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Genetic diversity analysis using phenotypic and SSR markers with trait association and multivariate analysis in cowpea (*Vigna unguiculata* (L.) Walp.) genotypes

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Abstract

The low productivity of cowpea is primarily attributed to inadequate utilisation of genetic diversity for the improvement of local cultivars. The present study was conducted to assess genetic diversity utilising 17 yield and biochemical traits along with simple sequence repeat (SSR) markers. Fifty cowpea genotypes were assessed during summer 2024 at Chaudhary Charan Singh Haryana Agricultural University (CCSHAU), India. Genotypes were planted with three replications in a randomised block design. Significant genetic variability was observed in the studied traits. The minimal differences between phenotypic and genotypic coefficients of variation (CV) indicated that the observed variation primarily stemmed from the genetic component. Most traits showed high heritability, with varying levels of genetic advance. Trait association revealed a positive interrelationship among yield-contributing traits, suggesting their utility for selection for cowpea yield improvement. Cluster I possessed better-performing genotypes for yield traits. Principal component analysis emphasised that pods per cluster (PCL), pods per plant (PPL) and clusters per plant (CPL) were the major contributing traits in principal component 1 (PC1). Out of 64 SSR markers screened, 40 showed successful amplification and 18 were highly polymorphic and used for diversity analysis, with an average of 2.94 alleles per marker. PIC values varied from 0.11 to 0.78. Highly informative markers (Vm 39, Vm 31, Vm 27, CP 1) were valuable for diversity assessment. Overall, the genotypes PGCP-89, PGCP-70, PGCP-90, KVCP 17-15, GC 2202 and GC 2105 were found to be superior for yield and contributing traits. These genotypes can be useful for further breeding and hybridisation for cowpea improvement; however, they require multi-environment validation.

Keywords: character associations; cowpea; genotypic variability; multivariate analysis; SSR markers

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1. Introduction

Cowpea [*Vigna unguiculata* (L.) Walp.] is a versatile and hardy legume crop that is adaptable in water-deficient areas and low-fertility soils. It belongs to the family Fabaceae, is diploid (2n = 22) and has an estimated genome size of 640.6 megabases (Mb) (1). It is self-pollinated in nature and extensively cultivated in arid, semi-arid and subtropical regions. It is utilised in various forms, including green beans, pulses and dry seeds and also serves as a valuable fodder for animals. Cowpea is valued for protein (23–32 %), carbohydrates (50–60 %), essential minerals such as zinc, iron, magnesium, calcium, potassium and phosphorus and a considerable amount of fat (F), dietary fibre and phytochemicals (2, 3). Cowpea, through its nitrogen fixation ability, increases soil nitrogen up to 40–80 kg per hectare (4). Therefore, enhancing cowpea yield and productivity is imperative to meet the increasing global demand for plant-based protein-rich diets, ensure food security, improve resilience under changing climate conditions and optimise resource use in sustainable agriculture.

The low productivity of cowpea is largely due to a low harvest index, various biotic and abiotic stresses and limited utilisation of genetic variability. A priori knowledge of genetic diversity is very important for the success of a breeding programme. Consequently, to develop cowpea varieties that are both locally adapted and high-yielding, breeding programmes must incorporate a diverse array of genotypes (5). Knowledge of genetic variability and trait interrelationships in a crop assists plant breeders in developing productive varieties (6). Since yield is influenced by multiple interrelated factors, a clear understanding of the associations among component traits is essential for yield improvement (7). Genetic

improvement for yield cannot be effectively achieved without identifying traits that contribute most significantly to it. The correlation coefficient helps to quantify the direction and strength of the relationship between component and the desired trait. However, it fails to explain how much each trait contributes directly or indirectly to the main trait. Therefore, path analysis is a standardised partial regression analysis that permits the partitioning of correlation coefficients into components of direct and indirect effects, thereby providing a more reliable interpretation of cause-and-effect relationships among the studied traits (8). Furthermore, principal component analysis (PCA) identifies key yield-related traits and cluster analysis helps choose diverse parents for crossing (9).

While phenotypical descriptors are affected by the environment, the molecular markers prove to be a precise and reliable tool for assessing genetic variation. Simple sequence repeats (SSRs) are particularly advantageous due to a high degree of polymorphism, reproducibility, co-dominant transmission and relatively high abundance in the genome (10). SSR markers have been effectively used to assess genetic diversity in cowpea (11). Several studies have assessed genetic diversity using morphological traits (6) and molecular SSR markers in cowpea (4). Likewise, independent investigations have assessed the nutritional quality of cowpea (6). While these studies provide valuable information, they primarily utilise individual or partially combined approaches to characterise cowpea genotypes. However, integrating these approaches with character association studies and multivariate analysis on the same set of genotypes provides a more reliable and comprehensive assessment of genetic diversity. Therefore, this study aims to explore the genetic diversity present in a large group of cowpea genotypes at the morphological and molecular levels. In-depth trait interrelationships and multivariate analysis have been incorporated into this study for identifying the key traits that can contribute to the development of resilient and high-yielding cowpea varieties.

2. Materials and Methods

The experimental material consists of 50 cowpea genotypes sourced from different sites across India. The study was conducted in the Dryland Area of Forage Section, Department of Genetics and Plant Breeding, CCS Haryana Agricultural University, Hisar, Haryana, India during Summer 2024. The experimental area was situated at 29.10 °N latitude and 75.46 °E longitude, at an elevation of 215.2 m above mean sea level (AMSL). This location experiences a tropical monsoonal climate and is classified as arid. The climate of the Hisar district is characterised by its dryness, temperature variations and limited rainfall. The average annual rainfall of the district is 450 mm and the maximum rainfall is received during June to September. The experimental field had sandy loam soil. The crop received optimum rainfall during the monsoon season and standard agronomic practices, including timely weeding, were followed throughout the crop growth period. The crop's quality parameters were estimated in the forage quality lab of this department. Each genotype was planted in two rows, 2 m long, in three replications, with a crop geometry of 45 × 10 cm, adopting a randomised block design. Genotypes were evaluated for 17 quantitative traits, including agronomic traits, such as days to 50 % flowering (DF), pods per plant (PPL), pod length (PL), days to maturity (DM), seeds per pod (SP), seed length (SL), seed test weight (STW), peduncle length (PedL), plant height (PH), branches per plant (BP), pods per cluster (PCL), clusters per plant (CPL) and seed yield per plant (SYP) and four biochemical traits.

Yield and yield-attributing traits

Yield and yield-associated parameters were assessed at the proper growth stage of the plant and full expression of the concerned trait by following the guidelines issued by the Protection of Plant Varieties and Farmers' Rights Authority (PPV & FRA, New Delhi). Data were recorded from three randomly selected plants from each genotype.

Biochemical estimation

Evaluation of crude fat, protein, crude fibre (CF) and tannin (T) content was carried out in 50 cowpea genotypes. Mature and healthy seeds from cowpea genotypes were ground into fine powder and were stored in an airtight container for estimation of these biochemical parameters.

Estimation of crude fat

Crude F (%) was estimated following the soxhlet method as per AOAC (2000)(using petroleum ether as the extraction solvent (12). Results were expressed as percentage (%).

Estimation of protein content

Protein (%) analysis was done using micro-Kjeldahl's method according to AOAC (2000) (12). The crude protein (P) content was calculated by multiplying the nitrogen content by a conversion factor of 6.25 and expressed as percentage (%).

Estimation of crude fibre

Crude fibre (%) was determined using the Foss FibertecTM 8000 (Auto Fibre Analysis System), according to standard AOAC (2000) procedure using defatted, finely ground seed samples (12). Acid and alkali digestion was carried out, followed by drying and ashing and CF content was expressed as a percentage (%).

Estimation of tannin

Tannin content was estimated using the Vanillin Hydrochloride method using finely ground seed samples extracted with methanol. Absorbance was recorded at 500 nm using a spectrophotometer and T content was

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quantified using a standard catechin calibration curve. The results were expressed as Catechin Equivalent (mg CE g^{-1}).

Genetic variability, character association and statistical analysis

Genetic variability was assessed using genotypic coefficients of variation (GCV) and phenotypic coefficients of variation (PCV) (13). The broad-sense heritability (percentage) was estimated following standard procedure (14), while the expected genetic advance was calculated (15). Hierarchical cluster analysis was performed using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) method (16). Correlation coefficient and Path coefficient analyses were performed using the methods and following equations:

$$r_p(xy) = \frac{Cov_p}{\sqrt{V_p(x) \times V_p}} \quad \text{(Eq. 1) (17)}$$

Where,

$r_p(xy)$ = Phenotypic correlation coefficient between traits x and y

Cov_p (xy) = Phenotypic co-variance between trait x and y

$V_p(x)$ = Phenotypic variance of trait 'x'

V_p (y) = Phenotypic variance of trait 'y'

$$r_{iy} = P_{iy} + \sum r_{ij}P_{jy} \quad \text{(Eq. 2) (18)}$$

Where,

r_{iy} = Phenotypic correlation coefficient between the i^{th} trait and seed yield

P_{iy} = Direct effect (path coefficient) of the i^{th} trait on seed yield

r_{ij} = Phenotypic correlation coefficient between the i^{th} and j^{th} traits

P_{jy} = Direct effect (path coefficient) of the j^{th} trait on seed yield

$\sum r_{ij}P_{jy}$ = Sum of the indirect effects of the i^{th} trait on seed yield through other traits

R (Residual effect) = $\sqrt{1- \sum r_{iy}P_{iy}}$

Statistical analyses were conducted using RStudio (version 2025.05.0 + 496) and OPSTAT (19).

