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Generation mean analysis to elucidate predominant gene effects and interrelationships of yield and contributing traits in chickpea under irrigated conditions

S.A. Shendekar[1], N.S. Kute[1]*, Banoth Madhu[2], A.S. Totre[3], P.L. Kulwal[4] and G.C. Shinde[1]

[1]Department of Agricultural Botany (Genetics and Plant Breeding), Mahatma Phule Krishi Vidyapeeth, Rahuri- 413 722, India
[2]Department of Genetics and Plant Breeding, School of Agriculture, SR University, Warangal-506 371, India
[3]Department of Agricultural Botany (Genetics and Plant Breeding), DUS testing on Chickpea, Mahatma Phule Krishi Vidyapeeth, Rahuri- 413 722, India
[4]Department of Agricultural Botany (Genetics and Plant Breeding), State Level Biotechnology Center, Mahatma Phule Krishi Vidyapeeth, Rahuri- 413 722, India

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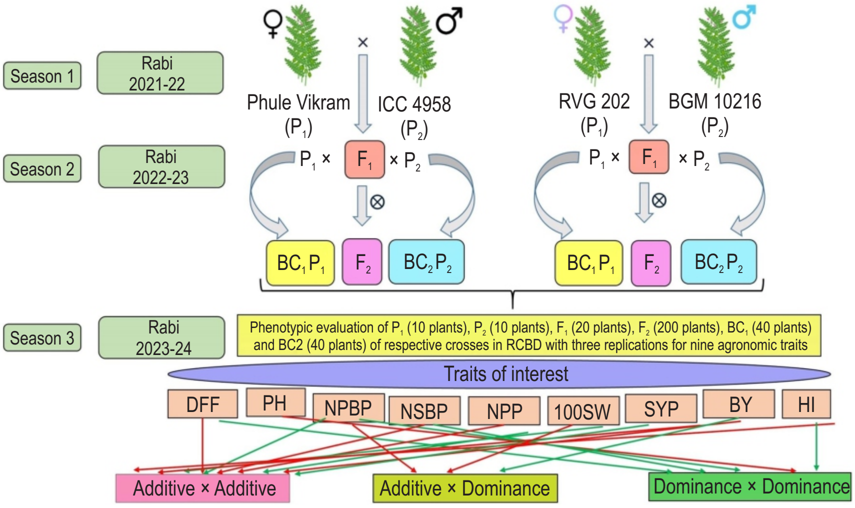
***Corresponding Author Email:** nskute2019@gmail.com ***ORCiD:** https://orcid.org/0000-0003-4259-3126

Abstract

Aim: The study aimed to estimate the gene action for yield and its components in chickpea through generation mean analysis and assess variability and trait interrelationships.



Methodology: The experiment was conducted at the Pulses Improvement Project, Department of Genetics and Plant Breeding, Mahatma Phule Krishi Vidyapeeth, Rahuri, India in *Rabi* 2023-24. The study used six generations (P_1, P_2, F_1, F_2, BC_1, & BC_2) from two crosses: Phule Vikram × ICC 4958 and RVG 202 × BGM 10216.

Results: The adequacy of the additive-dominance model was assessed using the joint scaling test. Significant results for all traits, except NPBP (No. of primary branches per plant) in Cross I, indicated model applicability. The dominance component exceeded the additive for most traits like NPP (No. of pods per plant) and 100SW (100 seed weight) in both the crosses, and DFF (days to 50% flowering), NPBP, SYP (seed yield per plant), BY (biomass per plant) and HI (harvest index) in Cross I. Both additive and non-additive gene actions contributed significantly. Implications for breeding strategies were discussed based on the type of gene action observed. Higher PCV (phenotypic coefficient of variation) than GCV (genotypic coefficient of variation) indicated environmental influence. Moderate heritability, genetic advance, and high heterosis for SYP were observed. Strong correlations between SYP and key yield components suggest that simultaneous selection for these traits can enhance chickpea productivity.

Interpretation: Identifying gene action and variability aids breeders in applying selection strategies, guiding breeding programs for development of high-yielding chickpea cultivars.

Key words: Agronomic traits, Chickpea, Gene action, Generation mean analysis

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Introduction

Chickpea (*Cicer arietinum* L.) is a major global pulse crop, with India, Australia, and Mexico as leading exporters (Muehlbauer *et al.,* 2017). It ranks third among pulses, covering 14.09 million ha and producing 16.51 million tons with a productivity of 1171 kg ha^{-1}. In India, it occupies 9.46 million ha, yielding 11.58 million tons at 1224 kg ha^{-1} (FAO, 2023–24). Despite India's leading contribution, chickpea productivity remains low due to its cultivation by resource-poor farmers under marginal conditions, which highlights the urgent need to enhance production to meet the increasing food demand. Therefore, the development of smart, high-yielding varieties adapted to diverse agro-climatic environments is essential (Kumar *et al.,* 2012; Kaur *et al.,* 2021). It is a diploid (2n = 2x = 16) crop with a genome size of ~931 Mbp and is highly self-pollinated, with an outcrossing rate below 1% (Singh *et al.,* 2008). Chickpea is nutritionally important, especially in vegetarian diets, providing rich carbohydrates (≈60%), protein (17–22%), essential vitamins, and minerals such as Ca, Mg, P, and K. Its tender leaves are also consumed as leafy vegetables, adding valuable micronutrients. (Jukanti *et al.,* 2012; Ibrikci *et al.,* 2003). Additionally, they enrich soil fertility through Rhizobium-mediated biological nitrogen fixation (Nagpal *et al.,* 2023).

Yield and other key traits are highly affected by the environmental factors, and understand their effects on yield is important (Watson, 1952). Moreover, knowledge of the inheritance pattern of economically important traits such as yield is fundamental for breeding programmes targeting diverse environments (Baenziger *et al.,* 2006). Understanding gene action is critical for effective breeding strategies. Many studies on chickpea gene action, based on diallel mating, do not capture non-allelic interactions, leading to biased estimates of additive and dominance components (Deshmukh and Gawande, 2016; Rahman *et al.,* 2022). Conventional methods like diallel, partial diallel, and line × tester analysis estimate additive and dominance effects but fail to fully capture epistatic (non-allelic) interactions, which play a major role in the inheritance of complex traits. The analysis of generation mean analysis includes test of epistasis, which gives information about the presence or absence of epistasis. If epistasis is present, it will give detailed estimate of different components of non-allelic interactions (Panse and Sukhatme, 1995; Nehra *et al.,* 2020).

