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ORIGINAL RESEARCH

Variance components, correlation and path analyses in cowpea (*Vigna unguiculata* L., Walp)

Olawale Mashood Aliyu[1] · Adeyemi Odunola Tiamiyu[1] · Muinat Usman[1] · Yusuf Folorunsho Abdulkareem[1]

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Abstract

Cowpea as a low-input crop has a potential to significantly ameliorate poor nutrition and food insecurity in sub-Sahara Africa if problem of poor seed yield is addressed. Adequate information on the relationship between yield components and seed yield is, however, crucial for the development of better quality varieties to improve farmers' field yield. To this end, twelve cowpea accessions of different seed sizes and mixed pedigrees were evaluated for two years in field trials of three replications laid out in a randomized complete block design. Data collected on plant vigour indices, yield components and seed yield were analyzed for variance components, Pearson correlation coefficient and structural equation modeling for path analysis. The accessions exhibited significant variation for all yield components including seed yield. In addition, the variance estimates indicated that substantial variations recorded were mostly genetic with high heritability values. Earliness in flowering and pod maturity recorded highly significant correlations and direct effect with yield components and seed yield. Positive correlation between precocity and high yield could be exploited in the development of improved varieties with early maturity for the savannah ecology with a characteristic short wet season. Importantly, all seed yield components are significantly correlated with each other and to total seed yield. Pods per plant, however, recorded highest coefficient values ($r = 0.85$; $P < 0.001$; 1.38**) for both Pearson correlation and path analysis, respectively, suggesting its importance as a yield component with highest direct effect on seed yield and should be a core selection index in cowpea breeding. The effect of size-number trade-off accounts for the counter-balance of direct effects of seeds per pod/plant (number) and seed weight (size) in cowpea and should be determined on genotype and/or seed size basis during selection. Plant vigour characters had no direct contribution to seed yield.

Keywords Cowpea · Correlation · Path analysis · Seed yield components · Variance components

Introduction

Increasing devastating effects of climate change, soil degradation and nutrient depletion in the sub-Sahara Africa (Animasaun et al. 2015) require innovative approach that incorporate short gestation, low-input, and resilience crops like cowpea into farming components of the smallholder farmers to ameliorate poor nutrition and perennial food shortage in the region. Cowpea, *Vigna unguiculata* L. Walp., is an important annual crop grain legume in the sub-Saharan Africa (Mortimore et al. 1997; Uarrota 2010), with global production estimated at about 4.5 million metric tons (Diouf 2011). It is an important source of human dietary nutrients because of high protein (25%) (see Dakora and Belane 2019; Goncalves et al. 2020) and lysine contents (Nielson et al. 1997). In addition to its grains and fresh leaves being used as vegetables, and cropping residue as fodder (Hall et al. 2003), cowpea has been incorporated as an integral component of farming system in savannah region with highly nutrient-deficient soil because of its ability to improve soil fertility. Despite the numerous benefits of cowpea, its production has been hindered by poor yield with average grain yield as low as 0.1–0.45 ton/ha in small holder farms (Kebede and Bekeko 2020) because of continuous planting of poor varieties by farmers and devastating effect of insect pest attack among other factors. The effect of low yield has reduced investment in the cultivation of cowpea and national production has been on the decline (Kebede and Bekeko 2020; Bolarinwa et al. 2021). The development and release

✉ Olawale Mashood Aliyu
walealiyu@mail.com; olawale.aliyu@kwasu.edu.ng

[1] Department of Crop Production, Kwara State University, Malete, P. M. B. 1530, Ilorin, Nigeria

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genetically modified variety with resistance to Maruca pod borer to address problem of pest attack has not been successfully adopted by farmers (Addae et al. 2020) because of (mis)information about GMOs. Small holder farmers will prefer natural variety over genetically modified type in many years to come because of tradition and safety issue. Recent studies had shown that some cowpea accessions have yield potential of 4–6 t/ha (Aliyu and Makinde 2016) that could be used along other breeding lines with broad genetic attributes (variability) as candidates for selection and/or as parents in long-term breeding programme. Falconer (1989) had opined that variation in genetic attributes among population of individuals is the bedrock of crop improvement. Continuous exploration of genetic variation and understanding relationships among plant genetic attributes especially yield components are critical to breeding progress. Variance component analysis has remained an important tool for assessing genetic variability among individuals in a population (Burton, 1952; Johnson et al. 1955; Allard 1960) and correlation analysis used to determine the relationship between plant characters. Studies on genetic variability and phenotypic stability (Omoigui et al. 2006; Nwosu et al. 2013; Aliyu and Makinde 2016) nutrient analysis (Henshaw 2008) of cowpea are well documented and will continue to receive greater attention because of its importance to the advancement of the crop. There are reported studies on the correlation analysis of cowpea (Singh et al. 1982; Ogunbodede 1989; Peksen 2004; Udensi et al. 2012; Sapara and Javia 2014; Srinivas et al. 2017) but none on path analysis using structural equation model (SEM).

