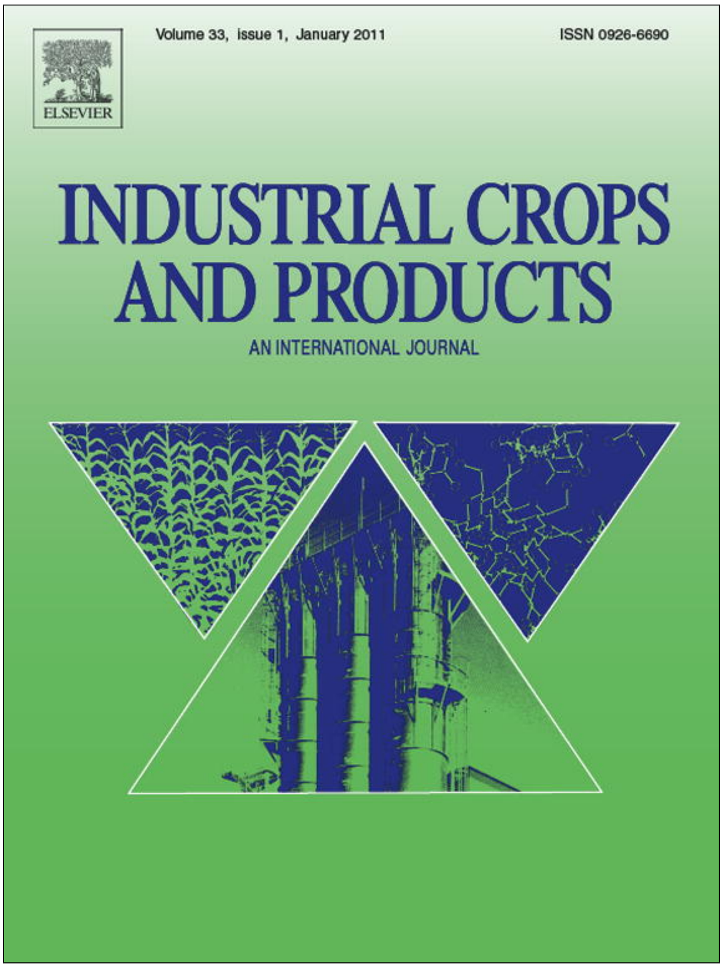

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Inheritance pattern and genetics of yield and component traits in opium poppy (*Papaver somniferum* L.)

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ABSTRACT

Opium poppy (*Papaver somniferum* L.) is an important medicinal plant produces more than 80 alkaloids belonging to various tetrahydrobenzylisoquinoline derived classes. These alkaloids are obtained from the capsules and straw of the plant. Information on the nature and magnitude of gene effects are required for genetic improvement. Therefore, the continuous assessment of newer breeding materials is mandatory on part of breeders. The objective of this study was undertaken to understand the particular gene action involved in the inheritance of yield and component traits. Two families (VG26 × VG20 and SG35II × VE01) of opium poppy were analyzed to study the gene actions involved in the inheritance of yield and component traits (plant height, leaves per plant, capsules per plant, peduncle length, capsule index, seed and straw yield per plant and morphine content). Simple additive, dominance, and epistatic genetic components were found to be significant. Dominance effect (‘*h*’) was higher than additive effect (‘*d*’) for capsule index and morphine content. Digenic interaction indicated the prevalence of dominance × dominance (‘*l*’) followed by additive × dominance (‘*j*’) type epistasis. The opposite sign of dominance (‘*h*’) and dominance × dominance (‘*l*’) indicated duplicate epistasis for all the traits. Biparental mating followed by recurrent selection involving desired recombinants may be utilized to improve the component traits.

