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RESEARCH ARTICLE

Gene actions for yield and its attributes and their implications in the inheritance pattern over three generations in opium poppy (*Papaver somniferum* L.)

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Abstract

The gene actions for yield and its attributes and their inheritance pattern based on five parameter model have been explored in four single crosses (NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1, NBMHT-1 × NBIHT-6 and NBMHT-2 × NBMHT-1) obtained using thebaine rich pure lines of opium poppy (*Papaver somniferum* L.) for three consecutive generations. All the traits showed nonallelic mode of interaction, however, dominance effect (*h*) was more pronounced for all the traits except thebaine and papaverine. The dominance × dominance (*l*) effects were predominant over additive × additive (*i*) for all traits in all the four crosses except for papaverine. The seed and opium yield, and its contributing traits inherited quantitatively. The fixable gene effects (*d*) and (*i*) were lower in magnitude than nonfixable (*h*) and (*l*) gene effects. The estimates of heterosis were also higher in comparison to the respective parents which suggested preponderance of dominance gene action for controlling most of the traits. The phenotypic coefficient of variation was marginally higher than those of genotypic coefficient of variation for all the traits. The traits thebaine, narcotine, morphine and opium yield had high heritability coupled with high genetic advance. The leaf number, branches per plant and stem diameter showed positive correlation with opium and seed yields. The selection of plants having large number of leaves, branches and capsules with bigger size would be advantageous to enhance the yield potential.

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Introduction

In recent years, genetically improved varieties/cultivars of economic value can only suffice the ever increasing commodity demand put forward due to population pressure. Among the vast array of commodity products, drugs obtained from opium poppy (*Papaver somniferum* L.) have great value for its extensive medicinal properties due to the presence of more than 80 different alkaloids. Among these alkaloids, demand for five most valuable alkaloids namely, morphine, codeine, thebaine, narcotine and papaverine is highly elevated (Shukla *et al.* 2015). Morphine and thebaine are used as pain killer, analgesic, respiratory, sedative etc. Codeine is used as cough suppressant; narcotine is used in arresting cell division of cancerous cell and papaverine is used in various surgeries (Chatterjee *et al.* 2010; Mishra *et al.* 2013; Shukla *et al.* 2015).

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At present, India is one of the largest producer and exporter of opium, and its derivatives accomplishing national and international demands. Besides meeting its domestic demand, India exported opium and its derivatives worth £3533 million in 2013–14. The production of opium during the crop year 2013–14 was 287 metric tonnes from an area of 5896 ha and the total number of cultivators were 44,354 (Annual Report 2014–15, Ministry of Finance, Govt. of India). Despite successful history of development of several high opium-yielding lines rich in specific alkaloids, the ever increasing global demand puts compulsive pressure for the development of newer high latex-yielding varieties rich in specific alkaloids.

The nature and extent of gene actions involved in the inheritance of different qualitative and quantitative traits plays a crucial role in genetic improvement of a crop through formulating an appropriate breeding plan. Since, improvement in crop plants is a continuous process so as to develop better plant types, information on genetic parameters

Keywords. gene action; global demand; heterosis; inheritance; opium poppy; *Papaver somniferum* L.

is prerequisite. The information on correlation, heterosis, inbreeding depression, heritability and genetic advance for various traits also helps in deciding the best breeding procedure aiming to genetic improvement of a crop. Therefore, the present study was undertaken in opium poppy with the objectives: (i) to decipher the nature and magnitude of gene action involved in the inheritance of different traits based on generation mean analysis, (ii) to study the genetic parameters and correlation to find out the traits responsible for yield and (iii) to sort out heterotic hybrids for exploitation.

Materials and methods

The experimental material comprised of three phenotypically distinct thebaine lines (NBIHT-4, NBIHT-5 and NBIHT-6), which were developed through interspecific hybridization between two species of opium poppy, i.e. *Papaver somniferum* ($2n = 22$) and *P. setigerum* ($2n = 44$) and other three distinct thebaine lines (NBMHT-1, NBMHT-2 and NBMHT-3) developed through mutation breeding. These lines were homozygous and pure as they were advanced upto F_{10} generations. The parents involved in the development of these lines were of a high opium yielding variety 'Madakini' of *P. somniferum* used as a parent for interspecific cross and mutation breeding, while other parent used was *P. setigerum*, a wild species. *P. somniferum* is a cultivated species for production of opium and seeds, and is the source of medicinally important alkaloids, while *P. setigerum* is characterized by large number of dehiscent capsules with very small size and is not under cultivation (figure 1). These lines were hybridized in full diallel mating design in 2009–10 at the experimental field of CSIR-National Botanical Research Institute, Lucknow, India, located at 26°4′N latitude and 80°45′E longitude and altitude of 129 m above sea level. Of the 30 crosses obtained, four phenotypically most distinct promising crosses (NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1, NBMHT-1 × NBIHT-6 and NBMHT-2 × NBMHT-1) were selected based on contrasting thebaine profiles of their respective parents. The genetic information obtained from these distinct crosses could better imply on the whole dataset of similar parentage rather than handling number of crosses to gather such information. These crosses were evaluated up to F_3 generation in randomized block design with three replications. The developed lines, NBIHT-5 and NBMHT-2, used in the present study are rich in thebaine (>10%) in comparison with the existing varieties/germplasm lines (<2%) and other two lines, NBIHT-6 and NBMHT-1, were moderate in thebaine (>3%). Plant to plant spacing was 10 cm and row to row spacing was 30 cm during the experimentation. Standard cultural practices were followed throughout the crop seasons (Yadav *et al.* 2006). Nine competitive plants from parental lines and F_1s and 30 plants from F_2 and F_3 generations per replication were randomly selected and tagged before flowering. The detailed observations were recorded on these tagged plants for days to 50% flowering (DOF), plant height (cm) (PH), peduncle length (cm) (PL), leaves per plant (LPP), branches per plant (BPP), capsules per plant (CPP), capsule size (cm^2) (CSz), stem diameter (cm) (SD), capsule weight per plant (g) (CWPP), husk yield per plant (g) (HYPP), seed yield per plant (g) (SYPP), opium yield per plant (mg) (OYPP), morphine % (M), codeine % (C), thebaine % (T), narcotine % (N) and papaverine % (P).

Statistical analysis

Data was analysed statistically using mean values of replicated data for each trait. The mean and variance were calculated as suggested by Hayman (1958). The presence of gene interactions were detected by using C and D scaling test as proposed by Hayman and Mather (1955). The component of

***P. setigerum* DC** ***P. somniferum* L.**

Figure 1. Plants of *P. somniferum* L. ($2n = 22$) and *P. setigerum* DC ($2n = 44$).

gene effects includes (m) = mean of F_2 generation, (d) = additive effect (joint estimates of d and $\hat{j}$ in 5-parameter model), (h) = dominance effect, (i) = additive × additive effect, (l) = dominance × dominance effect. Complementary epistasis was determined when dominance (h) and dominance × dominance (l) gene effects have same sign and duplicate epistasis when the sign was different (Kearsey and Pooni 1996). Heterosis over better and mid parent was calculated by deducting generation mean of F_1 from mean value of better and mid parent, respectively. Genotypic and phenotypic coefficients of variability were also calculated. Broad sense heritability was estimated as percentage of the ratio of genotypic variance to phenotypic variance in F_2 population as per Allard's (1960), $h^2B = 100 \times (\sigma^2F_2 - \sigma^2E)/\sigma^2F_2$, where σ^2F_2 is phenotypic variance of F_2 population and σ^2E environmental variance. Genetic advance in percentage was calculated as GA% = (GA/X) × 100, where GA = $k \times (\delta p) \times h^2B$ and k = standardized selection differential (2.06), δp = phenotypic standard deviation of F_2 population, h^2B = broad sense heritability and X = mean of the trait. The correlation among different traits for all the generations was calculated using the mean values of all the crosses as suggested by Johnson *et al.* (1955).

