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Research article

Genetic control of earliness in cowpea (*Vigna unguiculata* (L) Walp)

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ABSTRACT

Global climate change is expected to further intensify the already harsh conditions in the dry savannah ecological zones of sub-Saharan Africa, posing serious threats to food and income security of millions of smallholder farmers. Breeding cowpea for improved earliness could help minimize this risk, by ensuring that the crops complete their lifecycle before the cessation of rainfall. In this study, we crossed two sets of cowpea lines showing contrasting phenotypes for earliness in terms of days to 50% flowering (DFF). One set of the lines comprised three extra-early parents (viz.: Sanzi-Nya, Tobonaa and CB27, 30–35 DFF), and the other set consisted of three early-to-medium maturity lines (viz.: Kirkhouse-Benga, Wang-Kae and Padi-Tuya, 42–45 DFF). The derived crosses and their parents were evaluated for key earliness-related traits at Nyankpala and Manga sites of CSIR-Savanna Agricultural Research Institute (SARI), Ghana. To unravel the genetic control of measured traits, we compared the appropriateness of Chi-square goodness of fit tests using classical Mendelian ratios, and frequency distribution (histogram)-related statistics such as skewness and kurtosis. The Chi-square test suggested a single dominant gene mode of inheritance for earliness, whereas the quantitative methods implicated duplicate epistasis and complementary epistatic gene actions. Our results show that coercing segregating lines to fit into classical Mendelian ratios to determine the genetic control of earliness could be misleading, due to its subjectivity. Thus, the genetic control of earliness in cowpea is governed by complementary and duplicate epistasis. The most applicable breeding approach for traits influenced by duplicate epitasis is selection of desirable recombinants from segregating populations developed from bi-parental crosses. Complementary epitasis, as found in the Wang-Kae × CB27 cross, could be exploited in developing improved extra-early lines through backcrossing. Heritability and genetic advance estimates were high for days to first flower appearance (DFFA) and days to 95 % pod maturity (DNPM) in the Padi-Tuya × CB27 and Kirkhouse-Benga x CB27 crosses, indicating that breeding for extra-earliness is feasible. CB27 could be a good donor for introgression of earliness into medium to late maturing improved cowpea varieties, because crosses developed from it had high heritability and genetic advance estimates.

1. Introduction

Cowpea (*Vigna unguiculata* (L.) Walp; 2n = 2x = 22) is one of the world's most important grain legumes. In sub-Saharan Africa (SSA), cowpea is extensively grown in the dry savannah regions owing to its ability to thrive under drought stress and perform well in marginal soils where other crops may fail (Pule-Meulenberg et al., 2010; Lucas et al., 2013; Boukar et al., 2019). Millions of people in SSA consume the protein-rich cowpea grains and leaves as food, while the haulm constitute an important source of nutrient for livestock (Dakora and Belane, 2019). Alidu et al. (2020) identified a cowpea genotype with high crude protein content of 46.90 %. Its nitrogen fixing ability through symbiotic association with *Brady rhizobium* spp. helps to replenish marginal soils (Kuykendall et al., 2000; Muindi et al., 2021; Ayalew et al., 2022).

In Ghana, cowpea is cultivated in all the agro-ecological zones, but a large chunk (85 %) of the annual national output is grown in the northern part of the country (MoFA-SRID, 2016; Herniter et al., 2019), where precipitation is predominantly short and erratic. Global climate change is expected to further exacerbate the already harsh conditions in the dry savannah ecological zones of Ghana, posing serious threats to food and

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economic security of millions of smallholder farmers. Breeding cowpea for improved earliness could help minimize this risk by ensuring that the crops complete their lifecycle before the cessation of rainfall (Owusu et al., 2021). To this end, genetic improvement in earliness has become one of the most important breeding objectives of cowpea breeding programs in SSA (Padi 2007; Santos et al., 2020). Information on the genetic control of key earliness-related traits in cowpea could greatly contribute to the development of extra-early maturing cowpea varieties, which mature in ≤60 days, to mitigate terminal drought.

Previous studies have shown that both monogenic and polygenic genes modulate the inheritance of earliness-related traits in cowpea. For example, Yamamoto et al. (2016) and Owusu et al. (2018) noted that the inheritance of first flower appearance (DFFA) and days to 95 % pod maturity (DNPM) were under single dominant gene control. Flowering time and pod maturity in soybean (a crop, whose genome has homologs and exhibits synteny and colinearity with cowpea (Pottorff et al., 2012; Lucas et al., 2013; Purnamasari et al., 2019) were also found to be controlled by a single dominant gene. Contrary to these reports, Ishiyaku et al. (2005) found seven genes controlling DFFA, Ribeiro et al. (2014) found three genes controlling DNPM, whereas Santos et al. (2020) reported that four and five genes are involved in the genetic control of DFFA and MNPM in cowpea, respectively. Andargie et al. (2014) noted that more than one gene and/or a multiple allelic gene system controls the inheritance of flowering time in cowpea. Moreover, Duplicate gene epistasis for days to first flowering in cowpea has been reported by Ubi et al. (2001); Ishiyaku et al. (2005); Singh et al. (2006); Rashwan (2010); Lal et al. (2013) and Thakare et al. (2016). Days to flowering is conditioned by additive effect, and days to pod maturity is governed by additive and dominance gene effects (Tuba Bıçer and Şakar, 2008).

Genetic estimates of agronomic traits are influenced by the type of genetic material (Alidu et al., 2020), sample size, method of sampling, method of calculation and effect of linkage (Said, 2014). Gaur et al. (2014) classified F_2 plants of chickpea into two classes, late and early (early and extra-early) and found good fit to a 9:7 ratio in all the crosses, instead of 9:6:1 for late, early and extra-early, respectively. This makes Chi-square test subjective, particularly when dealing with a trait like earliness.

Estimation of skewness (symmetry) of the distribution of a measured trait in a given population is an important method for determining the genetic control of both quantitative and qualitative traits Neelima et al., 2020. Positive skewness implies complementary gene action, whereas negative skewness indicates duplicate gene action (Pooni et al., 1977). On the other hand, kurtosis describes an extent to which a peak of a probability distribution deviates from a normal distribution, and this indicates the number of genes that are involved in controlling a trait (Robson, 1956).

These diverse and contradictory opinions among cowpea researchers call for more research to elucidate the genetic control of key earliness-related traits in cowpea, hence the present study. In the present study, we unraveled the genetic control of earliness in cowpea by comparing the appropriateness of Chi-square goodness of fit tests using classical Mendelian ratios, and frequency distribution-related statistics such as skewness and kurtosis.

2. Materials and methods

2.1. Plant materials

Six genotypes comprising three early-to-medium maturing improved cowpea varieties and three extra-early maturing lines were used for this study. The early to medium maturing lines were Padi-Tuya (70–75 days to physiological maturity), Kirkhouse-Benga (65–70 days to physiological maturity), and Wang-Kae (65–70 days to physiological maturity). The three extra-early maturing lines used were Sanzi-Nya (50 days to physiological maturity) (Owusu et al., 2020), Tobonaa (50 days to physiological maturity) and CB27 (55 days to physiological maturity) (Ehlers et al., 2000).

