Euphytica (2018)214:63
https://doi.org/10.1007/s10681-018-2147-x

Genetic studies for seed size and grain yield traits in kabuli chickpea

Prity Sundaram · Srinivasan Samineni · Sobhan B. Sajja · S. P. Singh · R. N. Sharma · Pooran M. Gaur

Received: 8 September 2017 / Accepted: 2 March 2018

Abstract Seed size, determined by 100-seed weight, is an important yield component and trade value trait in kabuli chickpea. In the present investigation, the small seeded kabuli genotype ICC 16644 was crossed with four genotypes (JGK 2, KAK 2, KRIPA and ICC 17109) and F_1, F_2 and F_3 populations were developed to study the gene action involved in seed size and other yield attributing traits. Scaling test and joint scaling test revealed the presence of epistasis for days to first flower, days to maturity, plant height, number of pods per plant, number of seeds per plant, number of seeds per pod, biological yield per plant, grain yield per plant and 100-seed weight. Additive, additive × additive and dominance × dominance effects were found to govern days to first flower. Days to maturity and plant height were under the control of both the main as well as interaction effects. Number of seeds per pod was predominantly under the control of additive and additive × additive effects. For grain yield per plant, additive and dominance × dominance effects were significant in the cross ICC 16644 × KAK 2, whereas, additive × additive effects were important in the cross ICC 16644 × JGK 2. Additive, dominance and epistatic effects influenced seed size. The study emphasized the existence of duplicate epistasis for most of the traits. To explore both additive and non-additive gene actions for phenological traits and yield traits, selection in later generations would be more effective.

Keywords Chickpea · *Cicer arietinum* · Generation mean analysis · Additive · Dominance · Epistasis · Seed size

Introduction

Chickpea (*Cicer arietinum* L.), a self-pollinated diploid (2n = 2x = 16) crop species with a genome size of 740 Mb, is the second most important food legume after common bean (*Phaseolus vulgaris* L.) in terms of annual production (FAOSTAT 2016). It is grown in more than 55 countries on 12.65 million ha with 12.09 million tons of production and 956 kg ha^{-1} average productivity (FAOSTAT 2016). Seed size determined by 100-seed weight has always been a trait of consumer preference in chickpea (Singh 1987), besides an important component of yield and adaptation (Singh and Paroda 1986). A wide range of genetic

P. Sundaram · S. Samineni · S. B. Sajja · P. M. Gaur
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India

P. Sundaram · S. P. Singh · R. N. Sharma
Bihar Agricultural University, Sabour, Bhagalpur, India

P. M. Gaur (✉)
The UWA Institute of Agriculture, University of Western Australia, Perth, WA 6009, Australia
e-mail: p.gaur@cgiar.org

Published online: 08 March 2018

variability is present for seed size in chickpea. Large-seeded kabuli types are gaining importance, as the kabuli chickpea receives higher market premium compared to desi chickpea (Upadhyaya et al. 2006). Very large seeded (> 45 g) kabuli chickpeas are being sold at about three times the price of desi chickpea and about two times the price of medium-seeded (~ 25 g) kabuli chickpea in India (Gaur et al. 2006). It has also been considered as an important factor for subsequent plant growth parameters including germination, seedling vigour and seedling mass (Narayanan et al. 1981; Dahiya et al. 1985). A better understanding of gene actions involved in seed size will facilitate breeding for large seed size in kabuli chickpea. Earlier studies have reported monogenic (Argikar 1956), digenic (Ghatge 1993; Upadhyaya et al. 2006; Hossain et al. 2010), oligogenic (Patil and D'Cruze 1964) and polygenic (Niknejad et al. 1971; Kumar and Singh 1995; Malhotra et al. 1997; Kumhar et al. 2013) inheritance of seed size depending on the number of genes segregating in the populations studied. According to Athwal and Sandha (1967), Smithson et al. (1985) and Kumar and Singh (1995), small seed size was dominant over large one. In contrast, Niknejad et al. (1971) stated that large seed size was partially dominant over the small seed size. Both additive and dominance genetic effects have been reported to be important for seed size by previous researchers (Girase and Deshmukh 2000; Karami and Talebi 2013; Kumhar et al. 2013). As the additive gene action relates to homozygosity, standard selection procedures (like mass selection, progeny selection, etc.) would be advantageous for traits controlled by such additive genes, whereas production of hybrids will benefit in the presence of dominance genes (Edwards et al. 1975). Presence of non-allelic interactions also contributed significantly to the inheritance of quantitative traits (Malhotra and Singh 1989). Girase and Deshmukh (2000), Bhardwaj and Sandhu (2007), Hossain et al. (2010), Kumar et al. (2013) and Sharma et al. (2013) reported the contribution of non-allelic interaction for seed size. The aim of this study was to estimate the components of genetic variation for seed size and other traits in chickpea using generation mean analysis (Hayman 1958; Mather 1949).

Materials and methods

Experimental procedure

The parental genotypes included five kabuli chickpea genotypes (ICC 16644, JGK 2, KAK 2, KRIPA and ICC 17109). Four F_1s were developed by crossing ICC 16644 with JGK 2, KAK 2, KRIPA and ICC 17109 and consequently F_2 and F_3 populations by selfing respective F_1s. In the study, the crosses ICC 16644 × JGK 2, ICC 16644 × KAK 2, ICC 16644 × KRIPA and ICC 16644 × ICC 17109 were designated as C_1, C_2, C_3 and C_4, respectively. The P_1, P_2, F_1, F_2 and F_3 of four crosses were evaluated in a compact family block design with three replications during post-rainy season of 2013–2014 in vertisol at ICRISAT, Patancheru, India. The plots of different generations contained different number of rows, i.e., two rows of parents, one row of F_1, and six rows each of F_2 and F_3 generations. Seeds were treated before sowing with a mixture of 2 g of thiram and 1 g of carbendazim kg^{-1} of seed. The seeds were sown at a wider spacing of 60 cm × 20 cm with single seed per hill in 4 m long row. Care was taken to sow the seeds at uniform depth (5 cm). All the recommended agronomical practices and necessary plant protection measures were followed to raise a healthy crop. The traits assessed were days to first flower, days to maturity, plant height at maturity (cm), number of pods per plant, number of seeds per plant, number of seeds per pod, grain yield per plant (g), biological yield per plant (g) and seed size (100-seed weight in g). The sample sizes (i.e., numbers of plants analyzed per cross) for the experiment varied from 18 plants each in P_1, P_2 and F_1; 210 plants each in F_2 and 210 progenies in each F_3.