Improving yield and developing superior cultivars depend on the availability of adequate genetic variability (Alemu *et al.,* 2017). Since phenotypic variation is largely governed by genotype, environment and genotype × environment interactions, understanding genetic variability is crucial. Genotypic variation, being heritable, holds particular significance for plant breeders (Tadesse *et al.,* 2016). Sufficient genetic variability is essential because crossing diverse parents can produce heterotic progenies in later generations. Beyond variability, the transmission of genes to progenies measured by heritability is critical for guiding the selection process (Alemu *et al.,* 2017). However, heritability alone is insufficient; it must be considered alongside genetic advance (GA) and genetic advance as a percentage of the mean (GAM) to accurately predict genetic gains (Shukla *et al.,* 2006). Yield is a complex, environment-sensitive trait; hence, indirect selection via related components is more effective than direct selection (Sohail *et al.,* 2018). Therefore, the present study was undertaken to evaluate the nature of gene action controlling yield and its related traits and to estimate genetic parameters along with their associations in two chickpea crosses under investigation.

Materials and Methods

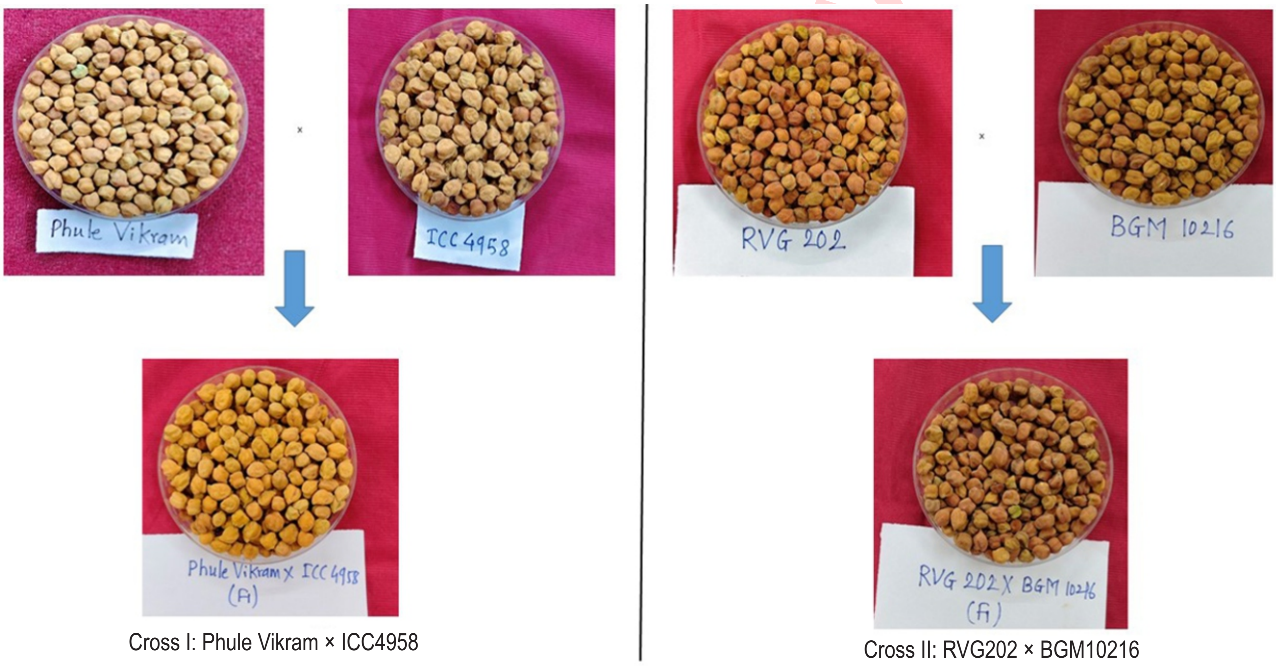
Selection and development of plant material: The experimental material consisted of six populations; parents (P_1, P_2), F_1 and F_2 generations and backcross generations (BC_1P_1, BC_1P_2) developed from two crosses, Phule Vikram × ICC 4958 and RVG-202 × BGM-10216. Four diverse parental lines (Phule Vikram, ICC 4958, RVG 202, BGM 10216) were purified by selfing single plants from each germplasm and selected based on yield and key traits (Table 1). Parents exhibited similar phenologies (46 days to flowering) and drought tolerance. F_1 hybrids were produced during *Rabi* 2021-22. In *Rabi* 2022-23, F_1 plants were either self-pollinated to develop F_2 populations or backcrossed to parents to produce BC_1P_1 and BC_1P_2. *Hybridity* of F_1 hybrids was confirmed by purple flowers and dark seeds, with seed coat color details are shown in Fig. 1.

Field experiment: The study was carried out in *Rabi* 2023-24 at the Pulses Improvement Project, Department of Genetics and Plant Breeding, Mahatma Phule Krishi Vidyapeeth (MPKV), Rahuri, India (19°23'26.5164"N, 74°38'53.1672"E; 657 m above MSL). The site features deep black clay soil with good drainage, moderate to high fertility, neutral to alkaline pH (6.5–7.76) and EC ranging from 0.23 to 0.48 dS m^{-1}. Soil organic carbon was 0.57%, with low available N (72.13 mg kg^{-1}), medium available P (13.2 mg kg^{-1}) and medium K (159 mg kg^{-1}). During season, the daily mean temperatures varied between 25°C to 27°C, total rainfall was approximately 253–296 mm and sunshine duration averaged 7–9 hours per day. Six populations from two crosses were evaluated using a randomized complete block design (RCBD) with three replicates. P_1, P_2, F_1, BC_1P_1 and BC_1P_2 were each represented by two replicated rows, while F_2 was unreplicated with eight rows. Rows were 1.80 m long with 30 × 10 cm spacing (row × plant). Sample sizes included ten plants each for P_1 and P_2, twenty for F_1, 200 for F_2, and forty each for BC_1P_1 and BC_1P_2. A single row of Phule Vikram was planted as a border to minimize edge effects. The study was conducted under irrigated conditions to ensure optimal moisture availability. This helped minimize environmental stress and allowed for accurate assessment of genotypic performance for genetic parameter and gene action analysis. Manual weeding and standard agronomic practices were followed.

