



Inheritance of Pod Length in Cowpea (*Vigna unguiculata* (L.) Walp.)

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Abstract

Confirming the contestable genes that control a trait of interest is indispensable for developing crop varieties. This underscores the importance of studying the mode of inheritance of pod length in cowpea. The objectives of this study were to estimate the gene numbers controlling pod length, its broad-sense heritability and its nature of dominance in cowpea. Three cowpea lines (Ife Brown, TVNu699 and TVu2723) were used to generate two crosses (Ife Brown x TVNu699 and TVu2723 x TVNu699) in the greenhouse. Four generations (P₁, P₂, F₁ and F₂) were evaluated in a randomized complete block design in 3, 3 and 4 replications for parents (P₁ and P₂), F₁ and F₂ respectively. Data on pod length and seed weight were subjected to statistical analyses. Additive variance (a) was higher than the dominance variance (d) in both crosses. Crosses: Ife Brown x TVNu699 with a = 2.82 and d = 0.43 and TVu2723 x TVNu699 with a = 3.49 and d = 1.69. The numbers of effective factors were estimated to be three and four in the two crosses; while the degrees of dominance were 15.2% and 42.9%, respectively. The broad-sense heritability estimates for pod length were 82.6% in the cross TVu2723 x TVNu699 and 71.2% in the cross Ife Brown x TVNu699. It was inferred that pod length in cowpea is controlled by multiple gene pairs, with additive gene action playing a significant role over dominance, and high values of the heritability estimates confirmed that the trait is transferable, indicating strong potential for selection.

Introduction

Legume pods offer Cowpea (*Vigna unguiculata* (L.) Walp.) is an annual crop from the family Fabaceae, genus *Vigna*, species *unguiculata*. Cowpea is a grain legume cultivated in the savannah regions of the tropics and subtropics. It is mostly adapted to diverse environments and it is considered a drought tolerant legume (Boukar *et al.*, 2019). Cowpea is a dicotyledonous crop and a diploid species with 2n = 22 chromosomes. It is usually grown as sole crop but could also be intercropped with cereals such as sorghum or millet in some parts of semi-arid humid tropics of sub-Saharan Africa, South and Central

America (Afe *et al.*, 2023) where it is being consumed. More than 5.4 million tons of dried cowpeas are produced worldwide, with Africa producing nearly 5.2 million. Nigeria is the largest producer and consumer and accounts for 61% of production in Africa and 58% worldwide, while Niger is the largest cowpea exporting country (FAOSTAT, 2021). Cowpea is the most commonly cultivated, consumed, distributed and traded African legume crop. It contains up to 30% protein in its grain and performs well in low fertile soils, drought tolerant and able to fix atmospheric nitrogen, improving poor soils (Horn *et al.*, 2022). Improvement in the agronomic practices will boost cowpea production, notwithstanding the prevailing production challenges of declining soil fertility,

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unreliable rainfall, pests and diseases (Boukar *et al.* 2016).

Legume pods offer a shielding envelope to developing seeds. It acts as catchments, transport link and temporary reservoir for solutes mobilized from vegetative parts to seeds; and if green and illuminated, it functions in photosynthetic fixation of CO₂ (Cho *et al.*, 2023). In cowpea, the total yield depends upon the number of pods and size of seed. It is established that the size and number of pods are characters that are quantitatively inherited (Atakora *et al.*, 2023). Pod length is an important yield component in cowpea cultivation, long pod variety, most times contains more numbers of seeds when compared to short pod varieties. There is a progressive increase in pod length with the advancing age of crop, up to 12 to 15 days after flowering which declines towards maturity due to drying of pods (Edematie *et al.*, 2021). Several genetic studies have been conducted to decode mode of inheritance on some important traits on cowpea. Egbadzor (2014) used different bi-parental crosses to estimate the number of genes that might control seed coat color in cowpea in order to decipher its mode of inheritance. Oladejo *et al.* (2020) used bi-parental to study the seed coat texture in cowpea, and they concluded that seed coat texture in cowpea is controlled by a pair of single genes. The study also revealed that smooth seed coat texture is completely dominant over rough seed coat texture. Furthermore, another study, Oladejo *et al.* (2021) examined the seed coat colour which is an important trait that determine consumers' preference in cowpea; they concluded that many genes were responsible for controlling coat color, arguing that many anthocyanins are known to be present in the seed coat of cowpea, and anthocyanin content of the various parts of a plant can be quantified. Pod length gave contrasting findings on the dominance of pod length. Abha and Meena (2024) who reported a high heritability of cowpea pod length; while other workers reported low heritability (Owusu *et al.*, 2020), but their report may be due to massive influence of the environment. There were contradictions on whether transgressive segregation was for long or short pods and in the estimates of the number of effective factors or genes controlling pod length in cowpea. This study was conducted to estimate the number of genes

controlling the inheritance of pod length in cowpea, the degree of dominance between short and long cowpea pod and, broad-sense heritability for pod length.