Generation means analyses of five populations (P_1, P_2, F_1, F_2 and F_3) and associated scaling tests (Mather 1949) were performed based on the assumption that populations have non-homogeneous variances (Mather and Jinks 1971). The validity of the additive-dominance model for scaling test and joint scaling test were examined using WINDOSTAT version 9.1 software (Indostat services, Hyderabad, India). The mean and variance were calculated as suggested by Hayman (1958). The generation means of traits were used to perform a simple scaling test to test the adequacy of additive–dominance model. The scaling tests, as given by Mather (1949) and Hayman and

Mather (1955) were used. Significance of any one or two scaling tests implies the inadequacy of additive–dominance model. The C and D scaling tests provide a test for dominance × dominance (l) and additive × additive (i) types of epistasis, respectively. Gene effects were estimated by joint scaling test as proposed by Hayman (1958) using WINDOSTAT. This program first tries to fit three parameter model, deletes those with t-values < 2.0, then tests the model significance by weighted χ^2 test. If significant, the program tries to fit a five-parameter model (m = mid parental values, d = additive effects, h = dominance effects, i = additive × additive, l = dominance × dominance) with a step-down for non-significant parameters. If all the parameters are significant then it computes weighted χ^2 test for joint scaling test. These parameters were estimated by weighted least squares method. The purpose of using weights was to account for differential precision with which means of different generations were estimated by virtue of the varying sample size.

Calculations

$$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2,$$

$$D = 4\bar{F}_3 - 2\bar{F}_2 - \bar{P}_1 - \bar{P}_2,$$

$$\text{Mean (m)} = \bar{F}_2,$$

$$\text{Additive effect (d)} = \frac{1}{2}\bar{P}_1 - \frac{1}{2}\bar{P}_2,$$

$$\text{Dominance effect (h)} = (4\bar{F}_1 + 12\bar{F}_2 - 16\bar{F}_3)/6,$$

$$\text{Dominance} \times \text{Dominance (l)} = (8\bar{F}_1 - 24\bar{F}_2 + 16\bar{F}_3)/3,$$

$$\text{Additive} \times \text{Additive (i)} = \bar{P}_1 - \bar{F}_2 + \frac{1}{2}(\bar{P}_1 - \bar{P}_2 + h) - \frac{1}{4}.$$

The variances of the estimates were computed using following formulae

$$V_C = 16V(\bar{F}_2) + 4V(\bar{F}_1) + V(\bar{P}_1) + V(\bar{P}_2),$$

$$V_D = 16V(\bar{F}_3) + 4V(\bar{F}_2) + V(\bar{P}_1) + V(\bar{P}_2),$$

$$V_m = V(\bar{F}_2),$$

$$V_d = \frac{1}{4}[V(\bar{P}_1) + V(\bar{P}_2)],$$

$$V_h = [16V(\bar{F}_1) + 144V(\bar{F}_2) + 256V(\bar{F}_3)]/36,$$

$$V_l == 256V(\bar{F}_3) + 576V(\bar{F}_2) + 64V(\bar{F}_1)]/9,$$

$$V_i = V(\bar{P}_1) + V(F_2) + \frac{1}{4}[V(\bar{P}_1) + V(\bar{P}_2) + V_h] + \frac{1}{16}(V_l),$$

where $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\bar{F}_2$, and $\bar{F}_3$ are the means of female parent, male parent, F_1, F_2 and F_3, respectively; and $V(\bar{P}_1)$, $V(\bar{P}_2)$, $V(\bar{F}_1)$, $V(\bar{F}_2)$, and $V(\bar{F}_3)$ are the variances of female parent, male parent, F_1, F_2 and F_3, respectively.

Results

Phenological traits, plant height and biological yield

Large variability in the mean performance (Table 1) for all the basic generations P_1, P_2, F_1, F_2 and F_3 was observed for phenological traits, i.e., days to first flower and days to maturity. The mean performance of F_1s exceeded the duration of late maturing parent suggesting the presence of over-dominance to those for early phenology. Either or both the C and D scale estimates showed significant deviation from zero for the phenological traits (Table 2) in all the four crosses which revealed the inadequacy of simple additive–dominance model and the presence of non-allelic interaction for these traits. The mean effect of F_2 performance (m) was highly significant in all the crosses. The additive effect (d), was found to be important in governing the phenological traits in all the crosses, whereas the dominance gene effect (h) was significant only for days to maturity in all the crosses except C_2. The analysis of interaction effect revealed that both additive × additive (i) and dominance × dominance (l) interactions were playing important role in governing phenological traits in all the crosses except C_2, where only additive × additive interaction was significant. The gene action was considered to be of duplicate type for days to first flower since the estimates of dominance and dominance × dominance had opposite signs. Days to maturity had duplicate gene effects in the crosses C_3

Table 1 Means and standard errors (±) for various traits in five generations of each of the four crosses of chickpea

