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Assessing genetic influence and inheritance patterns of yield components in cowpea introgressed with the *cry1ab* gene for the control of *Maruca vitrata* pest

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Abstract: Cowpea is an important food legume widely grown and consumed across the semi-arid regions of Africa, serving as a rich source of essential nutrients, including proteins, vitamins, carbohydrates, and minerals. However, cowpea cultivation faces major challenges due to the high prevalence of insect pests that adversely impact crop yield, with the Legume pod borer (*Maruca vitrata*) being one of the most damaging pests, capable of causing yield losses ranging from 20% to 80%. To combat this issue, genetically engineered cowpea event 709A, which incorporates the Cry1Ab gene from *Bacillus thuringiensis* (Bt) for resistance against *Maruca vitrata*, has been developed and released in Nigeria as SAMPEA 20-T. This study aimed to determine the heritability and primary gene effects of some yield related traits in cowpea lines introgressed with the pod borer resistance gene (Cry1Ab). A randomized complete block design was employed, involving six generations (P_1, P_2, F_1, F_2, BC_1, and BC_2) from four crosses (Padi-tuya x PBRC, Apagbaala x PBRC, Kirkhouse x PBRC, and Wang-kae x PBRC). These crosses were derived from four *M. vitrata*-susceptible varieties and an elite *M. vitrata*-resistant line (PBRC), and were evaluated at the confined field trial (CFT) site in Nyankpala. The results indicated that most traits in the four crosses exhibited duplicate epistasis among dominant decreasers, while a few traits showed complementary epistasis among dominant decreasers. A broad range of narrow sense heritability estimates were observed, ranging from 0% to 97%. Based on the analysis of gene effects—including additive, dominance, and epistasis—it was concluded that pedigree breeding would be the most effective approach for enhancing most of these traits.

Keywords: Generation mean analysis, Gene Action, Heritability, Additive, Dominance, Epistasis

Introduction

Cowpea (*Vigna unguiculata*) is a vital grain legume in sub-Saharan Africa, serving as a crucial food source for humans and livestock (Togola et al. 2017). It is widely cultivated due to its adaptability to diverse agro-ecological conditions and its multiple uses, including human consumption, livestock feed, income generation for farmers and food processors, and soil fertility improvement through nitrogen fixation (Sindhu et al. 2019; Timko et al. 2007). Cowpea contributes significantly to the livelihoods of millions of smallholder farmers and is an integral part of traditional cropping systems in West Africa. Its ability to grow in poor soils and withstand drought conditions makes it a preferred crop in regions with challenging growing environments.

Despite its importance, cowpea yields on farmers' fields remain low, typically ranging from 240 kg/ha to 492 kg/ha, far below the potential yields of up to 4 t/ha achievable under optimal conditions (Ahmed et al. 2009; Boukar et al. 2013). This significant yield gap is primarily due to various biological and environmental stressors. Among these, insect pests are the most critical constraints, causing substantial yield losses. *Maruca vitrata*, commonly known as the legume pod borer, is one of the most destructive pests of cowpea, inflicting damage at both the flowering and podding stages of the crop. Infestations by this pest can result in yield losses ranging from 20% to as high as 80%, and in severe cases, complete crop failure (Sodedji et al. 2020).

To manage these pests, farmers often resort to chemical pesticides. While effective in reducing pest populations, the use of chemical pesticides poses significant challenges, including health risks to humans and animals, environmental pollution, and high costs, particularly for resource-limited farmers (Ahmed et al. 2009; Singh et al. 2016). Moreover, reliance on pesticides can lead to the development of resistance in pest populations, further complicating pest management efforts. Consequently, there is a pressing need for more sustainable and affordable pest control strategies in cowpea cultivation.

Advancements in genetic engineering have provided new avenues for developing insect-resistant crops, including cowpea. One such innovation involves the incorporation of *Bacillus thuringiensis* (Bt) insecticidal proteins, which have been used successfully in a variety of crops such as cotton, eggplant, maize, and soybean to control lepidopteran pests. The Cry1Ab gene from Bt has been genetically engineered into the cowpea line IT86D-1010, resulting in the development of event 709A, which expresses Cry1Ab proteins that are toxic to *Maruca vitrata* (Addae et al. 2020). This Bt cowpea event has been introgressed into farmer-preferred varieties such as Songotra in Ghana and SAMPEA 10 in Nigeria. The resulting Pod Borer Resistant Cowpea (PBRC) was released in Nigeria to provide smallholder farmers with a viable solution to *Maruca vitrata* infestations.

While genetic modification offers a promising approach, exploring other sustainable pest management strategies remains critical. Host plant resistance, where cowpea varieties are bred to resist or tolerate pest attacks, is considered an economically viable, ecologically sound, and sustainable approach to pest control (Sobda et al. 2018). This method can significantly reduce pest prevalence in the field, thereby safeguarding crop yields without the need for chemical inputs. Genetic management through host plant resistance has been identified as a key strategy to combat insect pests in cowpea, offering a cost-effective and durable solution (Adeyanju et al., 2012).

Understanding the genetic basis of resistance traits is essential for the effective deployment of host plant resistance in breeding programs. This involves assessing the heritability of resistance traits and understanding the genetic interactions that govern these traits. Generation mean analysis is a valuable method that evaluates the primary genetic effects—additive, dominance, and digenic interactions—arising from the crossing of inbred lines (Zdravković et al. 2011). This approach helps breeders determine the mode of inheritance of key traits and select the most appropriate breeding strategies.

