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INHERITANCE OF QUANTITATIVE TRAITS IN OPIUM POPPY (*Papaver somniferum* L.)

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Generation mean analysis was carried out using five parameter model on five cross combinations with five generations i.e. parents, F_{1s}, F_{2s}, and F_{3s} randomly selected from partial diallel breeding experiment. The aim of study was to investigate the mode of gene actions involved in the inheritance of quantitative traits viz. days to 50% flowering, plant height, leaves/plant, capsules/plant, capsule size, capsule weight/plant, seed yield/plant and opium yield/plant. C and D scaling test showed the presence of non allelic interaction in the inheritance for all the traits except for plant height, seed yield/plant (ND1001xIS13) and capsule size (NBR5xND1002) which showed non interacting mode of inheritance. In general, the interaction effect together i.e. additive x additive [i] and dominance x dominance [l] found in higher magnitude than the combined main effects of additive [d] and dominance [h] effects for all the traits in all the five crosses. Dominance effect [h] was found pronounced for most of the traits

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except days to 50% flowering where additive effect [d] was found prevalent. Among the interaction effects dominance x dominance [l] was predominant over additive x additive [i] for all traits in all the five crosses except capsules/plant and capsule size in cross ND1001xNBRI11 and leaves/plant and opium yield/plant in cross NBRI5xND1002. As per sign of dominance (h) and dominance x dominance (l) duplicate epistasis were noticed for all the traits except plant height and leaves/plant in cross ND1001xUO1285. Potence ratio indicated presence of over dominance for almost all the traits. Substantial amount of realized heterosis, residual heterosis in F_2 and F_3 progenies and high heritability with moderate to high genetic advance in F_2 progeny and significant correlation among important traits in desirable direction were observed. A breeding strategy of diallel selective mating or biparental mating in early segregating generation followed by recurrent selection may be used for genetic improvement.

Key words: additive gene effects, epistasis, generation mean analysis; heritability, *Papaver somniferum,* residual heterosis

INTRODUCTION

Opium poppy (*Papaver somniferum* L.) occupies very important position among medicinal plants and chief source of raw opium and its pharmaceutically valuable alkaloids namely morphine, codeine, thebaine, narcotine and papaverine. These alkaloids and its derivatives are mainly used to prepare several life saving drugs mainly pain killer, analgesic, respiratory sedative, antispasmodic and vasodilator by pharmaceutical companies (SINGH *et. al.* 1995, YADAV *et. al.* 2006). The raw opium and its alkaloids are harvested from green but fully matured capsules of the plant. Thus, the productivity and availability of raw opium are always concern with high opium yielding varieties of opium poppy. Genetic improvement of quantitative traits of any crop plants through different breeding program desires the information on the nature and magnitude of gene effects. The genetic potential of the concern plant population can be predicted and measured by the estimates of genetic effects. Based upon the nature and relative magnitude of additive and non additive genetic variance various breeding strategies can be formulated towards the genetic improvement of important traits of the concerned population. Along with information on gene actions the knowledge about the nature and magnitude of correlation among various characters and heritability and genetic advance also help the breeders in deciding the most appropriate breeding procedure to enhance the genetic potentialities and to make breakthrough in the productivity of crop. Previous studies on various quantitative traits including seed and opium yield have showed the involvement of both additive and non additive gene actions. SINGH *et. al.* (1999, 2001), and YADAV *et. al.* (2009a,b) reported non-additive gene action for days to 50% flowering, plant height, peduncle length, branches/plant, capsules/plant, capsule size, capsule weight/plant, seed yield/plant, husk yield/plant, opium yield/plant. However, additive gene action for days to 50% flowering, plant height, leaves/plant, capsules/plant, capsule weight/plant, opium and seed yield/plant was reported by various workers (KHANNA and SHUKLA 1989; LAL and SHARMA 1991; SHUKLA 1992; KANDALKAR and NIGAM 1993; SINGH *et. al.* 1999). The genetic information on transmissibility of different traits and genetic relationship among important traits are also of interest to determine selection for genetic improvement.

Genetic improvement of quantitative traits is continuous process and to accumulate desirable gene pool for improved varieties requires informations on genetical parameters of each experimental setup. The genetical inferences obtained from one set of experimental material cannot be implemented to other set of experimental material with high accuracy. Thus, the generation mean analysis study was carried out to i) determine mode of gene action and type of epistasis, ii) estimate potence ratio, heterosis and inbreeding effect, iii) estimate broad sense heritability, genetic advance and genetic correlation among traits as selection parameters in opium poppy. The genetic informations will help to devise efficient breeding strategies for genetic improvement and development of high yielding varieties in opium poppy.