Correlation analysis nonetheless is an important tool for determining the relationships between plant characters; however, correlation coefficients can be misleading if the correlation between two traits is a consequence of the indirect effect of other traits (Bizeti et al. 2004). Path analysis on the other hand is an excellent platform for studying interrelated components of complex traits in plants (Singh and Chaudhary 1977), because it partitions the effect into component parts: (i) the direct effect, which is a standardized partial regression coefficient for the predictor variable and, (ii) the indirect effect, which involve the product of a correlation coefficient between two predictor variables (Dewey and Lu 1959). In the past, time-consuming statistical procedure using algebra method is used in the computation of path analysis (Chaudhary and Joshi 2005). But, in recent time, structural equation model (SEM) has been promoted over algebra path analysis method because the former considered relationships only among measured variables, whereas SEM examined both measured and latent variables. Among other advantages of SEM are automation, reliability, efficiency and time-saving (speed). In this study, twelve cowpea accessions were evaluated for variability extant and relationships between yield components and seed yield using variance component analysis, correlation coefficient and path analysis of structural equation model (SEM). The goal of this study is to apply structural equation model (path analysis) to plant data from 12 cowpea genotypes from genetically diverse background in order is to determine yield components that are critical to for selection and improvement of cowpea in savannah ecology with limited wet season.

Materials and methods

The experimental planting materials used in this study are twelve (12) cowpea accessions collected from the Genetic Resources Centre of the International Institute of Tropical Agriculture (IITA), Ibadan and their pedigrees and morphological characteristics presented in Table 1. The 12 accessions are of three different classes of seed

Table 1 Pedigree of 12 cowpea accessions and their seed morphological characteristics

Accession No	Country of Collection/origin	Biological Status	Cultivar Name	Seed weight (g)	Seed colour	Seed class
TVU 7157	Nigeria	Landrace	Ex TVU 4855	0.22	Dark brown	Large
IT89KD-288	Nigeria	Breeding	Ex TVU 16722	0.19	White	Large
TVU 10364	Cote d'Ivoire	Landrace	Ex TVU 7786	0.19	Brown	Large
IT10K-815-5	Nigeria	Breeding	–	0.22	Brown	Large
TVU 7769	Cote d'Ivoire	Landrace	Ex-Bouake Market	0.06	Light brown	Small
TVU 8252	Cote d'Ivoire	Landrace	Ex-Korhogo Market	0.08	Deep brown	Small
TVU 9267	Burkina Faso	Landrace	Douna No. 1	0.06	Ash	Small
TVU 10466	Burkina Faso	Landrace	–	0.09	Mixed colour	Small
TVU 11622	Burkina Faso	Landrace	Ex TVU 8297	0.10	Brown	Medium
TVU 6912	Niger	Landrace	Ex Pres Diori	0.13	White	Medium
TVU 13271	Burkina Faso	Landrace	Kamboinse Local	0.12	White	Medium
IT98K-503-1	Nigeria	Breeding	–	0.14	Off-white	Medium

size (large ≥ 0.16 g, medium 0.11–0.16 g and small seed ≤ 0.11 g) (Drabo et al. 1984) and of two major types (traditional landrace and breeding line) (Table 1). The experiment was sited at the research field of the Kwara State University Teaching and Research, Malete, located at the Latitude 08° and 26[1] N and Longitude 04° 291 E and about 345 m above sea level in the southern Guinea Savanna ecology of Nigeria.

The experimented was first conducted during the planting season 2016 and was repeated in 2017. Each experimental block consisting of twelve accessions laid out in a randomized complete block design (RCBD) and was replicated thrice. Sowing was done the same date in the month of July for both years of study to minimize variation between experimental years. Each accession was planted on treatment plot size of 3.0 m × 0.6 m with alley of 1.0 m between plots. Plant population was reduced to one per stand at three weeks after germination. Weeds in the experimental plots were manually control using hoe. The plants were prevented from insect pest attack by spraying with Cypermethrin at the rate of 2 ml/L every 2 weeks until pod maturity.

Plant data were collected on, plant vigour: number of main branches at flowering, number of leaves at flowering, plant height at flowering (cm); phenology: days to 50% flowering, days to 50% pod maturity; yield components: pods per plant, pod length (cm), seeds per pod, seeds per plant, hundred seed weight (g); and seed yield (kg/ha). Summarized data were analyzed for variance components as described by Burton (1952), Johnson et al. (1955) and Allard (1960), Pearson pairwise correlation coefficients and path analysis using Structural Equation Modeling (SEM). All the analyses were done using STATA 13.0 statistical software (Stata Corp. USA, www.stata.com).