Diversity analysis by SSR markers

Genomic DNA (Deoxyribonucleic acid) was isolated from the 50 cowpea genotypes using the CTAB (Cetyl Trimethyl Ammonium Bromide) extraction method (20). The concentration of the isolated DNA was determined using a Thermo Scientific NanoDrop spectrophotometer by measuring absorbance at 260 and 280 nm. Further, DNA quality was assessed by electrophoresis on a 0.8 % agarose gel. A total of 64 Molecular SSR markers were selected from the previously conducted studies based on their polymorphism and successful application in genetic diversity analysis of cowpea genotypes. In this study, these markers were used to assess the diversity of a distinct set of 50 cowpea genotypes. The list of primers used in the present study is mentioned in Table 1.

Polymerase chain reaction (PCR) was performed using a Bio-Rad thermo cycler machine in PCR tubes containing 2.0 µL DNA template (50 ng mL^{-1}), 1 µL of 1 X Green GoTaq Ò Flexi buffer, 1 µL 25 mM magnesium chloride ($MgCl_2$), 0.4 µL 10 mM dNTPs mix, 10 mM forward primer and reverse primer in 0.5 µL and 0.2 µL 5U Taq DNA Polymerase, finally the 4.4 µL autoclaved ddH_2O was added making a final volume of 10 µL for one PCR reaction. PCR amplification was done with initial denaturation at 94 °C for 4 min, followed by 35 cycles consisting of denaturation at 94 °C for 1 min, annealing at 45.5–58.5 °C (primer specific) for 1 min and extension at 72 °C for 1 min. This was followed by final primer extension at 72 °C for 7 min and the reactions were then held at 4 °C for further analysis. PCR-amplified DNA products were separated by electrophoresis on a 2 % agarose gel prepared in 1 X TBE buffer containing ethidium bromide. Electrophoresis was carried out at 100 volts for approximately 1.5 hr. Finally, the migrated DNA fragments were visually analysed by the Bio-Rad Gel Documentation system and the DNA band sizes were compared with the 100 bp DNA ladder. The amplified DNA generated by SSR markers was analysed after visualising the bands across genotypes. Each band was scored as '1' for presence and '0' for absence. Polymorphic information content (PIC) value was calculated by the formula:

$$PIC = 1-\sum (P_{ij})^2 \quad \text{(Eq. 3)}$$

Where P_{ij} represents the frequency of the j^{th} allele at the i^{th} locus, summed over all alleles.

To determine the genetic distance between the genotypes and group them into various clusters, a dendrogram was constructed using RStudio (version 2025.05.0+496) software.

3. Results and Discussion

Yield performance of cowpea genotypes and analysis of variance

Highly significant mean squares were observed for all the yield-related and biochemical traits in the analysis of variance (Table 2), reflecting considerable genetic variability among the studied genotypes. Such variability can be effectively exploited in cowpea breeding programmes to improve yield and quality.

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Table 1. list of SSR markers used in the study for diversity analysis of cowpea genotypes.

Sl. no	Primer Name	Forward sequence 5'<----------->3'	Reverse sequence 5'<----------->3'
1	Vm3	GAGCCAGGGCACAGGTAGT	GAGCCGGGTTCAATAGGTA
2	Vm 5	TTCCCTGCAACAAAAATACA	AGCGACGGCAACAACGAT
3	Vm11	CCCAGAGGCCGCTATTACAC	CGGGAATTAACGGAGTCACC
4	Vm12	CAACAGACGCAGCCCAACT	TTGTCAGCGAAATAAGCAGAGA
5	Vm13	GTCCCCTCCCTCCCACTG	CACCCGTGATTGCTTGTTG
6	Vm 14	ATAAAGGAGGGCATAGGGAGGTAT	AATTCGTGGCATAGTCACAAGAGA
7	Vm 19	TCGTGGCACCCCCTATC	TATTCATGCGCCGTGACACTA
8	Vm 22	GTACTGTTCCATGGAAGATCT	GCGGGTAGTGTATACAATTTG
9	Vm 23	AGACGCGTGGTACCCATG TT	AGACATGTGGGCGCATCTG
10	Vm 25	CAATTCCACTGCGGGACATAA	CCACAATCACCGATGTCCAA
11	Vm 26	TGTGGCATTGAGGGTAGC	GGCATCAGACACATATCA CTG
12	Vm 31	GTGTTCTAGAGGGTGTGATGGTA	CGCTCTTCGTTGATGGTTATG
13	Vm 33	CAGCGAGCGCGAACC	GCACGAGATCTGGTGCTCCTT
14	Vm 34	TAACCCAATAATAAGACACATA	AGCTCCCCTAACCTGAAT
15	Vm 35	ATGGCTGAAATAGGTGTCTGA	GGTCAATAGAATAATGGAAAGTGT
16	Vm 36	GTCGCTGGGGGTGGCTTATT	ACTTTCTGTTTTACTCGACAACTC
17	Vm 37	CGAGGATGAAGTAACAGATGATC	TGTCCGCGTTCTATAAATCAGC
18	Vm 39	AAAAGGATGAAATTAGGAGAGCA	GATGGTTGTAATGGGAGAGTC
19	Vm 40	CTCTAACACCTCAAGTTAGTGATC	TATTACGAGAGGCTATTTATTGCA
20	Vm 68	TCGAAGCAACAAATGGTCACAC	CAAGGCATGGAAAGAAGTAAGAT
21	Vm 70	GAAGGCAAAATACAT GGAGTCAC	AAAATCGGGGAAGGAAACC
22	Vm 71	TGGGTGGAGGCAAAAACAAAAC	TCGTGGCAGAGAATCAAAGACAC
23	CP37	TGTCCGCGTTCTATAAATCAGC	CGAGGATGAAGTAACAGATGATC
24	CP3	GAGCCGGGTTCAATAGGTA	GAGCCAGGGCACAGGTAGT
25	CP1	CACCCGTGATTGCTTGTTG	GTCCCCTCCCTCCCACTG
26	CP	CGCTGGGGGTGGCTTAT	AATTCGACTTTCTGTTTACTTG
27	CP2	GTAAGGTTTGGAAGAGCAAAGAG	GGCTATATCCATCCCTCACT
28	CP5	AGCGACGGCAACAACGAT	TTCCCTGCAACAAAAATACA
29	CP24	TCAACAACACCTAGGAGCCAA	ATCGTGACCTAGTGCCCACC
30	VM9	ACCGCACCCGATTTATTTCAT	ATCAGCAGACAGGCAAGACCA
31	VM10	TCCCACTCACTAAAATAACCAACC	GGATGCTGGCGGCGGAAGG
32	VM16	TCCTCGTCCATCTTCACCTCA	CAAGCACCGCATTAAAGTCAAG
33	VM17	GGCCTATAAATTAACCCAGTCT	TGTGTCTTTGAGTTTTTGTTCTAC
34	VM27	GTCCAAAGCAAATGAGTCAA	TGAATGACAATGAGGGTGC
35	VM28	GAATGAGAGAAGTTACGGTG	GAGCACGATAATATTTGGAG

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36	VM30	CTCTTTCGCGTTCCACACTT	GCAATGGGTTGTGGTCTGTG
37	VM38	AATGGGAAAAGAAAGGGAAGC	TCGTGGCATGCAGTGTCAG
38	E107111562	AACTCAGAGACAAAACTCACCCA	CCACTCGTTTTAGCTTCTTCAAA
39	E1081215711	CTCTAGCTTTGTTCGTCGTTGAT	ATACACGTGTGAACACCAAAACA
40	E1121316121	CTGAAGATCATCATCCCAATTCC	AAAATCTGATTGGCAACATAGGA
41	E1159516411	GCAATTGACCTAGACAACCTCAC	ATCACCCTCTCCTTCTCACTCTC
42	E1345417901	AAGATCCTTGCACTGAAATTGAA	CTTTCTCCAACTCACTCCTCTCA
43	E1429718451	TCATTCTTGTTCTGTGCTTCTCA	ATTAATGGGACAAGAAATGCAGA
44	E1502531	AGCAGAGATGAAGAAAACGATGT	CTTTTCATGACATTCGACCTCAC
45	E1573619231	ACTTTGCATGAAGAACCTCTCAG	CCCTGATATGGAGTTTGTGGATA
46	E1577519251	ATTTGCACTTTTCGACTCCAGTA	GAAGAAGAGAAGTTATCGTGCCA
47	E1684719591	TCAAAGCTCAAACCTAAACCAAA	GACACTGTTTCTACGCCATCTTC
48	E1735319801	ACACTTCCTAGGTGATTGTAGCG	ATCACCCAACCTTAACTCTCACA
49	E200215141	CACCTTAACAAAAGCTGCTCCTA	GAGGTCATTCAGAAAGAACATCG
50	E211515451	TAGTGCTGCTGGTAATTCTGGAT	CTCTTCTTCAAAGGGGTTGACTT
51	E251156091	ATTACATCACTCGACACCCAATC	TGACGATGCTTCTGAGCTAGGTA
52	E257216231	GGAAAAGAAACTCTAGCTTGGCA	ATCCCCATTGCATCTTCTTATTT
53	E272826501	TCATCAAAGATGTTTCCTTCCAT	ATAAGTTCATGTAATCGCATGGC
54	E2751841	CAGTACGATTTCTGAATGTCACG	TATCTTCTGCTCTGCTCTGCTCT
55	E354010801	GAGTTCAGCCTTGAGAGACTGC	ATTTGACGACAGCAAGAGAAAAC
56	E420011241	ACATTTCGGAGTATTTTGTCCTG	CCAATCAAAACGAACTCTTCAAC
57	E421111251	TCCTCTCCACCTCCTAAACAAAC	CTTTTTGAAAATGTCTTTCCAGC
58	E458029311	GATTTAGGATGCATCAGTCCAAC	CTGGATACTGCAACGGGAG
59	E470811451	CGTGCACCCTAGAGCTTTTATAC	AGATTAAACCTCTCACTCCACCC
60	E489829761	AAACATTTTTCTTAAACCGCCAC	GGCGTGGATATTAGGGATTACTT
61	E561611791	CTACACTTTCATCATCACCGTCC	AAAATAAACACTGCTGTGGATGC
62	E577311931	GTCATGCAACGATATTAAGCTCC	GGCAGGATACATGATGAGTTACC
63	E809213181	ACTATCACACCCAAAAGCACACT	CAAGAGCAGTGAAGAAGAAGAGC
64	E904513911	CCCAGAAAGCACTATTAACCAGA	TCCCCTTCTTATCCTTCACTTTC