Characters	P_1	P_2	F_1	F_2	F_3
Days to first flower					
ICC 16644 × JGK 2					
Means	30.33	34.95	50.47	40.12	43.44
Std. errors	± 0.18	± 0.18	± 0.26	± 0.53	± 0.54
ICC 16644 × KAK 2					
Means	31.50	36.77	51.33	47.30	47.64
Std. errors	± 0.18	± 0.18	± 0.33	± 0.76	± 0.73
ICC 16644 × KRIPA					
Means	30.70	38.70	52.97	42.31	45.48
Std. errors	± 0.24	± 0.13	± 0.26	± 0.64	± 0.69
ICC 16644 × ICC 17109					
Means	31.36	38.20	53.40	42.51	46.03
Std. errors	± 0.24	± 0.17	± 0.26	± 0.64	± 0.72
Days to maturity					
ICC 16644 × JGK 2					
Means	81.10	85.50	92.40	87.06	87.12
Std. errors	± 0.31	± 0.29	± 0.32	± 0.41	± 0.43
ICC 16644 × KAK 2					
Means	80.47	85.53	90.77	93.15	93.27
Std. errors	± 0.29	± 0.44	± 0.34	± 0.54	± 0.54
ICC 16644 × KRIPA					
Means	80.63	89.20	94.00	90.21	94.61
Std. errors	± 0.19	± 0.24	± 0.39	± 0.59	± 0.72
ICC 16644 × ICC 17109					
Means	81.36	90.50	96.47	91.24	95.36
Std. errors	± 0.27	± 0.32	± 0.33	± 0.67	± 0.76
Plant height at maturity (cm)					
ICC 16644 × JGK 2					
Means	43.26	48.40	44.50	48.37	45.69
Std. errors	± 1.47	± 1.26	± 0.77	± 0.39	± 0.39
ICC 16644 × KAK 2					
Means	44.83	50.33	46.30	49.07	46.71
Std. errors	± 0.67	± 1.10	± 1.09	± 0.37	± 0.44
ICC 16644 × KRIPA					
Means	42.56	60.03	50.83	52.71	50.37
Std. errors	± 1.00	± 0.69	± 0.56	± 0.41	± 0.50
ICC 16644 × ICC 17109					
Means	44.96	59.43	49.53	50.78	49.34
Std. errors	± 1.20	± 0.99	± 1.10	± 0.46	± 0.53
No. of pods per plant					
ICC 16644 × JGK 2					
Means	76.13	86.70	130.03	93.00	95.29
Std. errors	± 4.75	± 3.14	± 7.70	± 2.71	± 3.52
ICC 16644 × KAK 2					
Means	80.80	76.93	109.30	76.41	89.83

Table 1 continued

Characters	P_1	P_2	F_1	F_2	F_3
Std. errors	± 4.19	± 3.28	± 8.49	± 2.74	± 3.26
ICC 16644 × KRIPA					
Means	77.23	55.93	91.57	71.25	70.64
Std. errors	± 2.91	± 3.44	± 5.72	± 2.13	± 2.65
ICC 16644 × ICC 17109					
Means	75.43	47.97	85.33	64.46	66.58
Std. errors	± 2.37	± 3.53	± 7.55	± 2.19	± 2.43
No. of seeds per plant					
ICC 16644 × JGK 2					
Means	85.63	91.00	131.13	99.84	101.40
Std. errors	± 4.72	± 3.47	± 7.77	± 2.72	± 3.70
ICC 16644 × KAK 2					
Means	85.50	95.60	110.50	92.08	108.82
Std. errors	± 4.63	± 3.67	± 8.71	± 3.27	± 3.96
ICC 16644 × KRIPA					
Means	85.23	59.27	93.83	76.38	75.95
Std. errors	± 3.13	± 4.28	± 5.78	± 2.22	± 2.83
ICC 16644 × ICC 17109					
Means	82.66	50.53	88.07	69.32	73.18
Std. errors	2.55	3.86	± 8.13	± 2.37	± 2.65
No. of seeds per pod					
ICC 16644 × JGK 2					
Means	1.12	1.06	1.01	1.09	1.07
Std. errors	± 0.02	± 0.01	± 0.01	± 0.01	± 0.01
ICC 16644 × KAK 2					
Means	1.06	1.24	1.01	1.21	1.22
Std. errors	± 0.01	± 0.01	± 0.01	± 0.01	± 0.01
ICC 16644 × KRIPA					
Means	1.10	1.05	1.02	1.08	1.08
Std. errors	± 0.01	± 0.02	± 0.01	± 0.01	± 0.01
ICC 16644 × ICC 17109					
Means	1.12	1.05	1.02	1.08	1.10
Std. errors	± 0.01	± 0.01	± 0.01	± 0.01	± 0.01
Grain yield per plant (g)					
ICC 16644 × JGK 2					
Means	24.00	32.88	36.64	33.23	30.74
Std. errors	± 1.88	± 1.09	± 2.86	± 0.86	± 1.10
ICC 16644 × KAK 2					
Means	23.81	35.55	33.31	26.76	29.73
Std. errors	± 1.93	± 0.99	± 2.77	± 0.86	± 1.02
ICC 16644 × KRIPA					
Means	23.39	28.74	33.27	28.54	26.32
Std. errors	± 1.87	± 1.28	± 1.96	± 0.81	± 1.01
ICC 16644 × ICC 17109					
Means	23.88	29.94	33.37	28.75	27.67