For successful breeding of insect-resistant cowpea varieties, it is crucial to identify the most effective breeding methods based on a comprehensive understanding of the genetic regulation of resistance traits. This study aims to (i) determine the mode of inheritance of yield components in Bt cowpea across six cross combinations and (ii) estimate heritability and main gene effects (additive, dominance, and digenic epistasis) of yield-related traits. The findings from this research will provide valuable insights into the genetic architecture of resistance traits in cowpea, guiding the development of improved, resilient, and high-yielding cowpea cultivars that meet the needs of smallholder farmers in sub-Saharan Africa.

Results

Mean performance of four cowpea crosses

Table 4 presents the mean performance of four different cowpea crosses (Padi-tuya x PBRC, Kirkhouse x PBRC, Apagbaala x PBRC, and Wang-kae x PBRC) and their respective parental lines, evaluating several traits including pod length (PL), number of seeds per pod (NSP), number of primary branches (PB), days to 50% flowering (DFF), days to first pod maturity (DFPM), and the number of Maruca damaged pods per plant (NMDP/P). Among the six generations assessed, significant variations were observed for most traits, with some exceptions.

For the Padi-tuya x PBRC cross, all traits exhibited significant differences except for pod length, which did not show a significant difference (0.944). In the Kirkhouse x PBRC cross, significant differences were found across all traits, except for the number of seeds per pod (NSP), where no significant difference was detected. The Wang-kae x PBRC cross displayed significant differences in all traits, with the exception of DFF (0.5985), DFPM (1.228), and PB (0.2092), indicating non-significant differences for these traits.

In contrast, the Apagbaala x PBRC cross showed significant differences across all measured traits except for the number of primary branches (PB), which did not significantly vary. These findings underscore the variability in genetic expression across different crosses and traits, highlighting the importance of cross-specific evaluations in breeding programs.

Scaling tests A, B, and C for various traits in four cowpea crosses

Table 5 displays the results of various scaling tests (A, B, and C) conducted on four cowpea crosses (Padi-tuya x PBRC, Wang-kae x PBRC, Kirkhouse x PBRC, and Apagbaala x PBRC). Significant differences were observed among all traits across all crosses, highlighting the genetic variability in these populations.

For the Padi-tuya x PBRC cross, scaling tests A, B, and C showed significant differences for the number of seeds per pod (NSP). Tests B and C indicated significant differences for the number of primary branches (PB) and days to 50% flowering (DFF). For days to first pod maturity (DFPM) and the number of Maruca damaged pods per plant (NMDP/P), significant differences were only noted in scaling test B. No significant differences were found for pod length (PL) in scaling tests A and B, indicating consistent performance of PL in these specific tests.

In the Kirkhouse x PBRC cross, NSP showed no significant differences across any of the three scaling tests, indicating a lack of genetic variation for this trait. However, the remaining traits (PB, DFF, DFPM, NMDP/P, and PL) were significant in at least one of the scaling tests, suggesting that genetic effects are present for these traits.

Table 1. Attributes of parental varieties/lines for introgression.

Variety/Event	Description	Key attributes
Kirkhouse benga (P_1)	Erect, Large white seeds, black hilum colour,	Early maturity, resistance to aphids and Striga, short cooking time and yield potential is 2.4 t/ha. Susceptible to Maruca
Wang-kae (P_1)	Erect, Large white seeds, brown hilum colour,	Early maturity, resistance to aphids and Striga, short cooking time and yield potential is 2.4 t/ha. Susceptible to Maruca
Padi-tuya (P_1)	Erect Larger white seeds, black hilum colour	Medium maturity, moderate resistance to diseases, and potential yield of 2.4 t/ha. Susceptible to Maruca
Apagbaala (P_1)	Small white seed, brown hilum colour	Produces many pods, potential yield of 1.8t/ha. Susceptible to Maruca
PBRC (P_2)	Medium white seeds, black hilum colour	Early maturity, resistance to *Maruca vitrata*, Striga resistant

Table 2. Cross of generation and number of plants per generation.

Cross/ Generation	**Wang x PBRC**	**Padi-tuya x PBRC**	**Kirkhouse x PBRC**	**Apagbaala x PBRC**
P_1	85	90	75	85
P_2	56	95	71	89
F_1	30	30	30	40
F_2	150	150	150	150
BC_1P_1	84	75	60	78
BC_1P_2	60	62	60	60

Table 3. Description of traits used for the generational studies.

No.	**Variable**	**Code**	**Description**
1.	Days to 50% flower	DFF	Number of days to 50% of plants reaching 50% flower
2	Days to 1st pod maturity	DFPM	Number of days to 1st pod reaching physiological maturity
3	Number of primary branches per plant	PB	Counting the number of pods on each plant for each generation at the time of 95% physiological maturity
4	Pod length	PL	Length of pods measured from each plant in each generation
5	Number of seeds per pod	NSP	Number of seeds per each pod
6	Number of Maruca damaged pods per plant	MDPP	The number of pods that were damaged by *M. vitrata* on each plant

The Wang-kae x PBRC cross revealed that only DFF was significant in scaling tests A and B, while the other traits (PB, DFPM, NMDP/P, PL, and NSP) did not show significant differences in these tests. However, scaling test C showed significance for DFF, DFPM, and PB, highlighting the specific genetic contributions affecting these traits.

