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Genetic Variability, Heritability and Selection Potential of Seed Size and Associated Traits among Cowpea Populations Developed Through Marker-assisted Backcrossing

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ABSTRACT

Background: Cowpea [*Vigna unguiculata* (L.) Walp.] production, in sub-Saharan Africa is severely limited by the parasitic weed *Striga gesnerioides*.

Methods: This study assessed genetic variability, heritability and genetic advance for key agronomic and seed traits in F_2 and BC_1F_1 cowpea populations developed through marker-assisted backcrossing (MABC) to combine *Striga* resistance with large seed size. Fifteen quantitative traits, including plant height, canopy diameter, seeds per pod and 100-seed weight, were evaluated across maternal half-sib families.

Result: Analysis of variance (ANOVA) showed highly significant (P≤0.001) differences among genotypes for all traits, confirming substantial genetic variability among the population. Phenotypic coefficients of variation exceeded genotypic coefficients, indicating minimal environmental influence. Broad-sense heritability was high (93.33-100%) and several traits displayed high genetic advance, suggesting predominance of additive gene action and suitability for early-generation selection. Canopy diameter, pods per plant, seeds per pod and 100-seed weight emerged as reliable selection traits. Overall, MABC effectively integrated *Striga* resistance with desirable agronomic characteristics.

Key words: Cowpea, Genetic advance, Genetic variability, Heritability, Marker-assisted backcrossing, Seed size, *Striga gesnerioides*.

INTRODUCTION

Cowpea [*Vigna unguiculata* (L.) Walp.] is a key grain legume in sub Saharan Africa, valued for its nutritional quality, adaptability to marginal environments and role in sustaining smallholder livelihoods (Vaggar *et al*., 2022; Reddy *et al*., 2025). However, its productivity remains constrained by several biotic stresses, most notably the parasitic weed *Striga gesnerioides*, which significantly reduces yield in susceptible varieties and continues to challenge breeding efforts in *Striga* prone agro-ecologies (Horn and Shimelis, 2020).

A fundamental requirement for genetic improvement in cowpea is the exploitation of genetic variability for traits related to yield and stress resilience. Genetic variability provides the essential raw material for selection and genetic gain, enabling breeders to identify and recombine superior alleles for desirable traits (Devi and Jayamani, 2018; Choudhary *et al.*, 2025). Studies in cowpea have identified significant genotypic differences among lines for key quantitative traits, with genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) often indicating substantial variation that can be harnessed in breeding programmes (Vinay *et al*., 2022).

Closely linked to variability are the quantitative genetic parameters of heritability and genetic advance, which together inform the efficiency and potential of selection (Kumar *et al*., 2026). Heritability estimates the proportion of total phenotypic variation attributable to genetic factors, distinguishing genetic control from environmental influence, while genetic advance provides an expectation of the gain achievable through selection in a given generation. High heritability coupled with high genetic advance suggests that additive gene action predominates, indicating that selection based on phenotypic performance will be effective (Sheidu *et al*., 2023). Moderate to high heritability and substantial genetic advance have also been reported for yield contributing traits in cowpea, pointing to the feasibility of improving these traits through selection (Vinay *et al.,* 2022).

Despite the growing body of literature on resistance to *Striga gesnerioides* in cowpea germplasm and advanced lines, there remains a need for targeted evaluation of

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genetic variability, heritability and genetic advance in breeding populations developed under biotic stress conditions such as *Striga* infestation. Such evaluations are critical for informing early generation selection strategies and ensuring that gains made under controlled breeding environments translate into improved performance under field conditions.

Accordingly, the present study aimed to assess genetic variability, heritability and genetic advance for key agronomic and seed traits in F_2 and BC_1F_1 cowpea populations developed through marker assisted backcross breeding. The insights generated are intended to guide selection decisions and accelerate the development of *Striga* resistant, high performing cowpea cultivars adapted to *Striga* endemic cowpea-producing environments.

MATERIALS AND METHODS

Plant materials

Selected cowpea [*Vigna unguiculata* (L.) Walp.] parental lines differing in seed size and responses to *Striga gesnerioides* were employed. Four (4) high-yielding, large-seeded but *Striga*-susceptible advanced breeding lines (UCC15-03, UCC15-25, UCC15-36 and UCC15-41) were used as the recurrent parents, while four (4) *Striga*-resistant donor parents possessing known resistance loci (UCC15-07, Aluba Kpole, IT93K-693-2 and Kubi were used as the non-recurrent parents. These parental lines were obtained from the Department of Molecular Biology and Biotechnology of the University of Cape Coast and were chosen based on prior agronomic performance and resistance status (Table 1).