Table 1 continued

Characters	P_1	P_2	F_1	F_2	F_3
Std. errors	± 1.88	± 1.37	± 3.36	± 0.88	± 0.94
Biological yield per plant (g)					
ICC 16644 × JGK 2					
Means	39.22	53.79	63.95	55.53	53.60
Std. errors	± 2.96	± 1.57	± 5.10	± 1.38	± 1.75
ICC 16644 × KAK 2					
Means	43.27	57.32	60.58	49.29	57.01
Std. errors	± 2.99	± 1.81	± 4.10	± 1.41	± 1.76
ICC 16644 × KRIPA					
Means	40.58	49.61	57.31	51.79	49.93
Std. errors	± 2.50	± 2.27	± 2.94	± 1.39	± 1.70
ICC 16644 × ICC 17109					
Means	43.30	49.53	61.75	48.71	52.96
Std. errors	± 2.83	± 2.017	± 5.34	± 1.55	± 1.68
100-Seed weight (g)					
ICC 16644 × JGK 2					
Means	25.21	36.00	26.43	33.85	30.79
Std. errors	± 0.54	± 0.82	± 0.94	± 0.44	± 0.46
ICC 16644 × KAK 2					
Means	24.16	41.62	30.27	30.15	28.68
Std. errors	± 0.58	± 0.59	± 1.19	± 0.50	± 0.50
ICC 16644 × KRIPA					
Means	26.98	47.76	35.61	37.86	34.33
Std. errors	± 1.99	± 0.70	± 0.59	± 0.45	± 0.48
ICC 16644 × ICC 17109					
Means	26.67	55.56	37.58	39.28	38.50
Std. errors	± 1.71	± 0.56	± 0.89	± 0.53	± 0.54

and C_4, whereas it had complementary gene effect in the cross C_1.

For plant height, the character expressions in F_1s were closer to the short parent, ICC 16644 which revealed that short plant height was partially dominant over the tall plant height. Either or both of the scaling tests were significant which revealed the importance of epistasis for the trait. Both the main effects as well as interaction effects were governing plant height in all the four crosses except C_4, whereas dominance gene effects were not important in governing this trait. The gene action was considered to be of duplicate type for this trait.

For biological yield per plant, significant estimates of C and D scale in crosses C_2 and C_4 indicated the presence of epistasis for the trait in both the crosses. The mean performance of F_1s was found higher than that of their respective parents for this trait. Additive gene effect was important for all the crosses, while dominance gene effect was important for the cross C_2 only. Dominance gene effect played important role in governing the trait in C_2 only. Among the interaction effects, only dominance × dominance interaction was important for the crosses C_2 and C_4. The cross C_2 exhibited both the main effects, i.e., additive and dominance and interaction effect dominance × dominance for the inheritance of this trait. The opposite signs of dominance and dominance × dominance revealed that duplicate epistasis was involved in controlling the trait in the crosses C_2 and C_4.

Table 2 Estimates of scaling test (± SE of mean) and gene effects (± SE of mean) for various traits in the four crosses of chickpea using five-parameter model