For the Apagbaala x PBRC cross, scaling test A indicated significant differences for pod length (PL) and NSP only. Scaling test B revealed significant differences for all traits except DFF, showing a broad range of genetic variability. In scaling test C, significant differences were noted for DFF, NMDP/P, and NSP, while the remaining traits did not exhibit significant changes.

These results demonstrate that the genetic effects in the four cowpea crosses vary widely depending on the trait and the scaling test applied. Understanding these variations is essential for designing effective breeding strategies aimed at improving yield-related traits and resistance in cowpea breeding programs.

Estimates of genetic parameters based on the three parameters model

Supplementary Table 1 presents the genetic parameters for various traits analyzed using a three-parameter model, focusing on the crosses Padi-tuya x PBRC, Kirkhouse x PBRC, Wang-kae x PBRC, and Apagbaala x PBRC. These parameters include mean values, additive and dominance genetic effects, and the χ^2 statistic for assessing model fit.

For the trait number of primary branches (PB), the Padi-tuya x PBRC cross had a mean value of 2.8709 ± 0.1004, indicating a notable deviation from zero. The additive genetic effect (a) was 0.2291 ± 0.093, which was not statistically significant, and the dominance genetic effect (d) was 0.0755 ± 0.206, also non-significant. The χ^2 statistic was 6.37 with a p-value of 0.095, suggesting a reasonable fit of the model to the observed data. For the Kirkhouse x PBRC cross, the mean value for PB was 2.7284

± 0.108, significantly different from zero. The additive genetic effect (a) was 0.0352 ± 0.103, and the dominance genetic effect (d) was -0.0402 ± 0.219, both non-significant. The χ^2 statistic was 13.84 with a p-value of 0.003, indicating a poor model fit. The Wang-kae x PBRC cross showed a mean value of 0.325 ± 0.055 for PB, significantly different from zero. The additive genetic effect (a) was 0.1864 ± 0.055, and the dominance genetic effect (d) was -0.1898 ± 0.093, with neither being statistically significant. The χ^2 statistic was 5.66 with a p-value of 0.129, suggesting a good model fit. For the Apagbaala x PBRC cross, the mean value for PB was 2.6514 ± 0.075, significantly different from zero. The additive genetic effect (a) was 0.0239 ± 0.073, and the dominance genetic effect (d) was -0.04 ± 0.164, both non-significant. The χ^2 statistic was 10.62 with a p-value of 0.014, indicating a poor model fit.

For days to 50% flowering (DFF), all four crosses showed significant additive effects, but dominance effects were not significant. For Padi-tuya x PBRC and Wang-kae x PBRC, the p-values (0) suggested that the model was not adequate. Conversely, for Kirkhouse x PBRC and Apagbaala x PBRC, the p-values were 0.056 and 0.063, respectively, indicating that the model fit was adequate for these crosses.

In the case of days to first pod maturity (DFPM), the Padi-tuya x PBRC cross had a mean value of 62.6456 ± 0.389, significantly different from zero. The additive genetic effect (a) was 2.1515 ± 0.372, significant, while the dominance effect (d) was -1.6722 ± 0.797, not significant. The χ^2 statistic was 10.33 with a p-value of 0.016, suggesting the model was not adequate. For the Kirkhouse x PBRC cross, the mean value for DFPM was 61.6078 ± 0.441, also significantly different from zero. The additive genetic effect (a) was 2.0493 ± 0.434, significant, and the dominance effect (d) was -1.3559 ± 0.982, not significant. The χ^2 statistic was 21.9 with a p-value of 1e-04, indicating a poor model fit. The Wang-kae x PBRC cross had a mean value of 62.8299 ± 0.441 for DFPM, significantly different from zero. The additive genetic effect (a) was 2.7822 ± 0.434, significant, while the dominance effect (d) was -1.343 ± 0.881, not significant. The χ^2 statistic was 16.28 with a p-value of 0.001, suggesting a poor model fit. For the Apagbaala x PBRC cross, the mean DFPM value was 62.9493 ± 0.697, significantly different from zero. The additive genetic effect (a) was 3.0853 ± 0.663, significant, and the dominance effect (d) was -1.2613 ± 1.227, not significant. The χ^2 statistic was 19.57 with a p-value of 2e-04, indicating a poor model fit.

For the number of Maruca damaged pods per plant (NMDP/P), the intercept values for Padi-tuya x PBRC and Wang-kae x PBRC were non-significant, with values of 0.4296 ± 0.079 and 0.2802 ± 0.055, respectively. The additive genetic effect was significant for these two crosses, while the dominance effect was non-significant. The intercept for Kirkhouse x PBRC was 0.2057 ± 0.086, non-significant, with both additive and dominance effects being non-significant. The p-values for Padi-tuya x PBRC and Kirkhouse x PBRC were 0.022 and 2^{-04}, respectively, indicating that the model was not adequate. Conversely, Wang-kae x PBRC had a p-value of 0.201, suggesting that the model was adequate for explaining genetic effects.

For pod length (PL) and number of seeds per pod (NSP), significant differences were observed in the intercepts for all four crosses. Additive genetic effects were non-significant across all crosses. Dominance genetic effects were non-significant for all crosses except for Padi-tuya x PBRC on PL and Wang-kae x PBRC on NSP. The p-values for PL indicated that the model was not adequate for Kirkhouse x PBRC and Apagbaala x PBRC, with values of 0.049 and 3e-04, respectively. However, the model was adequate for Padi-tuya x PBRC and Wang-kae x PBRC. For NSP, the model was not adequate for Padi-tuya x PB.