Methods and Materials

Genetic materials

The varieties used in the study were TVNu699, TVu2723 and Ife Brown. TVNu699 is a wild variety of cowpea which possesses pubescence that makes it resistant to biotic factors such as insect pests. It is a short-pod variety gotten from the International Institute of Tropical Agriculture (IITA), Ibadan. Ife brown is an elite cowpea variety that is acceptable in the market, it is a long-pod variety developed by the Faculty of Agriculture, Obafemi Awolowo University, Ile-Ife in conjunction with the Institute for Agricultural Research and Training (IAR&T). TVu2723 is a long-pod variety, developed by the International Institute of Tropical Agriculture (IITA), Ibadan. The attributes of the cowpea genotypes are summarized in Table 1.

Below is the crossing pattern of the cowpea genotypes:

- i. TVu2723 (P₁) x TVNu699 (P₂)
- ii. Ife Brown (P₁) x TVNu699 (P₂)

Greenhouse management and practices

The parental lines (Ife Brown, TVu2723, and TVNu699) were planted in the greenhouse. Eight (8) buckets filled with topsoil were used to grow each variety and replicated three times. Two seeds were planted per hill for each bucket. Thinning was done 2-weeks after emergence, to one seedling per bucket, which sums up to twenty-four seedlings per variety. Manual wetting was done. At two weeks' interval, continuous planting was done to synchronize flowering. NPK 15:15:15 fertilizer was applied two weeks and four weeks after planting to boost the performance of the plants. Cypermethrin and Lambda-cyhalothrin at 0.8 liters per hectare 10% E.C were sprayed for the control of insects such as Flower bud thrips, *Megalurothrips sjostedti* and the pod sucking bugs, *Maruca vitrata*, *Clavigralla tomentosicolis* and *anoplocnemic curvipes*.

Table 1: Pod characteristics of the parental lines used in the crosses in this study

Variety	Origin	Description	Pod nature	Pod length (cm)	Dried pod colour
Ife Brown	OAU, Ile Ife	Cultivated, medium-duration landrace, day-length neutral, brown seeds, fast-cooking, drought-resistant, pest/disease tolerant	Long	12.97	Light Yellow
TVu2723	IITA, Ibadan	Extra-early maturity, cream-colored seeds with black eye, high protein/mineral content Cultivated	Long	17.6	Light Yellow
TVNu699	IITA, Ibadan	Wild, genetic diversity for seed coat color, pest resistance, low pod yielding cultivar. Useful in introducing novel traits into cultivated cultivars	Short	9.72	Dark Brown

Generation of crosses from the parental lines

TVu2723 (P₁) and Ife Brown (P₁) – female parents with long pod varieties, were crossed to TVNu699 (P₂) male parent, a short pod variety. TVNu699 was used as the male parent while the female parents were Ife brown and TVu2723 in the generation of the crosses. Flowers from TVNu699 were plucked, and the anthers were gently exposed and rubbed with the stigmas and styles of emasculated TVNu2723 and Ife Brown flower, then tagged after pollination. Crosses generated from the three parental lines were advanced to F₂ by selfing F₁ plants, while several backcrosses to parent one (BCP₁) and backcrosses to parent two (BCP₂) were not successful due to unfavourable environmental conditions.

Evaluation of generations

The parental lines (Ife Brown, TVu2723, and TVNu699) were evaluated in the greenhouse, where F₁ crosses were successfully obtained. Subsequently, the F₁ seeds were advanced to obtain F₂ plants for evaluation at the experimental field of the Faculty of Agriculture, Obafemi Awolowo University (OAU), Ile-Ife. All the four generations, (P₁, P₂, F₁ and F₂) for each of the two populations of crosses were evaluated at the OAU experimental field. The field was laid in randomized complete block design in 3, 3 and 4 replications for parents (P₁ and P₂), F₁ and F₂ respectively. Higher number of replications for F₂ was

necessary to facilitate wider expression of phenotypes in segregating generation.

Pod lengths were measured using twine and a 30 cm metre rule. Each parental line (Ife Brown, TVu2723, and TVNu699), five mature, dry, unthreshed pods were randomly selected from eight individual plants in each population. Successful cross-pollinated flower buds from these parental lines produced F₁ pods, which were also harvested at maturity. Thirty (30) F₁ seeds were planted to obtain the F₂ plants, from which pod length measurements were subsequently obtained.