Data collection: Data was collected for nine agronomic traits. Days to 50% flowering (DFF) were recorded as the number of days from sowing until half the plants in each genotype flowered. Plant height (PH) at maturity (cm) was measured from the base to

Table 1: Salient features of parent material used for the generation mean analysis experiment

Genotypes	Pedigree	Salient features	Source
Phule Vikram	ICCV 10 × ICCL 873212	High yielding, wilt resistant and suitable for mechanical harvesting.	MPKV, Rahuri
Raj Vijay gram 202 (RVG - 202)	(JAKI 9226 × DCP 20) × JG 412	Large seeded, suitable for late planting.	RVSKKV, Gwalior
Pusa Chickpea 10216 (BGM -10216)	[(Pusa 372 × ICC 4958) × 2 * Pusa 372]	High yield, drought tolerant variety, developed by MAS.	IARI, New Delhi
ICC 4958	Landrace collected from Jabalpur, MP, in 1973.	Internationally recognized drought tolerant donor.	ICRISAT, Hyderabad



Cross I: Phule Vikram × ICC4958

Cross II: RVG202 × BGM10216

Fig. 1: Seed coat color characteristics of parents and hybrids. Phule Vikram = Orange; ICC 4958 =Yellow; Phule Vikram × ICC 4958 (F_1) = Yellow; RVG 202 =Orange; BGM 10216 =Light brown; RVG 202 × BGM 10216 (F_1) = Brown.

the apex of the main shoot. NPBP were counted within 2.5 cm of the ground and secondary branches (NSBP) were counted from the primary branches at maturity. For NPP, the total number of mature pods was counted at harvest and their means were calculated. For 100 SW (g), clean seed samples were randomly taken and 100 seeds were counted and weighed. Seed yield per plant was determined by recording the total seed weight per randomly selected plant and calculating the average. The Biological yield included the mass of above-ground shoots, pods, stems, and foliage. Harvest index was calculated using the formula proposed by Donald and Hamblin (1976).

Statistical Analysis: Data were subjected to ANOVA using RCBD, as suggested by Panse and Sukhatme (1995). Average values for all nine traits across generations (P_1, P_2, F_1, F_2, BC_1 P_1, BC_1 P_2) in both crosses were analysed. Heat maps of mean performance were prepared using Seaborn's heatmap package in R-Studio (v.4.2.3) to assess significant differences ($P < 0.05$) among traits. A scaling test (A, B, C, D) following Mather (1949) and Hayman and Mather (1955) was used to detect non-allelic interactions. The adequacy of the additive-dominance model (three-parameter model) was tested by the joint scaling test (Cavalli, 1950). If the model was found to be inadequate based on a significant χ^2 test, six-parameter generation mean analysis (Hayman, 1958) was performed.

This analysis estimated the mean (m), additive (d), dominance (h), and epistatic interactions, including additive × additive (i), additive × dominance (j), and dominance × dominance (l). Statistical analyses were performed with WINDOSTAT 8.8 software (Indostat services, Hyderabad, India, http://www.windostat. org/index.html). Genotypic (GCV) and phenotypic coefficients of variation (PCV) were determined following Miller *et al.* (1958). Broad-sense heritability (h^2bs) was estimated using Warner (1952), and genetic advance over mean (GAM) following Johnson *et al.* (1955). Mid-parent heterosis (MPH) was calculated based on Fonseca and Patterson (1968). Inbreeding depression (ID) was assessed following Kempthorne (1957). Correlation matrices among traits in F$_2$ populations were generated using the Corrplot R-package (Wei *et al.* 2017).

Results and Discussion

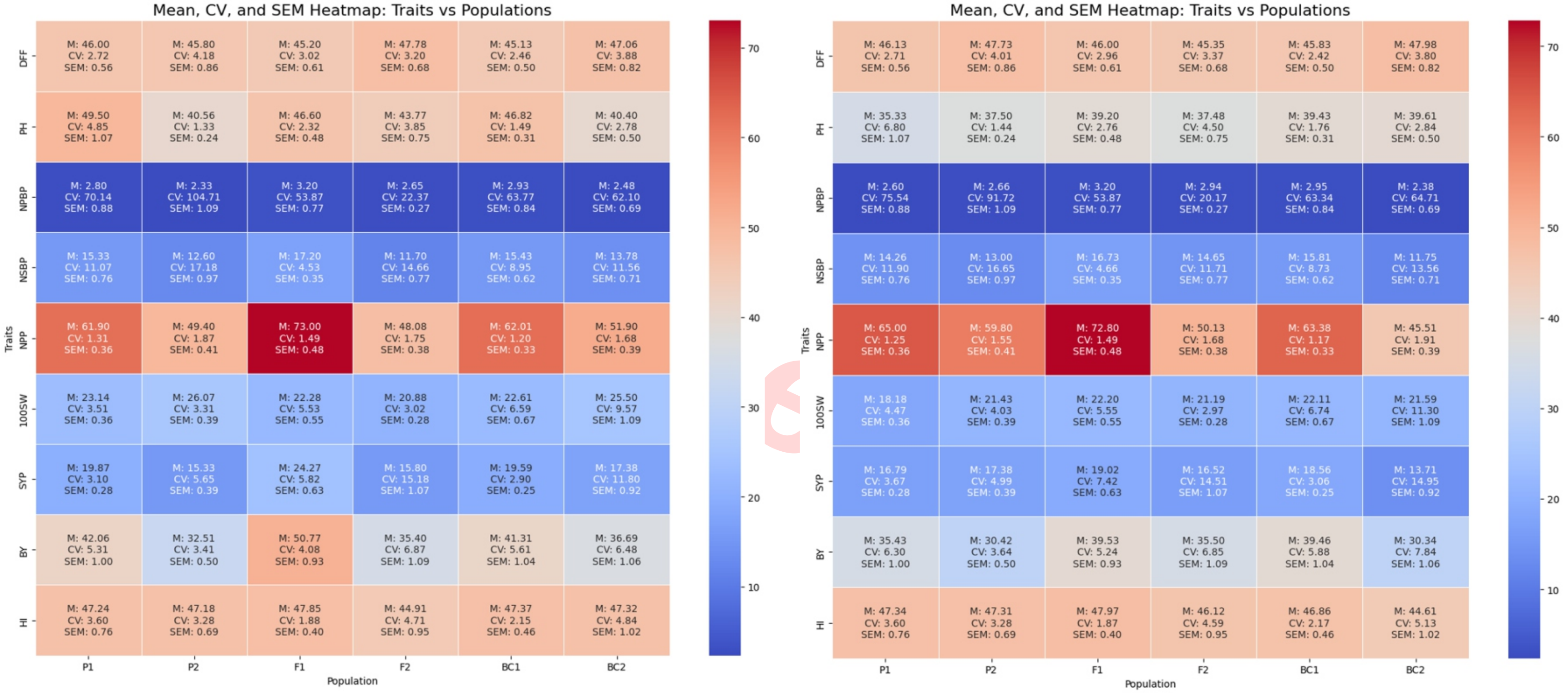
ANOVA revealed that the mean squares for generations were highly significant for all the traits studied (Table 2), indicating the presence of sufficient genetic variability among generations in both crosses. The mean values of nine chickpea traits across parents, F$_1$, F$_2$, BC$_1$, and BC$_2$ generations for Cross I and Cross II are presented in Fig. 2. In Cross I, the days to 50% flowering (DFF) ranged from 45.20 to 47.78 days. Among the parents, ICC 4958 flowered earliest, followed by Phule Vikram. The segregating generations showed DFF in the order BC$_1$ > F$_1$ > BC$_2$ > F$_2$. In Cross II, DFF varied from 45.35 to 47.98 days, with RVG 202 flowering earlier than BGM 10216. The segregating generations exhibited flowering in the order F$_2$ < BC$_1$ < F$_1$ < BC$_2$, indicating progressive delay in flowering. For PH, Cross I ranged from 40.40 to 49.50 cm. Phule Vikram recorded the tallest plants, while ICC 4958 was the shortest. Among generations, the highest PH was observed in BC$_1$, followed by F$_1$, F$_2$, and BC$_2$. In Cross II, PH varied from 35.33 to 39.61 cm, where RVG 202 produced the shortest plants and BGM 10216 the tallest. The generations showed the order F$_2$ < F$_1$ < BC$_1$ < BC$_2$. The NPBP in Cross I ranged from 2.33 to 3.20. Among parents, Phule Vikram had higher NPBP compared to ICC 4958. Among generations, F$_1$ recorded the highest NPBP, followed by BC$_1$, F$_2$, and BC$_2$. Similarly, in Cross II, NPBP varied from 2.38 to 3.20, with BGM 10216 exhibiting higher NPBP than RVG 202. The generation-wise trend remained consistent, with F$_1$ showing the maximum value, followed by BC$_1$, F$_2$ and BC$_2$. The NSBP in Cross I ranged from 11.70 to 17.20. Phule Vikram recorded the highest NSBP among parents, followed by ICC 4958. Among generations, F$_1$ exhibited the highest NSBP, followed by BC$_1$, BC$_2$, and F$_2$. In Cross II, NSBP varied from 11.75 to 16.73, with RVG 202 showing higher values than BGM 10216. Across generations, F$_1$ again recorded the maximum NSBP, followed by BC$_1$, F$_2$ and BC$_2$, indicating superior branching ability in hybrid generations.