Estimates of genetic parameters based on the six-parameter model

Padi-tuya x PBRC revealed significant positive additive effects and dominant-dominant effects and significant negative dominant effects, additive-additive effects and additive-dominant effects with duplicate epistasis between dominant decreasers for DFF (Supplementary Table 2). Significant positive additive effects were recorded for DFPM but dominance, additive-additive and dominant-dominant effects were found to be non-significant. NMDP/P recorded significant additive effect and additive-dominance effect but non-significant effects for dominance, additive-additive, and dominant-dominant effects. NSP revealed significant differences for all parameters studied with duplicate epistasis between dominant decreasers.

For Kirkhouse x PBRC non-significant effects were recorded for additive gene effects and additive-dominace effects. Dominance, additive-additive, and dominant-dominant effects were not significant for NSP. Significant additive and additive dominant effects were recorded for DFPM whilst dominant, additive-additive, and dominant-dominant effects were found to be non-significant but complementary epistasis between dominant decreasers was revealed by this trait. NMDP/P revealed significant additive and dominant-dominant effects whilst dominant, additive-additive and additive-dominant effects were not significant. Additive and additive-dominant gene effects were non-significant. Dominant and additive-additive effects were significant and negative for PL. Duplicate epistasis between dominant decreasers type of epistasis was found in all traits studied except NMDP/P which revealed duplicate epistasis between dominant increasers. For Wang-kae x PBRC significant additive and additive genetic effects were recorded for DFF, dominant, additive-dominant, and dominant were non-significant but complementary epistasis between dominant decreasers was revealed. DFPM was significant for all the measured genetic parameters except dominant–dominant effects. The cross Apagbaala x PBRC revealed non-significant gene effects for all the parameters except additive dominant gene effect, which was significant for PB, complementary epistasis between dominant decreasers was observed. DFPM recorded significant gene effects for all parameters studied only additive dominance effects were found to be non-significant, duplicate epistasis between dominant decreasers was observed. However, in NMDP/P additive and additive-additive effects were found to be significant. Dominant, additive-dominant and dominant-dominant effects were found to be non-significant.

Table 4. Means performance of four cowpea crosses evaluated during the 2020 cropping season.

Generation	PB	DFF	DFPM	NMDP	PL	NSP	PB	DFF	DFPM	NMDP	PL	NSP
	Padi-tuya x PBRC						Kirkhouse x PBRC					
P1	3.2	42	65	0.87	13.23	10	2.8	41	64	0.31	13.7	10
P2	2.7	37	60	0.1	13.37	11	2.8	37	59	0.01	13.4	9.6
F1	3.2	38	61	0.1	14.27	12	2.9	37	59	0.07	14.7	10.7
F2	2.8	40	62	0.3	14.1	10	2.7	39	61	0.28	14.3	10.6
BC1	3	39	62	0.31	13.77	9	2.6	40	62	0.4	13.3	10.1
BC2	2.8	38	61	0.25	13.6	9	2.6	38	61	0.33	13.8	10.5
Mse	0.009	0.301	0.568	0.005	0.269	0.307	0.02	0.476	0.387	0.004	0.257	0.261
LSD	0.175***	0.998***	1.371***	0.124***	0.944	1.008***	0.2594	1.255***	1.132***	0.1212***	0.921*	0.929
	Wang-kae x PBRC						Apagbaala x PBRC					
P1	3	41	66	0.53	13.4	9	2.723	42	65.9	0.445	13.88	10.567
P2	2.8	37	60	0.38	13	9	2.57	37	60.27	0.09	14.19	10.567
F1	3.2	37	61	0.1	13.7	10	2.547	40	62.3	0.123	15.49	11.733
F2	2.8	40	63	0.3	14.1	10	2.7	41	63.3	0.373	14.48	10.033
BC1	2.9	40	63	0.25	13.7	10	2.537	42	63.53	0.227	13.84	10.467
BC2	2.9	39	61	0.22	13.7	10	2.767	38	60.07	0.253	13.52	10.267
Mse	0.013	0.108	0.456	0.037	0.513	0.343	0.014	0.439	1.176	0.01	0.3	0.11
LSD	0.2092*	0.5985***	1.228***	0.3488	1.303	1.065	0.2127	1.2***	1.973***	.1794***	.996**	0.6.31***

Note: P1 = Parent 1, P2 = Parent 2, F1 = First filial generation, F2 = Second filial generation, BC1 = Backcross 1, BC2 =Backcross 2, PB = primary branches, DFF = days to 50% flowering, DFPM = days to first pod maturity, PL = pod length, NSP = seed per pod and NMDP/P = number of Maruca damaged pods per plant. *** = Significant at P ≤ 0.001, ** = Significant at P ≤ 0.01 and * = significant at P ≤ 0.05.

Table 5. Scaling test A, B and C for various traits in four cowpea crosses evaluated during the 2020 cropping season.