1. Introduction

Opium poppy (*Papaver somniferum* L.) is an important medicinal plant produces more than 80 alkaloids belonging to various tetrahydrobenzylisoquinoline derived classes (Weid et al., 2004). Pharmaceutically important alkaloids include analgesic morphine, codeine, thebaine, papaverine, etc. (Facchini and Park, 2003). These alkaloids are obtained from the capsules and straw of the plant. Information on the nature and magnitude of gene effects are required for genetic improvement. However, most of these information were generated through either of the two mating designs: diallel (Griffing, 1956; Hayman, 1954) and line × tester (Kempthorne and Curnow, 1961). The diallel mating designs have some unrealistic assumptions and limitations of handling fewer numbers of parental lines at a time, and the line × tester design mainly adopted for preliminary testing of large number of general combiners. In opium poppy, such genetic information was gathered by various workers from time to time using either diallel (Kandalkar et al., 1992; Kumar, 2007; Kumar et al., 2008; Lal and Sharma, 1991; Singh et al., 1996, 2004; Yadav et al., 2007, 2009) or line × tester (Singh et al., 2001) designs. Cavalli (1952) proposed the joint scaling test for testing the expected relationship between generation means in the additive–dominance model of Mather and Jinks (1971). This test has two important advantages over other first degree statistics methods: (i) the generation means are not, in general, known with equal precision and hence appropriate weights are given to them and their expectations (ii) the data used in this analysis are neither confined to single generation nor restricted in any other way. Furthermore, the analysis is less cumbersome in respect to calculations, errors are smaller and the estimates are reliable. The generation means and its partitioning provide the information on the type of gene action involved. The study on this aspect is, however, meager in opium poppy under concentrated poppy straw system, where the morphine is extracted from straw. The importance of additive, dominance and epistatic genetic components and the magnitude of their estimate seem to be material specific (Kumar and Patra, 2010). Therefore, the continuous assessment of newer breeding materials is mandatory on part of breeders. The present investigation was undertaken to understand the particular gene action involved in the inheritance of yield and component traits.

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Table 1
Estimates of gene effects in two non-interacting crosses used for important morpho-metric traits in opium poppy in 2004–2006.

Name of crosses	Scaling test				$\hat{m}$	$\hat{d}$	$\hat{h}$	χ^2	
	A	B	C	D				Value	df
Leaves/plant									
SG35II × VE01	NS	NS	NS	NS	$10.88^{**} \pm 0.22$	$0.54^{*} \pm 0.22$	0.78 ± 0.39	4.33	3
Seed yield/plant									
VG26 × VG20	NS	NS	NS	NS	$7.49^{**} \pm 0.32$	0.09 ± 0.31	-0.62 ± 0.55	6.21	3

NS: non significant; *m*, pooled mean; *d*, pooled additive effect; *h*, pooled dominance effect; df, degree of freedom.
* Significant at $p = 0.05$.
** Significant at $p = 0.01$.

2. Materials and methods

The material consisted of 6 generations: P_1, P_2, F_1, F_2, BC_1, and BC_2 of 2 crosses involving 4 parental lines, VG20, VG26, SG35II, and VE01 (Satpute, 2000; Kumar and Patra, 2010), their 2 single crosses (VG26 × VG20 and SG35II × VE01) along with their respective 2 F_2s and 4 backcrosses [BC_1's ($F_1 \times P_1$) and BC_2's ($F_1 \times P_2$)]. VE01 is a dwarf having small sized capsule, low seed and straw yield and high morphine content in straw; SG35II is a tall having low morphine content in straw, high seed and straw yield; VG26 is tall having big sized capsule, non waxy capsule surface, high seed yielder and medium morphine content in straw and VG20 is a tall, early flowering and medium sized capsule with high morphine content in straw (Kumar, 2007; Kumar and Patra, 2010). Thus, a total treatments of 12 [2 crosses and their 6 basic generations, P_1, P_2, F_1 ($P_1 \times P_2$), F_2 (selfed F_1's), BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$), respectively] were raised in a compact family block design (RBD) with 3 replications at Central Institute of Medicinal and Aromatic Plants (CIMAP), Lucknow, India during 2 consecutive years 2004–05 and 2005–06. The planting was done in 3 m long rows with row-to-row and plant-to-plant distances of 30 cm and 10 cm, respectively. Each generation was represented by 3 rows (as experimental rows) and 2 rows as non-experimental rows grown as the border rows in each replication in order to minimize competition of nutritional uptake. The data were recorded on 10 randomly selected competitive plants in each row for yield and component traits, namely plant height (cm), leaves per plant (number), capsules/plant(number), peduncle length (cm), capsule index (capsule width/capsule length), seed and straw yield/plant (gm) and morphine content (%). The morphine content (%) in straw was quantified through high performance liquid chromatography analysis (Akhila and Uniyal, 1983). Data were processed on HCL infiniti Pro computer (P4) using the software SPAR-1 (Doshi and Gupta, 1991).