MATERIALS AND METHODS

Experimental material and design

The experimental material for the present investigation consists of five randomly selected cross combinations derived from partial diallel experiment (YADAV 2004). These five crosses were NBRI5xBR231, NBRI5xND1002, ND1001xNBRI11, ND1001xIS13 and ND1001xUO1285. The final experimental trial were laid out with seven parental lines (NBRI5, BR231, ND1002, ND1001, NBRI11, IS13 and UO1285), their four cross combinations of F_1s, F_2s and F_3s during the crop season 2005–2006 at the experimental field of Genetics and Plant Breeding Division of National Botanical Research Institute, Lucknow. The field was located at to $26^0 40'$ N latitude and $80^0 45'$ E longitude and an altitude of 129 m a.s.l. All the entries were evaluated in a randomized block design with three replications. Two rows of each entry were grown in each replication with spacing of 10 cm within rows and 30 cm between rows. Standard cultural practices were followed throughout the crop season including pre-sowing addition of farmyard manure at the rate of 10 t/ha, 5–6 t/ha neem cake and 30, 50, 40 kg/ha of nitrogen, phosphorus and potassium, respectively as basal dressing. An additional dose of nitrogen of 60 kg/ha was top dressed in two equal splits at 40 days and 60 days after sowing and sprayed with the fungicide diethelene biscarbamate (Dithane M-45 0.2%) at 45 and 60 days after sowing. The field was irrigated as and when required. Ten competitive plants in parental lines and F_{1s} and twenty plants in F_2 and F_3 generations per replication were randomly selected and tagged before flowering. The detailed observations were recorded on *days to 50% flowering* (DOF) -as the duration of 50% flower opening from the date of sowing; *plant height* (PH) - measured in centimeter from the base of the plant i.e. at ground level to top of the main capsule at the time of maturity; *leaves/plant* (LP) - total number of leaves present on main stem of plant; *capsules/plant* (CP) -total number count of capsules borne by each tagged plant;

capsule size (CS) -measured in cm^2 by electronic vernier calipers in term of length and width at middle portion of capsule; *capsule weight/plant* (CWP) - total weight of capsules along with its seed weighed by electronic balance in the unit of gram; *seed yield/plant* (SYP) - weight of seeds from all the capsules of selected plant; *opium yield/plant* (OYP)- total opium obtained from each selected plant in unit of milligram.

Statistical Analysis

The data of various traits were compiled and mean values of the replicated data were used for statistical analysis. The means and variances were calculated as suggested by HAYMAN (1958). The presence of gene interactions was detected by using C and D scaling test as proposed by HAYMAN and MATHER (1955). The component of gene effects includes [m] = mean of F_2 generation, [d´] = additive effect (joint estimates of d and ĵ in 5-parameter model), [h] = dominance effect, [i] = additive x additive effect, [l] = dominance x dominance effect. The type of epistasis was determined as complementary when dominance [h] and dominance x dominance [l] gene effects have same sign and duplicate epistasis when the sign was different (KEARSEY and POONY 1996). Realized heterosis over better and mid parent was calculated by deducting generation mean value of F1 from mean value of better and mid parent respectively. Residual heterosis in F_2 and F_3 generation was estimated as the percentage of deviation of generation mean of F_2 and F_3 from mid parent value respectively. Broad sense heritability for all the crosses were estimated as a percentage of the ratio of genotypic variance to phenotypic variance in F_2 population as per Allard's formula (1960), $h^2_B= 100 \times (\sigma^2F_2-\sigma^2_E)/ \sigma^2F_2$, where, σ^2F_2 is phenotypic variance of F_2 population and σ^2_E environmental variance. Genetic advance in percentage was calculated as GA % = (GA/X) x 100 where, GA= k x (δp) x h^2_B and k= standardized selection differential (2.06), δp = phenotypic standard deviation of F_2 population, h^2_B = broad sense heritability and X = mean of the trait. The pooled data of all the generations mean and crosses were used to calculate phenotypic correlation (rp) using analysis of variance and covariance values as suggested by JOHNSON *et. al.* (1955a).

RESULTS

Scaling test

The C and D scaling test for almost all the crosses and traits showed that at least one or both were found significant indicating the presence of non allelic interaction in the inheritance of the traits under study (Table 2). However, some crosses for few traits like ND1001xIS13 for plant height, seed yield/plant and NBR5xND1002 for capsule size showed non significant values for both C and D scales indicating non interacting mode of inheritance. The detail genetic estimates for different traits are explained as:

Generation mean analyses

Substantial amount of variability in mean performance of basic generations P_1, P_2, F_1, F_2 and F_3 were noticed for almost all the traits in all the cross combinations (Table 1). The parental divergence was noticed for days to 50% flowering, capsule weight/plant, seed yield/plant for crosses NBR5xBR231 and NBR5xND1002. The mean performance of the parental lines of the cross ND1001xIS13 showed significant divergence for all the traits under study. However, contrary to this the parental mean performance of the crosses ND1001xNBRI11 and ND1001xUO1285 showed very low divergence for almost all the traits. The mean performance of F_1swas found better than either of parents for plant height, capsules/plant, capsule size, capsule weight/plant, seed yield/plant and opium yield /plant for four crosses i.e. NBRIxND1002, ND1001xNBRI11, ND1001xIS13 and ND1001xUO1285. However, the F_1 mean performance of cross NBRI5xBR231 was found better than parents only for capsule size, seed yield/plant and opium yield/plant. The days to 50% flowering showed that the F_1 flowers earlier than their respective parental lines in all the crosses. The mean performance of F_2 and F_3 generation showed significant decline over respective F_1s for almost all the traits in all the crosses except NBRI5xBR231 for plant height, capsules/plant and opium yield/plant, ND1001xNBRI11, ND1001xIS13 and ND1001xUO1285 for opium yield/plant where F_2 performance was better than F_1s but further comes down in F_3 generation. The F_3 generation mean performance was found higher than their respective F_1s and F_2s only for capsules/plant in all the crosses except NBRI5xND1002.