Table 2. Analysis of variance for various quantitative traits in cowpea genotypes

		Mean sum of squares							
Source	**df**	**DF**	**PH**	**BP**	**CPl**	**PPl**	**PCl**	**PL**	**PedL**
Replication	2	2.73	368.18	17.42	8.4	18.36	0.01	2.58	1.57
Genotypes	49	59.40**	840.86*	4.62*	50.21**	89.91**	1.69**	14.55**	56.48**
Error	98	5.5	175.55	1.22	2.17	3.08	0.15	1.99	4.58
CV %		5.76	12.38	12.92	9.04	9.62	16.04	9.94	16.06

Mean sum of squares

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Source	df	DM	SP	SL	STW	F	P	T	CF	SYP
Replication	2	67.39	7.46	0.22	0.83	0.007	2.33	0.19	0.09	9.78
Genotypes	49	109.44**	8.88*	2.858**	22.79**	3.37**	22.60**	8.20**	6.85**	319.81**
Error	98	5.21	2.19	0.32	0.79	0.01	0.27	0.053	0.04	10.53
CV %		3.01	12.76	9.12	7.86	3.39	2.13	4.43	3.71	10.67

*Significant at 5% level, ** Significant at 1% level Abbreviations: df: Degree of freedom; DF: Days to 50% flowering; DM: Days to maturity; PH: Plant height(cm); BP: Branches per plant; CPl: Clusters per plant; PPl: Pods per plant; PCl: Pods per cluster; PL: Pod length (cm); PedL: Peduncle length (cm); SP: Seeds per pod; SL: Seed length (mm); STW: Seed test weight (g); F: Fat %; P: Crude protein %; T: Tannin (CEmg/g); CF: Crude fibre; SYP: Seed yield per plant (g)

Analysis of trait means, CV and critical difference (CD) further demonstrated significant differences among genotypes for all traits, thereby confirming considerable genetic variability. In the present study, the mean DM was 76 days, whereas a previous study reported a mean of 74 days (6). The number of SP and PPL showed a mean of 11.61 and 18.25, respectively. Similar reports were found for these traits, focusing on the diversity analysis of cowpea genotypes (21, 22). Seed test weight was observed to be a maximum of 8.03 g, which is lower than the 27 g reported in earlier study (23). Seed yield per plant among the evaluated cowpea genotypes ranged from 14.55 g to 58.04 g with an overall mean of 30.42 g. Genotype PGCP-89 (58.04 g) was noted as the maximum seed-yielding genotype, followed by PGCP-70 (54.28 g), PGCP-90 (52.57 g), GC 2202 (50.19 g), KVCP 17-15 (48.51 g) and GC 2105 (48.41 g). Similarly, another study noted SYP ranged from 8.67–47.78 g (24). In this study, the quality estimation showed that P content varied widely among genotypes (17.12–28.86 %), with the highest value in PGCP-89, suggesting the importance of protein-rich genotypes in breeding. In another study, similar protein content ranging from 19.3 % to 27.9 % has also been reported (25). High fibre enhances the dietary quality of cowpea and benefits digestion. Crude fibre content ranged from 2 % to 8.25 %. Genotypes PGCP-70 and GC 3 had maximum fibre content and may be a valuable breeding source for fibre content. Fat content showed substantial variation (1.19-5.14 %) and the genotypes rich in F content (PGCP-90, GC 1802) can be included in the cowpea breeding programmes for developing nutrient-rich varieties. Tannin content varied from 2.2 to 9.5 mg CE g^{-1}, reflecting differences in anti-nutritional factors. Higher tannin content reduces the nutritional value of the crop because tannins interfere with nutrient absorption and digestibility (26). Genotypes CPD-249 and EC-724035 exhibited lower T levels; therefore, they should be preferred for improving the nutritional quality of cowpea. Detailed information on the mean values of the studied yield and quality traits in 50 cowpea genotypes is provided in Table 3. Nutritional improvement is a major objective in legume crops, such as protein and fibre content. Interestingly, % genotype PGCP-89 combined the highest seed yield with high protein content (26.86 %), while PGCP-70 showed superior yield and high CF content (8.25 %), suggesting the potential of these genotypes for yield combined with protein and fibre content. The results indicate that superior agronomic performance and desirable nutritional traits can be combined in a cowpea breeding programme.

Estimation of genetic variability parameters

The estimates of characteristics revealed that the PCV for almost all traits were slightly higher than their corresponding GCV, indicating a lesser environmental influence and strong genetic control on these traits. The GCV and PCV for yield traits were found to be high for seed yield $plant^{-1}$, T content, PedL, PPL, pods $cluster^{-1}$, F content, CF, CFL and STW, emphasising the importance of these traits for direct selection in cowpea crop breeding schemes. However, another study reported moderate values for PedL, PCL, PL and SP (21). On the contrary, our results found DF and protein content with low GCV and PCV values, thereby restricting the effectiveness of selection for these traits in cowpea. GCV and PCV were also high in one study for the branches $plant^{-1}$, PH, pod yield, PPL and SP in cowpea (27). Similar findings of higher PCV and GCV were reported in cowpea (22, 24, 28–32). Fig. 1 shows the genetic variability parameters for various quantitative traits.

Traits such as F content, CF, T, protein content, STW, SYP, PPL and CPL exhibited exceptionally high heritability values. A high magnitude of genetic advance, as a percentage of the mean (> 20 %), along with high heritability, was recorded for the following traits: CPL, PPL, PCL, PedL, STW, F content, T content, CF and SYP, suggesting the traits are governed by additive gene effects. Therefore, direct phenotypic selection of these characters is expected to be beneficial and can facilitate significant genetic improvement in cowpea breeding schemes. The previous investigation found high heritability along with high genetic advance for PH, number of racemes plant-1, PedL, PPL, CPL, PL and hundred seed weight (21). In another study, high heritability with high genetic advance was recorded for similar characters, such as number of CPL, SYP, PPL and PPL and highlighted that simple selection can be effective for improvement in these characters (24). Similarly, other studies confirm similar results with our studies, with high heritability coupled with high genetic advance (30–33). High heritability with high genetic advance, particularly for traits that directly contribute to yield, suggests that direct selection can be highly effective for overall yield improvement (34).

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Table 3. Mean values of various quantitative characters in studied cowpea genotypes