Breeding scheme and population development

Hybridization was carried out using a single backcross breeding strategy to introgress *S. gesnerioides* resistance genes into the genetic background of the elite large-seeded recurrent parent. Initial crosses were made between the recurrent parent (♀) and the resistant donor parent (♂) to generate F_1 progenies. The confirmed F_1 plants were subsequently backcrossed to the recurrent parent to produce the BC_1F_1 population.

To facilitate genetic evaluation, an F_2 population was also developed through selfing of selected F_1 plants. The breeding scheme followed principles of marker-assisted backcross breeding (MABC) to accelerate the recovery of elite seed traits while retaining *Striga* resistance genes. The overall mating design was structured in line with the North Carolina Mating Design II, enabling effective assessment of genetic contributions from parental lines (Fig 1).

Experimental site and field management

Field evaluations were conducted at the St. Joseph's College of Education School Farm in Bechem in the Ahafo Region from October to December, 2024. Bechem lies in the forest transition ecological zone at Latitude 7°4′50.808″N and Longitude 2°1′27.156″W (https://en.wikipedia.org/wiki/St._Joseph%27s_College_of_Education). Standard agronomic practices for cowpea production (Bassi *et al*., 2024) were followed throughout the growing season, including appropriate spacing, weed control and pest management.

Phenotypic evaluation of agronomic traits

Phenotypic data were collected on selected agronomic and seed traits, with particular emphasis on seed size attributes.

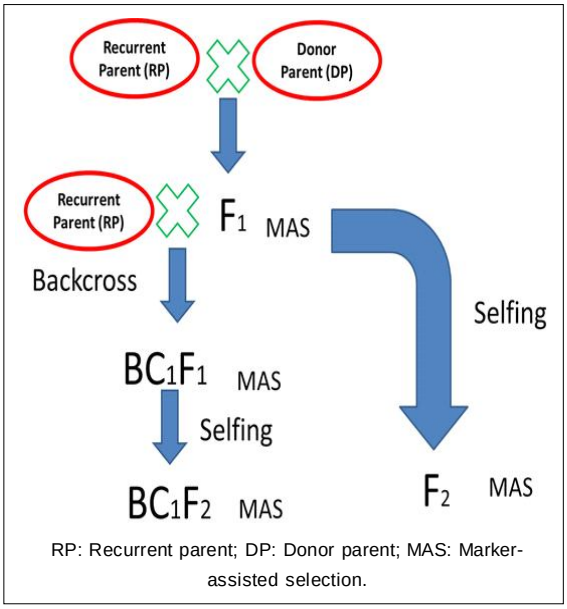


Fig 1: Scheme for introgression of genes for *S. gesnerioides* resistance and larger seed size using backcross breeding.

Table 1: Parental cowpea genotypes.

Genotype	Pedigree	Reaction to *S. gesnerioides*	Seed coat colour	100-seed weight (g)
IT93K-693-2	(IT88D-867-11 × IT90K-76) × IT89KD-374.	Resistant	Brown	13.25
Kubi	SARI	Resistant	White	18.58
UCC15-07	GH3684 × IT97K-499-35	Resistant	White	19.53
Aluba kpole	IITA	Resistant	Reddish brown	24.69
UCC15-03	GH3684 × IT97K-499-35	Susceptible	White	22.83
UCC15-25	GH3684 × SARC-1-57-1	Susceptible	White	22.98
UCC15-36	GH3684 × UCS01	Susceptible	Red	25.70
UCC15-41	GH3684 × UCS01	Susceptible	White	22.72

Traits evaluated included plant height, canopy diameter, terminal leaf length, terminal lead diameter, number of branches, days to flowering, days to pod maturity, number of peduncles per plant, pods per peduncle, seeds per pod, pod length, seed length, seed width, seed thickness and 100-seed weight. Measurements were taken following standard cowpea descriptors to ensure consistency and repeatability (IBPGR, 1983).

Statistical analysis

Phenotypic data were subjected to statistical analysis using [R.4.3 (2023) Version 12]. ANOVA was performed to determine significant differences among genotypes. Descriptive statistics were used to summarize trait performance and marker–trait associations were inferred based on concordance between molecular and phenotypic data.

RESULTS AND DISCUSSION

Agronomic and yield traits performance of F_2 and BC_1F_1 maternal half-sib families

Substantial variation was observed among the F_2 cowpea progenies analysed as maternal half-sib families for all 15 quantitative traits measured (Table 2). Mean performance differed across maternal families (UCC15-03, UCC15-25, UCC15-36 and UCC15-41), indicating effective segregation for both vegetative and yield-related traits at the F_2 generation.