Statistical analysis

Data were analyzed at a 5% level of significance to determine statistical differences among the generations (P₁, P₂, F₁, and F₂).

Based on Burton (1951), Number of effective factors (genes): $k = (0.25 (0.75 - h + h^2) D^2) / (\sigma^2 f_2 - \sigma^2 f_1)$ where, $D = P_1 - P_2$; $h = (F_1 - P_2) / (P_1 - P_2)$; $\sigma^2 f_2 =$ Variance of F₂ family; $\sigma^2 f_1 =$ Variance of F₁ family; $P_1 =$ Mean of parent 1; and $P_2 =$ Mean of parent 2

Broad-sense heritability (H²_b) of pod length was estimated using Ito and Brewbaker (1991) formula: Broad sense; $H^2_b = (\sigma^2 f_2 - \sigma^2_e) / \sigma^2 f_2$ (Ito and Brewbaker, 1991)

where, $\sigma^2_e =$ Error variance = $\frac{1}{4} (\sigma^2 p_1 + \sigma^2 p_2 + 2\sigma^2 f_1)$; $\sigma^2 f_2 =$ Variance of F₂ family; $\sigma^2 f_1 =$ Variance of F₁ family; $\sigma^2 p_1 =$ Variance of parent 1; and $\sigma^2 p_2 =$ Variance of parent 2.

The degree of dominance is the deviation from the mid-parent value towards one of them, as illustrated below.

Mid-parent value = $\frac{1}{2} (P_1 + P_2)$, where, P_1 = Mean of parent 1; P_2 = Mean of parent 2; Mid-parent value.

Degree of Dominance = Dominance variance (d) / Additive genetic variance (a)

where $d = F_1 - \frac{1}{2} (P_1 + P_2)$; $a = \frac{1}{2} (P_1 - P_2)$; F_1 = Mean of F_1 ; P_1 = Mean of parent 1; and P_2 = Mean of parent 2.

Broad-sense heritability (H^2b) and degree of dominance were also estimated for pod length. Collected data were analyzed appropriately.

Results and Discussion

Estimates of the cross Ife Brown x TVNu699

In the cross I, there are different phenotypic expressions of pod length at F_2 segregating generation as depicted (Figure 1). The mean values of pod length of the two parental lines: Ife Brown (15.35 ± 0.55 cm) and TVNu (9.72 ± 0.24 cm) are genotypically different as presented (Table 2) with the standard error of difference (SED) of 0.60 at the 5% level of significance between parent lines. The difference between the mean pod lengths of the two lines is 5.63 cm, which is greater than their SED (0.60). This further connotes that the two parental lines are genotypically different in their trait of interest - pod length. Furthermore, the cross between Ife Brown and TVNu699 produced an F_1 generation, which was advanced to F_2 progenies. The SED for this comparison was 0.68, suggesting that the difference observed between the mean pod lengths of the F_1 and F_2 generations, which was 3.75 cm, was also significantly different (Table 2). The F_1 generation exhibited an intermediate pod length of 12.97 cm, which is close to the mid-parent value (12.54 cm) compared to F_2 (9.22 cm).

Estimates of the cross TVu2723 x TVNu699

In the cross II, there are different phenotypic expressions of pod length at F_2 segregating generation as depicted (Figure 2), while the mean value of the pod length of the two parental lines: TVu2723



Figure 1. Cross of Ife Brown x TVNu699



Fig. 2. Cross of TVu2723 x TVNu699

(17.60 ± 0.54 cm) and TVNu699 (9.72 ± 0.24 cm) were genotypically different as presented (Table 2) with the standard error of difference (SED) at the 5% level of significance between the two parent lines (0.59). The difference between the mean pod lengths of the two lines was 7.88 cm, which is greater than their SED (0.52). This further connotes the two parental lines were genotypically different in their trait of interest - pod length as presented (Table 3). Furthermore, the cross between TVu2723 and TVNu699 produced an F_1 generation, which was advanced to F_2 progenies. The F_1 generation exhibited an intermediate pod length of 15.35 cm, which was close to the mid-parent value (13.66 cm) compared to F_2 (12.92 cm).

