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PATTERN OF QUANTITATIVE INHERITANCE OF YIELD AND COMPONENT TRAITS IN OPIUM POPPY (*Papaver somniferum* L.)

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Generation mean analysis of cross NB-5x58/1 and its reciprocal cross was carried out to understand the nature of gene action in opium poppy. The significance of A, B, C and D scaling tests indicated presence of non-allelic interaction in the inheritance of traits except capsule size and husk yield/plant for reciprocal cross. Additive as well as dominance components of gene action were found in both the crosses. Most of the traits had greater non fixable dominance 'h' and dominance x dominance effects 'l' than fixable additive (d) and additive x additive effects (i) except leaves/plant, branches/plant, capsules/plant, stem diameter, capsule weight/plant, husk yield/plant, opium yield/plant, codeine and narcotine content which showed greater importance of additive (d) and additive x additive effects (i) effects. Inter-mating of the best parents, diallel selective mating or biparental mating in early segregating generations followed by recurrent selections were suggested for genetic improvement of opium poppy.

Key words: *a*lkaloid, epistasis, gene action, Joint scaling test, *Papaver somniferum* L.

INTRODUCTION

Opium poppy (*Papaver somniferum* L.) is an important medicinal plant which is a source of commercial opium. Opium obtained by lancing semi-ripe capsules, is one of the historically well known pain killers and is a rich source of various alkaloids which are used in modern medicine for the production of analgesic, antitussive and antispasmodic drugs (PUSHPANGADAN and SINGH 2001; SHUKLA *et a*l. 2006). It produces more than hundred pharmaceutically active benzylisoquinoline alkaloids (FACCHINI and PARK 2003; WEID *et al.* 2004) out of which morphine ($C_{17}H_{19}NO_3$), methyl morphine or codeine ($C_{18}H_{21}NO_3$), dimethyl morphine or thebaine ($C_{19}H_{21}NO_3$), narcotine or noscapine ($C_{22}H_{23}NO_7$) and papaverine ($C_{20}H_{21}NO_4$) are major ones (WEID *et al*. 2004; FRICK *et al.* 2005; SHUKLA *et al.* 2006, 2010). Morphine palliates from about all kinds of grievous pains and

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contributes a major percentage (7-17%) of total alkaloids present in opium (SHUKLA *et al.* 2006; YADAV *et al.* 2009b).

Several basic and applied studies have been carried out for the genetic improvement of crop to enhance its yield potential following various conventional breeding approaches (ITENOV *et al.* 1999; SHUKLA and SINGH 2001; SHUKLA *et al.* 2010). A considerable genetic variability existing within the indigenous germplasms has been extensively exploited in various breeding programs such as diallel analysis, Line x Tester analysis and in different selection criteria (SINGH *et al* 1998; SHUKLA and SINGH 2001; YADAV *et al*. 2009a). For the past one decade global demand for opium alkaloids is increasing rapidly for the manufacturing of life saving drugs by the pharmaceutical industries. Seeing the global market of alkaloids and its derivatives, the scientific breeding approaches for the genetic improvement in *P. somniferum* to increase its specific alkaloids have been going on in India for the last two decades (SHARMA *et al.* 1999; PUSHPANGADAN and SINGH 2001; SHUKLA *et al.* 2010). The development of high yielding varieties and creation of genetic variability is a continuous process of plant breeding which requires knowledge about gene action for its genetic improvement. The present study was undertaken to find out the type of epistasis and nature of gene action for different quantitative traits. Based on the information generated through this study on various parameters, an effective breeding scheme may be devised for genetic improvement and enhancement of yield in opium poppy.

MATERIALS AND METHODS

Material

The material for present study comprised of two pure lines namely NB-5 and 58/1. NB-5 is medium heighted, white unfringe flowered, broad leaved with high opium and seed yield while 58/1 is relatively shorter than NB-5, having deeply serrated leaves and white fringed petals with opium and seed yield lower than NB-5 but have higher morphine content than NB-5. The F_{1s} and reciprocals were made in the year 2011-12 by crossing the two genotypes and advanced into F_{2s} and backcrosses were made in controlled climatic chamber (CG72, Conviron, Canada). The final trial comprising six generations i.e. P_1, P_2, F_1, F_2, B_1 and B_2 of crosses NB-5x58/1 and reciprocal 58/1xNB-5 were grown in a randomized block design (RBD) with three replications in year 2012-13.