Trait/Test	A	B	C	A	B	C
Padi-tuya x PBRC				Kirkhouse x PBRC		
PB	-0.3844±0.2628ns	-0.4225±0.24*	-1.043±0.4246*	-0.4792±0.1921*	-0.6026±0.1865**	-0.3951±0.3222ns
DFF	-0.7733±0.6689ns	1.9969±0.6882**	5.1088±1.1801***	1.375±0.6991ns	1.5128±0.6715*	2.8945±1.1777*
DFPM	-0.7956±0.8053ns	1.505±0.757*	2.4936±1.4143ns	0.3083±0.8225ns	2.8872±0.7586***	4.6355±1.2643***
NMDP/P	-0.3533±0.1812ns	0.3214±0.1521*	0.0386±0.2592ns	0.4333±0.2157*	0.5872±0.1822**	0.6738±0.2241**
PL	0.018±0.824ns	-0.3748±0.8254ns	1.2686±1.354ns	-1.7779±0.8905*	-0.5779±0.7672ns	0.8295±1.1604ns
SP	-3.8289±0.6092***	-5.4152±0.6047***	-4.8377±1.0224***	-0.4292±0.6689ns	0.6513±0.6249ns	1.3021±1.0579ns
Wang-kae x PBRC				Apagbaala x PBRC		
PB	-0.4073±0.2296ns	-0.2429±0.2655ns	-0.8958±0.4*	-0.2008±0.1622ns	0.4103±0.1881*	0.4047±0.3068ns
DFF	1.4568±0.5972**	2.7714±0.7078***	6.4825±1.06***	0.5198±0.6923ns	-0.6886±0.6458ns	2.4836±1.2118*
DFPM	-0.659±0.7679ns	1.4571±0.7649ns	4.1457±1.29**	-1.1647±1.0265ns	-2.3711±0.6813***	2.4128±1.8647ns
NMDP/P	-0.0485±0.1726ns	0.2143±0.1586ns	0.4401±0.2515ns	-0.1409±0.1674	0.3184±0.1542*	0.709±0.2669**
PL	0.1233±0.7745ns	0.6838±0.9215ns	2.1963±1.2622ns	-1.6408±0.6059**	-2.5727±0.6905***	-1.0068±3.0657ns
SP	0.1979±0.6513ns	1.0048±0.7887ns	1.2541±1.2211ns	-1.2877±0.5539*	-1.7031±0.617**	-4.4136±0.8409***

Note: PB = primary branches, DFF = days to 50% flowering, DFPM = days to first pod maturity, PL = pod length, NSP = seed per pod and NMDP/P = number of Maruca damaged pods per plant. *** = Significant at P ≤ 0.001, ** = Significant at P ≤ 0.01 and * = significant at P ≤ 0.05. A = Scaling test A, B = Scaling test B and C = Scaling test C.

Duplicate epistasis between dominant increasers was observed. For PL dominant-dominant gene effects were found to be significant, all other effect was non-significant with duplicate epistasis between dominant decreasers. NSP was non-significant for all the parameters measured with complementary epistasis between dominant increasers.

Additive-dominance epistasis and Chi-square values for the re-estimated parameters

The re-estimated genetic parameters are presented in Supplementary Table 3, which includes the additive-dominance epistasis and Chi-square values. In the plant cross Padi-tuya x PBRC, the mean value of DFF was 39.2167 ± 0.561, which was substantially different from zero. This indicated the presence of a significant additive genetic effect (a) of 2.2019 ± 0.5422, which contributes to the variation in DFF. The dominance genetic effect (d) was estimated to be -0.7912 ± 1.2092 (not statistically significant). The χ^2 score of 35.67 indicated a strong match between the model and the observed data. The mean value of DFPM was 62.0303 ± 0.3413, which was statistically distinct from zero. The variation in DFPM was significantly influenced by an additive genetic impact (a) of 2.0388 ± 0.5741. The dominance genetic impact (d) had a value of -1.6528 ± 2.4635 and did not reach statistical significance. The χ^2 statistic yielded a value of 22.16, which suggests that the model fits well with the observed data.

The mean value of NMDP/P was 0.2913 ± 0.0737, which was substantially different from zero. The additive genetic impact (a) was determined to be 0.232 ± 0.1082, indicating that it was not statistically significant. The dominance genetic impact (d) was determined to be -0.3669 ± 0.5861, indicating that it is not statistically significant. The χ^2 statistic yielded a value of 23.64, indicating a favorable alignment between the model and the observed data. The NSP had an average value of 14.8719 ± 1.0337, which was substantially different from zero. The presence of a notable additive genetic effect (a) of -0.3766 ± 0.1178, was found to contribute to the observed variation in NSP. The dominance genetic effect (d) was calculated to be -16.7558 ± 2.6125, signifying a statistically significant and large contribution. The χ^2 statistic yielded a value of 13.6506, indicating a favourable alignment between the model and the observed data.

For the Kirkhouse x PBRC cross, the mean value of PB was 2.5533 ± 0.3133, which was substantially different from zero. Additionally, the χ^2 statistic was 12.9, showing that the model suited the observed data well. The mean value of DFPM was 61.1474 ± 0.3485, which was substantially different from zero. Additionally, there was a significant additive genetic impact (a) of 2.2253 ± 0.5331, which contributed to the variation in DFPM. The dominant genetic impact (d) had a value of -2.5431 ± 2.9662 and did not reach statistical significance. The model exhibited a strong alignment with the observed data. The mean value of PL was 16.4767 ± 0.9962, indicating a considerable deviation from zero. The χ^2 statistic yielded a value of 5.1081, which suggests that the model fits well with the observed data.

The cross between Wang-kae and PBRC demonstrated that the mean value of DFF was 39.0885 ± 0.578, which was statistically different from zero. Additionally, there was a significant additive genetic effect (a) of 2.041 ± 0.642, which contributed to the variability observed in DFF. The χ^2 statistic yielded a value of 52.94, indicating a favourable alignment between the model and the observed data. Typically, the data includes average values and genetic influences for each characteristic, which show the extent to which additive and dominant genetic variables contribute. The χ^2 statistics indicate that the models generally provide a good match to the observed data.