The SED for these comparison was 0.82, which is far lesser the means difference of the two generations (2.43 cm). This still confirms that there is

Table 2: Mean Pod length (cm), variance (δ^2), standard deviation (δ) standard error of difference (SED) of the generations in the cross between Ife Brown x TVNu699

Generation	Pod length (cm)	Variance (δ^2)	Standard variation (δ)	Standard error difference (SED)
P ₁	15.35 ± 0.55	0.61	0.78	0.6
P ₂	9.72 ± 0.24	0.29	0.54	
F ₁	12.97 ± 0.33	0.56	0.75	0.68
F ₂	9.22 ± 0.60	1.77	1.33	

P₁: Ife Brown, P₂: TVNu699, F₁: First Filial generation, F₂: Second Filial generation

Table 3: Mean Pod length (cm), variance (δ^2), standard deviation (δ), and standard error of difference of the generation in the cross between TVu2723 x TVNu699.

Generation	Pod length (cm)	Variance (δ^2)	Standard variation (δ)	Standard error difference (SED)
P ₁	17.60 ± 0.54	1.44	1.2	0.59
P ₂	9.72 ± 0.24	0.29	0.54	
F ₁	15.35 ± 0.40	0.32	0.57	0.82
F ₂	12.92 ± 0.72	2.59	1.61	

Mid Parent Value = 13.66 cm , P₁: TVu2723, P₂: TVNu699, F₁: First Filial generation, F₂: Second Filial generation

significant difference in the pod length observed between the F₁ and F₂ generations as shown (Table 3).

Heritability, number of effective factors (number of gene pair) and degree of dominance of pod length

The estimated broad sense heritabilities for pod length were 71.2% and 82.6% for crosses I & II respectively (Table 4). The number of effective factors

(number of gene pairs) controlling pod length was estimated to be three (3) and four (4) respectively for crosses I and II. The estimated mid-parent values for both cross I (12.54 cm) and cross II (13.66 cm) were presented together with their degrees of dominance (15.2% & 42.9%) that measured deviation from the mid-parent value towards one of the parents (Table 4).

Table 4: Estimates of pod length heritability and other genetic parameters for both crosses.

Parameters	Ife Brown x TVNu699	TVu2723 x TVNu699
Broad-sense heritability of pod length	71.20%	82.60%
Number of effective factors (genes)	3	4
Mid parent value (P ₁ + P ₂)	12.54 cm	13.66 cm
Degree of dominance	15.20%	42.90%

TVu – Tropical *Vigna unguiculata*, TVNu – Tropical *Vigna non-unguiculata*

Significant differences ($p < 0.05$) in mean pod length were observed across generations derived from the Ife Brown \times TVNu699 cross, indicating the presence of genetic variability. The F_1 generation recorded the mean pod length of 12.97 cm, exceeding the mid-parent value of 12.54 cm, which indicated the partial dominance of the long pod trait. Broad-sense heritability estimated at 71.2% aligns with the findings of Abha and Meena (2024) who also reported a high heritability of cowpea pod length. This high heritability indicates that there is a high probability of effective selection to be made in early generations for pod length. The level of dominance is lower (15.2%), which indicates that there are greater effects of additive genes rather than dominant genes in this cross. This is advantageous for plant breeders because additive changes are more consistent and predictable across generations. In the same vein, Oladejo *et al.* (2020) pointed out the impact of additive gene effects for seed coat trait, in which case inheritance was primarily additive strengthening the effectiveness of early generation selection. These results support the premise that under strong additive effect, there is little interference from dominance or epistatic relations and considerable progress can be made from selection within the populations undergoing segregation. Edematie *et al.* (2021) also reported that the pod length in cowpea is primarily influenced by the additive gene effects and argued that selection through phenotypic evaluation in earlier segregating generations tends to be efficacious as long as heritability is more than 60%. The existence of three effective genetic factors ($k = 3$) confirms that the inheritance of pod length is controlled by more than one gene pair (i.e. few loci than other complex traits), and it does not follow Mendelian inheritance as seed coat texture, which is monogenic trait (Oladejo *et al.*, 2020).

Owusu *et al.* (2020) on the contrary, reported lower heritability estimates for pod length. This may arise from variation in the environment, genetics, or experimental errors. While only pod length represents a direct morphological trait associated with the pod, protein content and micronutrient concentration have also been shown to be influenced by genotype-by-environment interactions, as reported by Gerrano *et al.* (2022).

Multi-environment trials are likely to enhance heritability and selection efficiency. Moderate heritability with low dominance indicates that some success can be achieved in early generations (F_2) with selection strategies aimed at increasing pod length. This supports the findings of Fulgence *et al.* (2024), who reported that in *Citrullus mucosospermus*, certain traits, including fruit size and seed characteristics, had high heritability and low dominance, suggesting strong genetic influence and minimal environmental impact. Their study also showed that additive variance was greater than dominance variance across many traits.