Experimental site

Experimental field of Genetics and Plant Breeding Division at CSIR-National Botanical Research Institute, Lucknow, India was the experimental site for this study located at $26^0 40'$N latitude and $80^0 45'$E longitude and an altitude of 129m above sea level. The average rainfall during the crop season ranges from 3.8mm to 21.9mm and the average day/night temperature varies between 22-38.0^{0}C and 4.1-20.5^{0}C respectively.

Experimental design

The experiment was carried out in randomized block design with three replications. The plants were planted in three meter long rows with row to row and plant to plant spacing 30x10cm respectively. Standard agro-technological practices were followed during the crop season (YADAV *et al.* 2009b). Data were recorded on 5 plants each per replication in parents and F_1s while on 10 plants each per replication from F_2s and backcrosses for the traits plant height (cm), peduncle length(cm), leaves/plant, branches/plant, capsules/plant, stem diameter (cm), capsule weight/plant (g), capsule size (cm^2), husk yield/plant (g), opium/plant(mg), seed yield/plant(g), morphine(%), codeine(%), thebaine(%) and narcotine (%) content. The alkaloids in the dry latex were estimated through High Pressure Liquid Chromatography (HPLC) following KHANNA and SHUKLA (1986).

Statistical analysis

The statistical analysis was done using indostat software, Windostat, Hyderabad. The presence of gene interactions were detected by using A, B, C and D scaling tests ($A=2B_1-P_1-F_1=0$; $B=2B_2-P_2-F_1=0$; $C=4F_2-2F_1-P_1-P_2=0$; $D=2F_2-B_1-B_2=0$) as proposed by HAYMAN (1958) and JINKS and JONES (1958). The component of gene effects includes [m] = mean of F_2 generation, [d] = pooled additive effect, [h] = dominance effect, [i] =additive x additive effect, [j] = additive x dominance gene effect and [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). The observed and expected means were compared and goodness of fit was tested against the χ^2 value for 3 degree of freedom in order to judge the adequacy of additive-dominance model.

RESULTS AND DISCUSSION

The significance of A, B, C and D scaling tests for all the traits in both the crosses showed the presence of non-allelic interaction in the inheritance of the traits except capsule size and husk yield per plant for reciprocal cross 58/1xNB-5 (Table 2). The reciprocal cross 58/1xNB-5 was found to be the non-interacting cross for capsule size and husk yield per plant since no scales were found significant for these traits. For capsule size significant and positive estimate of additive (d) component and for husk yield per plant significant positive estimate of dominant component (h) were exhibited. The non-significance of h, i, j and l for capsule size and d, i and l for husk yield per plant may be attributed to their low estimates or very high standard error or near symmetrical distribution of positive and negative alleles among parents resulting in inter-cancellation of the effect of each other (KUMAR and PATRA 2010, 2012). No significant reciprocal differences were observed between $F_1$and F_2 means and their reciprocal populations (Table 1) for all the traits indicating the absence of maternal effect (NERISON *et al*. 2013).

Both the crosses for all the traits except capsule size and husk yield were interacting as evident from the significance of at least one of the four scales as well as χ^2 values. The similar signs of dominance (h) and dominance x dominance (l) indicated the presence of complementary (C) type of epistasis whereas the opposite signs indicated the predominance of duplicate (D) type of epistasis. Significant positive estimate of additive‘d’ component was exhibited for peduncle length, branches/plant, opium yield/plant and codeine content for cross NB-5x58/1 and leaves/plant, stem diameter, capsule weight/plant, capsule size/plant, seed yield/plant, percentage of morphine, thebaine and narcotine in latex for reciprocal cross suggested the involvement of associative additive gene pairs (KUMAR and PATRA, 2010). The negative significant estimates of additive (d) components for leaves/plant, capsule weight/plant and morphine content for cross NB-5 x 58/1 indicated the involvement of dissociative additive gene pairs in the inheritance of these traits which is in agreement with the findings of KUMAR and PATRA (2012); NARAIN *et al*.(2007).