Gene action and epistasis

One or both C and D scaling test was found significant for all the crosses exhibiting non allelic interaction for inheritance of all the traits studied (Table 2). In general, the interaction effect together i.e. additive x additive [i] and dominance x dominance [l] found in higher magnitude than the combined main effects of additive [d] and dominance [h] effects for all the traits in all the five crosses. However, for plant height in cross NBRI5xND1002 and ND1001xIS13, capsule size and opium yield/plant in cross NBRI5xND1002, the combined estimates of additive [d] and dominance [h] was found higher than interaction effects. The additive effect [d] was more pronounced for days to 50% flowering in all the five crosses. Contrary to this, dominance effect [h] was prevalent for plant height, leaves/plant, capsule size, capsules/plant, capsule weight/plant, seed yield/plant and opium yield/plant in all the crosses. Among the interaction effects dominance x dominance [l] was predominant over additive x additive [i] for all traits in all the five crosses except capsules/plant and capsule size in cross ND1001xNBRI11 and leaves/plant and opium yield/plant in cross NBRI5xND1002. Opposite sign for [h] and [l] was noticed for all traits in all the five crosses indicating duplicate type of epistasis except ND1001xUO1285 for plant height, leaves/plant, and NBRI5xND1002 for husk yield/plant.

Table 1. Mean performance of parents, F_{1s}, F_{2s} and F_{3s} of five cross combinations for various quantitative traits in opium poppy

Crosses	Generations				
	P_1	P_2	F_1	F_2	F_3
			Days to 50% flowering		
NBRI5x BR231	104.3±0.28	111.1±0.40	108.1±0.31	107.6±0.71	108.7±0.35
NBRI5xND1002	104.3±0.28	111.8±0.3	106.7±0.28	107.0±0.64	103.6±0.38
ND1001xNBRI11	110.1±0.47	111.7±0.32	102.9±0.26	105.1±0.54	104.2±0.46
ND1001xIS13	110.1±0.47	99.1±0.31	101.0±0.36	102.1±.071	100.2±0.43
ND1001xUO1285	110.1±0.47	110.9±0.42	105.4±0.45	106.0±0.75	107.7±0.47
			Plant height		
NBRI5x BR231	126.7±0.78	134.3±0.59	124.4±0.42	127.1±2.08	116.6±0.65
NBRI5xND1002	126.7±0.78	121.6±0.84	132.7±0.65	126.3±1.89	122.0±0.94
ND1001xNBRI11	124.4±0.89	128.4±1.84	131.8±1.70	131.2±2.63	117.6±2.76
ND1001xIS13	124.4±0.89	90.5±1.24	128.3±1.34	121.9±2.26	113.3±1.97
ND1001xUO1285	124.4±0.89	130.2±1.08	132.2±1.19	115.7±2.27	111.0±1.23
			Leaves/plant		
NBRI5x BR231	20.1±0.61	22.1±0.35	17.8±0.32	21.5±0.67	18.9±0.35
NBRI5xND1002	20.1±0.61	20.5±0.53	21.6±0.37	19.9±0.78	18.4±0.56
ND1001xNBRI11	20.3±0.33	17.6±0.33	19.3±0.32	19.9±0.39	17.2±0.31
ND1001xIS13	20.3±0.33	12.3±0.28	18.8±0.27	20.2±0.52	18.0±0.33
ND1001xUO1285	20.3±0.33	21.7±0.33	22.3±0.33	18.5±0.46	18.4±0.34
			Capsules/plant		
NBRI5x BR231	3.1±0.20	3.0±0.28	3.0±0.23	3.3±0.32	2.7±0.29
NBRI5xND1002	3.1±0.20	2.3±0.16	3.8±0.27	3.2±0.44	2.1±0.20
ND1001xNBRI11	2.6±0.17	2.3±0.16	3.7±0.24	2.6±0.29	2.0±0.17
ND1001xIS13	2.6±0.17	1.4±0.17	2.8±0.22	2.7±0.30	1.8±0.22
ND1001xUO1285	2.6±0.17	2.7±0.23	2.7±0.23	3.2±0.27	1.9±0.26
			Capsule Size		
NBRI5x BR231	12.7±0.21	13.2±0.32	14.1±0.26	13.7±0.42	14.4±0.34
NBRI5xND1002	12.7±0.21	14.4±0.15	14.9±0.19	14.2±0.43	13.6±0.38
ND1001xNBRI11	11.4±0.14	11.9±0.17	13.3±0.27	13.3±0.47	13.5±0.27
ND1001xIS13	11.4±0.14	8.3±0.22	12.0±0.16	10.7±0.26	12.3±0.34
ND1001xUO1285	11.4±0.14	14.6±0.21	13.8±0.17	13.2±0.50	14.1±0.35
			Capsule weight/plant		
NBRI5x BR231	15.6±0.24	12.6±0.28	14.8±0.29	14.6±0.51	13.3±0.33
NBRI5xND1002	15.6±0.24	10.7±0.22	17.5±0.21	16.1±0.49	12.7±0.40
ND1001xNBRI11	12.4±0.31	12.2±0.21	13.6±0.21	13.0±0.29	11.0±0.25
ND1001xIS13	12.4±0.31	8.6±0.24	12.8±0.23	12.8±0.39	11.5±0.33
ND1001xUO1285	12.4±0.31	10.6±0.19	13.4±0.29	13.3±0.39	11.9±0.52