In Cross I, NPP ranged from 48.08 to 73.00. Phule Vikram recorded the highest NPP, followed by ICC 4958. Among generations, F$_1$ showed the maximum NPP, followed by BC$_1$, BC$_2$ and F$_2$. In Cross II, NPP varied from 45.51 to 72.80, with RVG 202 registering the highest value, followed by BGM 10216. The generation-wise trend for NPP showed F$_1$ as the highest, followed by BC$_1$, F$_2$, and BC$_2$, indicating better pod formation in segregating generations. The 100SW in Cross I ranged from 20.88 to 26.07 g, with ICC 4958 exhibiting the highest value, followed by Phule Vikram. Among generations, BC$_2$ recorded the maximum 100SW, followed by F$_1$, BC$_1$ and F$_2$. In Cross II, 100SW varied from 18.18 to 22.20 g, where BGM 10216 had the highest value, followed by RVG 202. Among generations, F$_1$ showed the highest 100SW, followed by BC$_1$, BC$_2$, and F$_2$, suggesting a positive heterotic effect on seed size. Seed yield per plant (SYP) ranged from 15.33 to 24.27 g in Cross I. Phule Vikram recorded the highest seed yield, followed by ICC 4958. Among generations, F$_1$ exhibited the maximum SYP, followed by BC$_1$, BC$_2$, and F$_2$. In Cross II, SYP varied from 13.71 to 19.02 g, with BGM 10216 showing the highest yield, followed by RVG 202. The generation-wise trend remained similar, with F$_1$ showing the highest SYP, followed by BC$_1$, F$_2$, and BC$_2$, indicating superior productivity of hybrid generations. Biological yield (BY) in Cross I ranged from 32.51 to 50.77 g. Phule Vikram recorded the highest BY, followed by ICC 4958. Across generations, F$_1$ showed the highest BY, followed by BC$_1$, BC$_2$, and F$_2$. In Cross II, BY ranged from 30.34 to 39.53 g, with RVG 202 showing the highest BY, followed by BGM 10216. Among generations, F$_1$ displayed the

Table 2: Analysis of variance for six generations of two crosses for yield and yield contributing traits in chickpea

Traits	Mean sum of squares			
	C-I (Phule Vikram × ICC 4958)		C-II (RVG 202 × BGM 10216)	
	Generations (df =5)	Error (df = 10)	Generations (df =5)	Error (df = 10)
Days to 50% flowering (DFF)	2.75**	0.85	3.28**	0.65
Plant height (PH, cm)	37.37**	7.51	8.21**	1.45
Number of primary branches plant^{-1} (NPBP)	0.31**	0.05	0.26**	0.10
Number of secondary branches plant^{-1} (NSBP)	12.18**	1.79	9.97**	0.59
Number of pods plant^{-1} (NPP)	301.08**	46.31	304.36**	18.86
100 seed weight (100 SW, g)	12.86**	0.30	6.65**	0.29
Seed yield plant^{-1} (SYP, g)	33.95**	5.23	10.57**	2.79
Biomass plant^{-1} (BP, g)	133.18**	23.76	50.07**	6.27
Harvest index (HI, %)	3.24**	1.21	4.27**	1.05

*, ** indicates significance at $p < 0.05$ and $p < 0.01$ level of probability, respectively