Table 1. Means and Standard errors for some morphological and physiological traits in P_1, P_2, F_1, F_2, BC_1 and BC_2 generations of cross NB-5x58/1 and 58/1xNB-5 in opium poppy

Generation	P_1(NB-5)	P_2(58/1)	F_1	F_2	BC_1	BC_2
Plant height (cm)						
NB-5x58/I	114.40±0.27	122.80±1.09	126.30±1.15	125.50±1.12	128.90± 1.57	129.90±1.10
58/1xNB-5			125.90±0.53	123.40±1.59	128.20±1.24	129.10±0.64
Peduncle length(cm)						
NB-5x58/I	22.20±0.20	26.60± 0.98	28.20±0.49	30.20±0.77	28.70±0.34	27.00±0.42
58/1xNB-5			26.70±0.40	26.80±0.36	29.30±0.62	29.00±0.37
Leaves/Plant						
NB-5x58/I	18.80±0.49	18.90±0.64	18.80±0.29	15.10±0.32	15.80±0.2	18.00±0.21
58/1xNB-5			18.70±0.37	16.90±0.28	18.50±0.34	15.60±0.27
Branches/Plant						
NB-5x58/I	1.80±0.20	1.70±0.26	2.10±0.28	1.10±0.10	1.70±0.15	1.10±0.10
58/1xNB-5			1.80±0.25	1.30±0.15	1.90±0.28	1.60±0.16
Capsules/Plant						
NB-5x58/I	1.80±0.20	1.60±0.22	2.00±0.25	1.20±1.33	1.50±0.17	1.20±0.13
58/1xNB-5			1.60±0.27	1.10±0.10	1.40±0.27	1.20 ±0.13
Stem Diameter						
NB-5x58/I	1.22±0.05	1.13±0.13	1.31±0.09	0.89±0.06	1.01±0.05	1.04±0.07
58/1xNB-5			1.26±0.10	1.02±0.09	1.32±0.07	0.98±0.03
Capsule wt/plant						
NB-5x58/I	5.72±0.27	3.05±0.30	9.63±0.85	3.69±0.10	5.42±0.22	5.83±0.18
58/1xNB-5			9.26±0.003	5.87±0.01	6.68±0.05	5.11±0.03
Capsule Size						
NB-5x58/I	11.67±0.46	14.54±1.26	15.79± 0.90	12.31±0.92	13.80±0.56	15.14±0.54
58/1xNB-5			15.12±0.55	13.95±1.08	15.16±0.35	13.14±0.63
Seed Yield/Plant						
NB-5x58/I	3.42±0.24	1.60±0.13	3.68±0.28	1.24±0.05	1.63±0.08	1.81±0.11
58/1xNB-5			3.69±0.28	1.99±0.92	2.20±s0.12	1.67±0.06
Husk Yield/Plant	2.30±0.09	1.45±0.20				
NB-5x58/I			5.95±0.45	2.45±0.13	3.79±1.17	4.02±0.15
58/1xNB-5			5.57±0.06	3.89±1.12	4.49±0.56	3.44±0.09
Opium Yield/Plant						
NB-5x58/I	311.40±12.03	240.70±7.17	223.10±11.63	170.20±2.29	187.6±6.45	169.40±4.23
58/1xNB-5			330.20±12.82	153.90±7.50	231.9±12.69	208.80±4.24
Morphine						
NB-5x58/I	10.72±0.81	13.92±0.10	12.41±0.02	12.61±0.10	10.89±0.01	11.73±0.23
58/1xNB-5			13.98±0.09	13.51±0.10	13.29±0.01	12.82±0.041
Codeine						
NB-5x58/I	2.33±0.15	1.57±0.01	2.15±0.20	1.60±0.02	1.80±0.01	1.66±0.04
58/1xNB-5			1.58±0.06	1.39±0.02	1.53±0.12	1.50±0.01
Thebaine						
NB-5x58/I	2.55±0.03	2.75±0.01	2.64±0.02	2.60±0.12	3.49±0.01	3.36±0.17
58/1xNB-5			2.69±0.15	1.76±0.07	3.46±0.01	3.02±0.003
Narcotine						
NB-5x58/I	5.78±0.08	6.51±0.01	5.38±0.01	7.42±0.001	6.59±0.03	6.37±0.19
58/1xNB-5			7.12±0.10	6.66±0.10	7.15±0.03	6.90±0.01

Table 2a. Estimate of genetic parameters and components of variances for different quantitative traits in Opium Poppy.