Table 1 continue. Mean performance of parents, F_{1s}, F_{2s} and F_{3s} of five cross combinations for various quantitative traits in opium poppy

Crosses	Generations				
	P_1	P_2	F_1	F_2	F_3
			Seed yield/plant		
NBRI5x BR231	9.7±0.28	6.8±0.26	10.4±0.37	10.1±0.56	8.7±0.46
NBRI5xND1002	9.7±0.28	6.9±0.28	10.7±0.31	9.8±0.53	7.6±0.38
ND1001xNBRI11	7.0±0.27	7.5±0.28	8.2±0.21	7.4±0.26	6.3±0.34
ND1001xIS13	7.0±0.27	4.7±0.28	7.2±0.23	7.1±0.34	6.1±0.19
ND1001xUO1285	7.0±0.27	5.8±0.20	7.5±0.25	7.2±0.33	6.3±0.27
			Opium yield/plant		
NBRI5x BR231	248.0±4.34	262.5±3.89	283.8±3.61	304.8±7.87	272.2±6.04
NBRI5xND1002	248.0±4.34	211.7±4.24	303.3±6.50	256.1±9.25	232.2±7.34
ND1001xNBRI11	219.7±4.73	194.9±3.11	241.4±3.83	258.3±4.80	233.6±4.52
ND1001xIS13	219.7±4.73	108.0±4.39	248.8±6.00	263.4±8.72	221.4±5.28
ND1001xUO1285	219.7±4.73	204.2±4.97	242.3±4.82	254.1±5.33	222.8±4.98

Table 2. Scaling tests of generation mean and estimates of genetic components for various quantitative traits in opium poppy based on five parameter model

Crosses	Scaling test		Estimates					Type of epistasis
	C	D	m	d	h	i	l	
				Days to 50% flowering				
NBRI5x BR231	-1.2	4.25**	107.6**	-3.4**	-2.7	-3	7.3	D
NBRI5xND1002	-1.2	-16.0**	107.0**	-3.7**	9.1**	10.5**	-19.7**	D
ND1001xNBRI11	-7.1**	-15.4**	105.1**	-0.8	1	9.0**	-11.0**	D
ND1001xIS13	-2.8	-12.6**	102.1**	5.5**	4.3**	7.9**	-12.9*	D
ND1001xUO1285	-7.9**	2.3	106.0**	-0.4	-4.8**	0.2	7.4	D
				Plant height				
NBRI5x BR231	-1.5	-48.6**	127.1**	-3.8**	25.9**	32.1**	-62.7**	D
NBRI5xND1002	-8.3	-13.0**	126.3**	2.6**	15.8**	7.3	-6.2	D
ND1001xNBRI11	8.3	-44.7**	131.1**	-1.9	36.5**	31.2**	-70.7**	D
ND1001xIS13	16.2	-5.4	121.9**	16.9**	27.1**	6.3	-28.9	D
ND1001xUO1285	-56.4**	-42.1**	115.7**	-2.9**	23.5**	18.6**	19	C
				Leaves/plant				
NBRI5x BR231	7.8**	-96**	21.5**	-0.9**	4.5**	7.7**	-23.3**	D
NBRI5xND1002	-4.3	-6.6**	19.8**	-0.2	4.9*	3.7	-3.1	D
ND1001xNBRI11	3.0	-8.6**	19.9**	1.4**	6.7**	6.3**	-15.6**	D
ND1001xIS13	10.5**	-1.1	20.2**	4.0**	4.9**	2.5	-15.6**	D
ND1001xUO1285	-12.8**	-5.1**	18.4**	-0.6**	2.6*	1.3	10.1**	C

Table 2continue. Scaling tests of generation mean and estimates of genetic components for various quantitative traits in opium poppy based on five parameter model