Characters/crosses	Scales		Genetic parameters					Gene action
	C	D	m	d	h	l	i	
Days to first flower								
ICC 16644 × JGK 2	− 6.27** (± 2.20)	27.67** (± 2.41)	40.12** (± 0.53)	1.58** (± 0.13)	− 1.94 (± 1.79)	45.26** (± 5.16)	− 16.33** (± 1.67)	Duplicate
ICC 16644 × KAK 2	18.33** (± 3.14)	27.75** (± 3.32)	47.30** (± 0.76)	2.67** (± 0.13)	1.79 (± 2.49)	12.56 (± 5.31)	− 10.11** (± 2.35)	
ICC 16644 × KRIPA	− 6.11* (± 2.64)	27.90** (± 3.08)	42.31** (± 0.64)	4.00** (± 0.14)	− 1.35 (± 2.27)	45.35** (± 6.39)	− 11.62** (± 2.08)	Duplicate
ICC 16644 × ICC 17109	− 6.26* (± 2.62)	29.60** (± 3.17)	42.51** (± 0.64)	3.45** (± 0.15)	− 2.12 (± 2.32)	47.81** (± 6.43)	− 13.87** (± 2.10)	Duplicate
Plant height at maturity								
ICC 16644 × JGK 2	15.90** (± 2.94)	− 2.54 (± 2.60)	48.37** (± 0.41)	3.02** (± 0.21)	4.56** (± 1.42)	− 24.58** (± 4.06)	10.38** (± 1.36)	Duplicate
ICC 16644 × KAK 2	8.58** (± 2.94)	− 6.46** (± 2.31)	49.09** (± 0.37)	2.92** (± 0.63)	4.45** (± 1.58)	− 20.05** (± 4.80)	11.24** (± 1.75)	Duplicate
ICC 16644 × KRIPA	2.57 (± 2.34)	− 10.51** (± 2.51)	52.71** (± 0.41)	6.73** (± 0.62)	4.97** (± 1.63)	− 17.45** (± 4.52)	20.91** (± 1.87)	Duplicate
ICC 16644 × ICC 17109	2.74 (± 3.28)	− 5.53* (± 2.80)	50.79** (± 0.46)	5.77** (± 0.78)	3.01 (± 1.85)	− 11.04* (± 5.52)	15.68** (± 2.24)	Duplicate
Days to maturity								
ICC 16644 × JGK 2	− 3.15 (± 1.79)	7.77** (± 1.95)	87.06** (± 0.41)	2.20** (± 0.21)	3.39* (± 1.42)	14.57** (± 4.06)	− 1.31 (± 1.36)	Complementary
ICC 16644 × KAK 2	25.06** (± 2.33)	20.77** (± 2.47)	93.15** (± 0.54)	2.53** (± 0.26)	− 1.91 (± 1.81)	− 5.71 (± 5.27)	− 4.60* (± 1.73)	
ICC 16644 × KRIPA	3.04 (± 2.50)	28.17** (± 3.15)	90.22** (± 0.59)	4.28** (± 0.16)	− 9.19** (± 2.28)	33.20** (± 6.17)	− 9.70** (± 2.02)	Duplicate
ICC 16644 × ICC 17109	0.34 (± 2.78)	27.26** (± 3.33)	91.24** (± 0.67)	4.65** (± 0.21)	− 7.50** (± 2.43)	35.90** (± 6.75)	− 8.82** (± 2.21)	Duplicate
Number of pods per plant								
ICC 16644 × JGK 2	− 50.90* (± 19.71)	32.33* (± 16.14)	93.00** (± 2.72)	5.28 (± 2.85)	18.58 (± 12.02)	110.97** (± 35.35)	− 19.47 (± 12.34)	Complementary
ICC 16644 × KAK 2	− 70.68** (± 20.91)	48.75** (± 15.15)	76.41** (± 2.74)	− 1.99 (± 2.66)	− 13.85 (± 11.76)	159.24** (± 36.04)	− 48.15** (± 12.16)	Duplicate
ICC 16644 × KRIPA	− 33.31* (± 15.05)	4.91 (± 12.38)	71.25** (± 2.13)	− 11.65** (± 2.38)	15.16 (± 9.09)	50.96* (± 26.91)	− 32.13** (± 9.20)	Complementary
ICC 16644 × ICC 17109	− 32.65 (± 18.00)	17.57 (11.51)	64.46** (± 2.19)	− 11.95** (± 2.15)	8.26 (± 9.31)	66.96* (± 29.71)	− 41.05** (± 9.59)	Complementary
Number of seeds per plant								
ICC 16644 × JGK 2	− 39.55* (± 19.87)	29.29 (± 16.84)	99.84** (± 2.73)	2.68 (± 2.93)	16.70 (± 12.42)	91.78* (± 35.99)	− 20.75 (± 12.96)	Complementary
ICC 16644 × KAK 2	− 33.78 (± 22.59)	− 70.03** (± 18.14)	92.08** (± 3.27)	− 5.45 (± 2.97)	− 32.37* (± 13.71)	138.41** (± 40.88)	− 62.41** (± 13.87)	Duplicate
ICC 16644 × KRIPA	− 36.62* (± 15.66)	− 3.48 (± 13.43)	76.39** (± 2.23)	− 17.98** (± 2.84)	12.80 (± 9.58)	44.19 (± 27.98)	− 39.75** (± 9.73)	
ICC 16644 × ICC 17109	− 31.61 (± 19.41)	21.31 (± 12.53)	69.32** (± 2.37)	− 15.85** (± 2.33)	2.21 (± 10.10)	70.55* (± 32.12)	− 51.17** (± 10.37)	Complementary
Number of seeds per pod								
ICC 16644 × JGK 2	0.16** (± 0.04)	− 0.07 (± 0.05)	1.09** (± 0.01)	− 0.03** (± 0.01)	− 0.01 (± 0.03)	− 0.31** (± 0.08)	− 0.01 (± 0.04)	Complementary
ICC 16644 × KAK 2	0.52** (± 0.05)	0.16** (± 0.06)	1.21** (± 0.01)	− 0.04** (± 0.01)	− 0.16** (± 0.003)	− 0.48** (± 0.11)	− 0.09* (± 0.04)	Complementary
ICC 16644 × KRIPA	0.01 (± 0.04)	− 0.08 (± 0.05)	1.08** (± 0.01)	− 0.07** (± 0.01)	− 0.05 (± 0.03)	− 0.11 (± 0.08)	− 0.08* (± 0.03)	
ICC 16644 × ICC 17109	0.06 (± 0.04)	0.05 (± 0.04)	1.08** (± 0.01)	− 0.05** (± 0.01)	− 0.10** (± 0.03)	− 0.01 (± 0.07)	− 0.12** (± 0.03)	Complementary
Grain yield per plant								
ICC 16644 × JGK 2	2.75 (± 7.04)	− 0.40 (± 5.22)	33.23** (± 0.87)	4.44** (± 1.09)	8.93* (± 3.92)	− 4.19 (± 11.88)	− 9.60* (± 4.26)	Duplicate
ICC 16644 × KAK 2	− 20.95** (± 6.90)	4.065** (± 4.94)	26.76** (± 0.86)	4.87** (± 1.09)	− 3.56 (± 3.72)	33.32** (± 11.49)	3.55 (± 4.17)	Duplicate
ICC 16644 × KRIPA	− 7.92 (± 5.60)	− 7.32 (± 4.92)	28.54** (± 0.81)	0.37 (± 1.16)	9.07** (± 3.40)	0.80 (± 9.92)	4.30 (± 3.81)	Complementary
ICC 16644 × ICC 17109	− 12.94 (± 7.95)	3.99 (± 4.79)	26.75** (± 0.89)	2.80* (± 1.17)	1.956 (± 3.81)	22.59 (± 12.49)	0.77 (± 4.37)	