Cross	Scaling Tests			
	A	B	C	D
Plant Height				
NB-5x58/I	17.10*±3.35	10.70**±2.71	12.20*± 5.15	-7.80*±2.94
58/1xNB-5	7.70**±2.76	17.90**±1.41	4.60±6.56	-10.50**±3.48
Peduncle Length				
NB-5x58/I	7.00**± 0.85	-0.80±1.38	15.60**±3.39	4.70**±1.64
58/1xNB-5	5.30**±1.62	9.10**±0.85	5.00*±0.85	-4.70**±1.01
Leaves/Plant				
NB-5x58/I	-6.00**± 0.70	-1.70*±0.82	-14.90**±1.60	-3.60**±0.69
58/1xNB-5	-0.60±1.01	-6.30**±0.81	-7.50**±1.55	-0.30±0.70
Branches/Plant				
NB-5x58/I	-0.50±0.46	-1.60**±0.43	-3.30**±0.76	-0.60*±0.27
58/1xNB-5	0.30±0.66	-0.40±0.46	-1.90*±0.85	-0.90*±0.44
Capsule/Plant				
NB-5x58/I	-0.80±0.47	-1.20**±0.43	-2.60**±0.80	-0.30±0.34
58/1xNB-5	-0.40±0.64	-1.00*±0.43	-2.20**±0.73	-0.40±0.36
Stem Diameter				
NB-5x58/I	-0.51**±0.15	-0.36±0.21	-1.41**±0.34	-0.27±0.15
58/1xNB-5	0.25±0.22	-0.52**±0.12	-0.79±0.42	-0.26±0.19
Capsule Weight/Plant			-	
NB-5x58/I	-4.51**±0.99	-1.03±0.98	3.29**±1.80	-3.87**±0.35
58/1xNB-5	1.06±1.59	-4.76**±0.90	-3.81*±1.88	-0.06±0.78
Capsule Size				
NB-5x58/I	0.14±1.50	-0.05± 1.89	-8.53±4.29	- 4.31*±1.99
58/1xNB-5	0.67±1.54	-0.52±1.45	-0.67±4.65	- 0.41±2.28
Seed Yield/Plant				
NB-5x58/I	-3.84**±0.40	-1.67**±0.38	-7.43**±0.64	-0.96**±0.16
58/1xNB-5	-0.89**±0.39	-3.76**±0.39	-4.45**±0.72	0.10±0.23
Husk Yield/Plant				
NB-5x58/I	-0.67±0.74	-0.64±0.74	-5.86**±1.41	-2.91**±0.33
58/1xNB-5	1.95±1.25	-0.99±0.60	0.64±1.24	-0.16±0.61
Opium Yield/Plant				
NB-5x58/I	-159.3**±21.13	-125.0**±16.08	-317.5**±28.66	-16.60±8.98
58/1xNB-5	-107.1**±29.32	-224.0**±19.52	-596.9**±41.87	-132.9**±20.1
Morphine Content (%)				
NB-5x58/I	-1.35**±0.10	-2.88**±0.42	0.99*±0.41	2.61**±0.28
58/1xNB-5	-1.42**±0.16	0.94**±0.16	1.35**±0.44	0.91**±0.21
Codeine Content (%)				
NB-5x58/I	-0.87**±0.03	-0.40**±0.09	-1.82**±0.09	-0.27**±0.06
58/1xNB-5	-0.09±0.24	-0.91**±0.06	-1.52**±0.14	-0.26*±0.13
Thebaine Content (%)				
NB-5x58/I	1.79**±0.04	1.33**±0.33	-0.19±0.47	-1.65*±0.29
58/1xNB-5	1.49**±016	0.81**±0.15	-3.63**±0.41	-2.96*±0.14
Narcotine Content (%)				
NB-5x58/I	2.02**±0.10	0.86*±0.39	6.65**±0.10	1.89*±0.20
58/1xNB-5	0.67**±0.1	0.90**±0.11	0.12±0.46	-0.73*±0.21

Table 2b. Estimate of genetic parameters and components of variances for different quantitative traits in Opium Poppy.