Results

Analysis of variance revealed presence of substantial amount of variability in mean performance of all five generations for most of the traits except for seed yield per plant in all the cross combinations (table 1). The parental divergence was noticed for branches per plant, opium yield per plant, morphine, thebaine and narcotine for all the crosses (table 2). The mean performance of parental lines of the crosses NBIHT-5 × NBMHT-1, NBMHT-1 × NBIHT-6 and NBMHT-2 × NBMHT-1 showed significant divergence for capsules per plant and seed yield per plant. The parental mean performance of the crosses NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1 and NBMHT-2 × NBMHT-1 for husk yield per plant; NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1 and NBMHT-1 × NBIHT-6 for capsule weight per plant; NBIHT-5 × NBIHT-6 and NBIHT-5 × NBMHT-1 for plant height and leaves per plant; NBIHT-5 × NBIHT-6 and NBMHT-1 × NBIHT-6 for peduncle length and NBMHT-2 × NBMHT-1 for days to 50% flowering showed significant divergence. The mean performance of F_1s was found better than either of parents for plant height for all the crosses. The mean performance of crosses NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1 and NBMHT-1 × NBIHT-6 for peduncle length, leaves per plant and morphine; NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1 and NBMHT-2 × NBMHT-1 for codeine; NBMHT-1 × NBIHT-6 and NBMHT-2 × NBMHT-1 for narcotine; NBIHT-5 × NBIHT-6 and NBIHT-5 × NBMHT-1 for thebaine; NBIHT-5 × NBMHT-1 and NBMHT-2 × NBMHT-1 for opium yield; NBMHT-1 × NBIHT-6 and NBMHT-2 × NBMHT-1 for capsule size; NBIHT-5 × NBIHT-6 and NBMHT-1 × NBIHT-6 for capsules per plant; NBMHT-2 × NBMHT-1 for days to 50% flowering; NBIHT-5 × NBIHT-6 for branches per plant; NBIHT-5 × NBIHT-6 for stem diameter and seed yield per plant showed better performance than either of parents. The F_2 mean performance was better than respective parents and F_1s for peduncle length, branches per plant, capsules per plant, capsule size, stem diameter, capsule weight per plant, husk yield per plant, opium yield per plant and morphine. However, F_3 performance was lower than respective parents and F_1s for all the traits except for peduncle length. Three crosses, namely NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1 and NBMHT-1 × NBIHT-6 in F_1 and two crosses namely NBIHT-5 × NBMHT-1 and NBMHT-1 × NBIHT-6 in F_3 showed early flowering than their respective parental lines. The mean performance of F_2 and F_3 generations showed significant decline over respective F_1s in almost all the four crosses for all the traits.

The scaling test revealed that the value of either C or D, or both were significant in all the crosses for all traits except for stem diameter and papaverine that indicated nonallelic mode of inheritance of the traits under study (table 3). All the crosses showed nonsignificant values of both C and D for stem diameter and papaverine indicating noninteracting mode of inheritance. In general, additive × additive (i) and dominance × dominance (l) interaction effects were together higher in magnitude than the combined main effects of additive (d) and dominance (h) for all the traits in all the crosses. The dominance effect (h) was found more pronounced for all the traits except thebaine and papaverine that exhibited additive effect (d). Dominance × dominance (l) interaction was noticed predominant over additive × additive (i) in all the crosses of all the traits except papaverine. The crosses NBIHT-5 × NBIHT-6, NBMHT-1 × NBIHT-6 and NBMHT-2 × NBMHT-1 for plant height and narcotine; NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1 and NBMHT-2 × NBMHT-1 for codeine; NBIHT-5 × NBMHT-1 and NBMHT-2 × NBMHT-1 for thebaine, NBMHT-2 × NBMHT-1 for days to 50% flowering, NBMHT-1 × NBIHT-6 for leaves per plant and NBIHT-5 × NBIHT-6 for branches per plant showed complementary type of epistasis as having similar sign of (h) and (l). Some crosses in few traits exhibited duplicate type of epistasis having opposite sign for (h) and (l).

Heterosis and inbreeding depression

The heterosis over mid and better parent ranged from −100.00 to 49.96 and 100.00 to 33.65, respectively, in the cross NBIHT-5 × NBIHT-6. However, the inbreeding depression ranged from −222.00 to 57.87 in this cross. In the cross NBIHT-5 × NBMHT-1, heterosis over mid parent ranged from −100.00 to 15.61, while over better parent, it ranged from −100.00 to 4.44. The range of inbreeding depression was from −134.36 to 59.13 in this cross. In the cross NBMHT-1 × NBIHT-6, heterosis over mid parent was

Table 1. Analysis of variance for four cross combinations for various characters in *P. somniferum* L.

Character	Cross	Generation (df = 4)	Replication (df = 2)	Error (df = 8)
Days to flowering	NBIHT-5 × NBIHT-6	5.500*	0.067	0.900
	NBIHT-5 × NBMHT-1	15.067***	0.600	0.266
	NBMHT-1 × NBIHT-6	8.100**	0.266	0.600
	NBMHT-2 × NBMHT-1	10.600***	0.466	0.300
Plant height	NBIHT-5 × NBIHT-6	198.920*	92.302	39.828
	NBIHT-5 × NBMHT-1	165.807*	86.055	36.553
	NBMHT-1 × NBIHT-6	153.146***	17.698	8.196
	NBMHT-2 × NBMHT-1	215.065**	29.016	15.968
Plant length	NBIHT-5 × NBIHT-6	52.253***	3.298	2.754
	NBIHT-5 × NBMHT-1	25.234***	0.695	0.447
	NBMHT-1 × NBIHT-6	34.225**	1.007	2.508
	NBMHT-2 × NBMHT-1	4.056	1.360	3.160
Leaves per plant	NBIHT-5 × NBIHT-6	2.753***	4.301	2.659
	NBIHT-5 × NBMHT-1	24.428**	4.115	3.328
	NBMHT-1 × NBIHT-6	9.334	3.779	4.022
	NBMHT-2 × NBMHT-1	7.779*	1.836	1.554
Branches per plant	NBIHT-5 × NBIHT-6	2.151	0.600	0.914
	NBIHT-5 × NBMHT-1	5.129*	0.185	0.868
	NBMHT-1 × NBIHT-6	6.929***	0.447	0.462
	NBMHT-2 × NBMHT-1	4.730**	0.278	0.601
Capsules per plant	NBIHT-5 × NBIHT-6	2.157	0.385	0.987
	NBIHT-5 × NBMHT-1	2.203*	0.009	0.411
	NBMHT-1 × NBIHT-6	6.163	4.036	3.389
	NBMHT-2 × NBMHT-1	6.315***	0.002	0.209
Capsule size	NBIHT-5 × NBIHT-6	2.384	6.800	1.453
	NBIHT-5 × NBMHT-1	10.607*	0.429	1.951
	NBMHT-1 × NBIHT-6	14.467**	0.706	1.592
	NBMHT-2 × NBMHT-1	14.751***	1.662	0.296
Stem diameter	NBIHT-5 × NBIHT-6	0.147**	0.013	0.266
	NBIHT-5 × NBMHT-1	0.158*	0.006	0.027
	NBMHT-1 × NBIHT-6	0.165**	0.002	0.015
	NBMHT-2 × NBMHT-1	0.141*	0.009	0.034
Capsule weight per plant	NBIHT-5 × NBIHT-6	31.912*	4.133	6.908
	NBIHT-5 × NBMHT-1	29.017*	1.690	4.663
	NBMHT-1 × NBIHT-6	77.425*	8.348	12.177
	NBMHT-2 × NBMHT-1	99.657***	10.152	5.669
Husk yield per plant	NBIHT-5 × NBIHT-6	45.558**	0.865	3.832
	NBIHT-5 × NBMHT-1	20.452*	3.569	3.055
	NBMHT-1 × NBIHT-6	56.285*	2.100	11.200
	NBMHT-2 × NBMHT-1	105.341***	13.543	3.413
Seed yield per plant	NBIHT-5 × NBIHT-6	3.004	1.447	1.423
	NBIHT-5 × NBMHT-1	3.100	2.763	3.044
	NBMHT-1 × NBIHT-6	4.739	2.084	3.697
	NBMHT-2 × NBMHT-1	1.810	7.708	3.668
Opium yield per plant	NBIHT-5 × NBIHT-6	7541.293*	41.272	1635.169
	NBIHT-5 × NBMHT-1	4052.396*	1194.068	889.464
	NBMHT-1 × NBIHT-6	8051.142*	255.338	1193.641
	NBMHT-2 × NBMHT-1	38012.501**	5941.640	2799.951
Morphine %	NBIHT-5 × NBIHT-6	57.399***	11.540	3.294
	NBIHT-5 × NBMHT-1	51.674**	1.410	5.687
	NBMHT-1 × NBIHT-6	33.532	0.581	10.821
	NBMHT-2 × NBMHT-1	18.393	8.377	4.841
Codeine %	NBIHT-5 × NBIHT-6	3.587*	0.975	0.695
	NBIHT-5 × NBMHT-1	6.184*	1.912	1.339
	NBMHT-1 × NBIHT-6	1.069	0.582	0.826
	NBMHT-2 × NBMHT-1	15.794	8.310	7.136
Thebaine %	NBIHT-5 × NBIHT-6	98.606***	3.141	5.176
	NBIHT-5 × NBMHT-1	99.192***	0.103	6.811
	NBMHT-1 × NBIHT-6	6.923*	2.305	1.351
	NBMHT-2 × NBMHT-1	52.286**	3.283	3.956