Plant height ranged from 39.72 cm in UCC15-03 to 54.95 cm in UCC15-36, while canopy diameter varied widely, with the highest mean recorded in UCC15-25 (95.71 cm). Phenological traits showed relatively narrow ranges, with days to flowering varying from 35.91 to 37.96 days and days to pod maturity from 55.28 to 57.40 days across maternal families. Yield components, such as number of pods per plant, seeds per pod and 100-seed weight also exhibited clear differences among families, with UCC15-25 and UCC15-36, generally, having higher mean values for yield-associated traits.

The BC_1F_1 cowpea population also exhibited appreciable variation among maternal half-sib families for all 15 quantitative traits evaluated (Table 3). Mean values differed across the four maternal backgrounds (UCC15-03, UCC15-25, UCC15-36 and UCC15-41), indicating the persistence of genetic variability following backcrossing to the recurrent parent.

Plant height ranged from 39.18 cm in UCC15-03 to 47.70 cm in UCC15-36, while canopy diameter varied between 53.84 cm (UCC15-25) and 66.22 cm (UCC15-36). Phenological traits showed relatively narrow variation, with days to flowering ranging from 35.39 to 39.18 days and days to pod maturity from 53.32 to 54.68 days across maternal families. Yield-related traits, such as number of pods per plant, seeds per pod and 100-seed weight, displayed notable differences among maternal families, with UCC15-25 and UCC15-36 generally having higher mean values for number of pods, number of seeds and seed size attributes.

Analysis of variance (ANOVA)

The analysis of variance revealed highly significant ($P \leq 0.001$) differences among maternal half-sib families for all 15 traits evaluated (Table 4). This pattern was consistent across all four maternal backgrounds, confirming the presence of substantial genetic variability within the F_2 population.

Replication effects were generally non-significant for most traits, suggesting minimal environmental influence and reinforcing the reliability of the observed genetic differences. The significant maternal family effects for key traits, such as plant height, canopy diameter, number of pods, seeds per pod and 100-seed weight, indicate that maternal lineage played an important role in trait expression at this stage of segregation. Analysis of variance revealed highly significant ($P \leq 0.001$) differences among maternal half-sib families for all traits studied in both F_2 and BC_1F_1 populations (Table 4 and 5). This indicates that substantial genetic variation was retained after backcrossing.

Replication effects were generally non-significant or of low magnitude, suggesting limited environmental influence on trait expression. Significant maternal family effects were consistently observed for key agronomic and yield traits, including plant height, canopy diameter, number of branches, number of pods, number of seeds per pod, pod length and 100-seed weight, highlighting the importance of maternal lineage in shaping phenotypic performance in the BC_1F_1 generation.

Phenotypic and genotypic coefficients of variation

The phenotypic coefficient of variation (PCV) was marginally higher than the genotypic coefficient of variation (GCV) for all traits across maternal families, indicating limited environmental influence on trait expression. High PCV and GCV values were recorded for canopy diameter, terminal leaf diameter, number of branches, number of pods and number of seeds per pod, suggesting considerable genetic variability for these traits within the F_2 population (Table 3).

Conversely, relatively low PCV and GCV values were observed for days to flowering, days to pod maturity, pod length and pods per peduncle, reflecting greater phenotypic stability for these traits.

Across all traits in the BC_1F_1 population, phenotypic coefficients of variation (PCV) were only slightly higher than genotypic coefficients of variation (GCV), indicating minimal environmental contribution to total phenotypic variance. Moderate to high PCV and GCV values were recorded for canopy diameter, terminal leaf traits, number of branches, number of pods and number of peduncles, reflecting considerable genetic variability among maternal families.

Lower PCV and GCV values were observed for phenological traits, such as days to flowering and days to pod maturity, as well as for pod length and pods per peduncle, suggesting greater phenotypic stability for these traits in the BC_1F_1 population compared to yield components (Table 6).

Table 2: Means of morphodescriptors, phenotypic and genotypic coefficients of variance of 15 quantitative characters among F_2 cowpea progenies.