2.2. Development of F_1 populations

The six genotypes were sown in plastic pots (filled with loamy soil) measuring 35 cm in height, with a base and top diameter of 20 and 30 cm, respectively in a screen house at CSIR-SARI, Nyankpala-Tamale (9^0, 25′, 41N, 0^0, 58′, 42W and 183 m.a.s.l) in 2018 and Manga (10. 273° N, 0.422° W; 712 m.a.s.l) in 2019. The extra-early maturing genotypes (Sanzi-Nya, Tobonaa and CB27) were sowed seven days later than their early-to-medium counterparts in order to ensure flowering synchrony. At flowering, female flower buds (fully matured non-opened) were emasculated between 6 am to 8 am using forceps. Pollen grains from opened male flowers were placed on the stigma of the emasculated flower buds before 9 am. The three extra-early maturing genotypes were crossed to Kirkhouse-Benga, Wang-Kae and Padi-Tuya in a direct crossing without reciprocals to generate nine F_1 populations (i.e. Kirkhouse-Benga × Sanzi-Nya; Kirkhouse-Benga × Tobonaa; Kirkhouse-Benga × CB27; Wang-Kae x Sanzi-Nya; Wang-Kae x Tobonaa; Wang-Kae x CB27; Padi-Tuya x Sanzi-Nya; Padi-Tuya × Tobonaa and Padi-Tuya × CB27). At maturity, the F_1 pods were harvested separately, seeds were extracted, sun-dried and kept in a desiccator for next season trial.

2.3. Hybridity test of F_1 plants, and development of F_2 and $BC_{1:1}$ and $BC_{1:2}$ populations

The parental lines and the F_1s were stager-sown in the screen house at CSIR-Manga research station. Genomic DNA was extracted from leaf samples collected from individual plants of the parental lines and the F_1 plants. CTAB (cetyltrimethylammonium bromide) method by Doyle and Doyle (1990) was used. Purified DNA samples were genotyped with a polymorphic SSR marker having these primers: MS-3F GGAATTGAAAT TGATCTAATG; MS-3R GTATTTAAGTGGCTTATGAGGTTG, to check for successful F_1 crosses. Successful F_1 plants were backcrossed to their respective recurrent and donor parents to generate $BC_{1:1}$ and $BC_{1:2,}$ respectively, while some were allowed to self to produce F_2 seeds.

2.4. Field evaluation of parental lines, their derived F_1, $BC_{1:1}$ and $BC_{1:2}$and F_2 populations

The F_2 plants of Padi-Tuya × Sanzi-Nya, Padi-Tuya × Tobonaa, Kirkhouse-Benga × Sanzi-Nya and Wang-Kae × Tobonaa crosses and their parental lines were evaluated at the CSIR-SARI experimental field at Nyankpala-Tamale during the 2019/2020 main cropping season. The six basic generations (viz.: parents, F_1, $BC_{1:1}$ and $BC_{1:2}$ and F_2) of all derived crosses were evaluated at CSIR-SARI, Manga research station during the 2020/2021 main cropping season. The families for each of the seven crosses were arranged in a randomized complete block design (RCBD) with three replications. Plots sowed with the non-segregating populations, (P_1, P_2, and F_1s) consisted of two rows, each 4 m long. The F_2 populations were sowed in 20 rows, whiles the backcrosses ($BC_{1:1}$ and $BC_{1:2}$) were sowed in three rows each. At both locations, rows were spaced 80 cm apart and distance between stands was 40 cm. A hill consisted of one plant. Standard agronomic practices for cowpea production by Dugje et al. (2009) were followed. Field pests such as aphids, thrips, pod sucking buds and *Maruca* were controlled using K-Optimal (Cyhalothrin 15 g/l + Acetamiprid 20; EC) at the rate of 500 ml per ha. Weeds were manually controlled using hoes.

2.5. Data collection

Data were collected on single plants for number of days to first flower appearance (DFFA), as the number of days from sowing to first day of flower appearance. The number of days to 95 % pod maturity (DNPM)

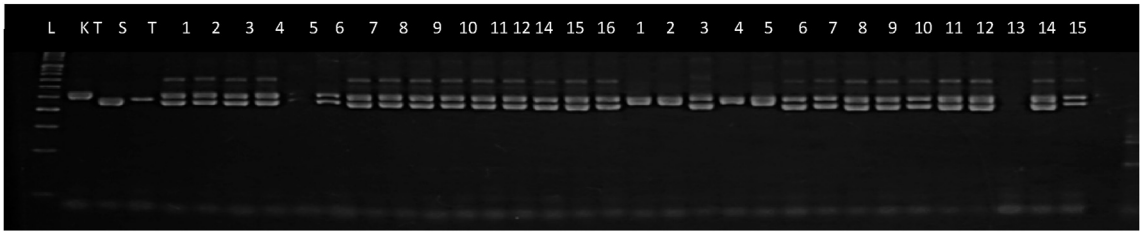

Figure 1. Gel picture showing successful crosses, Marker = MS-3, L = ladder (50 bp) KT = Kirkhouse-Benga, S=Sanzi-Nya, T = Tobonaa, the first 1–16 = KT x Sanzi-Nya and the last 1–15 = KT x Tobonaa. Non-adjusted image is presented in supplementary Figure 1.

was recorded as the number of days from sowing to when 95 % of the pods on each plant reached physiological maturity for seed production.

2.6. Data analysis

2.6.1. Determination of genetic control of earliness using Chi-square goodness of fit test

Mode of inheritance of earliness was analyzed by observing the ratios of extra-early maturity and early-to-medium maturity groups in the F_2 segregating populations. However, an intermediate group was included in all CB27 crosses, because 50 % of the plants were heterozygotes or intermediate between the two parental homozygotes. The observed extra-early and early-to-medium plants were compared with the theoretical expected ratios using Chi square goodness of fit tests. For DFFA, plants which flowered in ≤35 days after sowing (DAS), were classified as extra-early maturing, and 36–40 DAS were considered early-to-medium maturing. In the case of the CB27 crosses, the plants which flowered in ≤35 DAS were classified as extra-early, 36–39 DAS as intermediate, and ≥40 DAS were considered early-to-medium maturing. For DNPM, the plants were classified into maturity groups based on Freire Filho et al. (2005) method. In this classification, extra-early genotypes mature in ≤60 DAS, early maturing genotypes mature between 61-70 DAS, and medium maturing genotypes mature between 70-80 DAP. The Eq. (1) below was used for the Chi-square goodness of fit test.

$$x^2 = \sum \frac{(\text{Observed} - \text{Expected})^2}{\text{Expected}} \quad (1)$$

2.6.2. Determination of genetic control of earliness using descriptive statistics

Originlab statistical software (OriginLab.com) was used to generate the histograms for DFFA and DNPM distributions in the F_2 populations. Descriptive statistics such as, skewness and kurtosis were computed using Microsoft excel 2013.

2.6.3. Heritability estimate

Variance components were estimated according to Eq. (2) (Kearsey and Pooni (1996). Statistical analysis was done using the R statistical software version 4.1.1

$$V_A = (2\ VF_2 - VBC_{1:1} - VBC_{1:2}) \quad (2)$$

$$V_D = VBC_{1:1} + VBC_{1:2} - VF_2 - V_E$$

$$V_{AD} = ½\ (V\ BC_{1:2} - VBC_{1:1})$$

$$V_G = V_A + V_D$$

$$V_P = V_A + V_D + V_E$$

Where V_A = Additive variance, V_D = Dominance variance, V_E = Environmental variance, V_G = Genotypic variance, V_{AD} = Additive-Dominance variance, V_P = Phenotypic variance, VF_2 = variance of F_2, $VBC_{1:1}$ variance of BC_1:$_1$, $VBC_{1:2}$ = variance of $BC_{1:2}$.

Heritability estimates were calculated using Eqs. (3) and (4).