Table 1 (*contd*)

Characters	Crosses	Generation (df = 4)	Replication (df = 2)	Error (df = 8)
Narcotine %	NBIHT-5 × NBIHT-6	85.662***	2.174	1.100
	NBIHT-5 × NBMHT-1	21.659**	3.254	2.794
	NBMHT-1 × NBIHT-6	22.352**	7.820	2.928
	NBMHT-2 × NBMHT-1	30.464**	7.707	2.381
Papaverine %	NBIHT-5 × NBIHT-6	0.000	0.000	0.000
	NBIHT-5 × NBMHT-1	0.042*	0.007	0.007
	NBMHT-1 × NBIHT-6	0.042*	0.007	0.007
	NBMHT-2 × NBMHT-1	0.067	0.087	0.046

*, ** And *** significantly different at $P < 0.05$, 0.01 and 0.001, respectively.

from −45.29 to 59.25, while over better parent, it was from −60.06 to 24.51 and inbreeding depression was from −437.54 to 74.21. In the cross NBMHT-2 × NBMHT-1, heterosis over mid and better parent varied from −91.74 to 1686.93 and from −93.39 to 793.47, respectively, and inbreeding depression varied from −487.56 to 65.94. Cross NBIHT-5 × NBIHT-6 for stem diameter and thebaine, NBIHT-5 × NBMHT-1 for peduncle length, NBMHT-1 × NBIHT-6 for stem diameter and NBMHT-2 × NBMHT-1 for days to 50% flowering and narcotine content had positive and significant heterosis over mid parent. None of the crosses showed significant heterosis over better parent for all the traits except NBMHT-2 × NBMHT-1 for narcotine. The cross NBIHT-5 × NBIHT-6 for branches per plant, capsule weight per plant, seed yield per plant and opium yield per plant, NBIHT-5 × NBMHT-1 for capsule size and seed yield per plant, NBMHT-1 × NBIHT-6 for branches per plant, capsule weight per plant, seed yield per plant and opium yield per plant, NBMHT-2 × NBMHT-1 for branches per plant, capsules per plant, capsule size, stem diameter, capsule weight per plant, seed yield per plant and opium yield per plant showed negative and significant inbreeding depression. Cross NBMHT-5 × NBMHT-1 showed significant and positive inbreeding depression for days to 50% flowering. The narcotine showed highest values of heterosis over mid and better parent in the cross NBMHT-2 × NBMHT-1 (table 4).

Coefficient of correlation

The correlation coefficient among 17 agronomic traits was estimated from pooled mean data (table 5). The opium yield showed significant and positive correlation with capsules per plant in F_2. However, in F_3, opium yield had significant and positive correlation with days to 50% flowering, leaves per plant, branches per plant, capsules per plant, stem diameter, capsule weight per plant, husk yield per plant and thebaine. None of the traits showed significant correlation with opium yield per plant in F_1. Most of the traits in F_2 and F_3 had negative correlation. Seed yield per plant had significant positive correlation with peduncle length in F_1 and days to 50% flowering, stem diameter and thebaine in F_3. In F_1, all the traits had negative correlation with opium yield per plant except for peduncle length, stem diameter, morphine, codeine and thebaine, while in F_3, most of the traits had positive correlation with opium yield per plant. Days to 50% flowering, capsules per plant, stem diameter and leaves per plant had significant positive correlation with most of the traits in F_3.

Genetic parameters

Genotypic coefficient of variability ranged from 0.00 to 117.18 in F_1, 0.00 to 90.03 in F_2 and 0.00 to 122.29 in F_3, while phenotypic coefficient of variability ranged from 0.00 to 117.74 in F_1, 0.00 to 92.35 in F_2 and 0.00 to 123.62 in F_3. The highest value of GCV was for narcotine in F_1 followed by thebaine, capsules per plant and branches per plant; narcotine in F_2 followed by thebaine, opium yield and capsule weight per plant; narcotine followed by branches per plant, thebaine and opium yield in F_3. The highest value of PCV was for narcotine followed by capsules per plant, branches per plant and codeine in F_1; narcotine followed by husk yield, thebaine and opium yield in F_2; narcotine followed by branches per plant, seed yield and thebaine in F_3. The heritability estimates in broad sense ranged from −0.30 to 0.99 in F_1, −0.38 to 0.95 in F_2 and −0.21 to 0.98 in F_3. Highest value of heritability was for narcotine followed by days to 50% flowering, thebaine and peduncle length in F_1; thebaine and narcotine followed by morphine and peduncle length in F_2, while narcotine followed by days to 50% flowering, opium yield and capsule weight per plant in F_3. The genetic advance in percentage ranged from −51.68 to 240.25 in F_1, −4.31 to 180.80 in F_2 and −3.15 to 249.20 in F_3. The highest value for genetic advance was noticed for narcotine followed by thebaine, peduncle length and capsule size in F_1, thebaine, opium yield and capsule weight in F_2 and branches per plant, opium yield and thebaine in F_3 (table 6).

Discussion

All the four crosses showed presence of significant variability for all the traits except for seed yield per plant. A large variation between minimum and maximum mean values in all the four crosses for all traits was visible. Cross NBIHT-5 × NBIHT-6 showed high mean performance over parents in all three generations, which suggested that pureline or recurrent selection would be worthwhile in advance

Table 2. Mean performance of parents, F_1s, F_2s and F_3s of four cross combinations for various characters in *P. somniferum* L.