Results

Variation analysis showed that the 12 cowpea accessions substantially differ genetically in plant vigour and reproductive attributes (Table 2). Pod maturity ranged from as early as 42 days after sowing, to 85 days for late maturing types. Yield components also varied considerably among these accessions, which offer potential for selection and improvement (Table 2). These cowpeas also performed differently across the 2 years of evaluation and this underscores the important roles of environment, especially climatic variables, on cowpea production. The cowpea displayed plasticity for plant vigour and seed yield components as shown by genotype × environment (year) interaction data (Table 2). Pods per plant and seeds per pod were stable across years while other characters exhibited significant variation. In terms of quantum of variation (coefficient variation), seed yield components exhibited higher proportions compared to vigour indices (Table 2). Further analysis of the variation into variance components showed consistent higher phenotypic variance (σ^2p) compared to genotypic variance (σ^2g), but with very high broad sense heritability for all the characters except seeds per plant (Table 3). This trend is an indication that environmental factors partly account for variations recorded but with lower proportion in most cases (Table 3). Narrow variation observed between values of the phenotypic coefficient of variation and genotypic coefficient of variation accentuates that the observed variations are plausibly inherent and genetic in nature (Table 3). Broad sense heritability as high as 96.77% was obtained for seed weight and was as low as 14.68% in seeds per plant (Table 3).

Correlation matrix analysis showed that branching and leaveness are highly significantly correlated i.e. plant

Table 2 Descriptive statistics and mean squares of plant vigour, and reproductive (yield components) characters of 12 cowpea accessions evaluated in two crop seasons (years)

Characters	Mean	Range (Min–Max)	Std	CV (%)	MS *g*	MS *y*	MS *gxy*	MS *error*
Number of branches at flowering	3.40	1.20–5.00	0.89	26.18	3.04**	6.85**	0.68**	0.17
Number of leaves at flowering	175.40	73.30–433.00	78.56	44.79	36,786.50**	9180.10**	1109.10**	242.40
Plant height at flowering (cm)	43.76	26.00–75.00	14.28	32.63	1218.44**	312.04**	19.54 ns	10.77
Days to 50% flowering	50.98	35.00–69.30	7.80	15.30	365.56**	145.01**	5.38**	1.91
Days to 50% pod maturity	61.35	42.00–85.00	10.50	17.11	643.01**	260.68**	19.07**	5.46
Pods per plant	21.83	9.80–39.00	8.35	38.25	382.80**	334.84**	11.41 ns	6.03
Pods length (cm)	18.08	13.00–26.60	3.92	21.68	85.29**	50.33**	3.14*	1.37
Seeds per pod	20.35	8.80–44.00	9.13	44.86	513.65**	54.78**	1.83 ns	4.30
Seeds per plant	491.70	105.84–1498.00	352.64	71.72	726546.00**	355618.00**	18495.00**	6030.00
Seed weight (g)	0.12	0.04–0.22	0.05	41.67	0.02**	0.01*	0.00*	0.00
Seed yield (kg/ha)	2689.00	770.55–6063.27	1383.64	51.46	9512,366.00**	14290687.00**	520030.00**	24160.00

ns not significant; *Std* standard deviation; *CV (%)* coefficient of variation; *MS* mean square (*g*—genotype, *y* year, *gxy* genotype by year)

*:Significant at 0.05; **: Significant at 0.01 probability level

Table 3 Estimates of variance components and broad sense heritability of plant vigour, and reproductive (yield components) characters of 12 cowpea accessions evaluated in two crop seasons (years)

	σ^2p	σ^2g	σ^2y	σ^2gxy	σ^2e	PCV	GCV	ECV	h^2 (%)
Number of branches at flowering	1.01	0.48	0.19	0.17	0.17	29.56	20.38	12.13	47.52
Number of leaves at flowering	6870.25	6090.68	248.27	288.90	242.40	47.26	44.49	8.88	86.65
Plant height at flowering (cm)	223.34	201.28	8.37	2.92	10.77	34.15	32.42	7.50	90.12
Days to 50% flowering	67.66	60.61	3.98	1.16	1.91	16.13	15.27	2.71	89.58
Days to 50% pod maturity	123.36	106.25	7.09	4.53	5.49	18.10	16.80	3.82	86.13
Pods per plant	79.75	62.80	9.13	1.79	6.03	40.90	36.30	11.25	78.75
Pods per peduncle	0.62	0.22	0.23	0.00	0.17	28.53	16.99	14.93	35.48
Pods length (cm)	17.31	13.99	1.36	0.59	1.37	23.01	20.69	6.47	80.82
Seeds per pod	89.77	84.89	1.40	-0.82	4.30	46.56	45.28	10.19	94.56
Seeds per plant	23319.78	3424.00	9710.78	4155.00	6030.00	30.68	11.90	15.79	14.68
Seed weight (g)	0.0031	0.003	0.00001	0.000002	0.0004	46.40	45.64	16.67	96.77
Seed yield (kg/ha)	2167110.09	1581367.67	396292.42	165290.00	24160.00	54.75	46.77	5.78	72.97

$\sigma^2 g$ genotypic variance, $\sigma^2 gxy$ genotype × environment variance, $\sigma^2 e$ environmental variance, $\sigma^2 p$ phenotypic variance; *GCV* genotypic coefficient of variation, *PCV* phenotypic coefficient of variation, *ECV* environmental coefficient of variation, *h2* heritability (broad sense)

branching facilitates increased leaf (biomass) production. However, numbers of branches and leaves recorded significant negative correlations with all yield components except seed weight with significant positive correlations (Table 4).