Crosses	Scaling test		Estimates					Type of
	C	D	m	d	h	i	l	epistasis
			Capsules/plant					
NBRI5x BR231	1.2	-2.1	3.3**	0.01	1.5	1.6	-4.4	D
NBRI5xND1002	-0.2	-3.4**	3.2**	0.4**	3.3**	2.2	-4.3	D
ND1001xNBRI11	-1.8	-2.1**	2.6**	0.1	2.3**	1.1	-0.3	D
ND1001xIS13	1.1	-2.2**	2.7**	0.6**	2.4**	1.7	-4.4	D
ND1001xUO1285	2.5**	-4.2**	3.3**	-0.1	3.3**	3.2**	-8.9**	D
			Capsule Size					
NBRI5x BR231	0.7	4.36**	13.7**	-0.2	-1.6	-2.8*	4.8	D
NBRI5xND1002	-0.2	-0.9	14.2**	-0.83**	1.9	0.6	-1.1	D
ND1001xNBRI11	3.3*	4.4**	13.2**	-0.3*	-0.7	-2.4	1.4	D
ND1001xIS13	-0.9	8.1**	10.7**	1.5**	-3.3**	-5.5**	12.0**	D
ND1001xUO1285	-0.8	3.9**	13.2**	-1.6**	-1.9	-2.8	6.4	D
			Capsule weight/plant					
NBRI5x BR231	0.4	-4.1**	14.6**	1.5**	3.6**	2.7	-6	D
NBRI5xND1002	3.1**	-7.6**	16.1**	2.4**	9.9**	5.5**	-14.3**	D
ND1001xNBRI11	0.4	-6.7**	13.0**	0.1	5.8**	4.6**	-9.6**	D
ND1001xIS13	4.7**	-0.6	12.8**	1.8**	3.5**	1.2	-7.1	D
ND1001xUO1285	3.4*	-1.7	13.3**	0.8**	3.6*	1.7	-6.9	D
			Seed yield/plant					
NBRI5x BR231	3.1	-1.7	10.1**	1.5**	3.8*	1.6	-6.4	D
NBRI5xND1002	1.3	-5.9**	9.8**	1.4**	6.5**	4.1**	-9.5	D
ND1001xNBRI11	-1.1	-4.1**	7.5**	-0.2	3.5*	2.5**	-3.9	D
ND1001xIS13	2.3	-1.3	7.1**	1.2**	2.7**	1.2	-4.8	D
ND1001xUO1285	0.7	-2.1	7.2**	0.6**	2.6**	1.5	-3.7	D
			Opium yield/plant					
NBRI5x BR231	141.1**	-31.4	304.8**	-7.3**	73.1**	44.4	-230.0**	D
NBRI5xND1002	-41.8	-43.0	256.1**	18.1**	95.2**	21.7	-1.6	D
ND1001xNBRI11	135.8**	3.0	258.3**	12.3**	54.8**	20.6	-177.1**	D
ND1001xIS13	228.3**	31.3*	263.4**	55.8**	102.1**	17.2	-262.7**	D
ND1001xUO1285	107.9**	-41.0**	254.1**	7.7**	75.7**	45.3**	-198.7**	D

*,** significant at 5% and 1% probability respectively

D= Duplicate epistasis, C= Complementary epistasis

Heterosis and Inbreeding effect (%)

The realized heterosis estimates for days to 50% flowering varied from -9.1 to -3.0 over better parent and from -8.8 to 0.4 over mid parent (Table3). The residual heterosis calculated in percentage from F_2 and F_3 generation over mid parent varied from -6.0 to 0.9. The inbreeding effect in percent varied from -0.6 to 0.5. The plant height showed variability of realized heterosis ranging from -9.9 to 6.0 over better parent and -6.1 to 20.8 over mid parent. The maximum inbreeding effect was recorded as 12.5% in cross ND1001xIS13. The maximum residual heterosis of 13.4% in F_2 (ND1001xIS13) and 12.8% in F_3 (ND1001xUO1285) was noticed for plant height. The estimate of maximum realized heterosis for leaves/plant was noticed in cross ND1001xIS13 (2.5) over mid parent. The inbreeding effect for this trait varied from -20.0 (NBRI5xBR231) to 17.0% (ND1001xUO1285). The cross ND1001xUO1285 with maximum inbreeding effect in F_2 also showed maximum realized heterosis (12.4%) in F_3 generation. The cross ND1001xNBRI11 exhibited maximum realized heterosis both over mid (1.2) and better parent (1.1) and also higher degree of inbreeding effect (29.7%) in F_2 generation for capsules/plant. Residual heterosis in F_2 generation was recorded upto 35.0% (ND1001xIS13) but none of the crosses exhibited positive value for residual heterosis in F_3 generation showing sharp decline in next generation. The cross ND1001xIS13 exhibited substantial amount of realized heterosis over mid parent (2.1) but also showed highest inbreeding effect (10.8%). The cross ND1001xNBRI11 was found better in respect to maximum realized heterosis over better parent (1.4), maximum residual heterosis in F_2 (14.2%) with no inbreeding effect for capsule size. The cross NBR5xND1002 showed maximum realized heterosis both over better (1.9) and mid parent (4.3) and residual F_2 heterosis (22.4%) and highest inbreeding effect for capsules/plant among all the five crosses. The maximum residual F_3 heterosis (9.5%) with no inbreeding effect was recorded for cross ND1001xIS13. For seed yield/plant the realized heterosis over better and mid parent was recorded maximum in cross NBRI4xND1002 and maximum residual F_2 and F_3 heterosis with second lowest inbreeding effect for NBRI5xBR231.The cross ND1001xIS13 showed maximum realized heterosis over mid parent (84.9), residual F_2 (60.7%) and F_3 (35.1%) and negative inbreeding effect for opium yield/plant.

Potence ratio, heritability and genetic advance

The level of degree of dominance of for various traits computed using generation means and presented as potence ratio (Table 3). The estimate of potence ratio for days to 50% flowering showed lack of dominance (considering negative value as zero) for inheritance of this trait in all the crosses except ND1002xIS13 in F_1 generation where partial dominance was recorded. The cross NBRI5xBR231 showed no dominance for plant height, in both F_1 and F_2 generation and for capsules/plant in F_1. Partial dominance was recorded for capsule weight/plant in both the generations in cross NBRI5xIS13. Over dominance was prevailing in the inheritance of seed yield/plant, opium yield/plant in all the five crosses, capsule weight/plant in four crosses and capsules/plant in three crosses both in F_1 and F_2 generations. The broad sense heritability calculated in percentage for F_2 generation was found high for almost all the traits. It varied from 73.0% for seed yield (NBRI5xND1002) to 93.0 for capsule size (ND1001xNBRI11). The genetic advance in percentage ranged from 3.5% for days to 50% flowering (ND1001xNBRI11) to 80.8% for capsule weight/plant (NBRI5xBR231).