Cross	Generation				
	P_1	P_2	F_1	F_2	F_3
Days to 50% flowering					
NBIHT-5 × NBIHT-6	102.33 ± 0.16	100.33 ± 0.33	101.33 ± 0.16	100.66 ± 0.33	103.66 ± 0.16
NBIHT-5 × NBMHT-1	102.33 ± 0.16	102.66 ± 0.16	99.33 ± 0.16	101.33 ± 0.16	97.33 ± 0.16
NBMHT-1 × NBIHT-6	102.66 ± 0.16	100.33 ± 0.33	100.33 ± 0.16	101.66 ± 0.16	99.30 ± 0.16
NBMHT-2 × NBMHT-1	98.66 ± 0.16	102.66 ± 0.16	103.33 ± 0.16	100.66 ± 0.16	100.33 ± 0.16
Plant height (cm)					
NBIHT-5 × NBIHT-6	105.08 ± 3.75	116.33 ± 0.98	127.99 ± 1.64	114.55 ± 0.91	116.00 ± 1.54
NBIHT-5 × NBMHT-1	105.08 ± 3.75	120.33 ± 1.05	124.44 ± 0.69	114.77 ± 1.49	119.77 ± 1.20
NBMHT-1 × NBIHT-6	120.33 ± 1.05	116.33 ± 0.98	128.11 ± 0.80	110.55 ± 0.80	111.66 ± 0.91
NBMHT-2 × NBMHT-1	122.00 ± 0.45	120.33 ± 1.05	122.33 ± 2.00	105.77 ± 0.65	106.55 ± 1.40
Peduncle length (cm)					
NBIHT-5 × NBIHT-6	23.16 ± 0.25	18.50 ± 0.43	28.45 ± 0.19	28.44 ± 0.24	25.66 ± 0.91
NBIHT-5 × NBMHT-1	23.16 ± 0.25	25.75 ± 0.26	29.72 ± 0.03	29.99 ± 0.09	26.00 ± 0.25
NBMHT-1 × NBIHT-6	25.75 ± 0.26	18.50 ± 0.43	26.70 ± 0.59	26.33 ± 0.53	24.44 ± 0.14
NBMHT-2 × NBMHT-1	23.00 ± 0.99	25.75 ± 0.26	23.70 ± 0.07	22.99 ± 0.09	24.50 ± 0.31
Leaves per plant					
NBIHT-5 × NBIHT-6	14.22 ± 0.73	19.83 ± 0.22	21.22 ± 0.39	16.44 ± 0.22	24.88 ± 0.67
NBIHT-5 × NBMHT-1	14.22 ± 0.73	18.66 ± 0.22	20.66 ± 0.58	16.99 ± 0.41	21.22 ± 0.58
NBMHT-1 × NBIHT-6	18.66 ± 0.22	19.83 ± 0.22	20.66 ± 0.34	16.66 ± 0.16	16.88 ± 1.18
NBMHT-2 × NBMHT-1	20.16 ± 0.15	18.66 ± 0.22	20.10 ± 0.38	16.44 ± 0.29	17.61 ± 0.60
Branches per plant					
NBIHT-5 × NBIHT-6	1.19 ± 0.18	0.66 ± 0.08	1.43 ± 0.40	2.66 ± 0.28	2.44 ± 0.22
NBIHT-5 × NBMHT-1	1.19 ± 0.18	3.91 ± 0.36	0.66 ± 0.19	1.33 ± 0.19	1 ± 0.25
NBMHT-1 × NBIHT-6	3.91 ± 0.36	0.66 ± 0.08	0.77 ± 0.14	1.99 ± 0.16	0.11 ± 0.05
NBMHT-2 × NBMHT-1	2.25 ± 0.07	3.91 ± 0.36	1.00 ± 0.00	2.66 ± 0.16	0.88 ± 0.24
Capsules per plant					
NBIHT-5 × NBIHT-6	2.08 ± 0.18	1.66 ± 0.08	2.11 ± 0.47	3.66 ± 0.28	3.22.11
NBIHT-5 × NBMHT-1	2.08 ± 0.18	0.00 ± 0.00	1.66 ± 0.19	1.99 ± 0.16	1.77.20
NBMHT-1 × NBIHT-6	0.00 ± 0.00	1.66 ± 0.08	3.55 ± 1.19	2.99 ± 0.16	1.11 ± 0.05
NBMHT-2 × NBMHT-1	3.16 ± 0.08	0.00 ± 0.00	2.00 ± 0.00	3.76 ± 0.15	1.77 ± 0.20
Capsule size (cm^2)					
NBIHT-5 × NBIHT-6	10.37 ± 0.69	11.11 ± 0.35	10.55 ± 0.38	12.08 ± 0.43	9.70 ± 0.32
NBIHT-5 × NBMHT-1	10.37 ± 0.69	9.04 ± 0.20	10.33 ± 0.29	13.78 ± 0.22	9.40 ± 0.17
NBMHT-1 × NBIHT-6	9.04 ± 0.20	11.11 ± 0.35	13.29 ± 0.42	14.26 ± 0.48	9.98 ± 0.10
NBMHT-2 × NBMHT-1	10.57 ± 0.10	9.04 ± 0.20	12.63 ± 0.01	14.71 ± 0.32	10.41 ± 0.28
Stem diameter (cm)					
NBIHT-5 × NBIHT-6	0.81 ± 0.05	1.26 ± 0.03	1.32 ± 0.02	1.37 ± 0.03	1.17 ± 0.02
NBIHT-5 × NBMHT-1	0.8167 ± 0.05	1.4 ± 0.05	1.16 ± 0.02	1.23 ± 0.05	0.95 ± 0.02
NBMHT-1 × NBIHT-6	1.4 ± 0.05	1.26 ± 0.03	1.12 ± 0.02	1.27 ± 0.02	0.78 ± 0.01
NBMHT-2 × NBMHT-1	1.60 ± 0.05	1.4 ± 0.05	1.15 ± 0.01	1.50 ± 0.03	1.11 ± 0.06
Capsule weight per plant (g)					
NBIHT-5 × NBIHT-6	5.42 ± 0.20	8.16 ± 0.90	7.27 ± 1.20	13.88 ± 0.52	6.86 ± 0.20
NBIHT-5 × NBMHT-1	5.42 ± 0.20	11.23 ± 1.10	5.56 ± 0.31	8.76 ± 0.55	3.37 ± 0.15
NBMHT-1 × NBIHT-6	11.23 ± 1.10	8.16 ± 0.90	5.25 ± 0.50	15.88 ± 1.54	2.94 ± 0.27
NBMHT-2 × NBMHT-1	11.96 ± 0.92	11.23 ± 1.10	7.03 ± 0.62	19.22 ± 0.52	3.99 ± 0.05
Husk yield per plant (g)					
NBIHT-5 × NBIHT-6	3.37 ± 0.37	6.69 ± 0.62	3.86 ± 0.67	12.44 ± 0.58	3.29 ± 0.11
NBIHT-5 × NBMHT-1	3.37 ± 0.37	6.95 ± 0.99	3.03 ± 0.15	7.10 ± 0.39	1.15 ± 0.05
NBMHT-1 × NBIHT-6	6.95 ± 0.99	6.69 ± 0.62	2.27 ± 0.40	12.22 ± 1.4	1.40 ± 0.34
NBMHT-2 × NBMHT-1	9.21 ± 1.07	6.95 ± 0.99	2.76 ± 0.25	16.21 ± 0.22	1.25 ± 0.13
Seed yield per plant (g)					
NBIHT-5 × NBIHT-6	2.05 ± 0.28	1.46 ± 0.29	3.24 ± 0.54	1.44 ± 0.32	3.57 ± 0.17
NBIHT-5 × NBMHT-1	2.05 ± 0.28	4.27 ± 1.03	2.52 ± 0.18	1.66 ± 0.19	2.21 ± 0.16
NBMHT-1 × NBIHT-6	4.27 ± 1.03	1.46 ± 0.29	2.98 ± 0.12	3.66 ± 0.34	1.54 ± 0.33
NBMHT-2 × NBMHT-1	2.75 ± 0.20	4.27 ± 1.03	4.26 ± 0.40	3.00 ± 0.75	2.74 ± 0.15
Opium yield per plant (mg)					
NBIHT-5 × NBIHT-6	95 ± 14.45	145.33 ± 11.28	132.33 ± 7.80	231.77 ± 10.74	147 ± 5.96
NBIHT-5 × NBMHT-1	95 ± 14.45	116.66 ± 7.80	156.66 ± 9.92	106.55 ± 2.69	55 ± 4.50
NBMHT-1 × NBIHT-6	116.66 ± 7.80	145.33 ± 11.28	76.66 ± 2.77	188.11 ± 14.86	60 ± 1.52
NBMHT-2 × NBMHT-1	60.33 ± 5.26	116.66 ± 7.80	140 ± 23.86	329.55 ± 27.41	51.33 ± 4.34

Table 2 (*contd*)