Correlation between flowering and pod maturity was positive and highly significant ($r = 0.93$, $P < 0.01$), demonstrating that flowering precocity is associated with earliness in pod maturity (Table 4). Late flowering and pod maturity had significant correlations with seed size {(seed weight ($P < 0.01$), but had negative relationships ($P < 0.05$, $P < 0.01$) with almost all other seed yield components (Table 4). Although correlations between plant phenology (flowering and maturity period) and seed yield were not significant but they are nonetheless negative. Almost all seed yield components (pod & seed) showed highly significant positive correlation with total seed yield except seed weight (Table 4, Fig. 1). Furthermore, in the order of magnitude, pods per plant, seeds per plant and pod length had more contribution to seed yield than other yield components. Correlation between seed weight and total seed yield was negative but not significant (Table 4; Fig. 1).

Structural equation model (path analysis) showed that seed yield components had significant direct effects on seed yield including seed weight (Table 5, Fig. 2). In the descending order of magnitude, pods per plant (1.38, $P < 0.001$),

Table 4 Correlation coefficients (matrix) of plant vigour and seed yield component characters of 12 cowpea accessions

	NBR	NLV	PHT	DTF	DPM	POP	POL	SPO	SPP	SWH	YPH
NBR	–										
NLV	0.41**	–									
PHT	− 0.20 ns	0.09 ns	–								
DTF	0.22 ns	0.40**	− 0.44**	–							
DPM	0.30*	0.50**	− 0.44**	0.93*	–						
POP	− 0.24*	0.02 ns	0.47**	− 0.33*	− 0.20 ns	–					
POL	− 0.16**	0.06 ns	0.58**	− 0.43**	− 0.31*	0.59**	–				
SPO	− 0.47**	− 0.37*	0.25*	− 0.58**	− 0.51**	0.63**	0.34*	–			
SPP	− 0.46**	− 0.24*	0.36*	− 0.54**	− 0.44**	0.84**	0.49**	0.93**	–		
SWH	0.41**	0.35*	− 0.39*	0.44**	0.40**	− 0.49**	-0.25*	− 0.71**	− 0.67**	–	
YPH	− 0.11 ns	0.08 ns	0.23 ns	− 0.18 ns	-0.07 ns	0.85**	0.50**	0.47**	0.66**	− 0.08 ns	–

ns not significant; *NBR* number of branches at flowering; *NLV* number of leaves at flowering; *PHT* plant height at flowering (cm); *DTF* Days to 50% flowering; *DPM* days to 50% pod maturity; *POP* pods per plant; *POL* pods length (cm); *SPO* seeds per pod; *SPP* Seeds per plant; *SWH* seed weight (g), *YPH* seed yield (kg/ha)