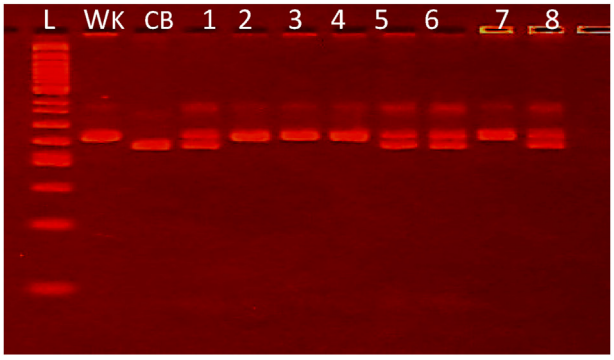

Figure 2. Hybridity test of F_1s. L = ladder (50 bp), marker; MS-3, WK = Wang-Kae, CB = CB27, WK x CB27 = 1–8. Non-adjusted image is presented in supplementary Figure 2.

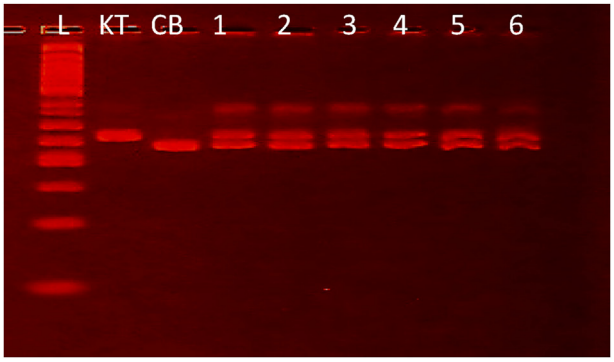

Figure 3. Hybridity test of F_1s. L = ladder (50 bp), marker: MS-3, KT = Kirkhouse-Benga, CB = CB27, KT x CB27 = 1–6. Non-adjusted image is presented in supplementary Figure 1.

$$\text{Broad sense heritability } (h^2_b) = V_G/(V_p) \quad (3)$$

$$\text{Narrow sense heritability } (h^2_n) = V_A/(V_p) \quad (4)$$

Genetic advance was calculated using the following Eq. (5):

$$GA = K \times \sqrt{Vp + h^2 n} \quad (5)$$

Where K = selection differential constant (2.06 at 5 % selection intensity) h^2 = heritability (narrow sense), V_P, = phenotypic standard deviation (Allard, 1960).

Genetic advance as a percentage of means (GAM) was calculated as indicated in Eq. (6) below.

$$GAM = (GA|\pi) \times 100 \quad (6)$$

Where GA is genetic advance and π is mean.

3. Results

3.1. Genotyping F_1 plants for hybridity test

The presence of two clear allele bands from the F_1 genotypes across the gel indicated successful crosses (Figures 1, 2 and 3). Crosses involving Kirkhouse-Benga and Sanzi-Nya produced 15 successful F_1 plants. The Kirkhouse-Benga x Tobonaa crosses yielded 10 successful F_1 plants, and six successful F1 plants were obtained from a cross between Kirkhouse-Benga and CB27. In the case of Wang-Kae cross combinations, nine, five and four true hybrids were produced with Sanzi, Tobonaa and CB27, respectively.

The summary statistics of DFFA and DNPM for the crosses are presented in Table 1. A total of 248 F_2 individuals were evaluated for Padi-Tuya × Sanzi-Nya cross, and segregated into 182 extra-early and 66 early to medium (3:1) for DFFA. The 116 F_2 plants obtained from Padi-Tuya × Tobonaa cross, 88 were extra-early and the remaining 28 were early to medium in terms of DFFA ($x^2 = 0.01$ and $p = 0.03$). In terms of DNPM, 91 out of the 116 F_1 plants were extra-early and 25 were early to medium ($x^2 = 0.32$ and $p = 0.53$). Both traits segregated into a 3:1 segregation ratio (Table 1).

The summary statistics for DFFA and DNPM of the six basic generations are shown in Tables 2 and 3. The Kirkhouse-Benga x Sanzi-Nya cross produced 155 extra-early and 55 early maturing F_2 plants for DFFA. For DNPM, a total of 210 F_2 plants (154 extra-early, and 56 early) were obtained from this cross. For Kirkhouse-Benga × Tobonaa, 134 extra-early and 48 early plants were observed for DFFA, whiles in the DNPM, 139 extra-early and 44 early maturing F_2 plants were obtained, A similar trend of 3:1 segregation ratio was observed for all other crosses. However, the 126 F_2 plants derived from Kirkhouse-Benga × CB27, followed 1:2:1 segregation ratio (extra-early: 33, intermediate: 64 and early to medium: 30) for DFFA in 2019 trial. However, for the same cross, a 3:1 segregation ratio (94 extra-early and 28 early) was obtained for DNPM. In the second trial, the same cross segregated into 44 (extra-early), 88 (intermediate) and 49 (early to medium) for DFFA, and 50 (extra-early), 87 (intermediate) and 44 (early) for DNPM with both traits fitting 1:2:1 segregation ratio. F_2 plants for the Wang-Kae × CB27 and Padi-Tuya × CB27 crosses segregated into a 1:2:1 segregation ratio for both traits. In all the seven crosses (evaluated in 2020/2021 cropping seasons), the $BC_{1:1}$ and $BC_{1:2}$ segregated into 1:1 for both DFFA and DNPM with the chi-square values less than the probability values.

The frequency distribution of the F_2 populations and parental were presented in the form of histograms (Figures 4 and 5).

Descriptive statistics were computed for the parents and F_2 generations for all crosses and evaluated in 2019/2020 and 2020/2021 cropping seasons (Tables 3 and 4, respectively). The results showed that the mean of the F_2 generation in all the crosses skewed to the early maturing parents. Low standard error and standard deviation values were observed in all the four crosses. Transgressive segregation was observed in both early and medium-to-late maturity groups (Table 3). For the four crosses evaluated in 2019/2020 cropping season, the kurtosis ranged from -1.14 (Wang-Kae × Tobonaa) to 2.43 (Padi-Tuya × Sanzi-Nya), whereas, skewness varied from -0.02 (Padi-Tuya x Sanzi-Nya) for DFFA to 1.12 (Padi-Tuya × Sanzi-Nya) for DNPM (Table 3). The following crosses had negative values of kurtosis in DNPM; Kirkhouse-Benga × Sanzi-Nya (−0.85); Padi-Tuya × Sanzi-Nya (−0.19); Wang-Kae × Tobonaa (−1.14); and Padi-Tuya x Tobonaa (−0.21). Kirkhouse-Benga × CB27 (−0.40) also had negative kurtosis for DFFA. Three crosses; Kirk-house-Benga x Sanzi-Nya (0.5); Padi-Tuya × Sanzi (2.43) and Wang-Kae × Tobonaa (0.76) had positive kurtosis for DFFA. Apart from Padi-Tuya × Sanzi-Nya which was negatively skewed (−0.02), the other three crosses were positively skewed (Table 3).

In Table 4, Kirkhouse-Benga × Sanzi-Nya (−0.41); Kirkhouse-Benga × Tobonaa (−0.33); Kirkhouse-Benga × CB27 (−0.26) and Wang-Kae × Sanzi-Nya (−0.47) had negative kurtosis for DNPM, but only Wang-Kae × Sanzi-Nya cross had negative kurtosis (−0.47) for DFFA. All other crosses had positive kurtosis for DFFA. Kirkhouse-Benga x CB27 cross was skewed at -0.22, Kirkhouse-Benga × Sanzi-Nya had coefficient of skewness of 1 for DFFA, all the other crosses had skewness <1 for both DFFA and DNPM.

Wang-Kae × CB27 had negative coefficient of kurtosis for DFFA (−0.42) and DNMP of (−0.38), whiles, that of Wang-Kae × Tobonaa was (0.0) for DFFA and (−0.18) for DNPM. Padi-Tuya × CB27 had the highest co-efficient of kurtosis of 4.57 in DFFA and 0.43 for DNPM. None of the

Table 1. Summary statistics for parents and F_2 progenies and Chi square goodness of fit tests for days to first flower appearance and Days to 95% Pod maturity for the study conducted in 2019/2020 cropping season.