Cross	Generation				
	P_1	P_2	F_1	F_2	F_3
Morphine %					
NBIHT-5 × NBIHT-6	7.97 ± 0.58	14.65 ± 1.15	16.86 ± 0.42	19.74 ± 0.19	13.60 ± 0.39
NBIHT-5 × NBMHT-1	7.97 ± 0.58	10.81 ± 0.96	16.03 ± 0.32	17.25 ± 0.57	16.81 ± 0.54
NBMHT-1 × NBIHT-6	10.81 ± 0.96	14.65 ± 1.15	16.32 ± 0.17	16.05 ± 0.31	8.83 ± 1.11
NBMHT-2 × NBMHT-1	15.02 ± 0.81	10.81 ± 0.96	14.99 ± 0.78	12.23 ± 0.11	9.49 ± 0.27
Codeine %					
NBIHT-5 × NBIHT-6	3.55 ± 0.12	2.41 ± 0.28	4.58 ± 0.39	1.92 ± 0.08	2.29 ± 0.23
NBIHT-5 × NBMHT-1	3.55 ± 0.12	3.44 ± 0.32	5.17 ± 0.63	2.11 ± 0.02	1.46 ± 0.29
NBMHT-1 × NBIHT-6	3.44 ± 0.32	2.41 ± 0.28	2.76 ± 0.23	2.51 ± 0.26	1.79 ± 0.11
NBMHT-2 × NBMHT-1	3.81 ± 0.23	3.44 ± 0.32	7.21 ± 1.69	2.45 ± 0.14	1.02 ± 0.08
Thebaine %					
NBIHT-5 × NBIHT-6	16.89 ± 0.76	3.52 ± 0.37	17.43 ± 0.86	9.77 ± 0.12	13.19 ± 0.70
NBIHT-5 × NBMHT-1	16.89 ± 0.76	5.08 ± 0.56	17.93 ± 0.63	8.35 ± 0.44	8.19 ± 0.87
NBMHT-1 × NBIHT-6	5.08 ± 0.56	3.52 ± 0.37	4.64 ± 0.23	1.19 ± 0.13	3.15 ± 0.33
NBMHT-2 × NBMHT-1	13.51 ± 0.80	5.08 ± 0.56	10.47 ± 0.69	4.12 ± 0.05	4.76 ± 0.36
Narcotine %					
NBIHT-5 × NBIHT-6	0.53 ± 0.26	12.07 ± 0.69	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
NBIHT-5 × NBMHT-1	0.53 ± 0.26	6.35 ± 1.01	0.00 ± 0.00	2.10 ± 0.31	0.00 ± 0.00
NBMHT-1 × NBIHT-6	6.35 ± 1.01	12.07 ± 0.69	12.68 ± 0.31	7.86 ± 0.12	8.80 ± 0.08
NBMHT-2 × NBMHT-1	0.87 ± 0.43	6.35 ± 1.01	9.78 ± 0.14	5.32 ± 0.26	5.23 ± 0.34
Papaverine %					
NBIHT-5 × NBIHT-6	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
NBIHT-5 × NBMHT-1	0.00 ± 0.00	0.26 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
NBMHT-1 × NBIHT-6	0.26 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
NBMHT-2 × NBMHT-1	0.28 ± 0.14	0.26 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

generations to develop varieties for dual purposes of seed and opium yield. The higher mean values in all three generations might be due to the accumulation of additive genes in the progenies. Earlier studies have also showed preponderance of additive gene action for opium and seed yields (Yadav *et al*. 2006; Maurya *et al*. 2014). The values of either C or D, or both obtained through scaling test were significant revealing nonallelic interaction for all the traits except for stem diameter and papaverine. These two traits had nonsignificant values of either C or D, or both which indicated noninteracting mode of inheritance. Most of the traits exhibited higher magnitude of dominance and dominance × dominance effect than the additive and additive × additive effect, which might be of great importance for all the crosses except for thebaine and papaverine. The preponderance of dominance gene action was also witnessed by the desirable estimates of both mid and better parent heterosis. Thus, the biparental mating followed by recurrent selection would be desirous. The results obtained are in conformity with Maurya *et al.* (2014). All the crosses depicted duplicate type of epistasis with exception in the crosses NBIHT-5 × NBIHT-6, NBMHT-1 × NBIHT-6 and NBMHT-2 × NBMHT-1 for plant height and narcotine; NBIHT-5 × NBIHT-6, NBIHT-5 × NBMHT-1 and NBMHT-2 × NBMHT-1 for codeine; NBIHT-5 × NBMHT-1 and NBMHT-2 × NBMHT-1 for thebaine; NBMHT-2 × NBMHT-1 for days to 50% flowering; NBMHT-1 × NBIHT-6 for leaves per plant and NBIHT-5 × NBIHT-6 for branches per plant which exhibited complementary type of epistasis. Earlier studies reported nonadditive type of gene action for capsules per plant, capsule weight per plant, leaves per plant, seed yield per plant, opium yield per plant (Kandalkar *et al.* 1992; Singh *et al.* 1996, 2001; Yadav *et al.* 2009a, b), days to 50% flowering, capsule size, plant height and husk yield per plant (Yadav *et al.* 2009a, b). Likewise, additive gene effect for days to 50% flowering, plant height, leaves per plant, capsule diameter, capsules per plant, capsule weight per plant, opium yield, seed yield per plant, husk yield per plant have been reported (Khanna and Shukla 1989; Lal and Sharma 1991; Kandalkar *et al.* 1992; Kandalkar and Nigam 1993; Singh *et al.* 1999). The inconsistency regarding the nature and magnitude of gene action for different traits might be due to the divergence in the parental population, size of population, design adopted and varied environmental conditions under which the study was performed (Yadav and Singh 2011; Maurya *et al.* 2014). The traits having significant negative magnitude of additive effect and significant positive magnitude of dominance effect suggest that these traits are governed by dominance gene action. In such cases, heterosis breeding would be advantageous. The negative estimates of additive × additive (i) suggested that the gene pairs accountable for leaves per plant and seed yield per plant were in dispersive form (Mather and Jinks 1977; Maurya *et al.* 2014).

The estimates of heterosis were also higher in comparison to the respective parents suggesting the preponderance of dominance gene action in controlling most of the traits. However, increase in heterozygosity also cannot be ignored as the parents used in these crosses were quite distinct in their

Table 3. Scaling test of generation mean and estimates of genetic components for various quantitative and qualitative characters in opium poppy based on five parameter model.