Estimates of variance components and heritability

Supplementary Table 4 indicates the results for each component of variance for the different traits across various parent combinations (Padi-tuya x PBRC, Kirkhouse x PBRC, Wang-kae x PBRC and Apagbaala x PBRC). For the Padi-tuya x PBRC parent combination, it was observed that the environmental factor contributed significantly to the variance for all traits. Additive genetic factors had a substantial impact on the observed variance in PB, DFF, DFPM, NMDP/P, PL, and NSP suggesting that these genes are under additive gene control. Moreover, dominant genetic factors have had a noticeable impact on DFF and NSP. Negative values were recorded for dominance and additive-dominance values except for DFF which was positive. Generally, heritability was moderate to high for most traits. DFF, DFPM and NSP recorded heritability values greater than 40% (0.45, 0.48 and 0.5 respectively) PB, NMDP/P recorded (0.21 and 0.25). PL had low narrow sense heritability (0.09). The results from Kirkhouse x PBRC parent combination had similar patterns to Padi-tuya x PBRC with additive genetic factors having a substantial impact on most traits. The additive variances recorded positive values for PB, DFF, DFPM and NSP (0.38, 2.7, 3.43 and 3.42 respectively).

Negative values were recorded for NMDP/P PL (-0.37 and -3.68 respectively). Negative dominant values were recorded for PB, DFF, DFPM and NSP. However positive values were recorded for NMDP/P PL (0.51 and 2.58 respectively). Narrow sense heritability was moderate for PB, DFF, DFPM, PL, and NSP (0.46, 0.40, 0.42, 0.30 and 0.40 respectively). NMDP/P recorded 0.00 heritability. For Wang-kae x PBRC parent combination, VE significantly contributed to variance for most traits. VA had a substantial impact on most traits, as positive additive variance was recorded for all traits under study except PL which recorded a negative additive variance of -2.91 indicating low genetic influence. VD was negative for all traits except pod length (1.56), suggesting a strong negative dominance effect.

VAD was small but present in most traits. VG was also positive for most traits, except for NMDP/P and PL which were negative. Hns was high for PB, DFF, DFPM, NMDP/P and NSP (0.12, 0.35, 0.46, 0.25 and 0.34 respectively) except for PL which was 0.00. In Apagbaala x PBRC cross, Similar patterns to Wang-kae x PBRC were observed with a significant impact of VE on most traits. High positive VA was recorded by all traits except NSP which was -1.25. High negative VD was recorded by all traits under study except NSP which had a positive value of 1.01. VAD was small but present in most traits. VG was positive for most traits.

Overall, heritability varied across traits, with PL showing a lower heritability. Additive genetic factors had a consistent and significant impact on most traits across different parent combinations. Dominance effects are present, but they vary in magnitude and direction across traits and parent combinations. The proportion of phenotypic variance attributable to genetic factors (heritability) varies across traits and parent combinations.

Discussion

Improving varieties for resistance to constraints involves combining different parental lines with diverse genetic potentials. As highlighted by Ajayi et al. (2020), utilizing genotypes adapted to specific ecological zones is crucial for breeding improved varieties. In this study, the varieties used are adapted to the Guinea savanna and Sudan savanna zones of Northern Ghana, and they exhibit varied maturity periods, which contribute to differences in traits such as Days to 50% Flowering (DFF), Days to First Pod Maturity (DFPM), and Pod Maturity (DPM) for the F1 progenies and their parents.

The generation mean analysis provides valuable insights into the genetic factors influencing various phenotypes across different plant crosses, specifically Padi-tuya x PBRC, Kirkhouse x PBRC, Wang-kae x PBRC, and Apagbaala x PBRC. The traits under consideration include DFF (related to flowering timing), DFPM (related to plant maturity), NMDP/P (related to insect damage), NSP (related to seed production), and PL (related to pod characteristics). Significant variations observed among the six generations for all traits indicate genetic variability, suggesting that breeding methods such as single seed descent, pedigree/marker-assisted selection, or marker-assisted backcrossing could be effective for improving these traits.

The lack of significant differences in Pod Length (PL), Number of Primary Branches (PB), and Number of Seeds per Pod (NSP) for the Padi-tuya × PBRC, Kirkhouse × PBRC, and Apagbaala x PBRC crosses suggests that dominance gene action plays a role in controlling these traits. The non-significant chi-square values indicate that a digenic interaction (6-parameter) model may adequately describe the genetic control for these traits.

In the Padi-tuya x PBRC cross, the DFF trait exhibited a substantial mean value with a significant additive genetic effect, indicating a genetic basis for variation in flowering time. However, dominance effects were not significant, suggesting that dominance does not play a major role in this trait. The chi-square statistic supports a good fit between the model and the observed data, affirming the reliability of these findings.

Significant differences were observed in scaling tests A, B, and C for NSP, while Pod Length and DFF showed significant differences in scaling tests A and B. For the Apagbaala x PBRC cross, NMDP/P exhibited significant differences in scaling tests B and C, indicating substantial epistasis and the inadequacy of the additive-dominance model. For DFPM, significant differences were only noted in scaling test B, whereas no significant differences were found for PL in Padi-tuya x PBRC in tests A and B. In Wang-kae x PBRC, no significant differences were found for any traits. These results suggest that the additive-dominance model may be inadequate for some traits, highlighting the importance of considering epistatic interactions.