Statistical analysis was performed separately for each cross. A Waller–Duncan *K* ratio was applied to determine the significant differences that existed among the generation means. The interacting and non-interacting crosses were identified following the methods of A, B, C, D scales ($A = 2B_1 - P_1 - F_1 = 0$; $B = 2B_2 - P_2 - F_1 = 0$; $C = 4F_2 - 2F_1 - P_1 - P_2 = 0$; $D = 2F_2 - B_1 - B_2 = 0$) suggested by Hayman and Mather (1955). The observed means of the 6 generations were used to estimate '*m*' (a constant),'*d*' (pooled additive effects), and '*h*' (pooled dominance effects) as per the joint scaling test of Cavalli (1952). The adequacy of additive–dominance model was tested by comparing the observed and expected means and goodness-of-fit tested against the χ^2 value for 3 degree of freedom (df) (the number of observed means available minus the number of parameters to be estimated). The 3 parameters – '*m*', '*d*', and '*h*' were estimated from the 6 generations by weighted least squares using reciprocals of the squared standard errors of each mean weight.

3. Results and discussion

3.1. Non-interacting crosses

The cross VG26 × VG20 for seed yields per plant and SG35II × VE01 for leaves per plant was the only non-interacting crosses (Table 1). Since the χ^2 (3df) values were non-significant, the additive–dominance model was found to be adequate for these traits and crosses. Significant positive estimate for '*d*' (additive) component was exhibited for leaves per plant in the cross SG35II × VE01. Non-significance of both the components i.e. additive ('*d*') and dominance ('*h*') for the cross VG26 × VG20 (seed yield/plant) may be ascribed to (i) either the estimates are very low or their standard errors are very high or (ii) near to symmetrical distribution of positive and negative alleles among the parents and hence leading to the inter-cancellation of the effect of each other (Kumar and Patra, 2010).

3.2. Interacting crosses

Interacting crosses too were identified through the scaling tests and a further confirmation was made through the adequacy test (χ^2) and the six parameters model was applied (Table 2). The opposite signs for '*h*' and dominance × dominance ('*l*') indicated the predominance of duplicate (D) type of epistasis and their similar signs indicated for complementary (C) type of epistasis. The observed findings on estimates of various genetic components have been briefly described below.

Significant positive estimates for '*d*' components were exhibited for peduncle length and capsule index in VG26 × VG20 and for plant height and peduncle length in SG35II × VE01 indicating that the inheritance of these traits was essentially controlled by associated additive gene pairs (Kumar and Patra, 2010). The occurrence of significant negative estimates for additive components were exhibited for leaves per plant and morphine content in the cross VG26 × VG20 and for capsule index and morphine content in the cross SG35II × VE01 indicating that these traits were essentially controlled by dissociated additive gene pairs (Kumar, 2007; Narain et al., 2007).

Significant positive estimates for '*h*' in the cross VG26 × VG20 for plant height, leaves per plant and capsule index as well as for plant height, capsule index and morphine content in the cross SG35II × VE01 are suggestive of the fact that there is a greater role of dominant gene effect for inheritance of these traits. Occurrence of significant negative estimates for dominance component in the cross VG26 × VG20 for peduncle length is suggestive of that genes with negative effects were dominant over the genes with positive effects (Kumar and Patra, 2010; Pawar et al., 1988).