Cross	Scaling test C	Scaling test D	Estimates *m*	Estimates *d*	Estimates *h*	Estimates *i*	Estimates *l*	Type of epistasis
Days to 50% flowering								
NBIHT-5 × NBIHT-6	−2.667**	10.667**	100.667	1.000	−7.556**	−5.556**	17.778**	D
NBIHT-5 × NBMHT-1	1.667**	−18.333**	101.333	−0.167	9.333	12.167	−26.667**	D
NBMHT-1 × NBIHT-6	−3.000**	−9.000**	101.667	1.167	7.333	7.833	−8.000**	D
NBMHT-2 × NBMHT-1	−5.333**	−1.333**	100.667	−2.000	2.667	−4.000	5.333**	C
Plant height								
NBIHT-5 × NBIHT-6	−19.203**	13.483**	114.550**	−5.625**	5.096**	−23.439**	43.582**	C
NBIHT-5 × NBMHT-1	−15.203**	24.149**	114.773**	−7.625**	−6.901**	−33.883**	52.469**	D
NBMHT-1 × NBIHT-6	−50.673**	−11.107**	110.553**	2.000*	8.736**	2.959**	52.756**	C
NBMHT-2 × NBMHT-1	−63.887**	−27.664**	105.777*	0.833	8.958**	9.462**	48.297**	C
Peduncle length								
NBIHT-5 × NBIHT-6	15.193**	4.120**	28.440	2.333	7.402**	4.452**	−14.764**	D
NBIHT-5 × NBMHT-1	11.617	−4.910**	29.997	−1.292	10.478*	2.626*	−22.036**	D
NBMHT-1 × NBIHT-6	7.670**	0.867**	26.330	3.625	5.275**	7.950**	−9.070**	D
NBMHT-2 × NBMHT-1	−4.163**	3.257**	22.997	−1.375	−3.540**	−5.615**	9.893**	D
Leaves per plant								
NBIHT-5 × NBIHT-6	−10.722**	32.614**	16.443	−2.806	−19.337**	−29.141**	57.781**	D
NBIHT-5 × NBMHT-1	−6.229**	18.007**	16.997	−2.222	−8.824**	−17.487**	32.315**	D
NBMHT-1 × NBIHT-6	−13.173**	−4.272**	16.663	−0.583	2.066**	−0.514**	11.868**	C
NBMHT-2 × NBMHT-1	−13.287**	−1.268**	16.440	0.750	−0.679**	0.131**	16.025**	D
Branches per plant								
NBIHT-5 × NBIHT-6	5.912**	2.596**	2.660	0.264	−0.243**	−0.218**	−4.421**	C
NBIHT-5 × NBMHT-1	−1.118**	−3.771**	1.330	−1.361	0.436**	−0.395**	−3.538**	D
NBMHT-1 × NBIHT-6	1.857**	−8.133	1.997	1.625	4.213	8.981	−13.319**	D
NBMHT-2 × NBMHT-1	2.487**	−7.937**	2.663	−0.833	3.623**	4.039*	−13.899**	D
Capsule per plant								
NBIHT-5 × NBIHT-6	6.670**	1.819**	3.660	0.208	0.134*	0.315**	−6.468**	D
NBIHT-5 × NBMHT-1	2.563**	1.041**	1.993	1.042	0.355*	1.817*	−2.030**	D
NBMHT-1 × NBIHT-6	3.213**	−3.216	2.997	−0.833	5.400**	1.013**	−8.572**	D
NBMHT-2 × NBMHT-1	7.887*	−3.583**	3.763	1.583	4.120*	6.870	−15.292**	D
Capsule size								
NBIHT-5 × NBIHT-6	5.718**	−6.850**	12.080	−0.369	5.325**	4.781**	−16.757**	D
NBIHT-5 × NBMHT-1	15.068**	−9.390**	13.787	0.668	9.391	10.107**	−32.612**	D
NBMHT-1 × NBIHT-6	10.301**	−8.733**	14.260	−1.037	10.749**	5.465**	−25.378**	D
NBMHT-2 × NBMHT-1	13.959**	−7.382**	14.710	0.764	10.074**	8.777**	−28.455**	D
Stem diameter								
NBIHT-5 × NBIHT-6	0.770	−0.118	1.373	−0.225	0.485	−0.243	−1.184	D
NBIHT-5 × NBMHT-1	0.377	−0.855	1.230	−0.292	0.688	0.050	−1.643	D
NBMHT-1 × NBIHT-6	0.187	−2.059	1.273	0.067	1.190	1.537	−2.994	D
NBMHT-2 × NBMHT-1	0.712	−1.555	1.507	0.104	0.804	1.364	−3.022	D
Capsule weight per plant								
NBIHT-5 × NBIHT-6	27.391**	−13.869**	13.882	−1.370	14.296**	11.072**	−55.013**	D
NBIHT-5 × NBMHT-1	7.297**	−20.712**	8.769	−2.905	12.258**	9.214**	−37.345**	D
NBMHT-1 × NBIHT-6	33.627**	−39.364**	15.883**	1.535*	27.407**	34.918**	−97.322**	D
NBMHT-2 × NBMHT-1	39.619**	−45.651**	19.220	0.368*	32.467**	37.774**	−113.694**	D
Husk yield per plant								
NBIHT-5 X NBIHT-6	31.967**	−21.773**	12.440	−1.663	18.673**	16.517**	−71.653**	D
NBIHT-5 X NBMHT-1	12.037**	−19.908**	7.107	−1.793	13.148**	11.693**	−42.593**	D
NBMHT-1 X NBIHT-6	30.682**	−32.472**	12.220**	0.129	22.209**	27.020**	−84.204**	D
NBMHT-2 × NBMHT-1	43.178**	−43.587**	16.217	1.129*	30.930	38.513**	−115.687**	D
Seed yield per plant								
NBIHT-5 X NBIHT-6	−4.242**	7.906**	1.442	0.294	−4.489**	−5.390**	16.197**	D
NBIHT-5 X NBMHT-1	−4.725**	−0.805**	1.662	−1.112	−0.893	−2.475**	5.227**	D
NBMHT-1 X NBIHT-6	2.952**	−6.892**	3.663	1.406	5.196**	7.899**	−13.125**	D
NBMHT-2 × NBMHT-1	−3.548**	−2.066**	3.003**	−0.761	1.534**	−0.736**	1.976**	C
Opium yield per plant								
NBIHT-5 × NBIHT-6	422.111**	−115.889**	231.778**	−25.167**	159.778**	97.278**	−717.333**	D
NBIHT-5 × NBMHT-1	−98.777**	−204.778**	106.556**	−10.833**	170.889**	98.389**	−141.334**	D
NBMHT-1 × NBIHT-6	337.112**	−398.223**	188.111**	−14.333**	267.334**	293.001**	−980.446**	D
NBMHT-2 × NBMHT-1	861.221**	−630.777**	329.555**	−28.167**	615.555**	507.722**	−1989.332**	D

Table 3 (*contd*)

Cross	Scaling test		Estimates					Type of
	C	D	*m*	*d*	*h*	*i*	*l*	epistasis
Morphine %								
NBIHT-5 × NBIHT-6	22.630**	−7.690**	19.747	−3.342*	14.448**	2.213**	−40.426**	D
NBIHT-5 × NBMHT-1	18.173**	13.973**	17.256	−1.422	0.351**	2.213**	−40.426**	D
NBMHT-1 × NBIHT-6	6.084**	−22.248**	16.053	−1.921**	19.437**	12.005**	−37.776**	D
NBMHT-2 × NBMHT-1	−6.893**	−12.324**	12.233	2.106*	9.136**	11.279**	−7.241**	D
Codeine %								
NBIHT-5 × NBIHT-6	−7.411**	−0.641**	1.930	0.573	0.787*	0.338*	9.027	C
NBIHT-5 × NBMHT-1	−8.891**	−5.356**	2.115	0.057	3.761**	2.202**	4.714**	C
NBMHT-1 × NBIHT-6	−1.301**	−3.711**	2.519	0.516**	2.090**	3.290**	−3.213**	D
NBMHT-2 × NBMHT-1	−11.863**	−8.083*	2.456	0.188	6.990**	3.787**	5.039**	C
Thebaine %								
NBIHT-5 × NBIHT-6	−16.175**	12.800**	9.779	6.681	−4.002**	2.133**	38.634**	D
NBIHT-5 × NBMHT-1	−24.411**	−5.918**	8.357	5.905	6.826**	11.686**	24.657**	C
NBMHT-1 × NBIHT-6	−13.111**	1.623**	1.199	0.777	−2.922**	−1.714**	19.645**	D
NBMHT-2 × NBMHT-1	−23.056**	−7.778**	4.123	4.216	2.522**	9.775**	20.371**	C
Narcotine %								
NBIHT-5 × NBIHT-6	−12.607**	−12.607**	–	−5.768	–	−5.232	–	–
NBIHT-5 × NBMHT-1	1.524**	−11.092**	2.103	−2.908	4.205*	1.834**	−16.821**	D
NBMHT-1 × NBIHT-6	−12.339**	1.088**	7.862	−2.860*	0.689	−8.503**	17.903**	C
NBMHT-2 × NBMHT-1	−5.517**	3.056**	5.322	−2.738	3.220**	−8.432**	11.430**	C
Papaverine %								
NBIHT-5 × NBIHT-6	–	–	–	–	–	–	–	–
NBIHT-5 × NBMHT-1	−0.265	−0.265	–	−0.133	–	−0.133	–	–
NBMHT-1 × NBIHT-6	−0.265	−0.265	–	0.133	–	0.398	–	–
NBMHT-2 × NBMHT-1	−0.546	−0.546	–	0.008	–	0.289	–	–

* And ** significantly different at $P < 0.05$ and 0.01, respectively.

origin. Large number of transgressive segregants was also obtained in F_2 generation which might be due to the accumulation of favourable genes from both the parents. This also suggest that alleles at multiple loci originated from both parents recombined in the F_1 hybrids, might have increased or decreased the values of phenotypes (Yadav and Singh 2011). Improvement in the yield potential of opium poppy should be based on judicious selection of transgressive segregants through sib-mating of F_1s'. To increase the frequencies of favourable alleles, intermating of superior segregants followed by recurrent selection could be a potential breeding technique. Low inbreeding depression followed by high heterosis in F_2 offers selection for superior and desirable plant type. The cross NBIHT-2 × NBMHT-6 for days to 50% flowering, branches per plant, capsule per plant, stem diameter, capsule weight per plant, seed yield per plant, opium yield per plant and morphine; the cross NBMHT-5 × NBMHT-1 for days to 50% flowering, peduncle length and morphine; the cross NBMHT-1 × NBIHT-6 for days to 50% flowering, stem diameter and opium yield; the cross NBMHT-2 × NBMHT-1 for capsule size and stem diameter can further be advanced for the respective trait(s) to improve the yield potential substantially.