The three-parameter model analysis revealed no significant differences between additive and dominant gene effects for PB across all crosses. DFF, DFPM, and NMDP/P showed significant additive gene effects, but dominant gene effects were non-significant, suggesting that pedigree selection could be effective for improving these traits. Significant additive gene action across crosses indicates that additive effects play a crucial role in the inheritance of these traits, making them suitable for improvement through selection of pure lines. Dominant gene effects were non-significant for all crosses except Apagbaala x PBRC. Negative significant values for dominance in most populations suggest that alleles responsible for these traits in cowpea are dominant. The absence of significant dominance gene effects for DFF aligns with previous studies by Adeyanju and Ishiyaku (2006) and Ishiyaku et al. (2005).

Epistasis type is determined when dominance and dominance × dominance effects are significant and have the same sign (complementary epistasis) or different signs (duplicate epistasis). DFF demonstrated additive and dominant gene action with duplicate epistasis between dominant decreasers. This finding is consistent with observations by Adeyanju and Ishiyaku (2006) and Ishiyaku et al. (2005), who reported duplicate epistasis for earliness-related traits in cowpea. The results suggest that non-allelic gene interactions, particularly duplicate epistasis, play a significant role in the inheritance of DFF and NMDP/P, which may pose challenges for breeders.

DFPM exhibited additive and additive-additive interactions with complementary epistasis between dominant decreasers, confirming findings by Abdelsatar et al. (2021) and Owusu et al. (2022). DFPM, PB, and NSP showed complementary gene action controlled by additive genes, suggesting that pedigree selection is a viable method for improving these traits. NSP's significance for all genetic parameters indicates that it is under polygenic control with both additive and non-allelic interactions involved.

Overall, many traits in cowpea are influenced by non-allelic interactions in addition to additive and dominant components, as demonstrated by studies from Edematie et al. (2021), Romanus *et al*. (2008), Singh and Singh (2015), and Thakare et al. (2016). The crosses Padi-tuya x PBRC, Kirkhouse x PBRC, and Wang-kae x PBRC showed narrow sense heritability values of 50% or less for all traits, suggesting that these traits are predominantly under the control of non-additive genes. Conversely, Apagbaala x PBRC exhibited heritability above 50% for DFF, PB, DFPM, and PL. Given the significant epistasis observed, selection for these traits would be most effective in later generations using pedigree and recurrent selection methods, as recommended by Fernandes et al. (2012).

Materials and methods

Parent material

Four (4) non-transgenic improved varieties which are Maruca susceptible, namely Apagbaala, Kirkhouse benga, Padi-tuya, and Wang-kae, were crossed with an improved transgenic line called PBRC (Pod borer resistant cowpea- which is resistant to *Maruca vitrata*) to produce four distinct populations. The non-transgenic types served as the recipient recurrent parents, whilst the transgenic line functioned as the Maruca-resistant donor parent. The aforementioned five lines were acquired from CSIR-SARI, and the process of introgression was conducted within a screen house located at the restricted Confined field trial (CFT) location of the cowpea project aimed at enhancing resistance against the Maruca pod borer. The attributes of the both the recurrent and donor parents are presented in Table 1.

Population development

The experiment involved utilizing buckets with a volume capacity of 15 liters, which were filled with the soil of a sandy-loam composition. A total of four seeds were first planted in each bucket, and subsequently reduced to two seeds at a time interval of three weeks following the initial planting. The buckets containing the plants were subjected to daily watering throughout the vegetative stage, and subsequently, watering was reduced to every two days during the flowering and maturity stages. The process of physically removing weeds from the planted buckets was conducted by hand picking, followed by the application of NPK fertilizer at a rate of 150kg/ha.

The crosses were produced using the methodology described by Myres (1996) with minor adjustments. The utilization of the capping method in the process of crossing was implemented to increase the likelihood of successful crosses and concurrently mitigate the risk of contamination. The flowers obtained from the donor parent were harvested during the early morning hours between 5:30 and 6:00 am, and thereafter stored in a refrigerated environment. The flowers were thereafter used in the evening between 4 - 6 pm, to pollinate emasculated recurrent (female) parents. The procedure of emasculation was conducted meticulously using sterilized forceps with sharp tips. To ensure the prevention of undesirable pollen contamination, the forceps was sanitized with 70% alcohol between each emasculation.

Subsequently, every cross was affixed with a label indicating the respective date of its pollination. The non-transgenic cultivars were crossbred with the transgenic line to produce four distinct groups of F_1 progenies. The non-transgenic lines (P1s) were utilized as the recipient recurrent parents, while the transgenic line (P2) was the donor parent that contained the Cry1Ab gene which confers the Maruca resistance to this line. A portion of the resultant F_1 progenies were selfed to generate F_2 progeny, while another portion were used in a backcrossing scheme with both the recurrent parents (P1) and the donor parent (P2) to generate the backcross populations. Before either selfing or backcrossing, an assessment was performed on each F_1 plant to determine the existence of the Cry1Ab protein. This evaluation was facilitated by employing immuno Bt test strips that are specifically designed for the Cry1ab/Ac gene.