Significant positive estimates for additive × additive (i) components in the cross VG26 × VG20 for plant height, leaves per plant and capsule index as well as for capsule index and morphine

Table 2
Estimates of gene effects in two interacting crosses for important morpho-metric traits in opium poppy in 2004–2006.

Name of crosses	Scaling test				$\hat{m}$	$\hat{d}$	$\hat{h}$	$\hat{i}$	$\hat{j}$	$\hat{l}$	Type of epistasis	χ^2	
	A	B	C	D								Value	df
Plant height													
VG26 × VG20	*	**	NS	**	$107.13^{**} \pm 3.08$	0.73 ± 0.77	$34.80^{**} \pm 8.40$	$12.67^{**} \pm 2.99$	-2.13 ± 2.86	$-25.60^{**} \pm 5.55$	D	26.17^{**}	3
SG35II × VE01	**	**	**	NS	$90.40^{**} \pm 5.17$	$32.67^{**} \pm 0.68$	$32.47^{*} \pm 12.33$	0.002 ± 5.13	$-81.33^{**} \pm 3.17$	$-24.94^{**} \pm 7.75$	D	845.63^{**}	3
Leaves/plant													
VG26 × VG20	**	NS	*	**	$8.27^{**} \pm 1.48$	$-0.93^{**} \pm 0.17$	$15.73^{**} \pm 3.65$	$5.47^{**} \pm 1.47$	$3.07^{**} \pm 0.99$	$-7.47^{**} \pm 2.28$	D	24.95^{**}	3
Capsules/plant													
VG26 × VG20	*	NS	NS	NS	$2.23^{*} \pm 0.88$	0.10 ± 0.14	-0.90 ± 2.04	0.27 ± 0.87	-0.73 ± 0.51	0.87 ± 1.23	D	7.84^{*}	3
SG35II × VE01	**	NS	NS	NS	$2.23^{**} \pm 0.80$	-0.17 ± 0.15	1.70 ± 1.86	0.13 ± 0.78	0.47 ± 0.49	-1.93 ± 1.16	D	9.06^{*}	3
Peduncle length													
VG26 × VG20	**	NS	NS	*	$30.20^{**} \pm 3.39$	$4.07^{**} \pm 0.41$	$-20.07^{*} \pm 7.51$	$-8.27^{*} \pm 3.36$	$-4.93^{**} \pm 1.60$	$17.73^{**} \pm 4.26$	D	38.60^{**}	3
SG35II × VE01	NS	**	**	*	$23.17^{**} \pm 2.11$	$1.10^{**} \pm 0.30$	-0.17 ± 4.81	$-5.33^{*} \pm 2.09$	$-7.00^{**} \pm 1.12$	2.00 ± 2.98	D	61.30^{**}	3
Capsule index													
VG26 × VG20	**	**	NS	**	-0.04 ± 0.16	$0.04^{**} \pm 0.01$	$2.16^{**} \pm 0.37$	$0.69^{**} \pm 0.15$	-0.10 ± 0.09	$-1.40^{**} \pm 0.23$	D	46.29^{**}	3
SG35II × VE01	**	**	*	**	$-1.50^{**} \pm 0.11$	$-0.06^{**} \pm 0.01$	$6.32^{**} \pm 0.25$	$2.28^{**} \pm 0.11$	$0.11^{*} \pm 0.04$	$-4.17^{**} \pm 0.16$	D	666.86^{**}	3
Seed yield/plant													
SG35II × VE01	*	NS	NS	NS	$6.82^{**} \pm 1.71$	-0.19 ± 0.40	4.20 ± 3.89	0.51 ± 1.66	0.19 ± 1.06	-4.21 ± 2.48	D	7.85^{*}	3
Straw yield/plant													
VG26 × VG20	*	NS	NS	NS	$5.10^{**} \pm 1.78$	0.17 ± 0.26	-3.14 ± 4.02	-0.13 ± 1.77	-1.30 ± 0.93	2.78 ± 2.37	D	7.95^{*}	3
SG35II × VE01	*	NS	NS	NS	$4.25^{*} \pm 1.56$	-0.35 ± 0.28	3.25 ± 3.67	0.36 ± 1.54	0.82 ± 0.97	-3.47 ± 2.27	D	7.92^{*}	3
Morphine content													
VG26 × VG20	NS	**	**	NS	-0.40 ± 1.21	$-0.03^{**} \pm 0.003$	3.81 ± 3.63	1.31 ± 1.21	1.28 ± 1.21	-2.50 ± 2.42	D	21.70^{**}	3
SG35II × VE01	**	**	**	**	$0.79^{**} \pm 0.01$	$-0.04^{**} \pm 0.003$	$0.19^{**} \pm 0.04$	$0.12^{**} \pm 0.01$	$0.09^{**} \pm 0.01$	$-0.10^{**} \pm 0.02$	D	204.69^{**}	3