The PCV was marginally higher than those of GCV for all the traits indicating that the variability present in different traits is due to genotypic effect. The genetic improvement of all these traits can easily be achieved by selection of promising plant type and also through crossing the desirable segregants among themselves followed by advance generation selections. Earlier, higher estimates of GCV and PCV were also reported by Yadav *et al.* (2004). Variability alone is not much helpful in determining the heritable portion of variation. Hence, the estimates of heritability should also be taken under consideration. Low to high estimates of heritability were observed for all the traits under study. The high heritability estimates for thebaine and narcotine in all the three generations, days to 50% flowering in F_1 and F_3, opium yield and morphine in F_2 and F_3 suggest that these traits are under strict genotypic control. High heritability does not necessarily mean high genetic gain and alone is not sufficient to make improvement through selection. Thus, the utility of heritability estimates is increased when it is used to estimate genetic advance (Johnson *et al.* 1955). The genetic advance provides information about the degree of gain obtained in a character under a particular selection pressure. The expected genetic advance is function of selection intensity, phenotypic variance and heritability. Thus, the genetic advance had an added edge over heritability as a guiding factor to breeders in selection programme. Maximum improvement can be achieved for thebaine and narcotine as these traits had high heritability coupled with high genetic advance. Improvement for opium yield and morphine content can also be made as these traits had high heritability and genetic advance in F_2 and F_3 generations. High heritability, GCV and genetic advance for the traits thebaine, narcotine, seed yield per plant and opium yield per plant suggest that these traits are primarily controlled by additive gene action. In such cases, simple selection model would be advantageous to obtain desired gain.

Table 4. Heterosis (mid and better parent) and inbreeding depression in opium poppy.

Trait	NBIHT-5 × NBMHT-6 MP	BP	ID	NBMHT-5 × NBMHT-1 MP	BP	ID	NBMHT-1 × NBIHT-6 MP	BP	ID	NBMHT-2 × NBMHT-1 MP	BP	ID
DOF	−1.82**	−2.94**	00.66	−2.89**	−4.43**	−2.01**	−3.68**	−4.44**	1.85**	6.05**	−6.65**	2.58**
PH	−0.26	−4.36	10.50**	0.12	−2.64	7.77**	−1.87	−1.91	13.70**	−9.15**	−9.19**	13.53**
PL	−2.81	−2.99	00.40	10.62*	4.44	−00.91	8.11	6.69	1.39	−16.28**	−16.67**	2.97
LPP	4.42	1.52	22.51**	−1.29	−2.55	17.74**	4.52	3.68	19.36**	−6.28	−7.25	18.24**
BPP	25.70	−5.83	−85.58*	−21.20	−27.83	−100.50	12.02	−22.33	−158.19*	−91.74*	−93.39*	−166.33**
CPP	15.41	−3.89	−73.46	−17.72	−22.33	−19.84	−22.08	−28.14	15.67	−52.39	−58.32	−88.17*
CSz	−7.71	−16.26	−14.47	−22.04**	−23.95**	−33.47**	−9.08	−13.49	−7.30	8.84	−1.56	−16.44*
SD	21.86*	13.91	−4.04	3.65	−10.44	−5.73	21.38*	14.88	−13.69	13.20	−2.18	−30.64**
CW	19.19	−15.75	−90.77**	−37.80	−49.05*	−57.66	−1.74	−18.59	−202.18**	−24.05	−27.31	−173.40**
HYPP	1.14	−24.83	55.59	−39.20	−50.17*	34.10	0.58	−12.24	−22.93	−4.72	−15.10	29.57
SYPP	38.77	−6.94	−222.00**	−32.35	−44.60	−134.36**	−5.78	−26.12	−437.54**	−41.23	−42.50	−487.56**
OYPP	26.05	−2.17	−75.15*	−6.01	−15.19	31.99	59.25	24.51	−145.36*	−53.51*	−56.75	−135.40**
M	10.58	3.76	−17.09	9.18	−2.73	−7.64	−11.80	−13.55	1.68	−2.50	−3.57	18.40
C	−18.92	−21.67	57.87*	−47.50*	−59.45**	59.13**	−45.29*	−60.06**	8.76	−43.68*	−46.27*	65.94**
T	49.96*	33.65	43.92**	15.61	−15.33	53.40**	−31.93	−56.65**	74.21	−83.18**	−84.26**	60.64**
N	−100.00**	−100.00**	0.00	−100.00**	−100.00**	0.00	23.22	−38.39**	38.01**	1686.93**	793.47**	45.63**

DOF, days to 50% flowering; PH, plant height (cm); PL, peduncle length (cm); LPP, leaves per plant; BPP, branches per plant; CPP, capsules per plant; SD, stem diameter (cm); CSz, capsule size (cm^2); CWPP, capsule weight per plant (g); SYPP, seed yield per plant (g); HYPP, husk yield per plant (g); OYPP, opium yield per plant (mg); M, morphine %; C, codeine %; T, thebaine %; N, narcotine %; P, papaverine %.

* And ** significantly different at $P < 0.05$ and 0.01, respectively.

Table 5. Genotypic correlations between all qualitative and quantitative traits in F_1, F_2 and F_3 generations in *P. somniferum* L.