Traits	P1	P2	F1	F2	BC1	BC2
DFF	M: 46.00 CV: 2.72 SEM: 0.56	M: 45.80 CV: 4.18 SEM: 0.86	M: 45.20 CV: 3.02 SEM: 0.61	M: 47.78 CV: 3.20 SEM: 0.68	M: 45.13 CV: 2.46 SEM: 0.50	M: 47.06 CV: 3.88 SEM: 0.82
PH	M: 49.50 CV: 4.85 SEM: 1.07	M: 40.56 CV: 1.33 SEM: 0.24	M: 46.60 CV: 2.32 SEM: 0.48	M: 43.77 CV: 3.85 SEM: 0.75	M: 46.82 CV: 1.49 SEM: 0.31	M: 40.40 CV: 2.78 SEM: 0.50
NPBP	M: 2.80 CV: 70.14 SEM: 0.88	M: 2.33 CV: 104.71 SEM: 1.09	M: 3.20 CV: 53.87 SEM: 0.77	M: 2.65 CV: 22.37 SEM: 0.27	M: 2.93 CV: 63.77 SEM: 0.84	M: 2.48 CV: 62.10 SEM: 0.69
NSBP	M: 15.33 CV: 11.07 SEM: 0.76	M: 12.60 CV: 17.18 SEM: 0.97	M: 17.20 CV: 4.53 SEM: 0.35	M: 11.70 CV: 14.66 SEM: 0.77	M: 15.43 CV: 8.95 SEM: 0.62	M: 13.78 CV: 11.56 SEM: 0.71
NPP	M: 61.90 CV: 1.31 SEM: 0.36	M: 49.40 CV: 1.87 SEM: 0.41	M: 73.00 CV: 1.49 SEM: 0.48	M: 48.08 CV: 1.75 SEM: 0.38	M: 62.01 CV: 1.20 SEM: 0.33	M: 51.90 CV: 1.68 SEM: 0.39
100SW	M: 23.14 CV: 3.51 SEM: 0.36	M: 26.07 CV: 3.31 SEM: 0.39	M: 22.28 CV: 5.53 SEM: 0.55	M: 20.88 CV: 3.02 SEM: 0.28	M: 22.61 CV: 6.59 SEM: 0.67	M: 25.50 CV: 9.57 SEM: 1.09
SYP	M: 19.87 CV: 3.10 SEM: 0.28	M: 15.33 CV: 5.65 SEM: 0.39	M: 24.27 CV: 5.82 SEM: 0.63	M: 15.80 CV: 15.18 SEM: 1.07	M: 19.59 CV: 2.90 SEM: 0.25	M: 17.38 CV: 11.80 SEM: 0.92
BY	M: 42.06 CV: 5.31 SEM: 1.00	M: 32.51 CV: 3.41 SEM: 0.50	M: 50.77 CV: 4.08 SEM: 0.93	M: 35.40 CV: 6.87 SEM: 1.09	M: 41.31 CV: 5.61 SEM: 1.04	M: 36.69 CV: 6.48 SEM: 1.06
HI	M: 47.24 CV: 3.60 SEM: 0.76	M: 47.18 CV: 3.28 SEM: 0.69	M: 47.85 CV: 1.88 SEM: 0.40	M: 44.91 CV: 4.71 SEM: 0.95	M: 47.37 CV: 2.15 SEM: 0.46	M: 47.32 CV: 4.84 SEM: 1.02

(A)

Traits	P1	P2	F1	F2	BC1	BC2
DFF	M: 46.13 CV: 2.71 SEM: 0.56	M: 47.73 CV: 4.01 SEM: 0.86	M: 46.00 CV: 2.96 SEM: 0.61	M: 45.35 CV: 3.37 SEM: 0.68	M: 45.83 CV: 2.42 SEM: 0.50	M: 47.98 CV: 3.80 SEM: 0.82
PH	M: 35.33 CV: 6.80 SEM: 1.07	M: 37.50 CV: 1.44 SEM: 0.24	M: 39.20 CV: 2.76 SEM: 0.48	M: 37.48 CV: 4.50 SEM: 0.75	M: 39.43 CV: 1.76 SEM: 0.31	M: 39.61 CV: 2.84 SEM: 0.50
NPBP	M: 2.60 CV: 75.54 SEM: 0.88	M: 2.66 CV: 91.72 SEM: 1.09	M: 3.20 CV: 53.87 SEM: 0.77	M: 2.94 CV: 20.17 SEM: 0.27	M: 2.95 CV: 63.34 SEM: 0.84	M: 2.38 CV: 64.71 SEM: 0.69
NSBP	M: 14.26 CV: 11.90 SEM: 0.76	M: 13.00 CV: 16.65 SEM: 0.97	M: 16.73 CV: 4.66 SEM: 0.35	M: 14.65 CV: 11.71 SEM: 0.77	M: 15.81 CV: 8.73 SEM: 0.62	M: 11.75 CV: 13.56 SEM: 0.71
NPP	M: 65.00 CV: 1.25 SEM: 0.36	M: 59.80 CV: 1.55 SEM: 0.41	M: 72.80 CV: 1.49 SEM: 0.48	M: 50.13 CV: 1.68 SEM: 0.38	M: 63.38 CV: 1.17 SEM: 0.33	M: 45.51 CV: 1.91 SEM: 0.39
100SW	M: 18.18 CV: 4.47 SEM: 0.36	M: 21.43 CV: 4.03 SEM: 0.39	M: 22.20 CV: 5.55 SEM: 0.55	M: 21.19 CV: 2.97 SEM: 0.28	M: 22.11 CV: 6.74 SEM: 0.67	M: 21.59 CV: 11.30 SEM: 1.09
SYP	M: 16.79 CV: 3.67 SEM: 0.28	M: 17.38 CV: 4.99 SEM: 0.39	M: 19.02 CV: 7.42 SEM: 0.63	M: 16.52 CV: 14.51 SEM: 1.07	M: 18.56 CV: 3.06 SEM: 0.25	M: 13.71 CV: 14.95 SEM: 0.92
BY	M: 35.43 CV: 6.30 SEM: 1.00	M: 30.42 CV: 3.64 SEM: 0.50	M: 39.53 CV: 5.24 SEM: 0.93	M: 35.50 CV: 6.85 SEM: 1.09	M: 39.46 CV: 5.88 SEM: 1.04	M: 30.34 CV: 7.84 SEM: 1.06
HI	M: 47.34 CV: 3.60 SEM: 0.76	M: 47.31 CV: 3.28 SEM: 0.69	M: 47.97 CV: 1.87 SEM: 0.40	M: 46.12 CV: 4.59 SEM: 0.95	M: 46.86 CV: 2.17 SEM: 0.46	M: 44.61 CV: 5.13 SEM: 1.02

(B)

Fig. 2: Heat map depicting the mean performance of generations studied for A= cross I and B= cross II. M, Mean; CV, coefficient of variation (P = 0.5%); SEM, standard error of mean.

maximum BY, followed by BC_1, F_2, and BC_2, reflecting enhanced biomass accumulation in hybrid combinations. The harvest index (HI) in Cross I ranged from 44.91 to 47.85. Phule Vikram recorded the highest HI, followed by ICC 4958. Among generations, F_1 exhibited the highest HI, followed by BC_1, BC_2, and F_2. InCross II, HI varied from 44.61 to 47.97, with RVG 202 showing the highest value, followed by BGM 10216. A similar trend was observed across generations, with F_1 recording the highest HI, followed by BC_1, F_2, and BC_2, indicating efficient partitioning of assimilates towards seed production in F_1 hybrids.

The Joint Scaling Test (Cavalli, 1950) was employed to identify epistatic gene interactions and estimate genetic parameters. The A, B, C, and D scaling tests, along with the Chi-square (χ^2) test, were found to be significant for all traits in both crosses, except NPBP in Cross I. The significance of any scaling test indicates the presence of non-allelic interactions, whereas non-significance suggests the absence of epistasis, thereby indicating the suitability of three-parameter model for NPBP in this cross. The Chi-square values further revealed that the additive-dominance model was inadequate, thus requiring the application of six-parameter model (Hayman, 1958). In cross I, DFF exhibited significantly negative additive and dominance effects. In Cross II, the additive effects (d) were significantly negative, while dominance effects (h) were significantly positive. Additionally, the additive × additive interaction (i) was positive and significant, and the dominance × dominance interaction (l) was negative and significant. In both crosses, the opposite signs of dominance (h) and dominance × dominance (l) confirmed the presence of duplicate epistasis, indicating that non-allelic gene interactions play an important role in governing these traits.