The outcomes of the crosses between TVu2723 (long-pod) and TVNu699 (short-pod) lines showed considerable variation among the other generations, supporting the assumption that pod length is a quantitatively inherited trait. The F_1 mean pod length was 15.35 cm, which is higher than mid-parent value (13.66 cm), highlighting that there is dominance for the long pod trait. The estimated broad-sense heritability (82.6%) within this cross exceeds that reported by Abha and Meena (2024), who reported heritability estimates between 70–80% for pod length in different genotypes of cowpeas. This suggests stronger genetic control of pod length in the TVu2723 \times TVNu699 cross. This is also supported by Oladejo *et al.* (2021) who reported complex inheritance patterns for cowpea seed traits such as, evidence of segregation beyond expected boundaries with deviation from Mendelian ratios, confirming the polygenic nature of these traits. In other words, they argued that such traits are influenced by multiple genes, which is further exacerbated by the environment's impact on the field.

Edematie *et al.* (2021), also reported high heritability estimates for crosses of cowpea with yard-long beans, especially in pod length. It has been concluded from these results that there is high heritability and therefore high genetic control. The TVu2723 cross has a moderate estimated degree of dominance of 42.9%. This still indicates partial dominance. These findings are in agreement with Abatchoua *et al.* (2018), who pointed out that cowpea pod length is determined by the interplay of several genes due to its polygenic characteristic. In contrary, Owusu *et al.* (2020) noted a lower heritability for pod length, suggesting a greater influence by environmental

factors. The greater pod length variability underscores the need to examine the interplay of environmental effects with the underlying genetic effects. Although some traits may display high heritability and an increased number of controlling genes, achieving optimal improvement through selective breeding often requires a sustained and carefully intensified selection over successive generations. Without such strategic continuity, the full genetic potential may remain untapped, particularly to reduce genetic drift. This underscores that short-term breeding strategies are likely to be insufficient, while long-term efforts hold greater promise for producing consistent and meaningful improvements in pod length.

TVu2723 \times TVNu699 exhibited the highest heritability for pod length at 82.6%, along with an additional contributing gene, totaling four effective factors, compared to 71.2% heritability and three genes in the Ife Brown \times TVNu699 cross. The dominance effect for pod length was also more pronounced in TVu2723 \times TVNu699 (42.9%), indicating stronger dominance expression within that genetic background. These results contradict with the findings of Abha and Meena (2024), who reported high heritability and genetic advance for pod length.

These conclusions are supported by Ousmane *et al.* (2022), who emphasized that high estimates of heritability and genetic gain are indicative of additive gene action rather than dominance effects in cowpea, particularly for traits such as pod length, in contrast to more complex traits like overall yield. Long-term genetic improvement in cowpea requires intensive selection, particularly within cross-pollinated populations such as those examined in this study. On the other hand, Owusu *et al.* (2020) reported lower heritability estimates for pod length, which suggests a great influence of environmental factors. This is needed to consider environmental interactions in genetics studies. Regardless, both crosses are useful for breeding programs. Ife Brown \times TVNu699 is more appropriate for selection in early generations because of low dominance and fewer genes. In contrast, TVu2723 \times TVNu699 is likely to respond better to selection in later generations or recurrent selection because of greater genetic intricacy and potential for sustained improvement.

This study provides insight for breeding cowpea varieties with longer pods for sowing as it increases pod and seed yield. Longer pods are partially dominant and higher heritability in both crosses, promising prospects for improvement. This is in alignment with Adeyanju *et al.* (2023) who observed that cowpea lines with high heritability for pod and seed traits responded well to selection and markedly improved yield in sub-Saharan Africa. Their research emphasizes the importance of purposeful hybridization and selection during the earlier generations driven by the pattern of inheritance. Transgressive segregation for short pods also suggests that undesirable recombinants will likely arise, therefore, highlighting the risk of not having proper selection methods in place. If cowpea breeders understood the patterns of inheritance, the number of genes, and the dominant genes, they would have better strategies through which selection could be made for enhanced yield under various environmental conditions.

Conclusion

This study confirms that the number of effective factors (gene pairs) controlling the inheritance of pod length trait was estimated to be three and four in the two crosses; and pod length is a highly heritable trait in cowpea. Although long pod length exhibited dominance over short pod length, the degree of dominance was low in both crosses. Transgressive segregation for short pods observed in the study suggests that selection for pod length in cowpea should be carried out in the early generations. Furthermore, the higher mean pod length in the F₁ generation compared to the F₂ generation indicates hybrid vigour.

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