Gen	Range	Mean	E-Early	E-Med.	Ratio	Chi-sq.	pr	Gen	Range	Mean	E.Early	Early		Chi-sq	Pr
Padi-Tuya (P1) ×Sanzi-Nya(P2)															
Days to first flower appearance								**Days to 95% Pod maturity**							
P_1	41–46	44.2 ± 1.57	0	30				P_1	66–72	69.9 ± 2.06					
P_2	30–34	30.8 ± 1.2	30					P_2	49–53	50.5 ± 1.33					
F_2	28–50	34.9 ± 3.66	182	66	3:1	0.34ns	0.56	F_2	47–75	58.8 ± 5.25	**183**	**65**	3:1	0.20ns	0.66
Padi-Tuya(P1) × Tobonaa(P2)															
Days to first flower appearance								**Days to 95% Pod maturity**							
P_1	41–47	44.63 ± 1.3	0	30				P_1	67–73	70.1 ± 2.41					
P_2	29–33	30.3 ± 1.26	30	0				P_2	48–52	50.2 ± 1.3					
F_2	28–47	35.5 ± 4.43	88	28	3:1	0.0ns	0.03	F_2	48–75	56.4 ± 5.72	91	26	3:1	0.32ns	0.53
Kirkhouse-Benga(P1) × Sanzi-Nya(P2)															
Days to first flower appearance								**Days to 95% Pod maturity**							
P_1	39–44	41.1 ± 1.74	0	30				P_1	63–69	65.2 ± 1.90					
P_2	28–34	30.6 ± 1.45	30	0				P_2	48–52	50.3 ± 0.99		0			
F_2	30–42	34.2 ± 2.20	87	26	3:1	0.24ns	0.89	F_2	48–67	55.5 ± 4.56	86	27	3:1	0.073ns	0.079
Wang-Kae(P1) × Tobonaa(P2)															
Days to first flower appearance								**Days to 95% Pod maturity**							
P_1	38–45	42.0 ± 1.95	0	30				P_1	63–71	65.4 ± 2.49					
P_2	28–33	28-33 ± 30.1	30	0				P_2	48–52	49.8 ± 1.03					
F_2	29–44	34.8 ± 5.25	74	28	3:1	0.33ns	0.57	F_2	50–68	56.3 ± 4.65	77	25	3:1	0.01ns	0.91

ns = Not significant.

Table 2. Summary statistics for the six basic generations and Chi square goodness of fit tests for segregating generations for DFFA and DNPM evaluated at Manga during 2020/2021 cropping season.

Gen	Range	Mean	E.Early	Early	Ratio	Chi-sq	Pr	Gen	Range	Mean	E.Early	Early		x^2	Pr
Kirkhouse-Benga(P1) × Sanzi-Nya(P2)															
Days first flower								**Days to 95 % pod maturity**							
P_1	38–44	41.6 ± 1.71	0	30				P_1	60–68	65.1 ± 1.77	0	30			
P_2	28–34	30.8 ± 1.72	30	0				P_2	47–52	49.5 ± 1.13	30	0			
F_1	32–39	35.3 ± 1.94	17	11				F_1	50–61	56.1 ± 2.0	28	2			
$BC_{1.1}$	33–43	37.3 ± 3.13	35	37	1:1	0.06 ns	0.814	$BC_{1:1}$	50–70	59.9 ± 4.26	38	34	1; 1	0.22 ns	0.64
$BC_{1.2}$	30–40	34.9 ± 3.0	37	33	1:1	0.23 ns	0.633	$BC_{1:2}$	49–67	57.6 ± 4.10	36	36	1; 1	0.00 ns	0.38
F_2	28–45	35.1 ± 3.75	155	55	3:1	0.16 ns	0.9	F_2	48–72	57.5 ± 4.82	154	56	3:01	0.31 ns	0.58
Kirkhouse-Benga(P1) × Tobonaa(P2)															
Days first flower								**Days to 95 % pod maturity**							
P_1	38–44	40.2 ± 1.71	0	29				P_1	62–67	64.6 ± 1.52	0	30			
P_2	29–33	30.9 ± 1.24	30	0				P_2	48–53	50.0 ± 1.29	30	0			
F_1	32–42	35.7 ± 1.19	20	10				F_1	52–65	55.3 ± 2.51	27	3			
$BC_{1:1}$	29–45	37.4 ± 3.71	40	44	1:1	0.19 ns	0.663	$BC_{1:1}$	50–71	59.8 ± 4.23	43	41	1; 1	0.42 ns	0.58
$BC_{1:2}$	28–44	34.9 ± 3.68	40	36	1:1	0.21 ns	0.646	$BC_{1:2}$	47–68	57.3 ± 4.34	46	40	1; 1	0.45 ns	0.55
F_2	28–47	35.3 ± 4.09	134	48	3:1	0.18 ns	0.669	F_2	48–75	57.5 ± 4.88	139	44	3; 1	0.20 ns	0.67
Wang-Kae(P1) × Sanzi-Nya(P2)															
Days first flower								**Days to 95 % pod maturity**							
P_1	39–45	41.1 ± 1.92	0	30				P_1	61–70	64.4 ± 1.53	0	30			
P_2	29–37	31.2 ± 1.51	30	0				P_2	48–54	50.4 ± 1.04	28	0			
F_1	33–38	34.1 ± 1.62	30	0				F_1	50–57	53.4 ± 1.13	29	0			
$BC_{1:1}$	29–43	37.1 ± 3.51	38	41	1:1	0.11 ns	0.736	$BC_{1:1}$	49–72	60.5 ± 4.0	40	38	1:1	0.51 ns	0.82
$BC_{1:2}$	30–41	34.2 ± 3.48	23	20	1:1	0.21 ns	0.647	$BC_{1:2}$	49–67	58.1 ± 3.83	23	20	1:1	0.21 ns	0.65
F_2	28–44	33.2 ± 3.99	147	51	3:1	0.06 ns	0.806	F_2	48–68	56.5 ± 4.70	143	52	3:1	0.28 ns	0.597
Wang-Kae (P1) × Tobonaa(P2)															
Days first flower								**Days to 95 % pod maturity**							
P_1	37–44	40.7 ± 1.64	0	30				P_1	62–69	63.5 ± 2.04	0	30			
P_2	29–34	31.7 ± 1.49	30	0				P_2	48–54	51.2 ± 1.79	25	0			
F_1	33–40	35.1 ± 1.99	18	9				F_1	49–55	52.3 ± 1.65	27	0			
$BC_{1:1}$	32–50	37.2 ± 3.59	25	29	1:1	0.30 ns	0.586	BC_1	48–69	58.2 ± 3.81	31	37	1:1	0.28 ns	0.60
$BC_{1:2}$	30–43	35.3 ± 3.43	39	41	1:1	0.05 ns	0.823	BC_2	48–69	58.3 ± 3.7	42	37	1:1	0.32 ns	0.57
F_2	29–45	34.9 ± 4.0	91	34	3:1	0.31 ns	0.577	F_2	49–70	56.8 ± 4.0	96	29	3:1	0.23 ns	0.63