Sl. no.	Genotypes	DF	DM	PH	BP	CPl	PPl	PCl	PL	PedL	SP	SL	STW	F	P	T	CF	SYP
1	PGCP-80	51.67	78.0	89.67	9.83	13.67	15.37	1.5	14.23	7.47	7.77	6.67	9.25	4.32	26.52	4.0	5.68	21.94
2	GC 2105	44.00	72.7	108.95	9.67	22.83	27.83	3.7	12.37	8.43	14.30	5.83	9.61	4.65	25.55	3.8	6.96	48.41
3	VCP-21023	41.33	75.0	100.43	8.83	15.33	14.00	2.0	18.13	12.03	10.77	4.57	7.93	2.31	23.30	5.2	5.82	23.56
4	TCM 314	42.00	76.3	76.89	7.50	21.23	15.60	1.7	11.50	12.37	10.73	5.87	7.78	2.87	25.76	5.3	6.86	20.70
5	CPD 307	39.33	80.3	101.48	7.17	16.67	18.17	2.8	14.27	24.17	13.00	6.50	12.93	3.32	26.16	3.8	6.36	31.19
6	CPD-331	43.33	89.0	94.43	9.17	16.00	10.17	1.0	15.60	14.80	13.33	6.33	13.38	3.19	25.66	3.3	5.87	20.78
7	PGCP-83	44.67	69.0	77.24	9.67	17.50	17.47	2.3	16.80	7.77	11.17	7.00	15.03	3.23	25.22	8.0	6.08	27.82
8	PGCP-82	45.33	74.0	77.84	8.00	17.33	18.50	2.3	11.80	14.17	12.00	6.50	8.88	2.87	24.18	3.5	6.04	27.53
9	GC 2115	40.33	74.0	84.40	9.00	20.67	16.50	2.3	13.77	14.17	11.00	4.30	8.48	2.02	25.26	8.0	6.14	28.33
10	GC 2108	40.67	75.3	122.40	10.50	19.33	16.63	2.3	13.63	9.93	11.17	6.83	9.15	3.86	26.27	4.2	5.82	28.90
11	PL-7	46.67	73.3	101.31	7.83	18.53	15.97	2.5	16.90	7.97	9.57	6.17	14.60	3.13	25.57	5.5	6.03	24.25
12	GC 3	40.00	87.3	104.35	10.00	15.00	16.77	2.5	14.27	13.13	9.43	6.03	13.04	3.15	26.53	6.1	8.05	33.63
13	PGCP-84	48.67	73.0	86.64	9.00	20.50	17.33	2.7	14.80	12.70	11.83	6.67	11.37	3.89	26.10	3.6	6.91	37.34
14	CPD 302	43.67	72.3	120.03	6.50	22.17	16.40	2.7	15.50	13.80	11.17	7.30	9.38	4.65	26.11	2.8	7.05	30.96
15	KVCP 17-15	39.00	68.3	103.97	8.17	21.00	23.67	3.7	9.90	12.23	12.63	7.60	14.06	4.91	26.04	5.4	6.92	48.51
16	GC 2006	47.00	73.3	93.81	7.83	22.83	18.87	2.7	11.40	15.57	12.90	4.40	6.91	2.07	25.63	3.7	6.67	25.49
17	GC 1905	45.67	81.0	101.01	7.17	17.17	20.93	2.7	15.50	16.90	11.50	6.50	7.98	3.32	25.19	4.2	5.59	28.60
18	GC 1801	35.67	70.0	97.60	9.33	15.50	23.47	3.5	13.03	12.43	12.53	5.97	14.74	1.84	25.25	5.5	3.64	47.36
19	VCP-17-19	45.33	91.7	125.50	10.67	14.00	15.33	2.7	14.10	22.00	10.40	4.70	16.59	4.29	25.66	4.3	6.79	29.08
20	GC 1805	42.00	88.3	100.68	11.43	19.17	15.07	3.2	20.50	18.87	15.87	6.17	13.56	4.46	26.18	3.6	5.73	33.08
21	PGCP-89	34.67	72.0	113.88	9.83	24.93	27.00	4.0	15.00	9.87	13.50	6.57	15.01	3.91	28.86	7.4	6.37	58.04
22	GC 2202	34.67	73.0	105.85	8.50	18.33	24.83	3.7	15.63	13.13	12.17	6.67	11.69	3.19	26.19	7.1	5.91	50.19
23	KMC 14	38.00	73.3	98.75	8.17	15.33	27.00	3.7	15.20	11.40	12.33	6.10	11.56	1.39	25.20	6.1	6.24	43.61
24	CPD-249	36.67	89.0	99.03	10.00	14.33	19.27	2.0	15.27	26.57	9.40	6.33	10.98	4.75	17.12	2.2	5.67	30.92
25	PL-3	44.67	69.3	129.60	10.00	14.33	15.50	2.5	13.40	14.77	10.67	6.00	11.66	3.57	26.90	6.5	5.15	27.96
26	IPCWP 2022-7	37.00	73.3	91.88	6.67	17.33	23.33	2.3	13.03	11.03	11.83	6.17	10.51	4.94	25.26	6.3	5.14	26.19
27	GC 2205	36.67	73.3	88.46	8.00	13.50	23.67	2.7	14.23	9.63	13.83	6.60	14.44	3.81	23.39	8.2	5.66	28.00
28	CPD-339	38.00	78.3	109.41	9.83	8.50	10.67	1.3	16.43	9.60	6.37	3.53	7.33	4.02	25.82	5.5	3.95	15.92
29	Pant Lobia 4	39.33	71.3	118.28	8.83	14.00	25.50	2.0	15.23	12.33	10.23	7.50	14.15	2.34	28.05	4.6	4.12	31.71
30	KMC 12	42.00	70.0	123.82	7.83	14.50	25.43	2.0	14.57	13.53	12.33	7.07	12.92	3.31	24.00	5.4	4.41	27.74
S.N.	Genotypes	DF	DM	PH	BP	CPl	PPl	PCl	PL	PedL	SP	SL	STW	F	P	T	CF	SYP
31	VCP 18-024	42.00	73.7	119.97	8.00	13.67	15.47	2.3	11.07	13.30	13.00	7.33	10.99	2.90	27.39	5.9	2.18	29.83
32	PCP-1124-1	40.67	76.0	101.69	6.50	10.47	11.87	1.3	14.10	12.63	9.83	6.73	8.53	4.41	24.77	6.0	4.81	19.22
33	GC 1802	44.00	76.7	90.07	9.17	12.67	16.83	2.0	13.13	8.87	12.60	6.67	9.40	5.09	25.38	9.5	4.88	31.63
34	KBC 9	52.33	86.3	107.35	7.17	12.00	13.60	2.7	16.30	9.67	12.97	3.90	8.78	5.14	25.42	7.3	2.17	24.08
35	PL-1	38.33	67.7	98.04	7.17	14.17	25.67	2.3	13.47	9.90	13.23	6.97	9.89	5.09	23.32	5.3	3.33	34.87
36	GC 1906	43.67	81.3	115.37	9.67	12.63	10.10	1.3	10.00	9.97	10.00	3.57	7.97	4.95	24.99	3.9	2.00	14.55
37	CPD 119	38.33	73.3	125.15	8.33	17.30	26.83	2.7	16.30	10.13	11.67	6.67	8.51	2.45	25.11	3.8	2.85	25.80
38	VCP 18-007	36.67	74.0	113.82	9.17	16.33	15.00	2.5	13.60	10.87	12.67	6.83	8.84	3.11	18.55	6.4	3.25	26.89
39	IPCWP 2022-10	38.67	74.3	121.34	9.17	11.17	22.10	2.0	12.97	11.37	13.50	6.53	10.50	3.37	22.11	8.1	5.26	36.04
40	PGCP-90	39.33	73.3	111.93	10.67	26.27	28.67	3.8	14.30	26.27	12.00	6.57	14.63	5.11	23.74	4.4	5.83	52.57

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41	RC 101	38.00	70.0	125.30	8.17	13.83	12.83	2.3	12.07	16.70	11.03	6.87	9.15	3.13	18.18	3.7	5.25	26.48
42	KBC 11	39.00	73.3	100.33	7.33	14.33	18.10	3.0	15.33	16.17	13.00	5.93	10.14	1.19	24.36	4.4	6.31	24.07
43	PGCP-70	40.67	72.3	127.23	9.00	25.77	28.67	4.0	16.97	15.93	13.87	6.73	13.99	3.91	24.70	5.7	8.25	54.28
44	PGCP-76	41.00	86.7	119.64	9.83	14.17	14.80	2.7	13.83	8.83	10.50	7.33	15.17	1.41	23.65	7.5	8.02	36.12
45	PGCP-73	40.33	83.3	117.02	7.83	13.50	9.83	1.7	8.43	12.33	8.33	6.43	13.83	2.95	17.23	4.4	4.24	19.33
46	TC-901	32.67	74.0	171.12	7.67	11.50	13.83	2.3	12.17	12.50	10.83	6.33	18.03	2.89	18.79	3.3	6.46	27.61
47	EC-724035	32.67	69.7	94.48	7.33	12.00	13.67	2.3	11.90	14.30	11.17	6.77	11.80	2.07	25.87	2.9	2.86	23.11
48	EC-528393	33.33	72.3	122.35	7.50	12.00	13.50	1.3	12.57	18.00	11.17	6.60	8.73	3.93	22.64	4.4	5.18	16.63
49	CPD 269	37.00	74.7	109.80	7.00	12.00	13.50	1.3	12.67	12.47	12.00	7.33	12.90	3.21	17.51	3.9	3.89	18.25
50	HC-46	36.67	73.3	110.90	6.67	17.87	11.33	1.7	11.67	12.93	11.47	5.73	9.14	2.90	23.66	4.8	5.87	21.93
	Overall Mean	40.67	75.83	107.01	8.56	16.30	18.25	2.45	13.98	13.32	11.61	6.25	11.32	3.46	24.41	5.17	5.41	30.42
	C.D. (5%)	3.81	3.71	21.50	1.80	2.39	2.85	0.64	2.25	3.47	2.41	0.93	1.44	0.07	0.84	0.37	0.33	5.27
	C.V	5.77	3.01	12.38	12.92	9.04	9.62	16.04	9.94	16.07	12.76	9.13	7.86	3.39	2.13	4.44	3.71	10.67

Abbreviations: DF: Days to 50% flowering; DM: Days to maturity; PH: Plant height(cm); BP: Branches per plant; CPl: Clusters per plant; PPl: Pods per plant; PCl: Pods per cluster; PL: Pod length (cm); PedL: Peduncle length (cm); SP: Seeds per pod; SL: Seed length (mm); STW: Seed test weight (g); F: Fat %; P: Crude protein %; T: Tannin (CE mg/g); CF: Crude fibre (%); SYP: Seed yield per plant (g)