Traits	Means				Phenotypic coefficient of variance				Genotypic coefficient of variance			
	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41
PH	39.72	54.26	54.95	50.50	14.08	22.06	14.15	29.74	14.07	22.00	14.15	29.74
CD	72.88	95.71	78.45	89.08	31.50	29.74	10.34	9.67	31.49	29.74	10.34	9.66
TLL	11.26	11.66	12.69	11.13	11.80	5.14	6.60	5.57	11.79	5.13	6.60	5.57
TLD	6.24	5.78	5.91	5.39	37.81	7.36	5.61	6.32	37.81	7.36	5.60	6.32
DF	35.91	36.82	37.96	36.03	5.09	1.59	1.59	1.44	5.09	1.59	1.59	1.44
DPM	55.28	55.74	57.40	56.74	2.88	1.72	4.14	2.72	2.88	1.72	4.14	2.72
NOB	2.70	3.40	3.02	2.86	22.97	14.52	24.59	30.42	22.96	14.51	24.59	30.41
NOP	12.43	15.63	15.42	16.01	29.27	7.78	10.20	6.25	29.23	7.73	10.19	6.23
PPP	3.67	3.58	3.61	3.58	1.05	0.68	1.00	1.81	1.02	0.68	1.00	1.81
PL	15.54	17.51	16.68	16.47	10.51	17.45	10.55	5.06	10.51	17.45	10.55	5.06
SPP	9.95	11.73	9.74	10.58	8.87	12.23	13.54	10.49	8.88	12.23	13.54	10.49
SL	9.77	9.42	10.05	9.55	6.97	5.32	1.71	5.01	6.97	5	.32	1.71
5.00												
SW	6.73	7.64	7.13	6.67	1.76	18.73	1.59	1.65	1.74	18.73	1.59	1.65
ST	5.29	5.38	5.72	5.28	3.36	2.34	3.96	1.28	3.36	2.34	3.96	1.28
100 SW	20.00	22.29	22.82	20.10	8.69	7.64	2.93	5.40	8.69	7.64	2.93	5.40

PH= Plant height, CD= Canopy diameter, TLL= Terminal leaf length, TLD= Terminal leaf diameter, NB= Number of branches, NP= Number of peduncles, DF= Days to flowering, DPM= Days to pod maturity, PPP= Pods per peduncle, PL= Pod length, SPP= Seeds per pod, S= Seed length, SW= Seed width, ST= Seed thickness, 100 SW= 100-seed weight.

Table 3: Means of morphodescriptors, phenotypic and genotypic coefficients of variance of 15 quantitative characters among BCF_1 cowpea progenies.

Traits	Means				Phenotypic coefficient of variance				Genotypic coefficient variance			
	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41
PH	39.18	39.27	47.70	44.42	8.64	38.46	8.31	9.29	8.64	38.45	7.85	9.29
CD	64.53	53.84	66.22	65.89	19.63	34.87	14.72	12.83	19.63	34.88	13.87	12.78
TLL	10.81	10.09	10.64	10.58	7.93	28.27	7.75	8.40	7.93	28.27	7.69	8.39
TLD	5.45	5.97	5.32	4.96	25.53	33.86	7.52	5.81	25.53	33.85	7.32	5.80
DF	35.84	36.90	39.18	35.39	4.93	26.78	2.46	3.77	4.93	26.78	2.23	3.77
DPM	54.68	53.32	54.51	54.52	1.27	26.55	0.55	0.16	1.27	26.55	0.54	0.14
NOB	2.66	3.08	2.54	2.61	24.18	24.06	37.91	41.82	24.18	24.05	35.79	41.81
NOP	11.68	19.26	12.61	12.29	7.76	68.80	20.84	14.35	7.75	68.80	18.81	14.33
PPP	3.58	4.52	3.78	3.62	1.85	35.16	5.07	2.55	1.85	35.16	5.07	2.55
PL	15.83	14.38	17.16	15.22	6.24	23.41	15.55	7.11	6.24	23.41	15.35	7.11
SPP	9.57	9.14	9.07	9.51	11.29	14.19	6.60	10.60	11.29	14.18	6.60	10.60
SL	9.87	10.99	10.45	9.44	6.64	23.66	11.24	6.86	6.64	23.65	10.67	6.86
SW	6.82	5.89	7.13	6.62	3.89	24.16	5.73	1.43	3.89	24.16	2.71	1.43
ST	5.39	4.74	5.66	5.27	3.82	26.26	3.63	3.10	3.82	26.26	2.42	3.10
100 SW	21.27	20.20	22.94	20.16	7.46	11.43	10.48	6.24	7.45	11.40	10.44	6.24

PH= Plant height, CD= Canopy diameter, TLL= Terminal leaf length, TLD= Terminal leaf diameter, NB= Number of branches, NP= Number of peduncles, DF= Days to flowering, DPM= Days to pod maturity, PPP= Pods per peduncle, PL= Pod length, SPP= Seeds per pod, SL= Seed length, SW= Seed width, ST= Seed thickness, 100 SW= 100-seed weight.