Gen	Range	Mean	Ex. Early	Inter	Early-Med	Ratio	Chi-sq	Pr	Gen	Range	Mean	Ex. Early	Inter	Early-Med	Ratio	Chi-sq	Pr.
Kirkhouse-Benga(P1) × CB27(P2)- prelim trial																	
Days first flower									**Days to 95 % pod maturity**								
P_1	37–44	40.8 ± 2.29			30				P_1	63–68	65.0 ± 2.74						
P_2	32–38	35.3 ± 2.0	30						P_2	53–59	55.7 ± 1.64						
F_2	32–44	37.3 ± 2.64	32	64	30	1:2:1	0.024 ns	0.877	F_2	50–67	56.2 ± 3.96	94	0	28	3:1	0.27	0.60
Kirkhouse-Benga(P1) × CB27(P2)																	
Days first flower									**Days to 95 % pod maturity**								
P_1	38–44	40.7 ± 1.79	0		30				P_1	61–68	64.2 ± 2.35	0		30			
P_2	32–39	34.8 ± 1.20	25						P_2	53–60	55.1 ± 1.80	25	0				
F_1	32–40	35.6 ± 1.80	15	8	2				F_1	55–61	59.2 ± 1.65	17	8	0			
$BC_{1:1}$	34–50	39.8 ± 3.33	10		64	1:1	39.41*	3.341	$BC_{1:1}$	55–75	62.4 ± 4.15	27		47	1:1	5.41*	0.02
$BC_{1:2}$	32–45	37.3 ± 3.61	34		38	1:1	0.22 ns	0.64	$BC_{1:2}$	53–70	60.4 ± 4.18	37		33	1:1	0.23ns	0.63
F_2	32–49	38.3 ± 4.14	44	88	49	1:2:1	0.41 ns	0.813	F2	50–73	61.4 ± 4.64	50	87	44	1:2:1	0.67ns	0.72
Wang-Kae(P1) × CB27(P2)																	
Days first flower									**Days to 95 % pod maturity**								
P_1	38–44	41.2 ± 1.98	0		30				P_1	61–69	64.66 ± 1.95		30				

(*continued on next page*)

Table 2 (*continued*)

Gen	Range	Mean	Ex. Early	Inter	Early-Med	Ratio	Chi-sq	Pr	Gen	Range	Mean	Ex. Early	Inter	Early-Med	Ratio	Chi-sq	Pr.
P_2	32–40	34.9 ± 1.82	29	0					P_2	33–38	35.13 ± 1.06	29					
F_1	34–40	35.9 ± 1.8	16	7	2				F_1	55–64	58.26 ± 2.0 21	5					
$BC_{1:1}$	30–45	37.9 ± 3.37	19		43	1:1	9.29*	0.00	$BC_{1:1}$	53–71	61.26 ± 3.58	24		36	1:1	2.4*	0.12
$BC_{1:2}$	30–44	36.5 ± 3.46	27		31	1:1	0.27 ns	0.59	$BC_{1:2}$	52–68	59.17 ± 3.27	30		28	1:1	0.67ns	0.79
F_2	32–47	38.2 ± 4.07	61	108	54	1:2:1	0.66 ns	0.719	F_2	53–72	62.44 ± 3.98	58	113	52	1:2:1	0.36ns	0.83
Padi-Tuya(P1) × CB27 (P2)																	
Days first flower									**Days to 95 % pod maturity**								
P_1	40–46	43.4 ± 1.94			30				P_1	66–74	69.8 ± 2.54			30			
P_2	33–38	35.3 ± 1.39	30						P_2	53–60	55.7 ± 1.66	30					
F_1	34–40	36.6 ± 1.54	21		6				F_1	53–62	58.3 ± 2.61	23	4				
$BC_{1:1}$	33–48	38.7 ± 3.27	11		67	1:1	40.21*	2.29	$BC_{1:1}$	55–80	63.7 ± 4.14	26		52	1:1	8.66*	0
$BC_{1:2}$	34–43	36.4 ± 2.24	21		24	1:1	0.20 ns	0.65	$BC_{1:2}$	52–66	59.1 ± 3.74	25		20	1:1	0.20ns	0.65
F_2	33–56	38.7 ± 3.98	26	52	30	1:2:1	0.44 ns	0.80	F_2	53–80	63.0 ± 5.10	29	55	24	1:2:1	0.50ns	0.78

Table 3. Descriptive statistics of days to first flower appearance and days to 95 % pod maturity for the parents and F_2 populations evaluated in 2019/2020 cropping season.

Trait	Gen	Mean	SE	SD	SV	Kurtosis	Skewness	Min	Maxi	No
Kirkhouse-Benga × Sanzi-Nya										
DFFA	F2	34.20	0.21	2.20	4.86	0.85	0.48	30	42	113
	KT	40.34	0.39	2.09	4.38			38	44	29
	Sanzi	31.23	0.24	1.33	1.77			29	33	30
DNPM	F2	55.55	0.43	4.56	20.75	-0.85	0.65	48	65	113
	KT	65.17	0.35	1.90	3.59			62	69	30
	Sanzi	50.30	0.18	0.99	0.98			48	52	30
Padi-Tuya × Sanzi-Nya										
DFFA	F2	34.92	0.23	3.66	13.42	2.43	1.12	28	50	248
	Pad	43.83	0.27	1.46	2.14			40	45	30
	Sanzi	30.87	0.45	2.45	5.98			20	33	30
DNPM	F2	62.30	0.30	4.80	23.05	-0.19	-0.02	50	75	248
	Pad	69.57	0.38	2.06	4.25			66	72	30
	Sanzi	50.47	0.24	1.33	1.77			49	53	30
Padi-Tuya × Tobonaa										
DFFA	F2	35.53	0.40	4.40	19.33	-0.21	0.74	28	47	118
	Padi	43.23	0.37	2.01	4.05			40	46	30
	Tob	31.57	0.26	1.41	1.98			29	34	30
DNPM	F2	60.27	0.47	5.01	25.12	-1.18	0.03	51	72	116
	Padi	70.10	0.44	2.41	5.82			67	73	30
	Tob	50.17	0.24	1.29	1.66			48	52	30
Wang-Kae × Tobonaa										
DFFA	F2	34.77	0.29	2.92	8.55	0.76	0.91	29	44	102
	Wk	40.73	0.42	2.29	5.24			37	44	30
	Tob	30.9	0.22667	1.24	1.54			29	33	30
DNPM	F2	56.21	0.45	4.59	21.10	-1.14	0.44	49	65	102
	Wk	65.40	0.45	2.49	6.18			61	71	30
	Tob	49.80	0.19	1.03	1.06			48	52	30

SE = Standard error; SD = Standard Deviation, SV = Sample variance, DFFA = Days to first flower appearance, DNPM = Days to 95 % pod maturity.