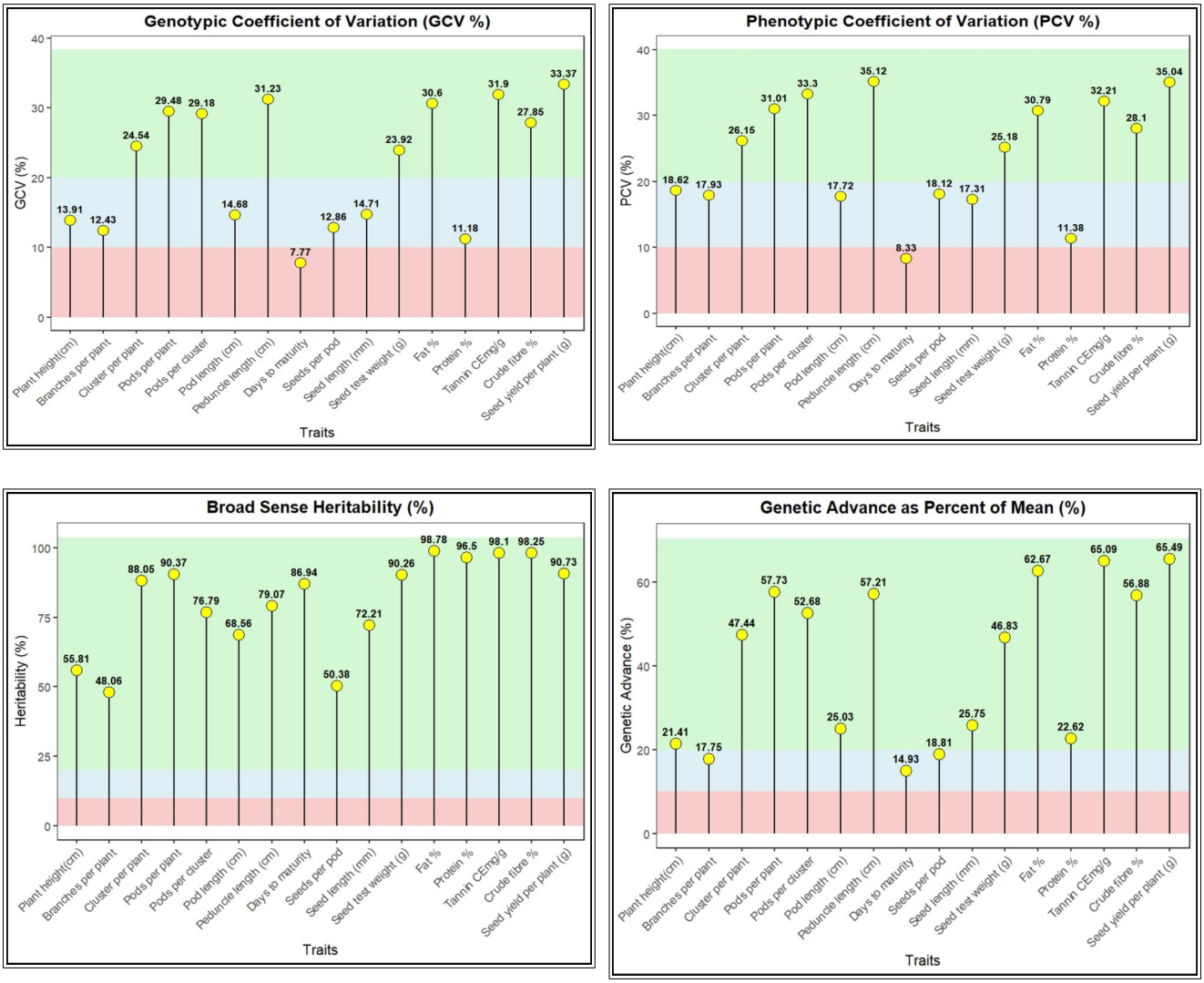


Fig. 1. Lollipop graph representing genetic variability parameters (A-D) for quantitative traits in cowpea genotypes.

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Character association studies in yield-attributing traits

Seed yield is a quantitative trait and is more complexly influenced by various factors and is the product of the contribution of other traits directly or indirectly (35). Therefore, information on the character association can improve selection efficiency and breeding success (6). Correlation measures the strength and direction of the association between two or more variables. The correlation coefficients for various yield-attributing traits are presented in a heat map (Fig. 2). SYP exhibited significant positive correlations with PCL, PPL, CPL, SP, STW and CF. The results indicate that these traits may serve as indirect selection criteria for yield improvement in cowpea. Similarly, another study noted that CPL and PPL had significantly h higher correlation coefficients with SYP in cowpea (35). We observed a negative correlation between seed yield and DM and DF. The correlation among these traits indicates strong interdependence among yield-contributing components and highlights the need to include correlated traits while designing breeding programmes. The present findings on correlations among yield attributes align with previous findings by several researchers (7, 9, 23, 24, 27, 35).

Since several yield-contributing traits are interrelated, path coefficient analysis was employed to quantify their direct and indirect effects and to identify traits with actual contribution to seed yield. Path analysis partitions the correlation coefficient into its individual components, thereby offering a more precise understanding of the relationships among traits (18, 36). In this study, a positive direct effect on seed yield was observed for PCL (0.816), followed by seed length (SL) (0.209), PPL (0.125) and BP (0.123). Seed test weight had a non-significant effect on yield. In contrast, STW had the most substantial positive direct effect on seed yield (0.440), followed by PPL (0.402) (32). The results of the path analysis for direct and indirect effects of various traits on seed yield are summarised in Table 4. In this study, the consistent identification of PCL and PPL as important yield-contributing traits by both correlation and path coefficient analyses indicates that these traits are direct contributors to seed yield and reliable selection criteria for cowpea seed yield improvement. These results in the path coefficient analysis are consistent with the previous studies conducted on the cowpea crop (9, 28, 35, 37). Furthermore, a very low residual effect value suggested that the selected traits adequately represented the variation in seed yield.

Hierarchical cluster analysis

Hierarchical cluster analysis is a statistically robust method used to interpret complex data matrices. To classify the 50 cowpea genotypes based on 17 yield attributes, hierarchical cluster analysis was performed using the D^2 statistic. The analysis grouped the 50 cowpea genotypes into six different clusters. The dendrogram is illustrated in Fig. 3, showing the genotype clustering. The cluster analysis revealed that cluster I had 21 genotypes. The cluster membership of each genotype is given in Table 5. Research done by (38, 39) classified cowpea genotypes into six and five clusters, respectively. Similarly, previous studies reported the grouping of 169, 33 and 430 genotypes into eight, five and seven clusters, respectively (23, 40, 41).

The Inter-cluster distance was noted to be maximum between cluster III and cluster V (50.45), while the minimum inter-cluster distance was between Cluster I and Cluster IV (31.03). The greater distance between clusters is a key factor in selecting parents with greater diversity for the hybridisation programme. Hybridisation between genotypes PGCP-90 from cluster V with higher seed yield (52.57 g) and GC-1805 from cluster III, with high protein (26.18 %) and F content (4.46 %), which belong to clusters showing maximum inter-cluster distance, is expected to produce hybrids combining higher yield with nutritional quality. Inter- and intra-cluster distances in cowpea genotypes have been presented in Table 6. Cluster I showed the maximum mean values for cluster per plant (18.30), PCL (2.70), CF (6.49 %), greater protein content (25.38 %) and SYP (33.65 g). The higher mean performance of cluster I for yield-related and quality traits indicates that the genotypes in this cluster can serve as promising donors for cowpea genetic improvement. Similarly, another study noted the highest STW in cluster VI and high SP in cluster I and suggested hybridisation from these clusters for developing high-yielding cultivars (23). In this investigation, cluster mean values calculated in different clusters are presented in Table 7.

Genotype PL-3 (Cluster VI) exhibited early maturity (69 days) and GC 1801 (Cluster II) showed high SYP (47.36 g). Thus, hybridization between the two can be advantageous for achieving early maturity along with high seed yield. One study conducted cluster analysis on 425 cowpea accessions and grouped the genotypes into seven clusters (23), while another study analyzed 142 mungbean genotypes and reported eight diverse clusters based on cluster analysis (42) all of which were consistent with present findings. Similarly, a separate study conducted cluster analysis for agro-morphological traits in 39 field pea genotypes and classified the genotypes into four major clusters (43).

Principal component analysis

This is a multivariate statistical technique that transforms a large set of correlated variables into a new set of fewer independent variables, called principal components, that represent the majority of the variation. In this study, the first five principal components were reported to have eigenvalues greater than one and they cumulatively explained 65.12 % of the total variation present in the 50 cowpea genotypes. These components captured most of the variability among the studied genotypes. The variance explained by principal components with eigenvalues > 1 in cowpea genotypes has been presented in Table 8. Eigenvalues important for identifying the principal components that contribute maximally to variation and components with eigenvalues more than one contribute more to variation (44).

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Table 4. Path coefficients for various quantitative traits indicating direct (bold & diagonal) and indirect effects (off-diagonal) on seed yield per plant in cowpea