Table 2 continued

Characters/crosses	Scales		Genetic parameters					Gene action
	C	D	m	d	h	l	i	
Biological yield per plant								
ICC 16644 × JGK 2	1.21 (± 12.08)	10.33 (± 8.24)	55.53** (± 1.38)	7.29** (± 1.68)	10.77 (± 6.40)	12.156 (± 19.86)	7.89 (± 6.96)	
ICC 16644 × KAK 2	− 26.96* (± 10.56)	26.88** (± 8.36)	49.29** (± 1.41)	6.02** (± 1.75)	− 13.07* (± 6.13)	71.29** (± 18.33)	10.30 (± 6.67)	Duplicate
ICC 16644 × KRIPA	2.37 (± 8.80)	5.96 (± 8.13)	51.80** (± 1.34)	4.51* (± 1.71)	8.64 (± 5.69)	4.79 (± 16.41)	1.44 (± 6.01)	
ICC 16644 × ICC 17109	− 16.423 (± 12.85)	26.63** (± 8.41)	48.72** (± 1.56)	5.64** (± 1.74)	− 2.64 (± 6.49)	57.40** (± 20.91)	− 9.21 (± 7.17)	Duplicate
100-seed weight								
ICC 16644 × JGK 2	17.32** (± 2.76)	− 9.77** (± 2.26)	33.85** (± 0.44)	3.40** (± 0.49)	3.22* (± 1.63)	− 36.13** (± 4.97)	16.19 (± 1.71)	Duplicate
ICC 16644 × KAK 2	− 11.72** (± 3.33)	− 17.34** (± 2.39)	30.12** (± 0.50)	5.71** (± 0.42)	3.99* (± 1.85)	− 7.50 (± 5.79)	21.07** (± 1.93)	Duplicate
ICC 16644 × KRIPA	3.49 (± 3.03)	15.13** (± 3.00)	37.86** (± 0.45)	9.39** (± 1.06)	7.90** (± 1.62)	− 24.83** (± 4.72)	29.44** (± 2.71)	Duplicate
ICC 16644 × ICC 17109	− 2.32 (± 3.30)	− 8.82** (± 3.02)	39.28** (± 0.53)	13.43** (± 0.90)	0.94 (± 1.90)	− 8.67 (± 5.68)	32.35** (± 2.63)	

m Mean effect, *d* additive effect, *h* dominance effect, *i* additive × additive effect, *l* dominance × dominance effects

*P > 0.05, **P > 0.01

Seed size, grain yield and yield components

The mean performance of F_1s generated from the crosses revealed that smaller seed size was partially dominant over larger seed size. Present study showed that the F_2 performance (m) was highly significant in all the crosses studied. Significance of either of the two scales indicated the presence of non-allelic interactions for seed size. Both the main effects, i.e., additive and dominance were significant for the trait in all the crosses except C_4, where only additive gene action was important. Additive × additive interaction was found to be important in all the crosses except the cross C_1, where only dominance × dominance interaction effect was important. Duplicate gene action was recorded in all the crosses for seed size.

For grain yield per plant, the estimated values of both scales C and D significantly deviated from zero for the cross C_2 only. The additive effect was found to be significant in all the crosses except C_3. The dominance gene effect played a significant role in crosses C_1 and C_3. Among interactions, dominance × dominance effect was significant for C_2 and C_3, while additive × additive was important for the cross C_1 only. Duplicate gene action was controlling the trait in C_1 and C_2.

Substantial amount of variability in the mean performance for all generations was observed for number of pods per plant. The mean performance of F_1s was found to be higher than either of the parents and the scaling test revealed the presence of epistasis for number of pods per plant in all the crosses, except C_4. Additive effect was found to be important for the crosses C_3 and C_4. Additive × additive and dominance × dominance interactions were governing the trait in all the crosses except C_1, where only dominance × dominance interaction was significant in governing the trait. The same sign of dominance and dominance × dominance interaction effects suggested complementary type of epistasis in all the crosses except C_2, which exhibited duplicate gene action for the trait.

The mean performance of F_1s was found to be higher than either of the parents for number of seeds per plant. Significance of the scaling test revealed the presence of epistasis for the character. Additive effect was found to be important for the crosses C_3 and C_4, whereas dominance effect was important for C_3 only for number of seeds per plant. Additive × additive

effect was important in the crosses C_2, C_3 and C_4, while dominance × dominance interaction was found significant in all the crosses except C_3. Duplicate gene action was present in C_3 and C_4, and complementary type in C_1.

Scaling test revealed the presence of epistasis for number of seeds per pod in the crosses C_1 and C_2. The additive effect was governing the trait in all the crosses, while the dominance effect was found to be significant in the crosses C_2 and C_4. Among the interactions, dominance × dominance was significant in C_1 and C_2 only. Additive × additive interaction was important in all the crosses except C_1. The same sign of dominance and dominance × dominance suggested complementary type of epistasis for number of seeds per pod.

Discussion

In this study, the mean effect of F_2 performance (m) was highly significant for all the characters in all the crosses. The variability observed for all the traits in F_2 and F_3 of all the four crosses suggests the scope for improvement of these traits through selection. It was observed that the estimate of a genetic parameter significant for a particular trait in one cross was not necessarily significant for the same trait in other crosses, which revealed that the genetic behavior was variable from cross to cross and trait to trait.

In addition to additive gene effects, additive × additive and dominance × dominance effects had high contribution in controlling the phenology. The negative estimate of additive × additive effects shows the gene pairs responsible for phenology are in dispersive form in their respective parents. The gene action was considered to be duplicate type for the character, since the estimates of dominance and dominance × dominance effect had opposite signs. Dispersion of alleles along with duplicate type of epistasis may lead to the faulty selection in early generations of segregants since presence of duplicate epistasis can hinder progress and make it difficult to fix genotypes at a high level of manifestation. Such gene effects can, however, be exploited by inter-mating the selected segregants and delaying the selection to advanced generations. Other possibilities could be a diallel selective mating system as proposed by Jensen (1970) or the recurrent selection procedures (Singh and Power 1990). Transgressive segregation in F_2 generation had been recorded for phenology as the mean value of F_2 progenies was found higher than the parental means. This might be due to the fact that alleles at multiple loci that originated from different loci from both parents recombine in the F_1 hybrids that might have increased the value of phenotypes (Bell and Travia 2005).