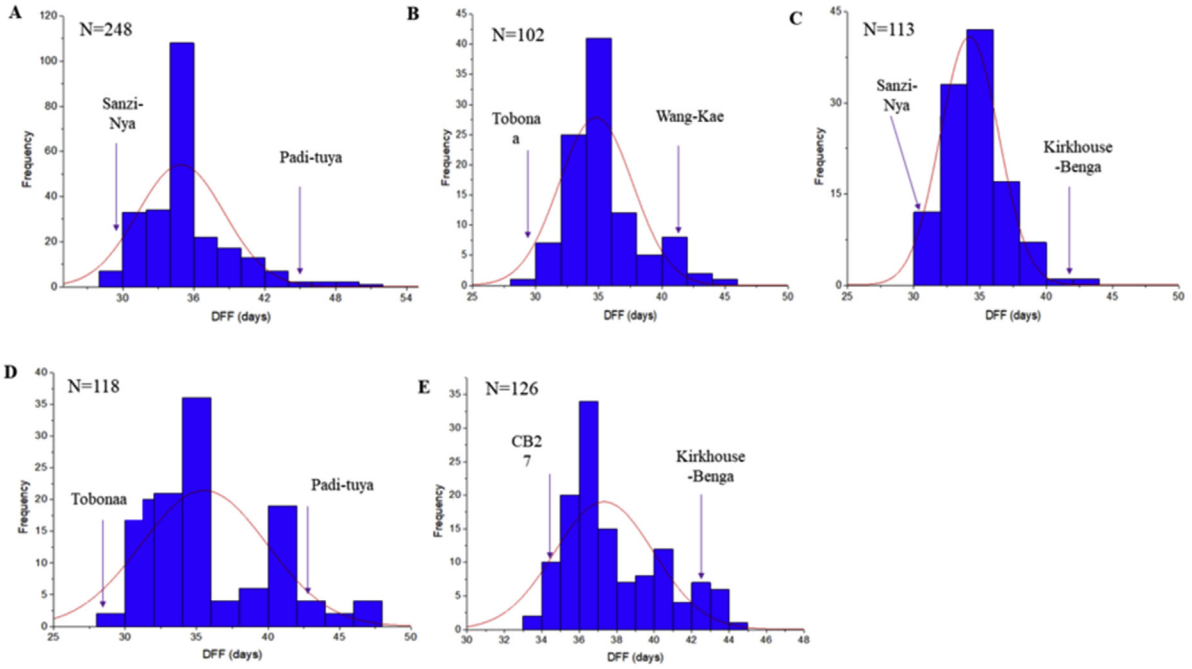

Figure 4. Frequency distribution of days to first flower appearance (DFF) of the parental and F_2 populations evaluated in 2019/2020 cropping season. N = number of F_2 plants evaluated. Non-adjusted image is presented in supplementary Figure 4.

crosses had more than co-efficient of skewness of ≥3, the highest was observed in Padi-Tuya × CB27 (1.66) (Table 4). Only Wang-Kae × CB27 cross (−0.21) was negatively skewed for DNPM (Table 4).

3.1.1. Estimates for heritability, genetic advance and genetic advance as a percentage of means

Broad sense heritability (h^2_b) estimates for DFFA ranged between 62 % (Wang-Kae × CB27) and 85 % (Padi-Tuya × CB27), and from 72 % (Kirkhouse-Benga × CB27) to 84 % (Kirkhouse-Benga × Sanzi-Nya) for DNPM. Narrow sense heritability (h^2_n) values varied from 18 % (Kirkhouse-Benga × Sanzi-Nya) to 85 % (Padi-Tuya × CB27) for DFFA and between 8 % (Kirkhouse-Benga × Sanzi-Nya) and 62 % (Kirkhouse-Benga × CB27) for DNPM. Genetic advance at 5 % selection intensity ranged from 1.32 (Kirkhouse-Benga × Sanzi-Nya) to 7.53 (Padi-Tuya × CB27) for DFFA, and from 0.89 (Kirkhouse-Benga × Sanzi-Nya) to 8.93 (Kirkhouse-Benga × CB27) for DNPM. Genetic advance as a percentage of mean ranged from 3.76 (Kirkhouse-Benga × Sanzi-Nya) and 19.84 (Padi-Tuya × CB27) for DFFA and from 1.44 (Kirkhouse-Benga × Sanzi-Nya) to 14.62 (Kirkhouse-Benga × CB27) for DNPM (Table 5).

4. Discussion

Heritability is an important parameter for crop genetic improvement, because it indicates how much of the phenotypic variance can be transferred from parents to progenies (Falconer, 1981). Also, it provides a clue of the appropriate breeding method to use and the extent to which the improvement of a particular trait could be achieved through selection (Akhshi et al., 2014). In this study, no significant segregation distortion ($p > 0.05$) was observed in the Chi square goodness of fit tests for DFFA and DNPM in all crosses where Sanzi-Nya and Tobonaa were used as donor parents. This suggests that there was no significant difference between the observed and the expected segregation ratios (3:1) for both traits. Thus, a single dominant gene could be responsible for the inheritance of DFFA and DNPM in this set of cowpea genotypes. These observations are consistent with the results of previous studies in cowpea (Ishiyaku et al., 2005; Yamamoto et al., 2016; Owusu et al., 2018) and in soybean (Bonato and Vello, 1999; Kong et al., 2014). However, the current finding contradicts that of Adeyanju and Ishiyaku (2007); Lo et al. (2018) and Santos et al. (2020) who noted that inheritance of earliness-related traits in cowpea is controlled by polygenes.

The segregation ratio 1:2:1 obtained for DFFA and DNPM in all crosses involving CB27 suggests that earliness in CB27 is controlled by a single gene acting additively (partial dominance mode of inheritance). Nonetheless, a 3:1 segregating ratio was observed for the cross between Kirkhouse-Benga x CB27 in DNPM during off-season. The disparity in segregation involving CB27 could be attributed to the high temperatures and low humidity during the period of evaluation (between April and June 2020). This observation is supported by the fact that non-significant segregation distortion of 1:2:1 was obtained for both DFFA and DNPM when the Kirkhouse-Benga × CB27 cross was evaluated together with Wang-Kae x CB27 and Padi-Tuya × CB27 during the optimal growing season. According to Gaur et al. (2014), number of days to flowering can be recorded with more precision than number of days to maturity, particularly during harsh or long period of unfavorable environmental conditions. Owusu et al. (2018) and Santos et al. (2020) noted that environmental conditions such as high temperatures have a stronger influence on pod maturation in cowpea than on flowering. This suggests that earliness in cowpea could be controlled by polygenes or largely influenced by the environment. Therefore, the use of quantitative methods to study the genetic control of earliness in cowpea could be beneficial.

The number of genes controlling a trait can be determined by third order statistics such as skewness and kurtosis and frequency distribution (Rani et al., 2016). Kurtosis describes the extent to which the peak of a probability distribution deviates from the normal distribution. If the peak is pointed, the distribution is leptokurtic (coefficient of kurtosis ≥3), and if it is flat, it is referred to as platykurtic (coefficient of kurtosis ≤3). For a normal distribution, coefficient of kurtosis is expected to be equal to 3. A normal distribution indicates that the trait is controlled by a single gene, whereas, leptokurtic distribution indicates that the trait is controlled by fewer genes, and a platykurtic distribution indicates that the trait is governed by many genes (Neelima et al., 2020). According to Neelima et al. (2020), a positive skewness indicates the traits could be controlled by dominant and complementary gene action, whereas a negative