Cross	Parameters						Type of epistase	χ^2	
	m	d	h	i	j	l		value	Df
Plant Height									
NB-5x58/I	125.50**±1.12	-1.0±1.91 -	23.30**±6.02	15.60*±5.89	3.20±2.00	-43.40**±9.23	D	37.23**	3
58/1xNB-5	123.40**±1.59	0.9±1.39	28.30**±7.00	21.00**±6.95	-5.10**±1.50	-46.60**±8.60	D	164.87**	3
Peduncle Length									
NB-5x58/I	30.20**±0.77	1.70**±0.5	-5.60±3.34	-9.40**±3.27	3.90**±0.74	3.20±4.02	D	88.38**	3
58/1xNB-5	26.80**±0.36	39 0.3±0.72	1.70**±2.13	9.40±2.03	-1.90±0.87	-23.80**±3.45	D	118.05**	3
Leaves/Plant									
NB-5x58/I	15.10**±0.31	-2.2**±0.29	7.15**±1.47	7.20**±1.39	-2.15**±0.50	0.50±1.98	C	124.63**	3
58/1xNB-5	16.90**±0.28	2.9**±0.43	0.45±1.51	0.60±1.41	2.85**±0.59	6.30**±2.33	C	66.48**	3
Branches/Plant									
NB-5x58/I	1.10**±0.10	0.60*±0.18	1.55*±0.63	1.20*±0.54	0.55*±0.246	0.90±1.05	C	22.92**	3
58/1xNB-5	1.30**±0.15	0.30±0.32	1.85±0.94	1.80±0.89	0.35±0.361	-1.70±1.54	D	6.82	3
Capsule/Plant									
NB-5x58/I	1.20**±0.13	0.30±0.21	0.90±0.75	0.60±0.58	0.20±0.26	1.40±1.17	C	14.99**	3
58/1xNB-5	1.10**±0.10	0.20±0.30	0.70±0.78	0.80±0.72	0.30±0.33	0.60±1.40	C	10.19**	3
Stem Diameter									
NB-5x58/I	0.89**±0.06	-0.03±0.09	0.68*±0.32	0.54±0.30	-0.08±0.11	0.33±0.49	C	21.89**	3
58/1xNB-5	1.02**±0.09	0.34**±0.08	0.61±0.40	0.52±0.39	0.39**±0.11	-0.25±0.53	D	26.67**	3
Capsule Weight/Plant						-			3
NB-5x58/I	3.69**±0.10	-0.41*±0.28	12.99**±1.12	7.745**±0.7	-1.74**±0.35	2.21±2.13	D	199.39**	3
58/1xNB-5	5.87**±0.2	1.56*±0.67	4.98**±1.78	0.11±1.56	2.91**±0.70	3.59±3.28	C	59.38**	
Capsule Size									
NB-5x58/I	12.31**±0.92	-1.34±0.78	11..312**±4.13	8.63*±3.98	0.09±1.02	-8.72±5.30 -	D	4.92	3
58/1xNB-5	13.95**±1.08	2.03*±0.72	2.84±4.63	0.82±4.55	0.59±0.98	0.97±5.47	D	0.43	3
Seed Yield/Plant									
NB-5x58/I	1.24**±0.05	-0.18±0.13	3.10**±0.44	1.92**±0.32	-1.09**±0.19	3.59**±0.83	C	160.38**	3
58/1xNB-5	1.99**±0.09	0.53**±0.14	0.97±0.55	-0.21±0.46	1.44**±0.19	4.86**±0.90	C	107.76**	3
Husk Yield/Plant									
NB-5x58/I	2.45**±0.13	-0.23±0.22	9.89**±0.94	5.83**±0.67	-0.66*±0.25	-5.79**±1.67	D	92.10**	3
58/1xNB-5	3.89**±0.12	1.05±0.56	4.01*±1.34	0.32±1.22	1.47*±0.57	-1.28±2.55	D	0.40	3
Opium Yield/Plant									
NB-5x58/I	170.2**±2.29	18.2*±7.72	-19.75±22.51	33.20±17.96	-17.15±10.42	251.1**±42.13	D	122.76**	3
58/1xNB-5	153.9**±7.50	23.1±13.38	319.95**±42.77	265.8**±40.2	58.45**±15.1	65.30±67.95	C	220.84**	3
Morphine Content (%)									
NB-5x58/I	12.61**±0.10	0.83**±0.20	-5.14**±0.56	-5.23**±0.56	0.77**±0.22	9.46**±0.91	D	264.70**	3
58/1xNB-5	13.51**±0.10	0.47**±0.08	-0.22±0.43	-1.82**±0.42	-1.18**±0.09	2.30**±0.53	D	173.68**	3
Codeine Content (%)									
NB-5x58/I	1.60**±0.02	0.14*±0.05	0.74**±0.12	0.54**±0.12	-0.24**±0.05	0.73**±0.20	C	1036.84**	3
58/1xNB-5	1.39**±0.02	0.04±0.02	0.15±0.26	0.52*±0.25	0.41**±0.12	0.47±0.50	C	224.93**	3
Thebaine Content (%)									
NB-5x58/I	2.60**±0.12	0.13±0.17	3.30**±0.58	3.31**±0.58	0.23±0.12	-6.43**±0.82	D	2162.002**	3
58/1xNB-5	1.76**±0.07	0.44**±0.01	5.97**±0.32	5.92**±0.28	0.34**±0.02	-8.22**±0.41	D	937.87**	3
Narcotine Content (%)									
NB-5x58/I	7.42**±0.01	0.22±0.20	-4..54**±0.40	-3.77**±0.40	0.58**±0.20	0.89±0.79	D	509.63**	3
58/1xNB-5	6.66**±0.10	0.25**±0.01	2.43**±0.43	1.45**±0.41	-0.12**±0.03	-3.03**±0.46	D	78.85**	3