In the genetic parameter analysis for PH, Cross I showed a significantly positive additive gene effect (d), while only the dominance × dominance interaction (l) was also significantly positive. In cross II, the dominance gene effect (h) was significantly positive, while the additive × additive interaction (i) was positively significant and the dominance × dominance (l) was significantly negative. The contrasting signs of (h) and (l) effects are indicative of duplicate epistasis. In Cross I, both additive (d) and dominance (h) effects were significantly positive, with no significant interaction components detected. In Cross II, the additive effect (d) was significant, the additive × additive (i) interaction was negatively significant, and the dominance × dominance (l) was positively significant, showing a similar interaction pattern. Furthermore, in Cross II, only the dominance × dominance (l) was significantly positive, along with a significant additive effect (d). Overall, in both Crosses I and II, additive (d), dominance (h), and additive × additive (i) effects were predominantly positively significant, highlighting the major role of both additive and non-additive gene actions in the inheritance of plant height. In Cross I, the additive gene effect (d) was significantly negative, whereas the dominance effect (h) was significantly positive. Among interaction components, the additive × additive (i) was significantly positive, while dominance × dominance (l) was significantly negative. In Cross II, dominance (h) and additive × additive (i) were also significantly positive

Table 3: Estimates of scaling tests, genetic components, and chi-square (X^2) values in two crosses of chickpea for nine traits

Traits	Crosses	Scaling tests				Genetic components						Type of epistasis	Chi square (X^2)
		A	B	C	D	m	d	h	I	j	l		
DFF	C-I	-0.93**	3.13**	8.93**	3.36**	47.78**	-1.93**	-7.43**	-6.73**	-2.03^{ns}	4.53**	Duplicate	532.08**
	C-II	-0.46^{ns}	2.23**	-4.46**	-3.11**	43.35**	-2.15**	5.30**	6.23**	-1.35^{ns}	-8.00**	Duplicate	317.00**
PH	C-I	-2.45^{ns}	-6.36**	-8.16*	0.32^{ns}	43.77**	6.42**	0.91^{ns}	-0.65^{ns}	1.95^{ns}	9.46**	--	42.20**
	C-II	4.33**	2.53*	-1.28^{ns}	-4.07**	37.48**	-0.18^{ns}	10.93**	8.15**	0.90^{ns}	-15.02**	Duplicate	35.69**
NPBP	C-I	-0.2^{ns}	-0.56^{ns}	-0.96^{ns}	-0.1^{ns}	2.52**	0.32**	0.38**	--	--	--	--	5.83
	C-II	0.1^{ns}	-1.10*	0.1^{ns}	0.55*	2.94**	0.56**	-0.53^{ns}	-1.00*	0.60^{ns}	2.10*	--	22.90**
NSBP	C-I	-1.66^{ns}	-2.23*	-15.53**	-5.81**	11.70**	1.65**	14.86**	11.63**	0.28^{ns}	-7.73*	Duplicate	65.09**
	C-II	0.9^{ns}	-6.23**	-1.83^{ns}	1.75^{ns}	14.65**	4.06**	-0.26^{ns}	-3.50^{ns}	3.56^{ns}	8.83*	--	39.77**
NPP	C-I	-10.76^{ns}	-18.60**	-64.86**	-17.75**	48.08**	10.11**	52.90**	35.50**	3.91^{ns}	-6.13^{ns}	--	39.71**
	C-II	-11.10^{ns}	-41.63**	-70.00**	-8.63^{ns}	50.13**	17.83**	27.83*	17.26*	15.26^{ns}	35.46^{ns}	--	69.22**
100SW	C-I	-0.18ns	2.66^{ns}	-10.23**	-6.35**	20.88**	-2.89**	10.38**	12.71**	-1.42^{ns}	-15.19**	Duplicate	88.06**
	C-II	3.83**	-0.44^{ns}	0.75^{ns}	-1.31^{ns}	21.19**	0.51^{ns}	5.02**	2.63*	2.14^{ns}	-6.02**	Duplicate	43.35**
SYP	C-I	-4.96**	-4.83**	-20.55**	-5.37**	15.80**	2.21*	17.42**	10.75**	-0.06^{ns}	-0.94^{ns}	--	50.87**
	C-II	1.30^{ns}	-5.97**	-3.11ns	0.77^{ns}	16.52**	4.84**	1.87^{ns}	-1.55^{ns}	3.64^{ns}	6.21^{ns}	--	14.33*
BP	C-I	-10.21**	-9.90**	-34.52**	-7.20*	35.40**	4.61**	27.88*	14.40*	-0.15^{ns}	5.70^{ns}	--	33.46**
	C-II	3.97^{ns}	-9.26*	-2.91ns	1.19^{ns}	35.50**	9.12**	4.22^{ns}	-2.38^{ns}	6.62^{ns}	7.67^{ns}	--	7.72*
HI	C-I	-0.33^{ns}	-0.37^{ns}	-10.46**	-4.87**	44.91**	0.05^{ns}	10.38**	9.75**	0.1^{ns}	-9.03**	Duplicate	42.47**
	C-II	-1.59*	-6.05**	-6.12**	0.76^{ns}	46.12**	2.24**	-0.89^{ns}	-1.53^{ns}	2.23^{ns}	9.18**	--	44.52**

ns, *, ** respectively for non-significant, significance at $p < 0.05$, significance at $p < 0.01$ level of probability; A, B, C, D represent the four scales generated from the scaling test. m, d, h, i, j, and l represent respectively the mean, additive, dominance, additive × additive, additive × dominance, and dominance × dominance parameters from the six parameters model.