For plant height at maturity, epistatic interactions were significant along with main effects with duplicate gene action. Negative sign of dominance × dominance effect indicated ambidirectional dominance but the positive sign of additive × additive effect reflected the association of alleles in the parental lines. Similar results were found by Bhardwaj and Sandhu (2007) and Kumar et al. (2013), while according to Girase and Deshmukh (2000) only main effects, i.e., additive and dominance were important for plant height in chickpea.

The main effect additive was governing biological yield per plant in all the crosses, while dominance effect was important for C_2 only. Additive gene effect, dominance effect and dominance × dominance effects were also important for this trait in C_2. For the cross C_4, additive effect and dominance × dominance effect were important. Duplicate type of epistasis was reported for the trait in both the crosses. For the crosses C_1 and C_3, only additive effect and dominance effect, respectively, were important. Since, additive and non-additive gene action were important for this trait, improvement may be possible by delaying selection to later filial generations. These findings are in agreement with Kumhar et al. (2013).

For number of pods per plant and number of seeds per plant, scaling tests indicated the presence of epistasis in three crosses (C_1, C_2, and C_3). Dominance × dominance component was higher in magnitude for the traits number of pods per plant and number of seeds per plant with complementary epistasis in C_1. Also, positive sign of dominance × dominance interaction showed unidirectional dominance whereas, for C_4, in addition to additive gene action, both the interaction effects were also significant. Negative and significant value of additive × additive interactions showed allelic dispersion in parents for both the traits. Additive gene effect and additive × additive interaction were playing important role for number of seeds per plant in cross C_3. In C_2, along with dominance gene action both the epistatic effects were important for number of seeds per

plant, while for number of pods per plant only epistatic effect was important. Pundir et al. (1991) and Panchbhai et al. (1992) also reported non-additive gene action for these traits. According to Girase and Deshmukh (2000) and Srinivasan et al. (2011) only the main effects were significant and there was no epistasis for these traits. The dominance × dominance component was higher in magnitude for these traits, hence selection should be delayed up to few generations till the dominance component is reduced.

All the components of gene action were found to be important in governing the number of seeds per pod which indicate the polygenic nature of the trait. Additive gene action played an important role in expression of the trait in all the crosses. Negative sign of additive gene action suggested the existence of higher proportion of alleles showing negative effect in the parents. Among interactions, dominance × dominance was important in C_1 and C_2, while additive × additive was important in all the crosses except in C_1 depicting the major role of additive × additive gene action. Complementary type of epistasis was observed for number of seeds per pod. Preponderance of additive effect, additive × additive interaction, along with complementary type of interaction showed effectiveness of selection for improving this trait. Similar results were observed by Bhardwaj and Sandhu (2007) and Kumhar et al. (2013) in chickpea.

For seed size, the mean performance of F_1s generated from the crosses revealed partial dominance of smaller seed size over larger seed size. Both the main effects, i.e., additive and dominance were important in all the crosses except C_4 where only additive effect was important. However, relatively higher magnitude of additive gene effects revealed the preponderance of additive gene action. The positive sign of dominance effect showed that increasing alleles were involved in dominant phenotype, i.e., small seed size. Dominance × dominance effect governed the trait in C_1 and C_3 only. In all the crosses, additive × additive interaction was important, except in C_1. Duplicate epistasis was evident from the opposite signs of dominance effect and dominance × dominance effect. Similar results were reported by Bhardwaj and Sandhu (2007), while Hossain et al. (2010) reported complementary gene action for this trait. Positive sign for additive × additive effect in all the crosses showed that there was association of alleles in parents for the trait. However, negative sign of dominance × dominance effect indicated ambidirectional dominance. The genetic control of seed size by additive and non-additive gene action indicated that selection for large seed size in early generations of C_4 would be effective.

Interestingly, for grain yield, differential role of individual genes and their interactions were found to be important in different crosses. The estimates of both the scales C and D significantly deviated from zero for the cross C_2 only. However, in the cross C_1 interaction components were significant. Mather and Jinks (1971) pointed out some conditions in which one or more of these generations means (i.e., B_1, B_2, F_2 and F_3 means those referred to as A, B, C and D scales) may not deviate significantly even when non-allelic interactions are present. These conditions are (a) with a dispersed pair of genes, the three groups of interactions, additive × additive, additive × dominance (j) and dominance × dominance may partly cancel out, and (b) with more than two interacting genes, cancellation can arise because of dispersion and because the individual i's, j's and l's may differ from one pair of interacting genes to another. Additive effect, dominance effect and additive × additive interaction were important for C_1 with preponderance of additive × additive interaction. It indicated that single plant selection should be delayed in segregating generations to minimise the dominance and epistatic effects. In C_2, additive effect and dominance × dominance interaction were governing the trait. In the crosses C_1 and C_2, both additive as well as non-additive gene action were important with duplicate type of epistasis governing the trait. Importance of additive as well as non-additive gene actions for grain yield was also reported by Bhardwaj et al. (2005), Deb and Khaleque (2009) and Karami and Talebi (2013). For the crosses C_3 and C_4, only dominance and additive gene effects, respectively, were significant and the absence of epistasis confirmed the results of scaling test for this trait. Srinivasan et al. (2011) reported that dominance effect in control condition, while additive effect in saline condition were governing the grain yield in chickpea. However, difference in gene actions among the crosses for grain yield in the study indicated that the four male parents might be different in their genetic constitutions.

In conclusion, seed size was controlled by both additive and dominance effects as well as duplicate epistasis. Similar trend was observed for phenological

traits and yield traits, i.e., number of pods per plant, number of seeds per plant and grain yield per plant. These traits were controlled by both additive and non-additive gene actions with duplicate type of epistasis suggesting that the selection for these traits would be more effective in later filial generations because useful genes will be fixed by then due to breakage of unfavourable linkages.

Acknowledgements CGIAR (Consultative Group on International Agricultural Research) Research Program on Grain Legumes for financial support.