*Significant at 0.05; **significant at 0.01 probability level

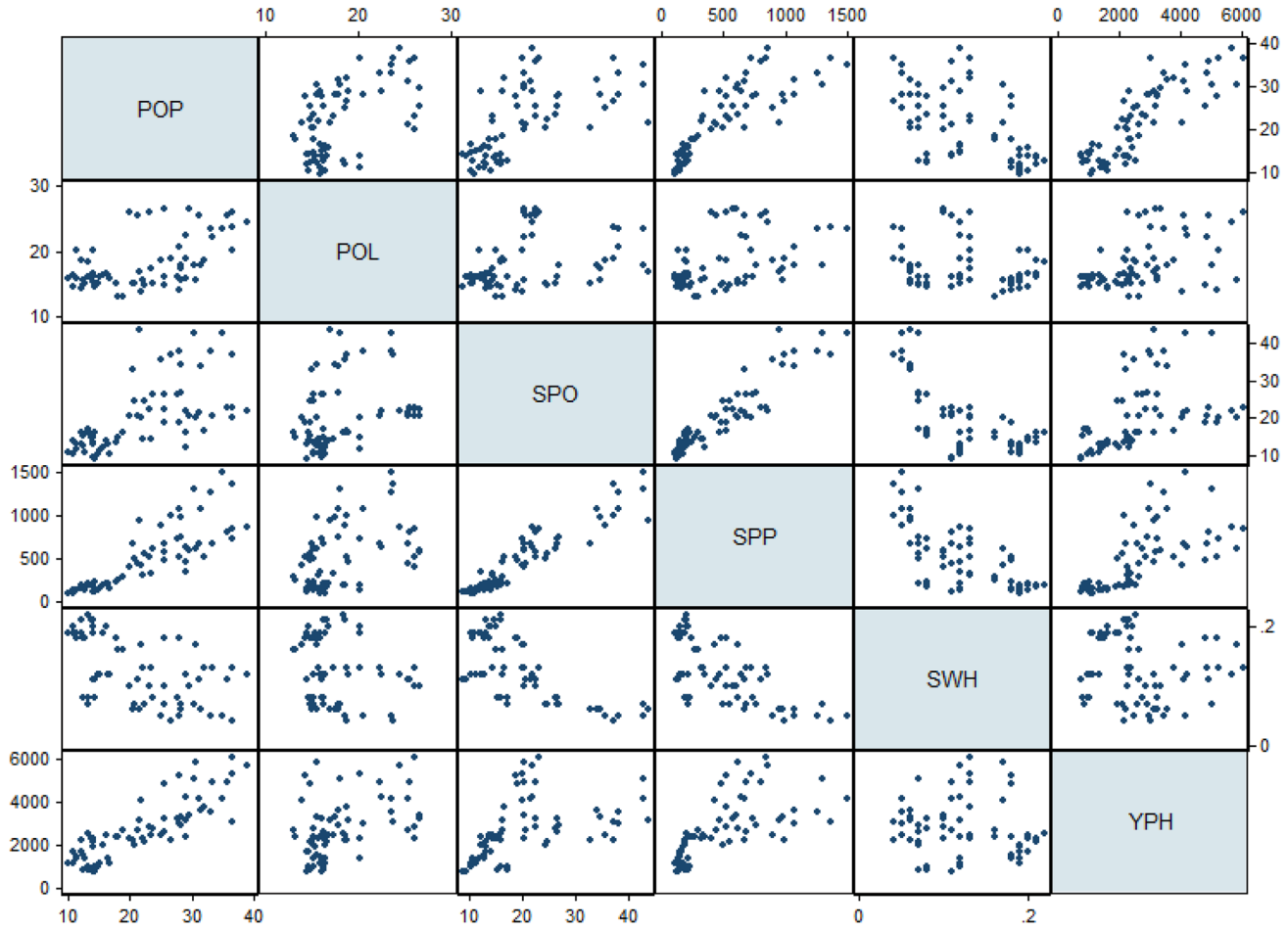


Fig. 1 Scattered diagrams showing relationships between yield components and seed yield (kg/ha). *POP* pods per plant; *POL* pods length (cm); *SPO* seeds per pod; *SPP* seeds per plant; *SWH* seed weight (g), *YPH* seed yield (kg/ha)

Table 5 Path analysis of structural equation model (SEM) showing direct and indirect effects of plant vigour and yield components on seed yield of 12 cowpea accessions

	NBR	NLV	PHT	DTF	DPM	POP	POL	SPO	SPP	SWH
NBR	− 0.13**	− 0.07	− 0.53**	− 0.04	− 0.15**	− 0.19**	− 0.106	− 0.26**	− 0.35**	− 0.01
NLV	− 0.07	0.03	0.02	− 0.10	− 0.07	0.01	0.039	0.12**	− 0.18	− 0.04
PHT	0.01	0.01	**− 0.24****	0.04	− 0.02	0.48**	0.331**	0.11	0.24**	− 0.02
DTF	− 0.01	0.07	− 0.09	− 0.18	0.67**	− 0.31**	− 0.237**	− 0.31**	− 0.43**	0.01
DPM	− 0.03	0.07	− 0.12	− 0.79**	0.03	− 0.19**	0.174*	− 0.30**	− 0.34**	0.02
POP	− 0.02	0.00	− 0.12	− 0.04	− 0.02	**1.38****	− 0.020	− 0.08	− 0.17	− 0.21**
POL	− 0.00	0.00	− 0.05	− 0.03	− 0.03	0.56**	0.038	0.11	0.28**	0.05
SPO	− 0.08	− 0.11	0.03	− 0.08	− 0.11	0.60**	0.147*	**0.40****	1.58***	− 0.39**
SPP	− 0.11	− 0.06	− 0.00	− 0.14	− 0.12	0.85***	0.130	− 1.02***	**− 0.63****	− 0.44**
SWH	− 0.03	0.04	− 0.11	− 0.09	− 0.02	− 0.52**	− 0.157*	− 0.60**	− 0.73**	**0.46****

Underline indicates direct effect

Residual effect (0.011): *significant at 0.05; **significant at 0.01; and ***significant at 0.001 probability levels

NBR number of branches at flowering; *NLV* number of leaves at flowering; *PHT* plant height at flowering (cm); *DTF* days to 50% flowering; *DPM* days to 50% pod maturity; *POP* pods per plant; *POL* pods length (cm); *SPO* seeds per pod; *SPP* seeds per plant; *SWH* seed weight (g), *YPH* seed yield (kg/ha)