m = mean; d = additive gene effect; h = dominance gene effect; i = additive x additive effect; j = additive x dominance effect; l = dominance x dominance effect; C = complimentary epistasis; D = duplicate epistasis; df = degree of freedom; ** and * = significant at 1% and 5% respectively

Greater role of dominant gene effect (h) for inheritance of plant height, capsule weight/plant, husk yield/plant and thebaine content for both the crosses, leaves/plant, branches/plant, stem diameter, capsule size, seed yield/plant and codeine content for cross NB-5x58/1 and for peduncle length, opium yield/plant and narcotine content in reciprocal cross 58/1 x NB-5 was evident from the positive significant value of pooled dominance effect 'h'. Genes with negative effects were dominant over the genes with positive effects in the inheritance of morphine and narcotine as evident from the negative significant values of dominant gene effect (h) for these traits for the cross NB-5 x 58/1.

Positive and significant estimates of additive x additive (i) component in both the crosses for plant height, codeine and thebaine content as well as for leaves/plant, branches/plant, capsule weight/plant, capsule size, seed yield/plant and husk yield/plant in cross NB-5 x 58/1 and opium yield/plant as well as narcotine content for the cross 58/1 x NB-5 reflected the involvement of associated gene pairs for these traits. For morphine content in both the crosses and for peduncle length and narcotine content in cross NB-5 x 58/1, negative and significant estimates of additive x additive (i) was exhibited which suggested that the gene pair responsible for these traits were in dispersive form (MATHER and JINKS 1971).

Peduncle length, branches/plant, morphine and narcotine content for cross NB-5 x 58/1 and leaves/plant, stem diameter, capsule weight/plant, seed yield/plant, husk yield/plant, opium yield/plant, codeine and thebaine content for reciprocal cross exhibited positive significant values of additive x dominance (j) while leaves/plant, capsule weight/plant, seed yield/plant, husk yield/plant and codeine content for cross NB-5 x 58/1 and plant height, morphine and narcotine content for reciprocal cross showed negative significant values of j. The positive significant value of j indicated the potential for enhancing these characters in subsequent generations (ADENIJI et al. 2007). The negative value of j for plant height indicated that the selection of short plants may be advantageous in subsequent generations (AKHTAR and ASLAM 2006). Positive significant estimate for dominance x dominance (l) component was observed for seed yield/plant and morphine content in both the crosses, for opium yield/plant and codeine content in cross NB-5 x 58/1 and for leaves/plant in reciprocal cross. The significant negative estimates of l were observed for plant height and thebaine content in both the crosses, for husk yield/plant in cross NB-5 x 58/1 and for peduncle length and narcotine content in reciprocal cross.