Table 3. Details of various genetic estimates as selection parameters in opium poppy

Crosses	Potence ratio		Realized Heterosis		Residual heterosis (%)		IE (%)	Heritability	Genetic Advance (%)
	F_1	F_2	BP	MP	F_2	F_3	F_2	F_2	F_2
				Days to 50% flowering					
NBRI5x BR231	0.1	-0.1	-3.0	0.4	-0.0	09	0.5	0.80	11.5
NBRI5xND1002	-0.4	-0.5	-5.1	-1.3	-0.9	-41	-0.3	0.78	9.2
ND1001xNBRI11	-9.8	-14.2	-8.8	-8.0	-5.2	-6.0	-2.1	0.86	7.4
ND1001xIS13	0.6	-0.9	-9.1	-3.6	-2.4	-4.2	-1.1	0.78	11.8
ND1001xUO1285	-12.7	-22.5	-5.5	-5.1	-4.0	-2.5	-0.6	0.82	13.5
				Plant height					
NBRI5x BR231	-1.6	-1.8	-9.9	-6.1	-2.61	-10.6	-2.1	0.85	89.6
NBRI5xND1002	3.3	1.6	6.0	8.5	1.7	-1.7	4.8	0.80	69.8
ND1001xNBRI11	2.7	4.8	3.4	5.4	3.8	-6.9	0.5	0.92	150.4
ND1001xIS13	1.2	1.7	3.9	20.8	13.4	5.4	5.0	0.79	102.5
ND1001xUO1285	1.7	-7.9	2.0	4.9	-9.1	12.8	12.5	0.80	109.6
				Leaves/plant					
NBRI5x BR231	-3.2	0.6	-4.2	-3.3	1.9	-10.4	-20.0	0.84	54.8
NBRI5xND1002	6.5	-4.0	1.0	1.3	-1.9	-9.4	7.8	0.72	68.0
ND1001xNBRI11	0.3	1.3	-1.1	0.3	5.0	-9.2	-3.1	0.82	19.1
ND1001xIS13	0.6	1.9	-1.5	2.5	23.9	10.4	-7.4	0.83	34.1
ND1001xUO1285	1.8	-7.1	0.6	1.3	-11.9	12.4	17.0	0.77	26.7
				Capsules/plant					
NBRI5x BR231	-1.0	10.0	-0.1	0.0	8.2	-11.4	-10.	0.80	75.1
NBRI5xND1002	2.7	2.5	0.7	1.1	18.5	-22.2	15.7	0.76	141.7
ND1001xNBRI11	8.3	2.0	1.1	1.2	6.1	-18.4	29.7	0.85	85.1
ND1001xIS13	1.3	2.3	0.2	0.8	35.0	-10.0	3.6	0.87	32.5
ND1001xUO1285	1.0	22.0	0.0	0.0	20.7	-28.0	-18.5	0.78	52.5
				Capsule Size					
NBRI5x BR231	4.6	6.1	0.9	1.1	5.7	11.2	2.8	0.91	35.8
NBRI5xND1002	1.6	1.5	0.5	1.3	4.8	0.3	4.7	0.85	33.6
ND1001xNBRI11	6.6	13.2	1.4	1.6	14.2	15.8	0.0	0.93	48.7
ND1001xIS13	1.4	1.1	0.6	2.1	8.6	24.8	10.8	0.91	17.7
ND1001xUO1285	0.5	0.2	-0.8	0.8	1.5	8.5	4.3	0.90	51.5
				Capsule weight/plant					
NBRI5x BR231	0.5	0.6	-0.8	0.7	3.5	-5.7	1.3	0.87	48.6
NBRI5xND1002	1.7	2.4	1.9	4.3	22.4	-3.4	8.0	0.90	41.2
ND1001xNBRI11	13.0	14.0	1.2	1.3	5.7	-10.6	4.4	0.85	16.7
ND1001xIS13	1.2	2.5	0.4	2.3	21.9	9.5	0.0	0.92	34.2
ND1001xUO1285	2.1	4.0	1.0	1.9	15.6	3.5	0.75	0.88	31.1

Table 3 continue. Details of various genetic estimates as selection parameters in opium poppy

Crosses	Potence ratio		Realized Heterosis		Residual heterosis (%)		IE (%)	Heritability	Genetic Advance (%)
	F_1	F_2	BP	MP	F_2	F_3	F_2	F_2	F_2
			Seed yield/plant						
NBRI5x BR231	1.4	2.55	0.7	2.1	22.4	5.4	2.9	0.83	77.3
NBRI5xND1002	1.7	2.1	1.0	2.4	18.0	-8.4	8.4	0.73	65.4
ND1001xNBRI11	3.8	1.2	0.7	0.9	2.1	-13.1	9.7	0.80	22.1
ND1001xIS13	1.2	2.1	0.2	1.3	21.3	4.3	1.4	0.86	42.3
ND1001xUO1285	1.8	2.6	0.5	1.1	12.5	-1.5	4.0	0.86	39.4
			Opium yield/plant						
NBRI5x BR231	3.9	13.6	21.3	28.5	19.4	6.6	-7.4	0.86	538.2
NBRI5x BR241	4.0	2.8	55.3	73.4	11.4	1.0	15.6	0.80	828.4
ND1001xNBRI11	2.7	8.2	21.7	34.0	24.6	12.7	-7.0	0.91	250.5
ND1001xIS13	1.5	3.5	29.1	84.9	60.7	35.1	-5.9	0.85	761.4
ND1001xUO1285	3.9	10.8	22.6	30.3	19.9	5.1	-4.8	0.80	276.7