Table 4: Mean squares for 15 characters among F_2 cowpea.

Sources	UCC15-03			UCC15-25			UCC15-36			UCC15-41		
	Mean sum of squares		Residuals (df=12)	Mean sum of squares		Residual (df=8)	Mean sum of squares		Residuals (df=8)	Mean sum of squares		Residuals (df=8)
	Replication (df=4)	Genotype (df=3)		Replication (df=4)	Genotype (df=2)		Replication (df=4)	Genotype (df=2)		Replication (df=4)	Genotypes (df=2)	
PH	0.01	156.27***	0.01	0.67	713.17***	0.75	0.02	302.09***	0.04	0.02*	1128.30***	0.00
CD	0.21	2632.97***	0.32	1.60	4050.00***	0.0	0.01	329.20***	0.01	0.13	370.46***	0.08
TLL	0.00	8.81***	0.00	0.00	1.79***	0.00	0.00***	3.51***	0.00	0.00	1.92***	0.00
TLD	0.00	27.83***	0.00	0.00	0.90***	0.00	0.00	0.55***	0.00	0.00*	0.58***	0.00
DF	0.00	16.70***	0.00	0.00	1.71***	0.00	0.00	1.82***	0.00	0.00	1.34***	0.00
DPM	0.01	12.64***	0.01	0.00*	4.58***	0.00	0.00	28.28***	0.00	0.00	11.88***	0.00
NB	0.00	1.93***	0.00	0.00	1.22***	0.00	0.00	2.76***	0.00	0.00	3.79***	0.00
NOP	0.04	66.04***	0.04	0.00	7.33***	0.02	0.00	12.36***	0.00	0.02*	4.98***	0.00
PPP	0.00	0.01***	0.00	0.00	0.00***	0.00	0.00	0.01***	0.00	0.00	0.02***	0.00
PL	0.00	13.34***	0.00	0.00	46.69***	0.00	0.00***	15.48***	0.00	0.00	3.48***	0.00
SPP	0.00	3.89***	0.00	0.00	10.29***	0.00	0.00	8.70***	0.00	0.00	6.16***	0.00
SL	0.00	2.32***	0.00	0.00	1.26***	0.00	0.00	0.15***	0.00	0.00	1.14***	0.00
SW	0.00	0.07***	0.00	0.00*	10.23***	0.00	0.00*	0.06***	0.00	0.00	0.06***	0.00
ST	0.00	0.16***	0.00	0.00	0.08***	0.00	0.00*	0.26***	0.00	0.00	0.02***	0.00
100 SW	0.00	15.10***	0.00	0.01***	14.49***	0.00	0.00	2.24***	0.00	0.00	5.89***	0.00

Heritability and genetic advance

Broad-sense heritability estimates were exceptionally high for all traits, ranging from 93.33% to 100% across maternal families (Table 7). Traits, such as plant height, canopy diameter, terminal leaf dimensions, number of pods, seeds per pod and 100-seed weight, consistently exhibited heritability values exceeding 99%, indicating that the observed variation was largely under genetic control.

Genetic advance and genetic advance expressed as a percentage of the mean were also high for most yield-related traits. Notably, genetic advance as a percentage of the mean for canopy diameter, number of branches, number of pods and plant height were high, suggesting the predominance of additive gene action and the potential for effective selection in early generations.

Broad-sense heritability estimates for BC_1F_1 maternal half-sib families were generally high, ranging from moderate to very high values across traits (Table 4). Estimates of broad-sense heritability for most traits, including canopy diameter, terminal leaf dimensions, number of branches, number of pods, number of seeds per pod, pod length and 100-seed weight, exceeded 90%, indicating strong genetic control of these characters.

Genetic advance and genetic advance expressed as a percentage of the mean were moderate to high for several yield-related traits, notably, canopy diameter, number of branches, number of pods, number of peduncles and 100-seed weight.

The comparative evaluation of the F_2 and BC_1F_1 cowpea populations, analysed as maternal half-sib families, provides valuable insight into the genetic consequences of segregation and backcrossing on agronomic performance, yield components and seed traits (Santos *et al*., 2024). The significant genetic variation observed in both populations demonstrates that substantial variability was generated at the F_2 stage and effectively retained in the BC_1F_1 generation following backcrossing to the recurrent parent. This outcome is particularly desirable in breeding programmes aimed at introgressing specific resistance traits while recovering elite agronomic backgrounds (Acquaah, 2012; Hospital, 2009).