	DF	DM	PH	BP	CPl	PPl	PCl	PL	PedL	SP	SL	STW	F	P	T	CF
DF	-0.117	0.033	-0.010	0.019	0.010	-0.025	-0.070	-0.018	0.006	0.010	-0.062	0.013	0.027	0.012	-0.002	0.003
DM	-0.036	0.106	0.000	0.048	-0.016	-0.053	-0.193	-0.023	-0.011	0.020	-0.076	-0.005	0.017	-0.003	-0.017	0.003
PH	0.039	-0.001	0.030	0.014	-0.015	-0.003	0.024	0.014	-0.004	0.011	0.029	-0.019	0.002	-0.010	-0.022	-0.002
BP	-0.018	0.041	0.003	0.123	0.015	0.012	0.235	-0.034	-0.004	0.002	-0.039	-0.016	0.019	0.007	0.013	0.006
CPl	-0.016	-0.024	-0.006	0.026	0.072	0.065	0.543	-0.015	-0.006	-0.044	0.026	-0.004	0.010	0.011	-0.009	0.016
PPl	0.024	-0.045	-0.001	0.011	0.037	0.125	0.623	-0.020	-0.002	-0.053	0.073	-0.012	0.006	0.009	0.021	0.005
PCl	0.010	-0.025	0.001	0.035	0.048	0.096	0.816	-0.026	-0.006	-0.062	0.035	-0.020	-0.003	0.010	0.017	0.011
PL	-0.020	0.024	-0.004	0.040	0.011	0.024	0.207	-0.103	-0.002	-0.018	-0.016	-0.005	0.003	0.010	0.011	0.006
PedL	0.022	0.034	0.003	0.016	0.013	0.006	0.135	-0.007	-0.033	-0.011	0.001	-0.008	0.010	-0.006	-0.053	0.006
SP	0.012	-0.022	-0.003	-0.002	0.032	0.067	0.514	-0.019	-0.004	-0.098	0.062	-0.009	0.005	0.005	0.019	0.002
SL	0.035	-0.039	0.004	-0.023	0.009	0.044	0.136	0.008	0.000	-0.029	0.209	-0.021	-0.003	-0.004	-0.003	0.004
STW	0.028	0.011	0.011	0.037	0.006	0.028	0.307	-0.011	-0.005	-0.017	0.084	-0.053	-0.007	-0.001	0.009	0.008
F	-0.029	0.016	0.001	0.021	0.007	0.007	-0.022	-0.003	-0.003	-0.004	-0.005	0.004	0.110	0.001	-0.001	-0.003
P	-0.043	-0.009	-0.009	0.025	0.024	0.032	0.246	-0.031	0.006	-0.015	-0.025	0.002	0.005	0.033	0.023	0.004
T	0.002	-0.016	-0.006	0.014	-0.006	0.023	0.123	-0.010	0.016	-0.016	-0.006	-0.004	-0.001	0.007	0.112	0.000
CF	-0.011	0.012	-0.002	0.026	0.039	0.024	0.310	-0.021	-0.007	-0.006	0.029	-0.015	-0.010	0.005	0.000	0.029

Residuals are 0.02209

Table 5. Cluster membership of cowpea genotypes in each cluster

Cluster no.	Genotypes	No. of genotypes
I	PGCP-80, GC 2105, TCM 314, CPD 307, PGCP-82, GC 2115, GC 3, PGCP-84, CPD 302, KVCP 17-15, GC 2006, GC 1905, PGCP-89, GC 2202, KMC 14, PCP-1124-1, KBC 11, PGCP-70, PGCP-76, EC-528393, HC-46	21
II	VCP-21023, GC 1801, VCP-17-19, CPD-339, GC 1906, TC-901, EC-724035	7
III	CPD-331, GC 1805	2
IV	PGCP-83, GC 2108, PL-7, IPCWP 2022-7, GC 2205, Pant Lobia 4, KMC 12, PL-1, CPD 119, CPD 269	10
V	CPD-249, VCP 18-007, PGCP-90, RC 101, PGCP-73	5
VI	PL-3, VCP 18-024, GC 1802, KBC 9, IPCWP 2022-10	5

Table 6. Inter (off-diagonal) and intra-cluster (diagonal) distances in cowpea genotypes

	Cluster I	Cluster II	Cluster III	Cluster IV	Cluster V	Cluster VI
Cluster I	26.60					
Cluster II	34.91	35.84				
Cluster III	41.58	45.75	33.13			
Cluster IV	31.03	36.95	42.50	28.03		
Cluster V	35.59	40.99	50.45	37.46	32.30	
Cluster VI	34.23	40.46	47.43	36.67	41.33	32.03

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Table 7. Cluster mean values for different traits in cowpea genotypes

Traits	Cluster I	Cluster II	Cluster III	Cluster IV	Cluster V	Cluster VI
DF	41.21	38.48	42.67	40.07	38.20	44.33
DM	75.37	77.14	88.65	72.12	77.92	76.06
PH	102.36	116.27	97.56	105.64	113.42	113.67
BP	8.25	9.05	10.30	8.18	9.17	8.70
CPl	18.30	12.78	17.59	15.82	16.85	12.77
PPl	19.19	14.44	12.62	21.40	17.12	16.70
PCl	2.70	2.20	2.10	2.24	2.46	2.30
PL	13.79	13.68	18.05	14.68	12.73	13.37
PedL	13.52	13.26	16.84	10.47	18.55	11.60
SP	11.72	10.30	14.60	11.70	10.69	12.55
SL	6.31	5.06	6.25	6.83	6.61	6.09
STW	10.65	12.06	13.47	12.21	11.49	10.27
F	3.25	3.20	3.83	3.54	3.81	4.01
P	25.38	24.24	25.92	24.37	18.96	25.44
T	5.12	4.37	3.45	5.52	4.22	7.46
CF	6.49	4.50	5.80	4.73	4.85	3.93
SYP	33.65	25.88	26.93	27.35	31.24	29.91

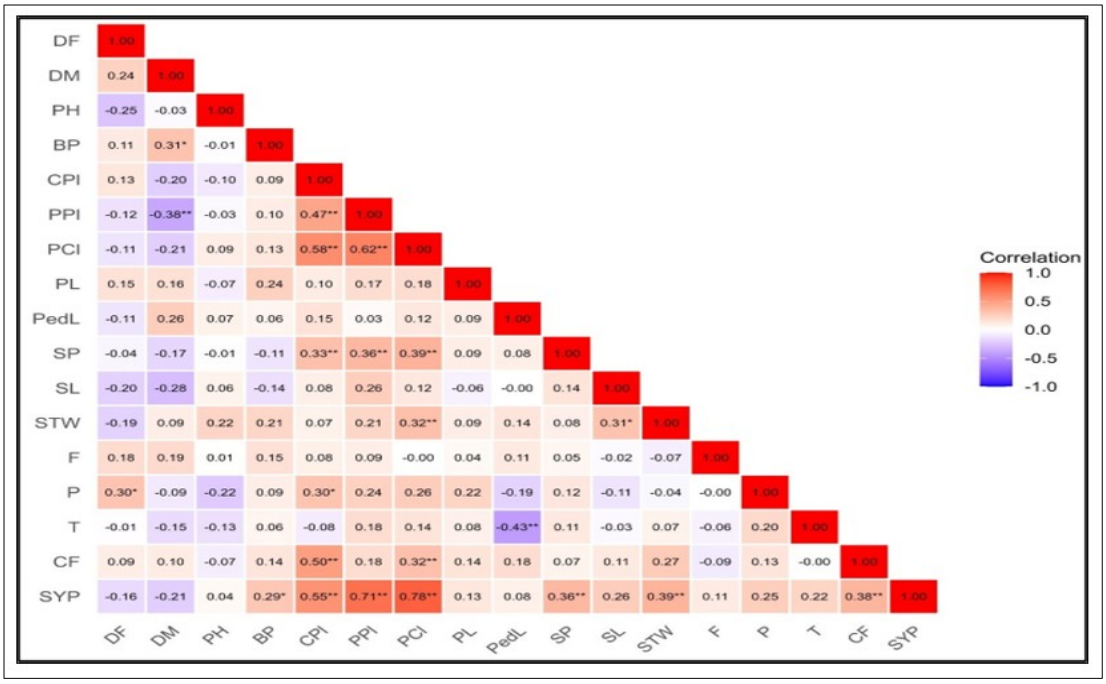


Fig. 2. Heat map representing the correlation coefficient between different 17 yield-attributing traits in cowpea. *Significant at 5 % level, ** Significant at 1 % level. DF: Days to 50 % flowering; DM: Days to maturity; PH: Plant height (cm); BP: Branches per plant; CPL: Clusters per plant; PPL: Pods per plant; PCL: Pods per cluster; PL: Pod length (cm); PedL: Peduncle length (cm); SP: Seeds per pod; SL: Seed length (mm); STW: Seed test weight (g); F: Fat (%); P: Crude protein (%); T: Tannin (CEmg/g); CF: Crude fibre (%); SYP: Seed yield per plant (g).

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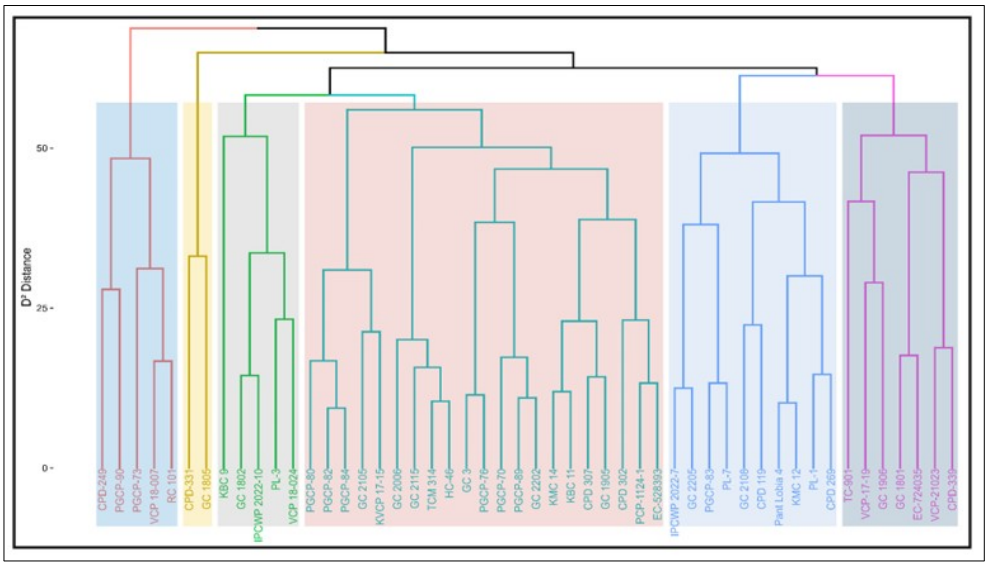


Fig. 3. Dendrogram revealing distribution of 50 cowpea genotypes into six clusters.