Correlation coefficient estimates

The correlations coefficient among eight agronomic traits were estimated from pooled mean data and presented in table 4. The yield component i.e. opium yield and seed showed positive and significant correlation with plant height, leaves/plant, capsules/plant, capsule size, capsule weight/plant, and among themselves. However, non significant correlation of capsule size with seed yield/plant was noticed.

Table 4. Genetic correlation among various quantitative traits in opium poppy

Traits	DOF	PH	LP	CP	CS	CW	SYP
PH	0.006^{NS}						
LP	0.164^{NS}	0.703^{**}					
CP	-0.239^{NS}	0.601^{**}	0.249^{NS}				
CS	-0.368^{**}	0.051^{NS}	0.011^{NS}	-0.057^{NS}			
CW	-0.380^{**}	0.686^{**}	0.604^{**}	0.496^{**}	0.212^{NS}		
SYP	-0.397^{**}	0.640^{**}	0.584^{**}	0.484^{**}	0.190^{NS}	0.910^{**}	
OYP	-0.620^{**}	0.415^{**}	0.380^{**}	0.444^{**}	0.407^{**}	0.782^{**}	0.770^{**}

*,** significant at 5% and 1% probability respectively

NS- non significant

Note: Trait name as described in material and methods

Days to 50% flowering was the trait, which had significant negative association with seed yield/plant, opium yield/plant, capsule weight/plant, and capsule size. Among the component traits plant height, leaves/plant, capsules/plant, capsule weight/plant showed positive and significant association among themselves. Capsule size showed either negative or non significant positive association with plant height, leaves/plant, capsules/plant, seed yield/plant. However, it had positive and significant correlation with opium yield/plant.

DISCUSSION

The generation mean analysis and scaling test revealed showed non allelic interaction in the inheritance of all the traits except few. The direct main effect of dominance and dominance x dominance interaction gene effect may be of great importance in all the crosses for plant height, leaves/plant, capsule size, capsules/plant, capsule weight/plant, seed yield/plant and opium yield/plant. Further, the estimates of both realized and residual heterosis in desirable direction also suggest the predominance of dominance gene action. All the crosses depicted duplicate type of epistasis with exception of ND1001xUO1285 for plant height, leaves/plant, and NBRI5xND1002 for husk yield/plant. Non-additive type of gene action has also been reported earlier for capsules/plant, capsule weight/plant, leaves/plant, seed yield/plant, opium yield/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/plant (YADAV *et. al.* 2009a,b). However, additive gene effect were reported for days to 50% flowering, plant height, leaves/plant, capsule diameter, capsules/plant, capsule weight/plant, latex yield, seed yield/plant, husk yield/plant, (KHANNA and SHUKLA 1989; LAL and SHARMA 1991; KANDALKAR *et. al.* 1992; KANDALKAR and NIGAM 1993; SINGH *et. al.* 1999). The discrepancies in the nature of gene action reported by different workers might be due to differences in parental diversity in the material, size of the population, design adopted and environmental conditions in which the experiment was conducted. The negative additive x additive (i) estimate shows the gene pairs responsible for capsule size are in dispersive form (MATHER and JINKS 1977) suggesting the gene contributing of both the parents. The mean performance of F_1 hybrids was found higher than either of the parental lines for most of the traits exhibiting the role of heterosis which was also evident from the estimates of realized heterosis in F_1 over better and mid parent. Transgressive segregation in F_2 generation has been recorded for most of the traits as the mean values of F_2 progenies was found higher or lower than the parental means. This might be due to the fact that alleles at multiple loci that originated from both parents recombined in the F_1 hybrids that might have increased or decreased the values of the phenotypes (BELL and TRAVIS 2005). Selection of transgressive segregants via sib-mating of F_1s' could be practiced to improve the yield potential in opium poppy. Furthermore, intermating of superior segregants followed by recurrent selection could be a potential breeding technique to increase the frequencies of favorable alleles. Comparatively low inbreeding effect in F_2 progenies and high level of residual heterosis in F_2 and F_3 generations also offers the selection of superior and desirable plant type. For instance, the cross ND1001xIS13 for capsules/plant, capsule weight/plant and opium yield/plant, and NBRI5xBR231 for seed yield/plant can be selected in advance generations for development of high yielding varieties.