Across most traits, the F_2 population exhibited relatively higher phenotypic and genotypic coefficients of variation compared to the BC_1F_1 population, reflecting the extensive segregation expected in early generations like the F_2. The reduction in variability observed in the BC_1F_1 generation is consistent with partial genome recovery of the recurrent parent following backcrossing. Nevertheless, the persistence of significant differences among maternal half-sib families in BC_1F_1 indicates that sufficient genetic diversity remained available for effective selection, particularly for yield-related and seed traits. Similar trends have been reported in cowpea and other self-pollinated crops undergoing backcross breeding (Falconer and Mackay, 1996; Gerrano *et al*., 2015).

Table 5: Mean squares for 15 characters among BC_1F_1 cowpea.

Sources	UCC15-03			UCC15-25			UCC15-36			UCC15-41		
	Mean sum of squares		Residuals (df=12)	Mean sum of squares		Residual (df=8)	Mean sum of squares		Residuals (df=8)	Mean		Residuals (df=8)
	Replication (df=4)	Genotype (df=3)		Replication (df=4)	Genotype (df=2)		Replication (df=4)	Genotype (df=2)		Replication (df=4)	Genotypes (df=2)	
PH	0.00	57.34***	0.00	0.03	1140.45***	0.05	1.53	71.75***	1.69	0.07.	85.09***	0.02
CD	0.04	802.26***	0.01	0.04	1761.97***	0.29	10.36	432.30***	10.72	0.37	354.82***	0.58
TLL	0.00	3.68***	0.00	0.01	40.70***	0.00	0.01	3.36***	0.01	0.00	3.94***	0.00
TLD	0.00	9.69***	0.00	0.00	20.40***	0.00	0.01	0.76***	0.01	0.00	0.41***	0.00
DF	0.00	15.61***	0.00	0.01	388.09***	0.02	0.17	3.98***	0.17	0.00	8.92***	0.00
DPM	0.00	2.40***	0.00	0.02	789.39***	0.01	0.10	8.05***	0.10	0.00	0.03***	0.00
NOB	0.00	2.07***	0.00	0.02	502.21***	0.01	0.10	4.24***	0.10	0.00	5.97***	0.00
NOP	0.00	4.10***	0.00	0.02	878.11***	0.01	1.17	29.39***	1.28	0.00	15.51***	0.01
PPP	0.00	0.02***	0.00	0.00	12.61***	0.00	0.00	0.18***	0.00	0.00	0.04***	0.00
PL	0.00	4.88***	0.00	0.01	56.69***	0.00	0.33	34.89***	0.19	0.01**	5.85***	0.00
SPP	0.00	5.83***	0.00	0.01	8.40***	0.00	0.41	8.21***	0.40	0.01**	5.08***	0.00
SL	0.00	2.15***	0.00	0.00	33.76***	0.01	0.16	6.35***	0.14	0.00	2.10***	0.00
SW	0.00	0.35***	0.00	0.00	10.13***	0.00	0.18	4.01***	0.20	0.00	0.04***	0.00
ST	0.00	0.21***	0.00	0.00	7.74***	0.00	0.02	0.11*	0.02	0.00	0.13***	0.00
100 SW	0.00	12.57***	0.00	0.02	26.54***	0.03	0.03	28.72***	0.05	0.00	7.92***	0.00

PH= Plant height, CD= Canopy diameter, TLL= Terminal leaf length, TLD= Terminal leaf diameter, NB= Number of branches, NP= Number of peduncles, DF= Days to flowering, DPM= Days to pod maturity, PPP= Pods per peduncle, PL= Pod length, SPP= Seeds per pod, SL= Seed length, SW= Seed width, ST= Seed thickness, 100 SW= 100-seed weight.

Table 6: Percentage heritability (Broad sense), genetic advance and genetic advance as percentage of mean, of 15 quantitative characters among F_2 cowpea progenies.