References

Argikar GP (1956) Some qualitative and quantitative observation on the genetic improvement of green seeded strain of *Cicer arietinum* L. Indian J Genet Plant Breed 16:52–56

Athwal DS, Sandha GS (1967) Inheritance of seed size and seed number per pod in *Cicer*. Indian J Genet Plant Breed 27:21–33

Bell MA, Travia MP (2005) Hybridization, transgressive segregation, genetic covariation and adaptive radiation. Trends Ecol Evol 20(7):358–361

Bhardwaj R, Sandhu JS (2007) Gene effects for yield and its components in chickpea. Crop Improv 34(1):48–51

Bhardwaj R, Sandhu JS, Sharma SR (2005) Gene action studies for yield and its component in chickpea (*Cicer arietinum* L.). In: Abstracts of fourth international food legumes research conference, 18–22 October, New Delhi, India, p 502

Dahiya BS, Solanki IS, Kumar R (1985) Germination rate and its genetics in chickpea. Int Chickpea Newsl 13:6–8

Deb AC, Khaleque MA (2009) Nature of gene action of some quantitative traits in chickpea (*Cicer arietinum* L.). World J Agric Sci 5(3):361–368

Edwards LH, Ketata H, Smith EL (1975) Gene action of heading date, plant height and other characters in two winter wheat crosses. Crop Sci 16:275–277

FAOSTAT (2016). http://faostat.fao.org/. Accessed 27 Feb 2018

Gaur PM, Pande S, Upadhyaya HD, Rao BV (2006) Extra-large kabuli chickpea with high resistance to Fusarium wilt. J SAT Agric Res 2:2

Ghatge RD (1993) Inheritance of seed size in chickpea (*Cicer arietinum* L.). J Soils Crops 3:56–59

Girase VS, Deshmukh RB (2000) Gene action for yield and its component in chickpea. Indian J Genet Plant Breed 60(2):185–189

Hayman BI (1958) The separation of epistatic from additive and dominance variation in generation means. Heredity 12:371–390

Hayman BI, Mather K (1955) The description of genetic interactions in continuous variation. Biometrics 11:69–82

Hossain S, Ford R, McNeil D, Pittock C, Panozzo JF (2010) Inheritance of seed size in chickpea (*Cicer arietinum* L.) and identification of QTL based on 100-seed weight and seed size index. Aust J Crop Sci 4:126–135

Jensen NE (1970) Diallel selective mating system or cereal breeding. Crop Sci 10:629–635

Karami E, Talebi R (2013) Nature of gene action and genetic parameters for yield and its components in chickpea. Afr J Biotechnol 12(51):7038–7042

Kumar S, Singh O (1995) Inheritance of seed size in chickpea. J Genet Breed 49:9–104

Kumhar BL, Singh D, Bhanushally TB, Koli NR (2013) Gene effects for yield and yield components in chickpea (*Cicer arietinum* L.) under irrigated and rainfed conditions. J Agric Sci 5(3):1–13

Malhotra RS, Singh KB (1989) Detection of epistasis in chickpea. Euphytica 40:169–172

Malhotra RS, Bejiga G, Singh KB (1997) Inheritance of seed size in chickpea. J Genet Breed 51:45–50

Mather K (1949) Biometrical genetics. Methuen and Co. Ltd., London

Mather K, Jinks JL (1971) Biometrical genetics. The study of continuous variation. Chapman and Hall Ltd., London

Narayanan A, Saxena NP, Sheldrake AR (1981) Varietal differences in seed size and seedling growth of pigeonpea and chickpea. Indian J Agric Sci 51:389–393

Niknejad M, Khosh-khui M, Ghorashy SR (1971) Inheritance of seed size in chickpeas (*Cicer arietinum* L.). Crop Sci 11:768–769

Panchbhai KM, Thote SG, Patil AJ, Wanjari KB (1992) Study of genetic variation in bulk populations of chickpea (*Cicer arietinum* L.) developed through different breeding methods. Ann Plant Physiol 6(1):73–76

Patil JA, D'Cruze R (1964) Inheritance of seed size in gram (*Cicer arietinum* L.). Poona Agric Coll Mag 54:21–22

Pundir RPS, Reddy KN, Mengesha MH (1991) Genetics of some physio-morphic and yield traits of chickpea (*Cicer arietinum* L.). Legum Res 14(4):157–161

Sharma S, Upadhyaya HD, Gowda CLL, Kumar S, Singh S (2013) Genetic analysis for seed size in three crosses of chickpea (*Cicer arietinum* L.). Can J Plant Sci 93:1–9

Singh KB (1987) Chickpea breeding. In: Saxena MC, Singh KB (eds) The chickpea. CAB International, Wallingford, pp 127–162

Singh O, Paroda RS (1986) Association analysis of grain yield and its components in chickpea following hybridization and a combination of hybridization and mutagenesis. J Agric Sci 56:139–141

Singh S, Power IS (1990) An appraisal of selection methods in self fertilized crops. In: Pehl RK, Meharchandani N (eds) Trends in crop improvement, India, p 17–26

Smithson JB, Thompson JA, Summerfield RJ (1985) Chickpea (*Cicer arietinum* L.). In: Summerfield RJ, Roberts EH (eds) Grain legume crops. Collins, London, pp 312–390

Srinivasan S, Gaur PM, Colmer TD, Krishnamurthy L, Vadez V, Siddique KHM (2011) Estimation of genetic components of variation for salt tolerance in chickpea using the generation mean analysis. Euphytica 182:73–86

Upadhyaya HD, Kumar S, Gowda CLL, Singh S (2006) Two major genes for seed size in chickpea (*Cicer arietinum* L.). Euphytica 147(3):311–315