The first principal component accounted for 24.85 per cent of the total variation. The variation explained by the 2nd, 3rd, 4th and 5th components was reported to be 13.43, 11.82, 8.31, 6.71 and 5.65 %, respectively. A study conducted on cowpea found that the first two principal components explained 59.84 % of the total variation (23), while another study reported 44.03 % (45) and yet another reported 51.66 % (5) in their PCA analyses. Cumulative variance explained by the first 2 principal components (PCs) in the present study was (38.28) lower than in these studies. SYP (20.52 %), PCL (19.14 %), PPL (15.89 %) and CPL (12.79 %) were the major contributing traits in PC1.

The percentage contribution of 17 yield and attributing traits to the major principal components is presented in Table 9. Principal component 1 was largely influenced by PPL, PCL, CPL, SP and seed yield, indicating the variation in these yield-contributing traits was the major factor differentiating the studied genotypes. The importance of these traits is further supported by the correlation and path coefficient analysis, which also identified these traits as key contributors to SYP, emphasising their significance as effective selection criteria in cowpea breeding programmes. In this study, a PCA biplot showing the distribution of yield-attributing traits and 50 cowpea genotypes on PC1 and PC2 is illustrated in Fig. 4. Genotype GC-2105 was associated with higher CPL, PGCP-90 with higher PCL, GC-2202 linked with PPL and seed yield was higher in PGCP-70 and PGCP-89. Genotype CPD-331 had higher DM values, while genotypes opposite the vector, such as PL-1, were identified as early-maturing genotypes. These genotypes exhibited strong positive associations with the key yield-contributing traits, indicating their potential utility in breeding programs aimed at enhancing seed yield and its related attributes. A similar pattern of results has been reported while studying various cowpea genotypes through principal component analysis (23, 45, 46).

The PCA biplot displayed similar vector orientations among seed YP, PPL, SP and STW, indicating similar patterns of variation. On the other hand, days to flowering and maturity exhibited contrasting patterns with yield-related traits. However, the morphological evaluation of genotypes was conducted at a single location during one growing season; therefore, further multi-environment and multi-season evaluation is necessary to support the validity of identified traits and genotypes.

Simple sequence repeat marker analysis

Detecting genetic diversity in plants by phenotypic traits becomes more reliable by using molecular markers to analyse variation at the DNA level (4). The amplification of SSR markers across cowpea genotypes showed clear banding patterns and a polymorphic nature of these markers. A total of 64 SSR markers were screened for analysis, of which 40 amplified and 18 markers showed high polymorphism. Most markers amplified, with allele sizes ranging between 140 and 350 bp. The total number of alleles per locus varied from two (Vm22, Vm9, E1735319801) to five (Vm39, Vm27), with an average of 2.94 alleles per marker. Similarly, a study detected one to three alleles with an average of 2.2 alleles per marker (47). They found that VM 25, VM 35, VM 36, VM 5 and CP 1 markers produced the highest number of alleles. On the other hand, all SSR markers analysed exhibited a higher polymorphism with 4 to 14 alleles per locus, with an average of 8.45 alleles per primer (4). Details of the polymorphic markers in this study are given in Table 10. In one study, SSR markers amplified the alleles within the size range of 153 to 302 bp (48). Markers with higher PIC values are considered more effective in revealing genetic variation and differentiating the individuals, thus preferred for diversity analysis. In the present investigation, the PIC values of SSRs varied from 0.11 (Vm 22) to 0.78 (Vm 39) with an average of 0.53. The maximum PIC value was observed for the marker Vm 39 (0.78), followed by Vm 31 (0.73), Vm 27 (0.65), CP 1 (0.65) and E1735319801

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(0.62). This suggests that Vm 39 and other highly informative markers, such as Vm 31, Vm 27 and CP 1, are particularly useful for studying genetic diversity in cowpea. Agarose gel electrophoresis showing polymorphism has been presented in Fig. 5 A-C. Previous research grouped the 33 cowpea genotypes into 3 main groups and concluded that cluster analysis based on polymorphic markers is a more reliable method for establishing relationships between genotypes (49). In our study, cluster analysis based on polymorphic markers using the UPGMA method grouped the genotypes into two major clusters with respective genotypes: A (33) and B (17), each further subdivided into two sub-clusters: A1 (18), A2 (15) and B1 (7), B2 (10), respectively (Fig. 6). The observed clustering patterns reflected the differences in allelic composition and provided information for identifying the genetically distant parents. Molecular markers and phenotype-based clustering showed different patterns because they capture different aspects of genetic variation. Several studies conducted molecular diversity analyses in cowpea and reported different clustering patterns for better categorisation of the accessions (4, 47, 48). Although the best-performing genotypes, namely, PGCP-70, PGCP-89, PGCP-90, GC 2202, KVCP 17-15 and GC 2105, based on phenotypic performance, were distributed across different SSR sub-clusters, indicating underlying molecular divergence and further supporting their suitability for crossing. Only 18 SSR polymorphic markers were used for diversity analysis. While they effectively differentiate the studied genotypes, they may not fully explain the genome-wide genetic diversity. Future research using a large number of polymorphic SSRs or SNP markers would support a more comprehensive diversity assessment.

Table 8. Variance explained by principal components with eigenvalues >1 in cowpea genotypes.

Principal component	Eigenvalue	Percentage of variance	Cumulative percentage of variance
PC 1	4.22	24.85	24.85
PC 2	2.28	13.43	38.28
PC 3	2.01	11.82	50.09
PC 4	1.41	8.31	58.41
PC 5	1.14	6.71	65.12

Table 9. Contribution of yield and attributing traits to major principal components

Traits/Variables	PC1	PC2	PC3	PC4	PC5
Days to 50 flowering	0.26	23.59	1.45	1.24	0.23
Days to maturity	1.96	12.67	16.74	1.73	0.01
Plant height (cm)	0.01	8.21	10.28	5.91	4.95
Branches per plant	1.74	9.87	7.15	13.84	1.07
Clusters per plant	12.80	2.11	0.01	12.88	0.62
Pods per plant	15.89	1.11	1.62	0.13	2.25
Pods per cluster	19.14	0.00	0.04	0.01	0.03
Pod length (cm.)	1.88	9.26	0.51	2.80	0.55
Peduncle length (cm)	0.41	0.01	24.89	13.61	0.30
Seeds per pod	8.47	0.48	1.05	2.08	4.77
Seed length (mm)	2.84	13.09	0.03	0.01	0.21
Seed test weight (g)	4.45	2.14	10.49	15.68	1.59
Fat content (%)	0.04	3.28	0.35	0.50	57.37
Crude protein (g)	3.11	11.40	7.95	0.14	0.41
Tannin (CE mg/g)	0.92	0.21	13.25	27.78	0.01
Crude fibre (%)	5.58	2.46	4.08	0.93	24.72
Seed yield per plant (g)	20.51	0.12	0.12	0.74	0.93

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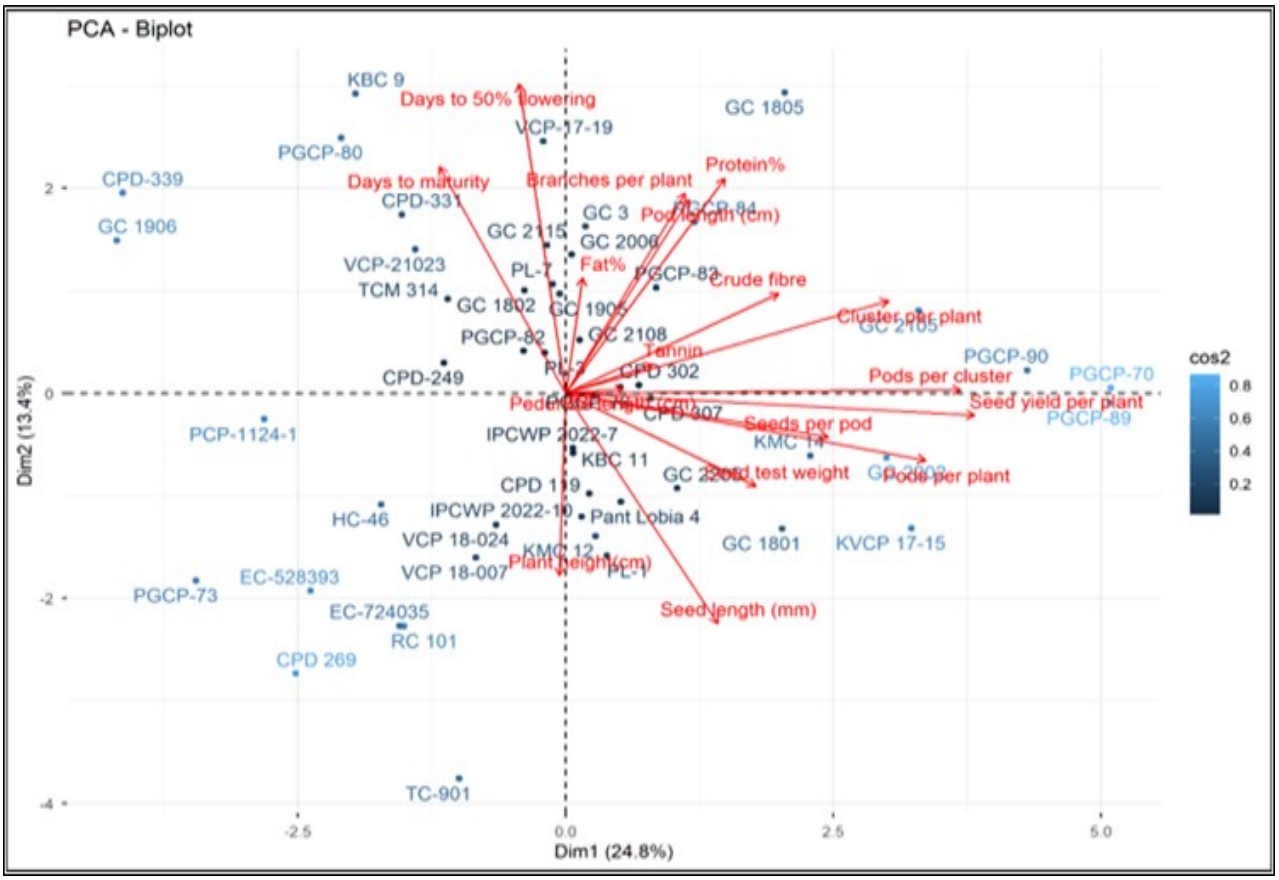


Fig. 4. PCA Biplot showing distribution of yield-attributing traits and 50 cowpea genotypes on PC1 and PC2.