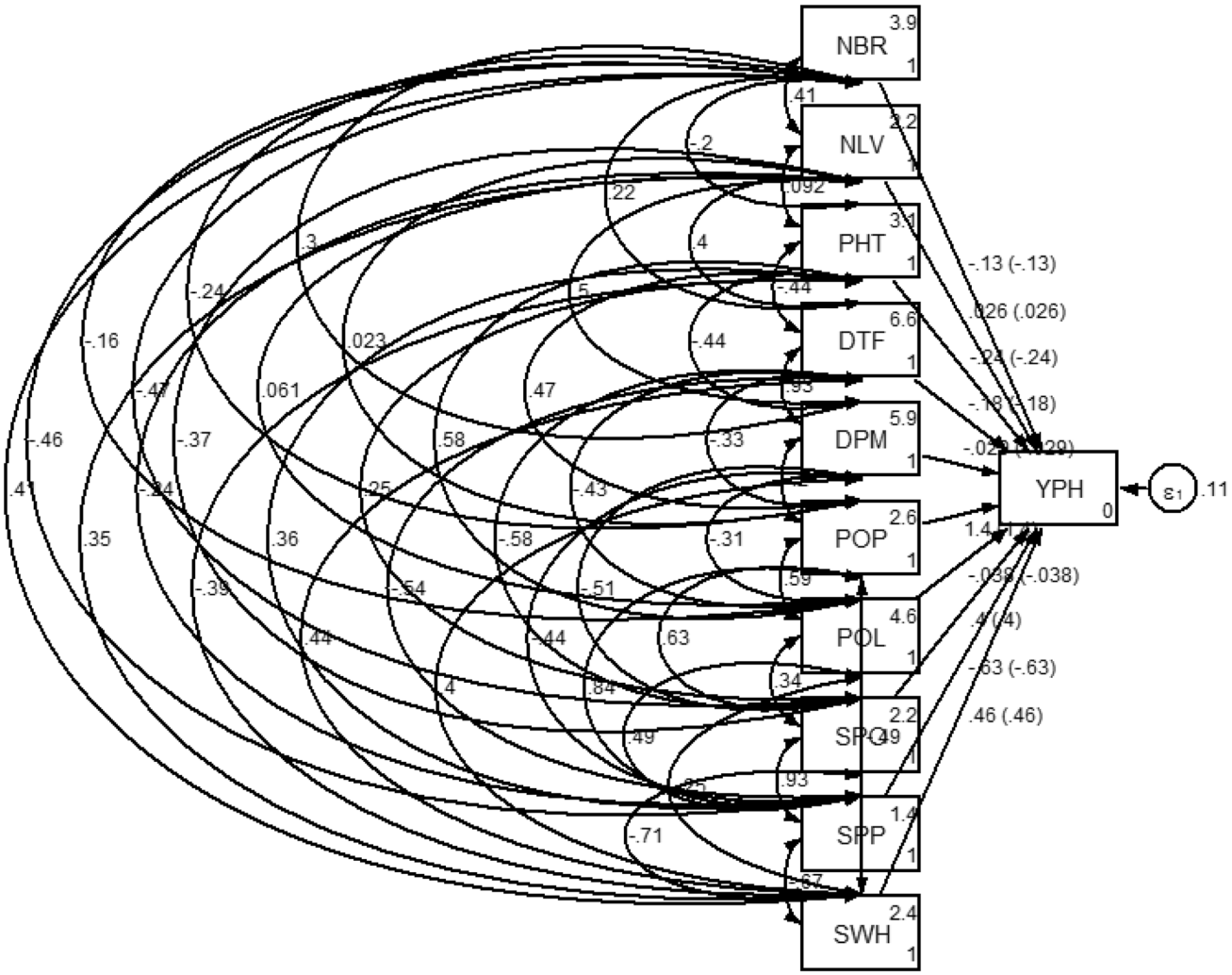


Fig. 2 Path diagrams showing relationships including direct effect of plant vigour and yield components with seed yield (kg/ha) in cowpea. *NBR* number of branches at flowering; *NLV* number of leaves at flowering; *PHT* plant height at flowering (cm); *DTF* days to 50% flowering; *DPM* days to 50% pod maturity; *POP* pods per plant; *POL* pods length (cm); *SPO* seeds per pod; *SPP* seeds per plant; *SWH* Seed weight (g), *YPH* seed yield (kg/ha)

seed weight (0.46, $P < 0.001$),) and seed per pod (0.40, $P < 0.01$) had significant direct effect on seed yield. (Table 5, Fig. 2). However, only seed per plant recorded significant negative direct effect (− 0.63, $P < 0.01$) on seed yield. Among the plant vigour characters, number of branches and plant height recorded significant negative direct effects (− 0.13, $P < 0.05$; (− 0.24, $P < 0.01$) respectively, on seed yield (Table 5). However, direct effects of number of leaves, days to flowering and pod maturity were not significant.

In terms of indirect effect of yield components on seed yield; seeds per pod had significant positive contributions through seeds per plant (1.58), and pods per plant (0.60). Seeds per plant also gave indirect positive effect through pods per plant (0.85). The counter-balance effects of seed number and seed weight were expressed through their negative indirect effects on seed yield (− 0.44, $P < 0.01$ and − 0.73, $P < 0.01$, respectively) (Table 5). Seeds per plant recorded negative significant indirect effects through seeds per pod (− 1.02), and seed weight (− 0.44). Seed weight also had significant negative indirect effects through seeds per plant (− 0.73), seeds per pod (− 0.60) and pods per plant (− 0.52). Seeds per pods also recorded significant negative indirect effect through seed weight (− 0.39) (Table 5, Fig. 2).