Study area description, field management and evaluation under natural conditions

The non-segregating F_1 progenies and their parents were evaluated under natural conditions at the confined field trial site at Nyankpala located in the Guinea Savannah agro-ecological zone which lies on Latitude: N 9^o, 23′, 12.81156″, Longitude: W 1^o, 0′, 7.80192″, and altitude 597ft above sea level. The experiment was planted during the 2020 main planting season for cowpea. The trial was laid out in a randomized complete block design with 3 replications with a spacing of 0.6m between rows and 0.2m within rows. The parents were planted in 3 rows of 2m long whiles the F_1s were planted in single rows. The field was maintained weed-free by manually weeding twice with a hoe 2 weeks after planting and during flowering. Fertilization was carried out by applying a basal dose of NPK fertilizer after the first weeding at a rate of 150kg/ha. Lagano (Lambda-cyhalothrin 2.5 EC) a non-systemic chemical insecticide was sprayed twice at a rate of 500ml/ha at flower bud initiation to control thrips and at podding to control pod-sucking bugs.

Data collection

The generations and number of plants that the data were collected from are presented in Table 2.

Data were collected from individual plants of the various generations for all four cross combinations on the following parameters; Days to 50% flower, Days to first (1st) pod maturity, Number of primary branches, Pod length, Number of seeds per pod and Number of Maruca damage pods per plant. These traits and their descriptions are presented in Table 3.

Statistical analysis

Mean performance

The mean performance of the generations for each trait was done using GenStat statistical software version 12. The means were separated using the Least Significant Difference (LSD) test at a significance level of 5%.

Generation mean analysis

The gene action of the traits of interest (PB, DFF, DFPM, PL, NSP and MDPP) was studied in the six basic generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of four crosses using scaling test proposed by Mather and Jinks. Scaling tests (A, B, and C) were performed in

all four crosses to determine the adequacy of the test in explaining the variations among the generation means. In cases where the scaling tests were inadequate in explaining the variations between the means, it was indicative of the inadequacy of the additive-dominance model in explaining the variability between the means in the crosses. In these cases, the data was further analyzed for the three-parameter model, thus m, [a], and [d] of the joint scaling test.

This procedure estimates the genetic parameters using weighted least squares and the inverse of the variance of each generation mean. The chi-square (χ^2) values were significant for some traits in the crosses valuated, indicating the presence of epistasis. Therefore, the joint scaling test was extended to include the six parameters model, to test for the di-genetic interaction. The A-D model was extended to include epistatic terms. The χ^2 adequacy test was not possible for this model, because the degrees of freedom were zero for each of the crosses. Therefore, non-significant parameters were removed from the full model to generate degrees of freedom for model adequacy χ^2 tests.

A perfect fit solution formula (six-parameter model) by Kearsey and Pooni was fitted for the four crosses, to determine the adequacy of the non-allelic interactions as suggested by Mather and Jinks. The data analysis was performed using R statistical software version 4.3.3. A simple linear regression model was fitted using Kearsey and Pooni method below:

$$Y = C + b_1x_{1i} + b_{2.}x_{2i} + b_3x_{3i} + b_{4.}x_{4i} + b_5x_{5i}$$

Where: c = intercept (m), b_1 = Additive gene effect [a], b_2 = Dominance gene effect, b_3 = Additive x Additive epistasis gene effects, b_4 = Additive x Dominance epistatic gene effects, b_5 = Dominance x Dominance epistatic gene effects, x = coefficients of the various gene effects. The results of the estimates of each of the genetic parameters using weighted least square weighed will be similar to the formulas below.

$$m = {}^1\!/_2\, P_1 + {}^1\!/_2\, P_2 + 4F_2 - 2BC_{1:1} - BC_{1:2}$$

$$a = {}^1\!/_2\, P_1 - {}^1\!/_2\, P_2$$

$$d = 6BC_{1:1} + 6BC_{1:2} - F_1 - 8F_2 - 1\tfrac{1}{2}P_1 - 1\tfrac{1}{2}P_2$$

$$aa = 2BC_{1:1} - 1BC_{1:2} - 4F_2$$

$$ad = 2BC_{1:1} - 2BC_{1:2} - P_1 + P_2$$

$$dd = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_{1:1} - 4BC_{1:2}$$

Where [m] = intercept, [a] additive genetic effects, [d] = dominance genetic effect, [aa] = additive x additive genetic effect, [ad] = additive x dominance genetic effect, and [dd] = dominance x dominance genetic effects.

Conclusion

Allelic and non-allelic interactions were found to be important in determining the expression of the traits under study in cowpea. The majority of the traits exhibiting digenic interaction were shown to depend heavily on duplicate gene activity. It would therefore be challenging for the breeder to use traditional breeding techniques, such as creating straightforward crossings and using the straight pedigree approach to exploit them. For the pedigree method, selection should be postponed to later generations and operated in bulk or by single-seed or single-pod descent. These methods are particularly expensive, time-consuming and laborious, marker-assisted selection would also be recommended for more efficiency. The breeding procedure involving multiple crosses, biparental crosses may be employed to get transgressive segregants. This is especially important to develop good pure lines having superiority in different characters.

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Author Contributions

Gloria Anyesom Adazebra, Samuel Amiteye, Francisca Addae-Frimpomaah, Nusrat Afful and Harry Amoatey: Conceived, designed and performed the experiments and edited the manuscript, Philip Agrengsore: Managed the experiments and collected the data. Emmanuel Amponsah Adjei and Jerry Nboyine: Analyzed, interpreted the data, wrote and edited the paper.

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Data Availability Statement
Data will be made available upon request.

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