Table 10. Details of polymorphic markers with amplification range, number of alleles and polymorphic information content (PIC)

Primer name	Amplification range (bps)	No. of alleles	PIC values	Primer name	Amplification range(bps)	No. of alleles	PIC values
Vm 22	200-300	2	0.11	Vm 10	170-200	2	0.534
Vm 9	200-300	2	0.467	Vm 31	200-280	3	0.732
Vm 13	180-200	2	0.32	CP 37	200-330	4	0.547
Vm 33	140-300	3	0.482	Vm 71	250-330	4	0.630
Vm 37	150-180	2	0.352	Vm 27	150-350	5	0.655
Vm 39	200-300	5	0.777	CP 1	200-300	3	0.654
Vm 68	200-300	3	0.654	CP 24	230-300	3	0.585
E1121316121	150-180	2	0.564	Vm 38	200-270	4	0.317
Vm 11	190-250	2	0.564	E1735319801	200-240	2	0.625

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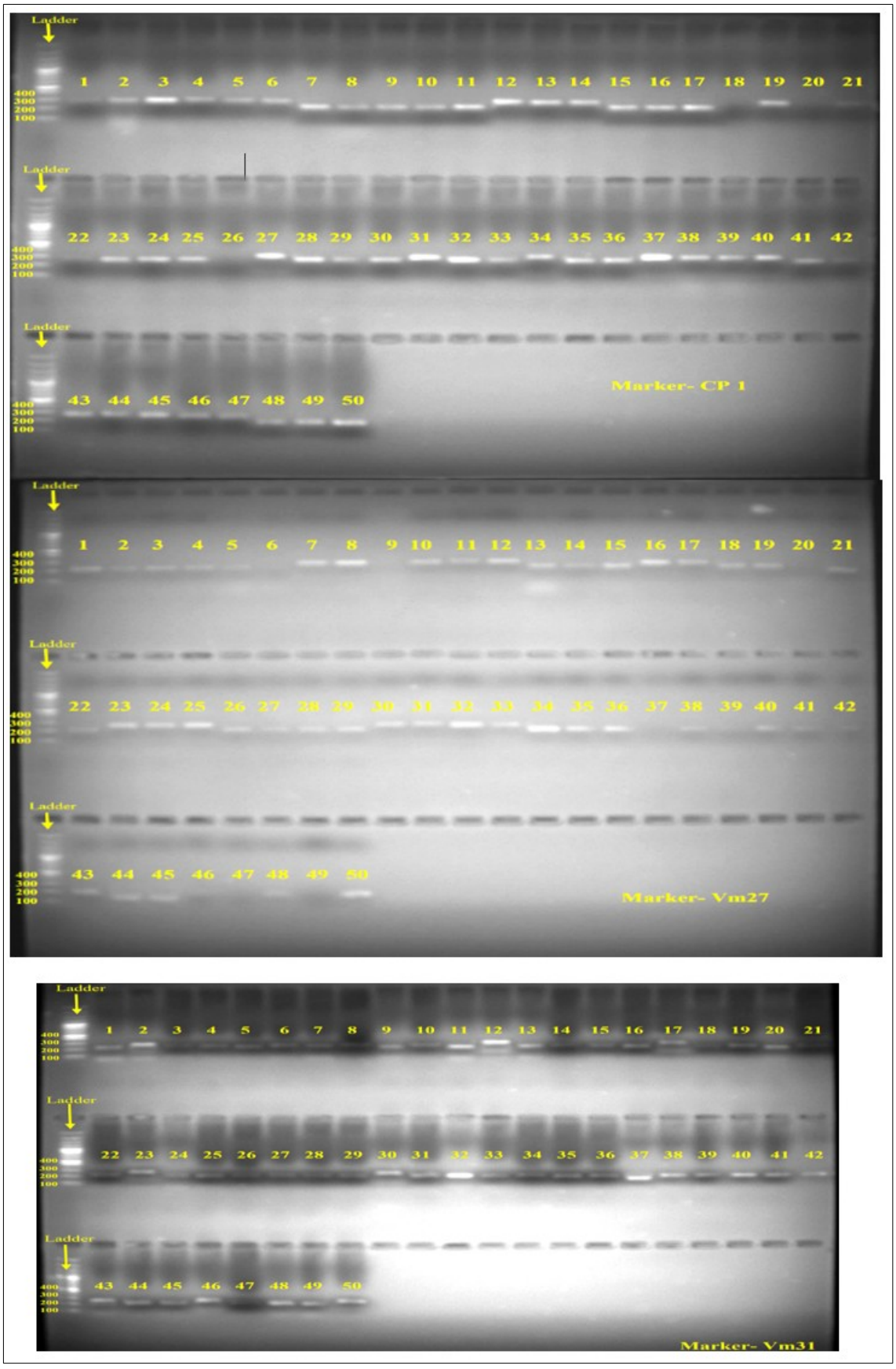


Fig. 5. Agarose gel electrophoresis image showing amplification of marker CP 1, Vm 27 and Vm 31 respectively in 50 cowpea genotypes.

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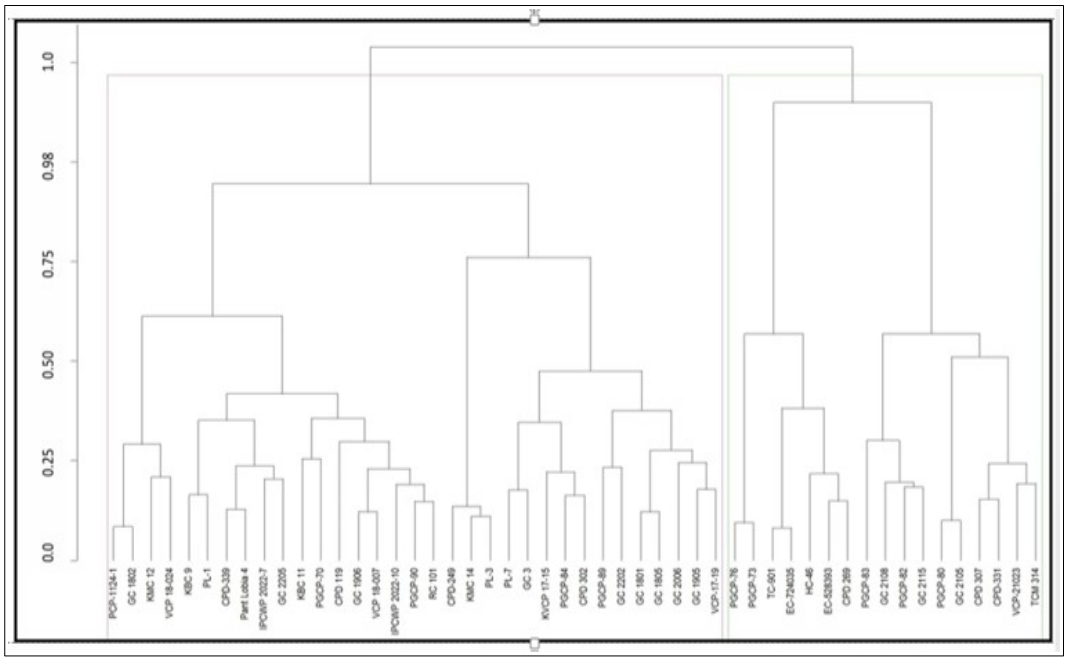


Fig. 6. Dendrogram showing genetic relationship among 50 cowpea genotypes using SSR markers.

4. Conclusion

Understanding the extent of genetic variability and selection of key yield-contributing traits is essential for designing effective breeding strategies. A high magnitude of variability was observed for yield-contributing and quality traits. Pods per plant, PCL, CPL, SP and STW were identified as the important yield-contributing traits. Cluster III and Cluster V were found to be genetically distant and hybridisation may be initiated to produce superior transgressive segregants. SSR marker analysis showed the genetic diversity among the genotypes and supported the phenotypic variation observed. Phenotypic and marker analyses jointly helped to identify diverse parents. Genotypes PGCP-70, PGCP-89, PGCP-90, GC 2202, KVCP 17-15 and GC 2105 exhibited higher yields and may be considered promising parents in breeding strategies. The findings of this study will be helpful in identifying the key traits and superior parental genotypes for designing effective breeding strategies to develop high-yielding cowpea varieties. However, multi-year and multi-environment evaluation is necessary to validate the stability of identified traits and genotypes.

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Authors' contributions

RD, RS and RP conceived the research idea and designed the research plan. RD carried out data collection, analysis and prepared the original draft of this manuscript. AK assisted with lab work and writing and editing the manuscript. AS and NK contributed to the editing, reference collection and proofreading of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

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