Traits	Heritability (Broad sense)				Genetic advance				Genetic advance as percentage of mean			
	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41
PH	99.96	99.48	99.94	100.00	11.51	24.52	16.01	30.95	28.99	45.20	29.13	61.27
CD	99.94	99.94	99.98	99.89	47.25	58.61	16.71	17.73	64.84	61.24	21.30	19.89
TLL	99.90	99.61	100.00	100.00	2.73	1.23	1.73	1.28	24.28	10.54	13.60	11.48
TLD	99.99	99.94	99.91	100.00	4.86	0.88	0.68	0.70	77.88	15.15	11.54	13.02
DF	99.96	99.62	100.00	100.00	3.76	1.20	1.24	1.07	10.48	3.26	3.27	2.96
DPM	99.71	99.98	99.99	100.00	3.27	1.97	4.90	3.18	5.92	3.54	8.53	5.60
NOB	99.97	99.88	100.00	99.97	1.28	1.02	1.53	1.79	47.30	29.88	50.66	62.65
NOP	99.71	98.76	99.86	99.65	7.47	2.47	3.24	2.05	60.13	15.83	20.99	12.82
PPP	93.33	100.00	100.00	100.00	0.07	0.05	0.07	0.13	2.03	1.41	2.06	3.73
PL	99.99	99.99	100.00	99.93	3.36	6.29	3.63	1.72	21.66	35.94	21.73	10.43
SPP	99.83	99.99	99.99	99.98	1.82	2.95	2.72	2.29	18.25	25.19	27.90	21.62
SL	99.91	99.92	99.66	99.96	1.40	1.03	0.35	0.98	14.35	10.95	3.51	10.31
SW	98.57	100.00	100.00	100.00	0.24	2.95	0.23	0.23	3.57	38.58	3.27	3.40
ST	99.68	100.00	100.00	100.00	0.37	0.26	0.47	0.14	6.90	4.81	8.15	2.64
100 SW	99.92	99.99	99.93	99.87	3.58	3.51	1.38	2.23	17.89	15.73	6.043	11.11

PH= Plant height, CD= Canopy diameter, TLL= Terminal leaf length, TLD= Terminal leaf diameter, NB= Number of branches, NP= Number of peduncles, DF= Days to flowering, DPM= Days to pod maturity, PPP= Pods per peduncle, PL= Pod length, SPP= Seeds per pod, SL= Seed length, SW= Seed width, ST= Seed thickness, 100 SW= 100-seed weight.

Table 7: Percentage heritability (Broad sense), genetic advance and genetic advance as percentage of mean, of 15 quantitative characters among BC_1F_1 cowpea progenies.

Trait	Heritability (Broad sense)				Genetic advance				Genetic advance expressed as per cent mean			
	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41	UCC15-03	UCC15-25	UCC15-36	UCC15-41
PH	99.98	99.98	89.24	99.88	6.98	31.11	7.28	8.49	17.81	79.21	15.27	19.12
CD	99.99	99.92	88.72	99.19	26.09	38.65	17.82	17.27	40.43	71.79	26.91	26.21
TLL	99.99	99.96	98.50	99.95	1.77	5.88	1.67	1.83	16.34	58.22	15.72	17.29
TLD	99.97	99.93	94.81	99.88	2.87	4.16	0.78	0.59	52.59	69.70	14.68	11.95
DF	99.99	99.98	81.80	99.96	3.64	18.15	1.63	2.75	10.16	55.15	4.15	7.77
DPM	99.90	99.99	94,92	84.72	1.43	25.88	0.07	0.15	2.61	54.70	3.13	0.27
NB	99.88	99.99	89.12	99.99	1.32	20.64	1.77	2.25	49.76	65.54	69.60	86.13
NP	99.88	100.00	81.43	99.77	1.86	27.30	4.41	3.62	15.96	141.72	34.97	29.49
PPP	100.00	99.99	100.00	100.00	0.14	3.27	0.40	0.19	3.82	72.42	10.44	5.24
PL	99.96	99.99	97.40	99.88	2.04	6.94	5.36	2.23	12.85	48.22	31.21	14.63
SPP	99.91	99.96	88.98	99.87	2.22	2.67	0.13	2.08	23.24	29.21	1.43	21.81
SL	100.00	99.93	90.12	99.95	1.35	5.35	2.18	1.33	13.68	48.70	20.87	14.13
SW	99.86	99.98	97.77	100.00	0.55	2.93	0.19	0.19	8.01	49.77	2.65	2.93
ST	100.00	99.99	44.55	100.00	0.42	2.56	0.19	0.34	7.87	54.09	3.33	6.39
100 SW	99.86	99.42	99.14	99.95	3.26	4.73	4.91	2.59	15.35	23.41	21.41	12.85

PH= Plant height, CD= Canopy diameter, TLL= Terminal leaf length, TLD= Terminal leaf diameter, NB= Number of branches, NP= Number of peduncles, DF= Days to flowering, DPM= Days to pod maturity, PPP= Pods per peduncle, PL= Pod length, SPP= Seeds per pod, SL= Seed length, SW= Seed width, ST= Seed thickness, 100 SW= 100-seed weight.