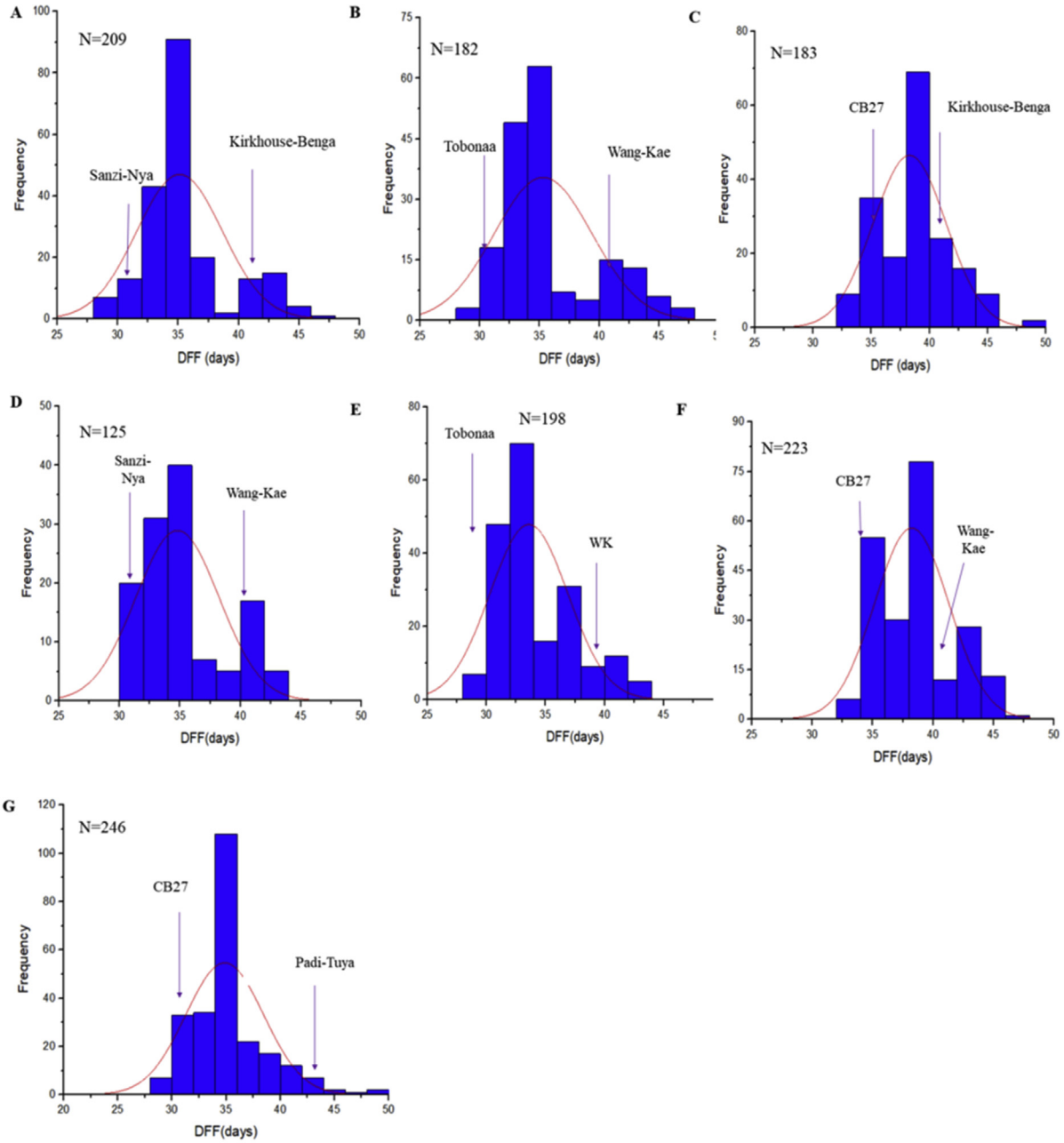

Figure 5. Frequency distribution of days to first flower appearance (DFF) of the parental and F_2 populations evaluated in 2020/2021 cropping season. N = number of F_2 plants evaluated.

skewness indicates the traits could be controlled by dominant and duplicate epistasis. The vast majority of crosses evaluated in this study were positively skewed for both DFFA and DNFM except Padi-Tuya x Sanzi-Nya, Kirkhouse-Benga × CB27 and Wang-Kae × CB27 which were negatively skewed. This implies that Padi-Tuya × Sanzi-Nya, Kirkhouse-Benga x CB27 and Wang-Kae × CB27 crosses are controlled by dominant and duplicate epistasis, whereas, all the other crosses are controlled by dominant and complementary gene action. The positive skewness observed for DFFA and DNPM showed that majority of the segregants were early maturing, thus direct selection for earliness could be effective. For the crosses with negative skewness, selection may be done from the lower end of distribution to obtain super early maturing segregants. In agreement with the findings of Neelima et al. (2020), platykurtic distribution was observed for all crosses in 2019 and 2020, expect Padi-Tuya × CB27, implying that DFFA and DNPM are controlled by polygenes. In addition, the asymmetrical distribution of the F_2 individuals observed for all the crosses in this study further emphasize that earliness in the studied cowpea genotypes evaluated is under polygenic control. Only Padi-Tuya × CB27 cross had leptokurtic, near normal distribution in the histogram and the highest positive skewness. This implies that fewer genes might be controlling earliness in this cross. These results are in agreement with the findings of previous authors who showed that earliness in cowpea is controlled by polygenes (Ishiyaku et al., 2005; Andargie et al., 2014; Ribeiro et al., 2014; Santos et al., 2020). The results however, contradict the monogenic mode of inheritance reported by Yamamoto et al. (2016), Owusu et al. (2018) and Wang et al. (2019). It is noteworthy that the result obtained via Chi-square test of goodness of fit in this study points to a single dominant gene mode of inheritance for

Table 4. Descriptive statistics of days to first flower appearance and days to 95 % pod maturity for the parents and F_2 populations evaluated in 2020/2021 cropping season.

	Trait	Mean	SE	SD	SV	Kurtosis	Skewness	Min	Max	No
Kirkhouse-Benga (P1) × Sanzi-Nya (P2)										
DFFA	F_2	35.11	0.25	3.55	12.59	0.93	1.00	28	47	209
	P1	41.63	0.31	1.71	2.93	-	-	38	44	30
	P2	30.77	0.31	1.72	2.94	-	-	28	34	30
DNPM	F_2	57.59	0.35	5.08	25.83	-0.41	0.33	48	72	208
	P1	65.13	0.32	1.78	3.15	-	-	60	68	30
	P2	49.50	0.21	1.14	1.29	-	-	47	52	30
Kirkhouse-Benga (P1) × Tobonaa (P2)										
DFFA	F_2	35.30	0.30	4.10	16.78	0.17	0.92	28	47	182
	P1	40.21	0.39	2.08	4.31	-	-	38	44	29
	P2	30.86	0.23	1.25	1.55	-	-	29	33	29
DNPM	F_2	57.52	0.41	5.58	31.16	-0.33	0.60	48	74	182
	P1	64.66	0.29	1.54	2.38	-	-	62	67	29
	P2	50.00	0.24	1.31	1.71	-	-	48	53	29
Kirkhouse-Benga (P1) × CB27 (P2)										
DFFA	F_2	38.29	0.23	3.14	9.84	0.39	0.47	32	49	183
	P1	40.73	0.42	2.29	5.24	-	-	37	44	30
	P2	34.84	0.39	1.95	3.81	-	-	32	40	25
DNPM	F_2	61.55	0.32	4.33	18.79	-0.26	-0.22	50	73	182
	P1	64.17	0.43	2.35	5.52	-	-	59	68	30
	P2	55.03	0.33	1.80	3.25	-	-	53	61	29
Wang-Kae (P1) × Sanzi-Nya (P2)										
DFFA	F_2	34.90	0.30	3.34	11.17	-0.47	0.81	30	43	125
	P1	40.73	0.42	2.29	5.24	-	-	37	44	30
	P2	31.72	0.29	1.43	2.04	-	-	29	34	25
DNPM	F_2	56.80	0.51	5.67	32.11	-0.44	0.70	49	70	125
	P1	63.50	0.55	3.04	9.22	-	-	57	68	30
	P2	51.16	0.36	1.80	3.22	-	-	48	54	25
Wang-Kae (P1) × Tobonaa (P2)										
DFFA	F_2	33.57	0.23	3.30	10.88	0.00	0.93	29	43	197
	P1	41.07	0.42	2.32	5.37	-	-	37	44	30
	P2	31.07	0.37	2.03	4.12	-	-	29	38	30
DNPM	F_2	56.53	0.32	4.50	20.26	-0.81	0.38	48	67	195
	P1	64.37	0.46	2.53	6.38	-	-	58	68	30
	P2	50.79	0.26	1.37	1.88	-	-	48	54	28
Wang-Kae (P1) × CB27 (P2)										
DFFA	F_2	38.23	0.21	3.07	9.45	-0.42	0.45	32	47	223
	P1	41.20	0.36	1.99	3.96	-	-	38	44	30
	P2	34.86	0.34	1.83	3.34	-	-	32	40	29
DNPM	F2	62.44	0.25	3.78	14.30	-0.38	-0.21	53	72	223
	P1	64.67	0.36	1.95	3.82	-	-	61	68	30
	P2	35.14	0.20	1.06	1.12	-	-	33	37	29
Padi-Tuya (P1) × CB27 (P2)										
DFFA	F_2	38.70	0.38	3.97	15.74	4.57	1.66	33	56	108
	P1	43.40	0.35	1.94	3.77	-	-	40	46	30
	P2	35.30	0.25	1.39	1.94	-	-	33	38	30
DNPM	F_2	63.03	0.52	5.42	29.41	0.43	0.44	53	80	108
	P1	69.83	0.47	2.55	6.49	-	-	66	74	30
	P2	55.73	0.30	1.66	2.75	-	-	53	60	30

SE = Standard error; SD = Standard Deviation, SV = Sample variance, DFFA = Days to first flower appearance, DNPM = Days to 95 % pod maturity.