Table 4: Estimates of genetic components for yield and yield attributing traits in two crosses evaluated in Rabi 2023-24

Genetic components	DFF		PH		NPBP		NSBP		NPP		100SW		SYP		BY		HI	
	C-I	C-II	C-I	C-II	C-I	C-II	C-I	C-II	C-I	C-II	C-I	C-II	C-I	C-II	C-I	C-II	C-I	C-II
GCV%	1.72	2.01	7.12	3.93	10.62	8.11	13	12.34	15.82	16.4	8.76	6.89	16.42	9.89	15.02	10.88	1.75	2.21
PCV%	2.63	2.65	9.43	5.05	13.71	14.25	16.01	13.46	19.66	17.96	9.08	7.35	20.43	14.26	19.3	13.01	2.93	3.12
h2bs	42.54	57.25	56.99	60.66	60	32.42	65	84.01	64.71	83.43	93.11	87.8	64.63	48.11	60.55	69.93	35.87	50.55
GAM	2.31	3.13	11.07	6.31	16.95	9.52	21.74	23.3	26.21	30.88	17.42	13.3	27.2	14.14	24.08	18.74	2.16	3.24
Heterosis (MP)	-1.52	-1.98	3.47	7.64	23.07	21.51	23.15	23.95	31.29	16.77	-9.46	12.08	37.88	22.02	36.14	20.06	1.34	1.35
ID	-5.71	1.41	6.06	4.36	16.92	8.07	31.97	12.4	34.13	31.19	6.26	4.53	34.9	13.11	30.27	10.2	6.13	3.85

GCV, genetic coefficient of variation; PCV, phenotypic coefficient of variation; h2bs, heritability broad sense; GAM, genetic advance percent over mean; Heterosis (MP), heterosis over mid parent; ID, inbreeding depression.

whereas dominance × dominance (l) remained significantly negative, confirming duplicate epistasis in both crosses. For SYP, Cross I showed positive and significant additive (d), dominance (h), and additive × additive (i) effects. In Cross II, only the additive effect (d) was significantly positive, with all interaction components remaining non-significant, indicating predominance of additive gene action. For the traits, Cross I exhibited significant and positive additive and dominance effects, with significant additive × additive interaction. In Cross II, only additive effects were significant, while interactions were non-significant, supporting epistatic influence.

The ANOVA displayed significant mean squares for treatments, indicating substantial variability across generations. The significant 'm' component for studied traits in both crosses suggested notable differences between generations. Scaling tests and Chi-square results showed that the additive–dominance model alone could not clarify the gene effects for yield and its components, implying the involvement of non-allelic gene actions. These results support earlier findings highlighting epistasis in chickpea (Deshmukh and Gawande, 2016; Sundaram *et al.,* 2018). For DFF, significant interactions and duplicate epistasis were observed, supporting Sundaram *et al.* (2018), though Nehra *et al.,* (2020) reported only main effects. In PH, significant epistatic interactions and duplicate epistasis were detected in Cross I, aligning with Kumar *et al.* (2012) and Farshadfar *et al.* (2008). For NPBP, Cross I was controlled by dominance effects, while Cross II showed significant additive and dominance × dominance interactions, which is in agreement with Kumar *et al.* (2012). For NSBP, the additive effects and all interaction components were significant, with duplicate epistasis in Cross I, consistent with Mali and Mundhe (2015). Additive and non-additive gene actions played significant roles in controlling NPP and 100 SW, matching Kumar *et al.* (2012) and Rahman *et al.* (2022).

SYP was governed by additive effects in Cross I and dominance effects in Cross II, with dominance interaction also contributing significantly. The additive gene action in Cross I corroborates with Nehra *et al.* (2020), while dominance effects in Cross II was consistent with Kumar *et al.* (2017). The significance of additive × additive interactions also corroborates with the previous findings of Sundaram *et al.* (2018) and Deshmukh and Gawande (2016). For BY and HI, the additive effects were important in Cross I, whereas dominance effects predominated in Cross II, with additive × additive interactions also influencing both traits. These outcomes were comparable with the findings of Kumar *et al.* (2017, 2020). Traits influenced by both additive and non-additive gene actions may benefit from delayed selection strategies, while those controlled by duplicate epistasis should be improved through inter-mating followed by delayed selection (Sundaram *et al.,* 2018). Traits governed mainly by additive gene action can be improved through direct selection.

Estimated genetic components for the studied traits in both crosses are presented in Table 4. The PCV (%) values were higher than GCV (%) for all characters, indicating environmental influence on trait expression. Moderate GCV (%) was evident for SYP and NPP in Cross II and NPP in Cross I, whereas low GCV (%) was recorded for DFF in Cross I, followed by HI in Cross I and DFF in Cross II. SYP in Cross I exhibited high PCV (%), while moderate PCV (%) was observed for NPP and BY in Cross I and NPP in Cross II. The lowest PCV (%) occurred in DFF for both crosses. Heritability reflects the proportion of genetic variability in phenotypic expression and indicates transmission efficiency from parents to progeny. Most traits exhibited high heritability, except DFF and HI. 100 SW recorded high heritability in Cross I and Cross II, along with NSBP in Cross II. Moderate heritability was observed for NPBP in Cross II, HI in Cross I and DFF in Cross I.

The highest GAM was recorded for NPP in Cross II, followed by SYP and BY in Cross I, whereas HI and DFF in both crosses showed low GAM. In F_1, both crosses exhibited positive heterosis over the mid parent, except DFF in both crosses and 100SW in Cross I, which showed negative heterosis. Cross I displayed pronounced heterosis for SYP, followed by BY and NPP. Low heterosis was observed in HI in cross I, followed by HI in Cross II and PH in Cross I. All traits exhibited positive inbreeding depression except DFF in Cross I, which showed negative depression. The maximum inbreeding depression was recorded