The consistently high heritability estimates observed for most traits in both populations highlight the strong genetic control governing trait expression. In the F_2 population, high heritability coupled with high genetic advance as a percentage of the mean for traits, such as plant height, canopy diameter, number of branches, number of pods and 100-seed weight suggests the predominance of additive gene action, making these traits highly amenable to early-generation selection (Johnson *et al.,* 1955). In the BC_1F_1 population, although genetic advance values were comparatively reduced for some traits, heritability remained high, indicating that favourable alleles were successfully transmitted through backcrossing and could be fixed in subsequent generations.

Seed traits, particularly, 100-seed weight, seed length and seed width, showed high heritability and appreciable genetic advance in both populations, underscoring their importance as reliable selection targets. The maintenance of superior seed traits in the BC_1F_1 generation is especially significant, as seed size is a key determinant of consumer preference, market value and adoption of improved cowpea varieties. Previous studies have similarly reported seed weight as one of the most heritable traits in cowpea, with limited environmental influence (Egbadzor *et al*., 2014; Mohammed *et al*., 2020).

From a breeding perspective, the results clearly demonstrate the effectiveness of marker-assisted backcross breeding (MABC) in combining *Striga* resistance with desirable agronomic and seed characteristics. While conventional backcrossing can lead to linkage drag and loss of elite traits, the retention of high-performing maternal families in the BC_1F_1 population suggests that marker-assisted selection facilitated the recovery of the recurrent parent genome while preserving favourable alleles for yield and seed size. This aligns with reports that MABC accelerates the introgression of resistance genes while minimizing disruption to elite genetic backgrounds (Collard and Mackill, 2008; Hospital, 2009).

The maternal half-sib analytical framework adopted in this study further enhanced selection efficiency by emphasizing additive genetic effects and reducing environmental variance within families. This approach is particularly useful in early backcross generations, where family-based evaluation improves the accuracy of identifying superior genotypes carrying both resistance and agronomic superiority (Hallauer *et al*., 2010). The consistent performance of certain maternal families across both F_2 and BC_1F_1 generations suggests genetic stability and highlights their potential as candidates for advancement in subsequent selection cycles.

In the context of *S. gesnerioides* resistance breeding, the ability to maintain high yield potential and large seed size alongside resistance is critical for the successful deployment of improved cowpea varieties in *Striga*-prone environments. The present findings demonstrate that the integration of molecular markers with conventional quantitative genetic analysis enables breeders to balance resistance introgression with agronomic performance. This integrated strategy enhances breeding efficiency and increases the likelihood of developing farmer-preferred *Striga*-resistant cowpea cultivars.

Overall, the comparative analysis of F_2 and BC_1F_1 populations confirms that early-generation selection, when guided by maternal half-sib evaluation and marker-assisted backcrossing, is an effective approach for simultaneous improvement of resistance and yield-related traits in cowpea. The results provide strong empirical support for the use of MABC in cowpea improvement programmes targeting *S. gesnerioides* resistance without compromising elite seed traits.

CONCLUSION

The present study revealed substantial genetic variability among the cowpea genotypes evaluated in the F_2 and BC_1F_1 populations for key agronomic and seed-related traits under *Striga gesnerioides* pressure. The wide ranges observed for number of pods per plant, number of seeds per pod and 100-seed weight indicate the presence of exploitable genetic diversity, providing a strong basis for effective selection in subsequent breeding generations.

Estimates of heritability varied among traits, with generally moderate to high heritability recorded for yield components and seed size attributes. The relatively high heritability of 100-seed weight suggests that this trait is predominantly under genetic control and can be reliably improved through selection.

The combination of high heritability and high genetic advance observed for several traits, particularly seed size and yield-related characters, suggests the predominance of additive gene action. This implies that phenotypic selection in early generations, including the BC_1F_1 and subsequent selfed generations, would be effective for improving these traits. Traits with high heritability but moderate genetic advance (pods per peduncle, days to flowering and days to pod maturity) may require prolonged selection or complementary breeding strategies to achieve substantial improvement.

From a breeding standpoint, these findings demonstrate that integrating genetic variability parameters with heritability and genetic advance estimates provides a reliable framework for identifying traits amenable to rapid genetic improvement. Selection focused on traits exhibiting high genetic advance as a percentage of the mean is expected to result in meaningful progress toward developing cowpea varieties that combine improved seed size and yield potential under *Striga*-infested environments. Overall, the results support the use of quantitative genetic parameters as effective tools for guiding selection decisions in cowpea improvement programmes.

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Conflict of interest

The authors declare that there is no conflict of interest regarding the submission and publication of this work.

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