Sanzi-Nay and Tobonaa, and partial dominant mode of inheritance of earliness for CB27 crosses. The disparity between the results obtained from Mendelian segregation approach and the other quantitative methods in this study, indicated that the qualitative approach may be misleading in the study of genetic control of earliness-related traits, due to its subjectivity.

Transgressive segregation, as a result of accumulation of favourable alleles for the earliness-related traits studied provides opportunity for the selection of segregants in either of the extremes. According to Rieseberg et al. (2003) and Bell and Travis (2005), transgressive segregation results from recombination between parental lines that possess quantitative trait loci (QTLs) with antagonistic effects. Moreover, heterosis, complementary gene or additive gene action, over-dominance and epistasis also contribute to transgressive segregation (Rieseberg et al., 1999). This also confirms that the inheritance of the key earliness-related traits are under the control of complementary or additive gene actions in most of the

Table 5. Genetic variance and heritability of days to first flower appearance (DFFA) and days to 95 % pod maturity (DNPM) for 2020/2021 cropping season.

Trait	VE	VA	VD	VAD	VG	VP	h^2_n	h^2_b	GA	GAM
Kirkhouse-Benga × Sanzi-Nya										
DFFA	3.20	2.34	7.16	-2.07	9.50	12.70	0.18	0.75	1.32	3.76
DNPM	4.14	2.04	19.87	-0.21	21.91	26.06	0.08	0.84	0.89	1.44
Kirkhouse-Benga × Tobonaa										
DFFA	3.98	9.72	3.09	0.27	12.80	16.78	0.58	0.76	4.89	13.85
DNPM	5.42	4.91	20.83	-0.50	25.74	31.16	0.16	0.83	1.84	3.19
Kirkhouse-Benga × CB27										
DFFA	4.71	10.03	-4.90	-2.49	10.03	14.74	0.68	0.68	5.38	14.18
DNPM	5.20	11.71	1.88	-3.26	13.59	18.79	0.62	0.72	8.93	14.62
Wang-Kae × Sanzi-Nya										
DFFA	3.78	4.44	2.95	0.55	7.39	11.17	0.40	0.66	6.88	19.51
DNPM	5.75	4.93	21.43	0.21	26.36	32.11	0.15	0.82	1.75	3.00
Wang-Kae × Tobonaa										
DFFA	4.04	2.40	4.44	0.79	6.84	10.88	0.22	0.63	1.49	4.26
DNPM	3.68	2.40	14.18	0.54	16.59	20.26	0.12	0.82	1.11	1.92
Wang-Kae × CB27										
DFFA	3.58	4.83	1.04	-1.16	5.87	9.45	0.51	0.62	3.23	8.62
DNPM	3.55	4.08	6.67	-1.43	10.75	14.30	0.29	0.75	2.25	3.72
Padi-Tuya × CB27										
DFFA	2.70	15.79	-2.75	-2.83	15.79	18.49	0.85	0.85	7.53	19.84
DNPM	5.33	18.34	5.74	-6.25	24.08	29.41	0.62	0.82	6.92	11.17

VE = Environmental Variance, VA = Additive variance, VD = Dominance variance, GV = Genetic variance, VP = Phenotypic variance, h^2_b = Broad sense heritability, h^2_n = Narrow sense heritability, GA = Genetic advance. GAM Genetic advance as the percentage of means.

crosses, and therefore selection of superior progenies would be beneficial. Low standard deviation values observed for all the crosses also confirms the opportunity for efficient selection (Abd El-Moghny et al., 2016).

An important objective of this study was to estimate the heritability (broad sense and narrow sense) and genetic advance of earliness-related traits in the set of cowpea genotypes evaluated. Both phenotypic and genotypic variances were high for DFFA and DNPM in all crosses, suggesting that environmental influence was minimal, and that the observed variation was largely due to the variation in the genetic background of the genotypes. Therefore, direct selection for DFFA and DNPM in the environments where the trials were conducted could accelerate progress in breeding cowpea for earliness. The results also suggest that imposing high selection intensity for earliness during the early generations in a cowpea breeding program would be rewarding (Olawuyi et al., 2015 Owusu et al., 2018). The broad sense heritability values obtained for DFFA and DNPM in this study are similar to those reported in previous studies (Sharma and Singhania 1992; Adeyanju and Ishiyaku 2007; Suganthi and Murugan, 2008; Sivakumar et al., 2013; Owusu et al., 2018; Santos et al., 2020). Moreover, the high narrow sense heritability and high genetic advance values recorded for DFFA, DNPM in Padi-Tuya × CB27 and Kirkhouse-Benga × CB27 crosses underscore the importance of both additive, and dominance gene effects in controlling earliness in these crosses. This result is very important in crop improvement because, narrow sense heritability provides a measure of the breeding value of a population (Kearsey and Pooni, 1996).

V_{AD} is a covariance and its sign will depend on the direction of dominance (Kearsey and Pooni, 1996). The following crosses: Kirkhouse-Benga × Sanzi-Nya, Kirkhouse-Benga × Tobonaa, Kirkhouse-Benga × CB27, Wang-Kae × CB27, and Padi-Tuya × CB27 had negative for V_{AD} for DFFA and DNPM, which implies that early maturity is dominant over late maturity. Since that of Wang-Kae × Sanzi-Nya and Wang-Kae × Tobonaa were positive but <1, dominance alleles for earliness may be involved. Additive gene effects are useful in the development of pure lines, whereas dominance and epistatic effects can be used to exploit hybrid vigor that may lead to transgressive segregation (Gawande et al., 2016).

The high (>20 %) and moderate (>10 %) values of genetic advance as percentage of mean (GAM) that were obtained in Padi-Tuya × CB27, Kirkhouse-Benga x CB27, Kirkhouse-Benga × Tobonaa and Wang-Kae × Sanzi-Nya, bode well for genetic improvement. Similar results were reported by Lesley (2005) and Nwosu et al. (2013). The other four crosses had low GAM, which corroborates the earlier report by Sivakumar et al. (2013).

5. Conclusions

The use of both qualitative (Mendelian segregation patterns) and quantitative methods provided useful information on the genetic control of earliness in cowpea, which will be useful in breeding programs. While the Mendelian segregation pattern suggested a single dominant gene mode of inheritance for earliness, the quantitative methods indicated that duplicate epistasis and complementary epistasis are responsible. It is, therefore, recommended that a robust quantitative method such as generation mean analysis could be used to identify the actual epistatic genetic effects controlling the inheritance of earliness in the set of cowpea genotypes used in this studies.

Declarations

Author contribution statement

Emmanuel Yaw Owusu: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Francis Kusi: Performed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Richard Akromah; Alexander Wireko-Kena: Conceived and designed the experiments; Wrote the paper.

Frederick Awuku Justice; Patrick Attamah; Gloria Mensah; Salim Lamini; Mukhtaru Zakaria: Performed the experiments.

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Data availability statement

Data will be made available on request.

Declaration of interests statement

The authors declare no conflict of interest.

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Additional information

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