Significant negative indirect effect of pods per plant on yield was recorded through seed weight (− .21, $P < 0.05$). Similarly, pod length had significant positive indirect effects through pods per plant (0.56), seeds per plant (0.27) and seeds per pod (0.11). Seeds per pod gave significant positive indirect contributions (effects) through seeds per plant (1.58), pods per plant (0.60) and pod length (0.15). Of note is the significant negative indirect effects of seeds per pod through seed weight (− 0.39).

Discussion

The application of statistical correlation tools in plant breeding is premised on the need to unraveling genetic relationship among phenotypic traits that characterized individual/or population of plants with a view to use such information in selection process for overall quality improvement in the crop species. Plant traits that are significantly correlated are presumed to be linked and may possibly be inherited together. However, complex nature of genes and their interaction with environments that defines phenotypes especially seed yield and its components sometimes makes such assumptions fallible in practice. Therefore, further dissection of correlation data into direct and indirect contributions through path analysis is useful in resolving such conundrum in conventional breeding practice (Aliyu 2006). Cowpea remains one of the most important legumes in sub-Sahara Africa and there are untiring efforts to solve problem of low seed yield through assessment of genetic variations and selection of better genotypes. Consequently, this study was set up to apply Pearson correlation analysis and structural equation model (path analysis) to plant data from 12 cowpea genotypes comprising mixture of traditional landrace and advance breeding lines to determine nature of correlations among yield components and partition the relationships of each component to seed yield into direct and indirect effects. Data presented here elucidate complex interaction among yield components that will facilitate seed yield improvement and/or breeding for multi-traits in this crop.

The variance components data depict high genetic variability of plant vigour characters and yield components in cowpea as documented in previous studies (Omoigui et al. 2006; Nwosu et al. 2013; Aliyu and Makinde 2016; Aliyu et al. 2019). Wide genetic variation with high heritability obtained in the yield components and seed yield is an indication of scale of genetic improvement existing in the accessions on the one hand and rate of advancement in yield improvement that can be accomplished during breeding programme. Besides faster rate of improvement, high heritability (h^2) with higher phenotypic coefficient of variation comparative to genotypic coefficient of variation is a further indication of high phenotypic stability of most of the yield components. This was underscored by low values of environmental variance (σ^2e) and it coefficient (ECV). Studies in cowpea have shown high heritability in yield components (Manggoel et al. 2012; Nwosu et al. 2013; Aliyu and Makinde 2016). Since heritability is the genotypic proportion of phenotypic variation of a trait in plant population, low heritability (14.68%) recorded in seeds per plant indicates that environmental factor(s) accounted for major portion of the variation and may not be a reliable selection indices. Dempster and Lerner (1950) established heritability threshold of < 20% as low with slow rate of genetic gains during selection.

There is strong evidence from coefficient values suggesting that highly vigorous plant with many branches and higher leaf biomass had negative significant direct effect on total yield. Plants with large seeds tend to produce more branches and higher quantity of leaf biomass without direct contribution to increase yield components and seed yield. Recent study on phosphorus supplementation for improved pod and seed development has shown luxuriant growth and higher biomass without commensurate yield at the rate of 60 kg ha^{-1} P (Aliyu et al. in press). In contrast, plant height significantly correlated with seed yield components (Table 4). Cowpeas with small-medium seeds produced vigorous plants with superior yield components like longer pods and large number of seeds. These set of cowpeas demonstrated earliness to medium maturity in flowering and fruiting.

A very high correlation coefficient ($r = 0.93$) recorded between flowering and pod maturity in this study is suggestive that the two phenological characters are genetically linked and days to flowering will be a reliable indicator for selection of maturity period in cowpea. Undensi et al. (2012) recorded significant positive correlation between flowering and pod maturity in some landraces of cowpea and opined strong linkage between period of plant growth to flowering initiation and time of pod and/or seed development. Earliness in flowering and pod maturity (precocity) is crucial to enhance seed yield in regions with short period of wet season. The significant negative correlations between phenological attributes (days to flowers and pod maturity) and yield components underscores devastating effect of delay flowering and/or late maturity on cowpea yield. Singh et al. (1982), Sapara and Javia (2014) obtained negative relationships between flowering and pods per plant in the crop. It is important to note that the effects of flowering and pod maturity on seed yield were indirect through components like pods per plant, seeds per plant and seeds per pod. In other words, delay in flowering and pod maturity can hinder quality pod and seed developments in cowpea. Data from previous studies have shown consistent significant negative correlations between phenological characters and yield components (Aliyu and Makinde 2016; Aliyu et al. 2019). This consistency across different studies underscores stable nature of these characters and its potential use in breeding precocious quality varieties for savannah ecology. Mekonnen et al. (2016) reported similar negative indirect effect of pod maturity through yield components on seed yield in 228 accessions of cowpea in Ethiopia.