Trait	Gen.	PH	PL	LPP	BPP	CPP	CSz	SD	CW	HY	SYd	OYd	M	C	T	N
DOF	F_1	0.32	−0.89**	−0.28	0.23	1.27	1.13	−0.30	0.77*	1.16	−0.40	−1.08	−0.67*	−0.07	−0.90**	0.90**
	F_2	0.33	0.37	0.05	−1.54	−1.17	1.02	−1.35	−0.32	1.05	−0.50	−0.99**	0.07	4.44	−0.71	0.81**
	F_3	−0.20	−0.19	0.62	0.86**	0.88**	0.17	0.76*	0.94**	0.98**	0.98**	0.89**	−0.24	0.93**	0.64	−0.19
PH	F_1		1.82	−0.80**	−0.45	−0.82**	−1.04	0.50	−2.18	−1.73	−0.50	−5.21	1.27	−3.99	−0.51	−0.30
	F_2		1.08	0.09	−0.54	−0.57	−1.06	−0.94**	−0.99**	−2.25	−0.10	−0.82**	0.95**	−7.57	0.72*	−0.70*
	F_3		2.82	0.60	0.30	0.25	−2.59	−0.02	0.22	−0.07	0.46	0.33	1.12	0.79**	0.64	−0.78*
PL	F_1			1.16	−0.05	0.11	−0.97**	0.50	−0.96**	−1.86	0.87**	0.22	1.82	−1.03	0.67*	−0.78*
	F_2			0.65*	−0.74*	−0.73*	−0.88**	−0.92**	−1.00**	−1.89	−1.01	−0.96**	0.88**	−8.08	0.66	−0.63
	F_3			1.28	0.20	0.21	−2.72	0.10	0.41	−0.04	0.45	13.88	2.57	−0.26	2.94	−3.38
LPP	F_1				−0.78**	−1.21	−0.59	0.00	−0.50	−1.89	−0.21	−4.56	−0.01	−0.20	1.34	−2.06
	F_2				−0.21	−0.27	0.23	−0.05	−0.61	0.06	−0.67*	−10.31	−0.03	0.02	−0.10	0.08
	F_3				1.01	0.97**	−1.20	0.90**	0.99**	0.88**	1.16	0.93**	0.89**	0.99**	1.12	−0.99**
BPP	F_1					−1.31	−0.40	0.01	−0.84**	−1.70	−0.86**	−6.15	0.65	0.10	1.10	−0.78*
	F_2					1.04	0.15	0.98**	1.04	−0.16	1.27	1.22	−0.16	2.77	0.01	−0.10
	F_3					1.02	−0.12	1.15	1.11	1.09	1.21	0.95**	0.53	0.71*	1.06	−0.96**
CPP	F_1						0.57	−0.09	−1.21	−1.65	−1.67	−28.36	0.07	−1.52	−3.74	3.66
	F_2						0.07	0.92**	0.98**	0.43	1.14	1.06	−0.23	2.44	−0.12	0.03
	F_3						−0.08	1.12	1.06	1.05	1.15	0.96**	0.46	0.92**	0.99**	−0.82**
CSz	F_1							−1.01	−1.08	0.24	−1.17	−1.79	−0.40	−0.38	−1.11	1.14
	F_2							0.56	0.44	3.90	0.11	0.12	−1.20	6.57	−1.04	1.05
	F_3							0.04	−0.12	−0.03	−0.09	−5.67	−1.42	−0.25	−0.79**	1.15
SD	F_1								0.01	−0.02	0.02	0.45	0.05	−0.05	0.85**	−0.83**
	F_2								1.10	1.07	1.22	1.30	−0.66*	5.80	−0.11	0.03
	F_3								0.98**	1.45	0.70*	0.67*	0.28	0.31	0.84**	−0.67*
CW	F_1									−1.51	−1.19	−15.48	0.96**	1.31	4.11	−1.95
	F_2									1.84	1.01	0.99**	−0.69*	5.51	−0.64	0.56
	F_3									1.06	1.04	0.99**	0.24	1.14	0.91**	−0.62
HY	F_1										−2.76	−16.10	1.06	1.43	−0.39	2.16
	F_2										2.11	1.03	−2.08	28.78	−2.87	3.09
	F_3										1.19	0.94**	0.45	0.52	0.97**	−0.81**
SYd	F_1											1.30	1.44	0.03	4.42	−3.81
	F_2											1.09	−0.62	3.59	−0.46	0.35
	F_3											1.12	0.10	1.70	0.95**	−0.51
OYd	F_1												11.27	5.81	1.68	−1.27
	F_2												−0.59	1.19	−0.26	0.19
	F_3												0.24	1.45	0.89**	−0.52
M	F_1													−1.52	0.11	−2.53
	F_2													−8.21	0.65	−0.67*
	F_3													0.06	0.73*	−0.99**
C	F_1														0.89**	−0.38
	F_2														−10.23	9.82
	F_3														1.29	−0.51
T	F_1															−1.00
	F_2															−1.00
	F_3															−0.90

* And ** significantly different at $P < 0.05$ and 0.01, respectively.

Table 6. Coefficients of variability, heritability and genetic advance (%) in *P. somniferum* L.

	GCV			PCV			Heritability (BS)			Genetic advance (%)		
Trait	F_1	F_2	F_3	F_1	F_2	F_3	F_1	F_2	F_3	F_1	F_2	F_3
DOF	1.86	0.37	2.62	1.92	0.68	2.68	0.93	0.29	0.95	3.70	0.41	5.27
PH	0.67	3.56	4.56	3.78	4.23	5.83	0.03	0.71	0.61	0.24	6.17	7.34
PL	9.32	11.03	3.32	10.18	11.66	7.23	0.84	0.89	−0.21	17.58	21.47	−3.15
LPP	3.33	3.41	16.20	6.05	5.54	21.84	−0.30	−0.38	0.55	−3.76	−4.31	24.74
BPP	42.89	23.90	76.65	86.03	38.27	106.07	−0.25	0.39	0.52	−44.06	30.74	114.10
CPP	48.06	24.48	41.60	92.08	29.45	51.56	−0.27	0.69	0.65	−51.68	41.91	69.14
CSz	11.02	6.43	3.39	15.45	11.33	8.94	0.51	0.32	−0.14	16.19	7.52	−2.64
SD	6.49	7.52	15.23	9.20	11.16	20.84	0.50	0.50	0.53	9.42	11.59	22.94
CWP	21.23	28.06	40.23	41.14	34.33	42.97	−0.27	0.67	0.88	−22.57	47.25	77.61
HYPP	9.64	14.70	28.46	41.56	72.74	43.23	−0.05	0.04	0.43	−4.61	6.12	38.59
SYPP	22.90	27.91	52.68	50.45	36.86	65.16	−0.21	0.57	0.65	−21.42	43.53	87.74
OYPP	15.28	41.71	57.64	42.33	46.62	60.52	0.13	0.80	0.91	11.36	76.87	113.10
M	4.84	18.85	28.28	10.91	19.82	34.99	−0.20	0.90	0.65	−4.42	36.93	47.09
C	14.72	1.24	18.28	60.95	21.46	50.26	0.06	0.00	0.13	7.32	0.15	13.70
T	48.84	66.44	58.90	52.26	68.14	63.81	0.87	0.95	0.85	94.02	133.44	111.98
N	117.18	90.03	122.29	117.74	92.35	123.62	0.99	0.95	0.98	240.25	180.80	249.20
P	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

DOF, days to 50% flowering; PH, plant height (cm); PL, peduncle length (cm); LPP, leaves per plant; BPP, branches per plant; CPP, capsules per plant; SD, stem diameter (cm); CSz, capsule size (cm^2); CWPP, capsule weight per plant (g); SYPP, seed yield per plant (g); HYPP, husk yield per plant (g); OYPP, opium yield per plant (mg); M, morphine %; C, codeine %; T, thebaine %; N, narcotine %; P, papaverine %.

The study on correlation becomes more important because it provides reliable information on the nature, extent and direction of selection. The opium yield showed significant and positive correlation with capsules per plant in F_2, while it had significant correlation with days to 50% flowering, leaves per plant, branches per plant, capsules per plant, stem diameter, capsule weight per plant, husk yield per plant and thebaine in F_3. Increase in leaf number, branches per plant and stem diameter advocates higher metabolic rates due to which opium and seed yields may increase. Earlier, Shukla *et al.* (2010) have reported that increase in yield related traits leads to higher pot yield in vegetable *Amaranthus*. Positive association of seed and opium yield with plant height, capsules per plant, leaves per plant, capsule size and capsule weight per plant has also been reported earlier (Singh *et al.* 2004; Yadav *et al.* 2005; Yadav and Singh 2006). The positive and significant association between seed yield and opium yield suggests that selection would be effective to improve both the traits simultaneously. Thus, selection of plants with more number of leaves, branches and capsules of bigger size would be advantageous to enhance the yield potential.

The present study concluded that seed and opium yields and its contributing traits are inherited polygenically. The fixable gene effects (*d*) and (*i*) were found lower in magnitude than nonfixable (*h*) and (*l*) gene effects that suggested nonadditive effect have major role in the inheritance of agronomic traits. Genetic improvement of opium poppy can be achieved through heterosis breeding or biparental mating in early segregating generation followed by recurrent selection. It is recommended that selection based on days to 50% flowering, leaves per plant, branches per plant, capsules per plant, capsule weight per plant, capsule size and stem diameter individually or simultaneously would directly and indirectly influence the opium and seed yields as both these traits have positive correlation among themselves. The developed thebaine rich lines are low opium yielding due to the presence of genetic background of *P. setigerum* which are wild species having very poor opium yield. In this perspective, gene actions involved in the inheritance of opium yield and its associated traits in this dataset can certainly be advantageous in formulation of future breeding programme aiming to develop varieties with high opium yield rich in specific alkaloids.

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