The greater value of 'h' and 'l' than that of 'd' regardless of their signs for plant height, peduncle length, husk yield/plant, thebaine and narcotine content for both the crosses and for branches/plant in reciprocal cross 58/1 x NB-5 and for opium yield/plant and capsule weight/plant in cross NB-5 x 58/1 indicated greater importance of duplicate epistasis in the inheritance of these traits. This implies the difficulty in selection for these traits as a result of restricted variability (KUMAR and PATRA 2010, 2012; TEFERA and PEAT 1997). Trigenic or higher order interactions are necessitated to understand the inheritance pattern of those traits which have non-significant values of 'd', 'h', 'i', 'j' and 'l' (KUMAR and PATRA 2010, 2012).

The present study revealed the presence of both additive as well as dominance type of gene effects in the inheritance of different traits. Earlier studies on various quantitative traits indicated the role of additive as well as non additive gene actions in the inheritance of yield and yield related component traits. Non-additive gene action for plant height, peduncle length, branches/plant, capsules/plant, capsule weight/plant, capsule size, seed yield/plant, husk yield/plant and opium yield/plant were also reported by SINGH *et al.* (1999, 2001) and YADAV *et al.* (2009a,b). Additive gene action for plant height, leaves/plant, capsules/plant, capsule weight/plant, seed yield/plant and opium yield/plant was reported by KANDALKAR and NIGAM (1993) and SINGH *et al.* (1999). In the present study both duplicate as well as complementary epistasis were noticed. The presence of duplicate epistasis reduces the variability in advance generation, subsequently reducing the progress of selection (KUMAR and PATRA 2012). The disagreements in the nature of gene actions for some of the traits with the findings of different workers may be the consequence of differences in variability in material, population size, design adopted and agro-climatic as well as environmental conditions of the experiment (YADAV and SINGH 2011).

CONCLUSION

It is concluded from the present study that for most of the traits the value of non fixable dominance 'h' and dominance x dominance effect 'l' is of greater magnitude than the value of fixable additive (d) and additive x additive effects (i) except some traits showing greater importance of dominance (h) and dominance x dominance (l) effects in the inheritance of these traits. This suggests that pedigree selection might be a useful breeding strategy for improving these traits. Selection may be delayed in this case to later generation so that dominant effect may diminish. It is obvious from this study that the breeding strategy for genetic improvement in opium poppy (*P. somniferum* L.) should be trait oriented and the selection of parents should be done carefully as genetic improvement in opium poppy is not practicable wholly (KUMAR and PATRA 2012). Strategies like inter-mating of the best parents, diallel selective mating or biparental mating in early segregating generations followed by recurrent selections, which exploit both additive and non-additive gene effects, might be suitable for genetic improvement of opium poppy (YADAV and SINGH 2011; SHARMA et al. 2003).

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KVANTATIVNO NASLEĐIVANJE PRINOSA I KOMPONENTI PRINOSA KOD OPIJUMSKOG MAKA (*Papaver somniferum* L.)

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Izvod
Vršena je analiza proseka generacije ukrštanja i recipročnog ukrštanja NB-5x58/1 u cilju razumevanja prirode akcije gena u opijumskom maku. Značajnst A, B, C i D skale testova ukazuje na prisustvo nealelne intearcije u nasleđivanju osobina izuzev veličine kapsule i prinosa ljuske po biljci u recipročnom ukrštanju. Nađene su kako aditivne tako i dominantne komponente u direktnom i povratnom ukrštanju. Većina osobina je imala veću ne fiksiranu dominantnost "h" i dominantne x dominantne efekte nego fiksirane aditivne (d) i aditivne x aditvne efekte (i) izuzev broja listova po biljci, broja grančica po biljci, dijametra tučka, težine kapsule po boljci, prinos ljuske po biljci, prinosa opijuma po biljci i narkotina. Ovo pokazuje veći značaj aditivnog (d) i aditivnog x aditivnog efekta (i). Predlaže se ukrštanje najboljih roditelja, dialelno selektivno ukrštanje ili biparentalno ukrštanje najboljih roditelja u ranim segregirajućim generacijama a posle toga rekurentna selekcija, što bi dovelo do genetičkog poboljšanja opijumskog maka.

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