In addition to other genetic parameters, the degree of dominance, here estimated as potence ratio, is also of interest to plant breeders (GARDNER 1963). In the present investigation, all the traits showed prevalence of over-dominance for almost all the traits except few traits where either no dominance or partial dominance was recorded. Over dominance has also been reported for plant height, capsules/plant, capsule weight/plant, opium yield/plant and seed yield/plant (KANDALKAR *et. al.* 1992; SHUKLA and KHANNA 1992; SINGH *et. al.* 1996, 2001; YADAV *et. al.* 2009a,b). However, partial dominance was reported for husk yield (KANDALKAR *et. al.*, 1992), latex yield, (LAL and SHARMA 1991), capsules/plant and morphine (SINGH *et. al.*, 1999), capsules/plant, capsule weight/plant, seed yield/plant and opium yield/plant. Partitioning of genetic variances of segregating generation into additive or dominance component through epistasis may result in bias estimates. Thus, the broad sense heritability in combination with genetic advance in F_2 segregating generation was estimated. The knowledge of the heritability of a trait is important to the breeders because it indicates the possibility and extent to which improvement is possible through selection (ROBINSON *et. al.*, 1949). It measures genetic relationship between parents and progeny and has been widely used in determining the degree to which a character may be transmitted from parent to offspring. The estimates of broad sense heritability were high for all the traits. High heritability was also reported for yield (seed and opium) and its component traits by various authors (LAL and SHARMA 1999; SINGH *et. al.* 2000; YADAV and SINGH 2006). 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 increased when it is used to estimate genetic advance (JOHNSON *et. al.* 1955b), which provides the information about the degree of gain in a character obtained under a particular selection pressure. The expected genetic advance is function of selection intensity, phenotypic variance and heritability. Thus, the genetic advance has an added edge over heritability as guiding factor to breeders in a selection programme. The genetic advance as percent of mean suggests that maximum genetic improvement may be achieved for opium yield/plant, seed yield/plant, capsule weight/plant, and capsule since these trait has high heritability coupled with high genetic advance.

The genetic correlation studies provide reliable information on the nature, extent and direction of selection. Thus, the studying correlation becomes more important. The genetic correlation analysis in the present study showed that opium yield and seed yield are positively associated with its major component traits i.e. leaves/plant, plant height, capsules/plant, capsule weight/plant. The earlier studies also showed positive association of seed and opium yield with plant height, capsules/plant, leaves/plant, capsule size, capsule weight/plant (SINGH and KHANNA 1993; 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 simultaneously improve both the characters. Thus for the improvement in opium and seed yield simultaneously by selection of tall plant height with more leaves, more capsules/plant of bigger size would be advantageous.

It is concluded from the present investigation that seed and opium yield and its contributing traits inherited quantitatively and fixable gene effects [d] and [i] were lower in magnitude than non fixable [h] and [l] gene effects showing non additive effect in the inheritance of agronomic traits in opium poppy. Breeding strategies like diallel selective mating or biparental mating in early segregating generation followed by recurrent selection might be appropriate approach toward genetic improvement of opium poppy. Based on different direct and indirect selection parameters it is emphasized that individual or simultaneous selection for capsule weight/plant, capsule size, plant height, and leaves/plant would influence directly and indirectly towards opium yield due to positive association among themselves helps to improve yield.

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NASLEĐIVANJE KVANTATIVNIH OSOBINA KOD OPIJUMSKOG MAKA (*Papaver somniferum* L.)

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I z v o d

Analiza proseka generacije je vršena koristeći model pet parametara u pet kombinacija ukrštanja sa pet generacija, na pr. roditelji, , F_{1s}, F_{2s}, and $F_{3s,}$ odabrani slučajno iz parcijalnog dialelnog seta u program oplemenjivanja. Cilj eksperimenta je bio istraživanje načina dejstva gena uključenih u nasleđivanje kvantativnih osobina kao što su broj dana do 50 % cvetanja, visina biljke broj listova po biljci, broj kapsula po biljci, veličina capsule, težina capsule po biljci, prinos semena po biljci i prinos opiuma po biljci. C i D test skale pokazuje prisustvo nealelnih interakcija u nasleđivanju svih osobina izuzev za visinu biljke , prinos semena po biljci (ND1001xIS13) I veličina kapsule (NBR5xND1002) koji pokazuju neinteraktivni način nasleđivanja. Generalno, interakcioni efekat zajedno sa na primer aditivni x aditivni (i) i dominantni x dominantni(1) nađenih u širem obimu nego kombinovan glavni efekat aditivnog (i) i dominantnog (h) efekta za sve osobine u svih pet ukrštanja. Dominantni efekat (h) je nađen za većinu ispitivanih osobina izuzev 50 % gde preovladava aditivni efekat (d). U okviru efekta interakcije, dominantnos x dominantnos (1) je bio predominantan nad aditivni x aditivni (i) za sve osobine u svih pet ukrštanja izzuzev za broj kapsula po biljci i veličini capsule u ukrštanju ND1001xNBRI11 i broja listova po biljci i prinosa opiuma po biljci u ukrštanju NBRI5xND1002. Kao za dominantnost (h) i dominantnost x dominantnost (1) utvrđena je duplirana epistaza za sve osobine izuzev visine biljke i broja listova po biljci u ukrštanju ND1001xUO1285 . Odnos potence ukazuje prisustvo over dominantnosti za gotovo sve osobine. Utvrđena je substancialna količina realizovanog heterozisa, rezidualni heterozis u F_2 i F_3 potomstvu i visoka naslednost sa umerenim do visokim genetičkim doprinosom u F_2 potomstvu i značajnu korelaciju između značajnih osobina u poželjnom pravcu.

Strategija oplemenjivanja dialelnog ili biparentalnog oprašivanja u ranim segregirajućim generacijama sa nastavkom u procesu rekurentne selekcije može da se primeni za genetičko poboljšanje.

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