the candidate gene *Vigun05g039500* (Herniter et al., 2018).

## 4. Conclusion

Conclusively, it has been shown in the present study that crosses between the accessions of cowpea involved were possible, and that maternal effect also play a significant role in the expression of traits such as number of pods set, percentage pod set, pod length and number of days to pod maturity. The results of the study also suggest that seed coat colour trait in cowpea is a polygenic trait. Further studies into the  $F_2$  and subsequent generations are required for better understanding of the patterns of inheritance of seed coat colour in the crop. Also, the relationships between seed coat colour and pattern and drought stress tolerance is one of the future tasks of the study. Knowledge of the seed coat characteristics and other desirable traits such as drought stress tolerance can aid breeders in breeding programs of cowpea for improved yield for environments with moisture deficit as well as consumer preference in terms of seed coat colour.

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