Path analysis accounts for direct and indirect contributions of each plant variable to seed yield in cowpea (Table 5, Fig. 2). Among the yield components with positive direct

contributions to seed yield are pods per plant, seed weight and seeds per pod. Two of these three components (pods per plant and seeds per pod) are the most reliable because they combine significant positive indirect effect through all other yield components with their direct effects. The positive direct effect of seed weight was negated by negative indirect effects through other yield components, which strongly suggests trade-off complex in cowpea yield. This result partly corroborate previous studies (Peksen 2004; Udensi et al. 2012; Sapara and Javia 2014; Aliyu and Makinde 2016; Sharma et al. 2016; Srinivas et al. 2017; Aliyu et. al. 2019) that seeds per plant and pods per plant are the most contributory factors to seed yield in cowpea, however, contradict Santos et al. (2014) that reported significant negative direct effect of pods per plant in Brazil. Difference in genotype, environment and/or growth habit could account for such variation between experimental studies. Although seeds per plant recorded strong correlation with seed yield, path analysis indicated otherwise with negative direct effect (-0.63; $P<0.01$). The strong effect of higher number of seeds (prolificacy) was progressively weakened by increasing seed size. Accessions with small seeds (< 0.06 g/seed) produced large quantity of seeds (number) (> 850 seed/plant) but eventually translated to fewer kg ha^{-1}. However, seeds per plant contributed significantly to increase seed yield through pods per plant. In other words, increases production of pods will increase seed yield significantly. Crammer and Wehner (2000) described path coefficient of > 0.7 as strong and as such signpost strong direct causal effects of such traits on yield. In this study, path coefficient of 1.38 was recorded for direct effect of pods per plant on seed yield. Coefficient values > 1.00 is not impossible depending on the analytical procedures adopted. Here, a structural equation modeling (SEM) of multiple regressions (Carey 1998) was used for path analysis in place of conventional algebra method (Dewey and Lu 1959; Singh and Chaudhary 1977).

Contribution of seed weight to seed yield has been controversial. Ogunbodede (1989) and Aliyu and Makinde (2016) observed significant positive correlation between seed weight and seed yield, thus contrasting non-significant negative correlation (Srinivas et al. 2017; Aliyu et al. 2019) and significant negative correlation (Udensi et al. 2012; Sapara and Javia 2014) reported. In this study, correlation coefficient showed non-significant negative correlation between seed size and seed yield and thus agrees with Rachie and Roberts (1974), Drabo et al. (1985), Srinivas et al. (2017) and Aliyu et al. (2019), but structural equation model (path analysis) indeed showed that seed weight had significant direct significant correlation to total seed yield in cowpea. This positive direct effect was significantly counterbalanced by numbers of pod and seeds (Table 5). Many factors including sample size, extent of seed size variability, climatic/environmental factors, and breeding history of the genotypes sometimes account for variation in data across studies. Average seed size of the accessions used in this study was 0.12 g and were of wider variability (0.04–0.22 g), compared to 0.19 g (0.11–0.27 g) and 0.14 g (0.79–0.19 g) in Aliyu and Makinde (2016) and Aliyu et al. (2019), respectively. Drabo et al. (1984) had reported additive gene action for seed size in cowpea, and this suggestive that contribution of seed size to seed yield is cumulative (additive) with increasing seed size until trade-off equilibrium threshold is attained. Here, there was progressive increase in seed yield with increasing seed size until 18.0 g/100 seeds (0.18 g) threshold was reached (see Fig. 1). Accessions with seed yield < 2000 kg/ha are predominantly of large seeds (> 0.19 g) (Fig. 1). Furthermore, correlation coefficient and path analysis showed clearly the trade-off effect of seed size for number through significant negative correlations with other yield components. Selection for yield improvement in cowpea should therefore focus more on pods per plants and seeds per pod rather than seeds per plant because of the strong influence of seed size-number trade-off. Combining seed size with other yield components as part of selection indices in cowpea breeding should be on genotype-basis and still need further studies, because of significant negative indirect effects through all yield components. Data set presented here showed evidence of seed size-number trade-off in cowpea that need to be taken into consideration during varietal development.

Another significance of path analysis in this study was evident in the limited contribution of plant vigour to seed yield. While Pearson correlation coefficient analysis showed no significant correlations between plant vigour (number of branch, number of leaves, and plant height) and seed yield (Table 4), path analysis, however, revealed that number of branches and plant height had significant negative direct effect on seed yield. Although plant height recorded significant indirect effect through pods per plant and pod length on seed yield, it will nonetheless contribute to biomass than seed yield. Plant height as yield component could further facilitate high density planting and mechanized harvesting. Accessions with high plant biomass are less prolific for pod and seed production but could be used in the development of dual-purpose varieties.

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Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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