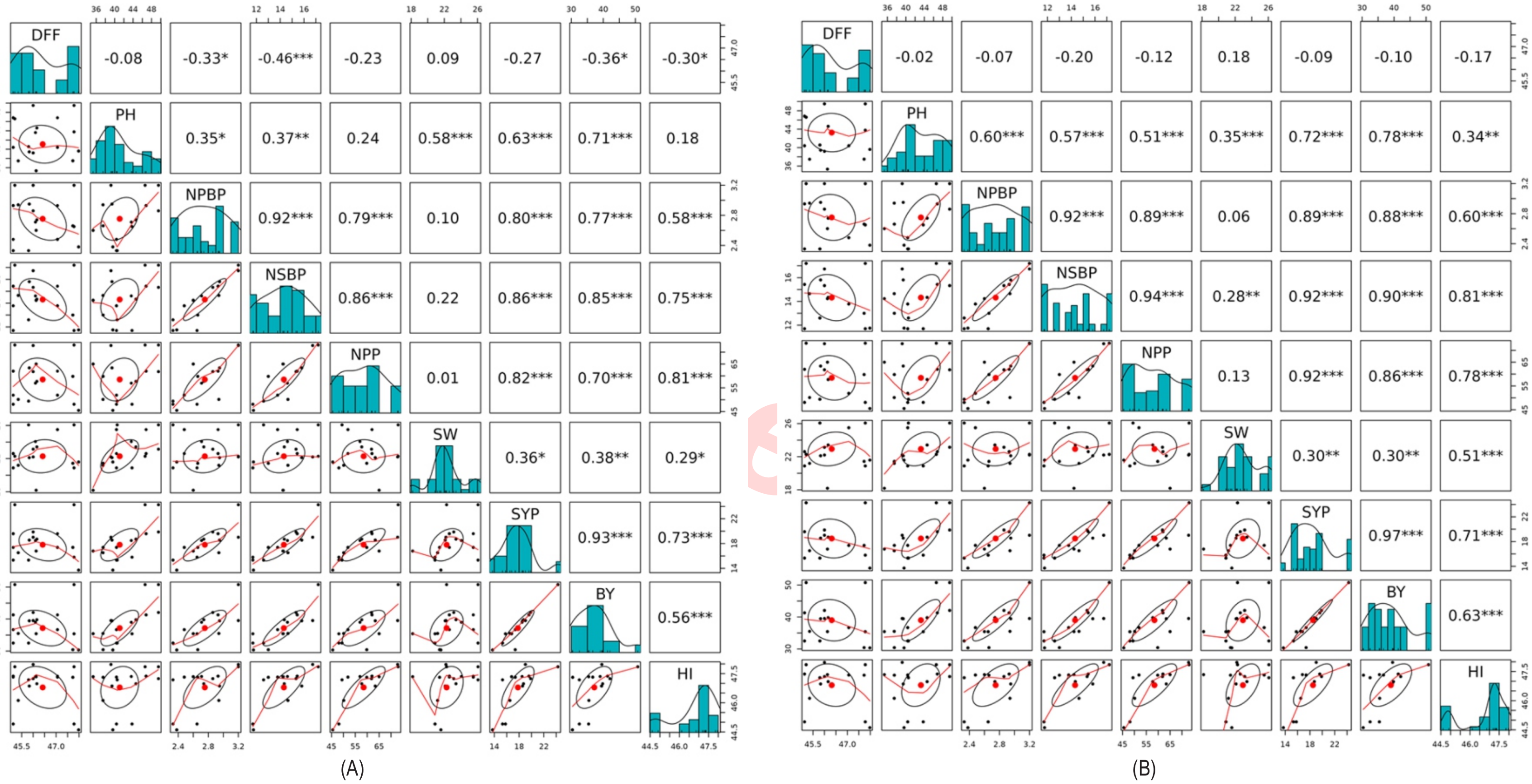


Fig. 3: Correlation matrixes (upper panels with numerical indicates positive and/or negative correlations), frequency distribution (diagonal panels) and scatter plots (lower panels) of F2 generation of A= cross I and B = cross II. *, **, and *** indicate significance at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively.

for SYP, followed by NPP and NSBP in Cross I, while it was negligible for DFF in Cross I, HI in Cross II and PH in Cross II. In all characters, PCV values exceeded those of GCV, suggesting a considerable environmental influence on character expression. These results are consistent with the findings of Thakur *et al.* (2018) and Anusha *et al.* (2020). Characters exhibiting low PCV and GCV may result in unreliable selection, and such traits could be improved by crossing with diverse parents to enhance variability (Karthikeyan *et al.,* 2022). Heritability, defined as the ratio of genetic to phenotypic variance, indicates the potential for trait improvement through simple selection when high (Kaur, 2021). In the present investigation, many characters exhibited high or moderate heritability, except DFF and HI. Traits showing high heritability could be improved through early-generation selection, whereas those with moderate and low heritability may benefit from delayed selection to minimise non-additive gene effects. This observation supports the findings of Kumar *et al.* (2012) and Anusha *et al.* (2020), who also reported moderate variability for NPBP and HI.

Traits with high genetic advance as a percentage of mean, such as NPP, SYP and BY, can be effectively improved through simple selection in early generations. For traits exhibiting moderate or low genetic advance, selection should be delayed to reduce the confounding influence of environmental factors. The high genetic advance recorded for NPP, SYP and BY supports the observations of Kumar *et al.* (2012). Similarly, Miller *et al.* (1958) reported low genetic advance for DFF and HI. According to Sagar and Chandra (1977), heterosis in legumes serves as a useful indicator for identifying superior crosses, thereby increasing the likelihood of obtaining desirable segregants. In the present study, high heterosis for SYP, BY and NPP suggests greater potential for recovering favourable genotypes. These hybrids may be further advanced for single-plant selection. The observed heterosis pattern is in agreement with Hedge *et al.* (2002), Jeena and Arora (2002), and Gupta *et al.* (2003). Most traits exhibited high, and some moderate, inbreeding depression, indicating that F_2 means were generally lower than F_1 means. This pattern facilitates the identification of crosses capable of generating superior pure lines, as reported by Chauhan *et al.* (2013) also.

The correlation of yield with different traits in the F_2 generation of Cross I is shown in Fig. 3A. SYP showed a strong positive association with PH and a weak positive correlation with 100 SW. It exhibited a strong by positive correlation with NPBP, NSBP, and NPP. BY was very strongly and positively correlated with NSBP and SYP, while showing a weak negative correlation with DFF and a weak positive correlation with 100SW. BY also displayed a strong positive association with PH, NPBP and NPP. HI was strongly and positively correlated with NSBP and SYP and showed a very strong positive correlation with NPP. It exhibited weak negative and weak positive associations with DFF and 100 SW, respectively, and moderate positive correlations with NPBP and BY. In the F_2 generation of Cross II (Fig. 3B), SYP showed a very strong positive correlation with NPBP, NSBP and NPP, along with a fairly strong positive association with PH and a weak positive correlation with 100SW. BY was very strongly correlated with primary and secondary branches, NPP and SYP and showed fair to weak positive correlations with PH and 100SW. HI exhibited a fairly strong positive correlation with NPBP, NPP, SYP and BY, and was very strongly correlated with NSBP while showing a moderate positive correlation with 100 SW. Correlation analysis is fundamental in plant breeding, as it supports indirect selection of complex traits like yield through associated characters. Traits such as BY, HI, NPP, NPBP and NSBP exhibited strong associations with SYP, indicating that their enhancement could contribute to improved yield.

The present results revealed strong correlations between SYP and PH, NPBP, NPP, BY and HI, while the association with 100SW was moderate, implying a comparatively lower influence on yield. BY and HI were identified as key selection indices due to their strong relationship with SYP (Toker and Ilhan, 2004). Similar associations between SYP and NPP, PH, and NSBP were also reported by Petrova and Desheva (2016) and Agrawal *et al.* (2018). Furthermore, increased PH may enhance NPP and facilitate better mechanical harvesting efficiency (Singh *et al.,* 2019).

Thus it can be concluded that both additive and non-additive genetic factors play a significant role in determining seed yield and its components in chickpea. Traits controlled by additive gene action are more amenable to improvement through simple selection methods, whereas traits influenced by non-additive gene action require biparental mating or selection in later generations for effective genetic progress. The strong correlations between SYP and key yield components indicate that simultaneous selection for these traits would contribute to enhanced chickpea productivity.

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