NS : non significant; *m*, pooled mean; *d*, pooled additive effect; *h*, pooled dominance effect; *i*, additive × additive gene effect; *j*, additive × dominance gene effect; *l*, dominance × dominance gene effect; D, duplicate type epistasis; df, degree of freedom.

* Significant at $p = 0.05$.

** Significant at $p = 0.01$.

content in the cross SG35II × VE01 indicated presence of associated forms of gene pairs for these traits. For peduncle length in both the crosses have exhibited significant negative estimates for additive × additive component.

Significant positive estimates for additive × dominance (j) components were exhibited in the cross VG26 × VG20 for leaves per plant as well as for capsule index and morphine content in the cross SG35II × VE01. Occurrence of significant negative estimates for additive × dominance component in the cross VG26 × VG20 for peduncle length and for plant height and peduncle length in the cross SG35II × VE01 suggests that there is a greater role of additive × dominance gene effect for controlling these traits.

Significant positive estimates for dominance × dominance (*l*) components were exhibited in the cross VG26 × VG20 for peduncle length, but for none of the characters in the cross SG35II × VE01. Significant negative estimates of dominance × dominance component in the cross VG26 × VG20 for plant height, leaves per plant and capsule index as well as for plant height, capsule index and morphine content in the cross SG35II × VE01.

The magnitude of '*h*' and '*l*' was larger than the '*d*' irrespective of their signs for plant height, leaves/plant, capsules/plant, peduncle length, capsule index, straw yield/plant and morphine content in the cross VG26 × VG20 and for capsules/plant, capsule index, seed and straw yield/plant and morphine content in the cross SG35II × VE01 implying the major role of duplicate epistasis. This suggested that the selection for these traits of both crosses might be difficult due to restricted variability (Kumar and Patra, 2010; Tefera and Peat, 1997). Non significant estimates of '*d*', '*h*', '*i*', '*j*', and '*l*' for the capsules/plant and straw yield/plant in both crosses and for seed yield/plant in the cross SG35II × VE01 suggest that trigenic or higher order of interactions are required for understanding the inheritance pattern of yield and component traits (Kumar and Patra, 2010).

Overall, the gene effects analysis in the present study has highlighted the greater existence of dominance effects and dominance × dominance non-allelic interactions for the characters studied. The epistasis in both the crosses for all studied characters is duplicate type. The presence of duplicate epistasis may reduce the variability in F_2 and further generations, thereby reducing the progress of selection. It was also evident from this study that in opium poppy breeding strategies for overall improvement would not be feasible and that it should be trait oriented and parent selection must be done with utmost care. Under these circumstances, the use of intermating of the best parents followed by recurrent selection holds promise for genetic improvement of these traits in opium poppy (Kumar and Patra, 2010).

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References

Akhila, A., Uniyal, G.C., 1983. Quantitative estimation of opium alkaloids. Indian Pharm. Sci. 45, 236–238.

Cavalli, L.L., 1952. An analysis of linkage in quantitative inheritance. In: Reeve, E.C.R., Waddington, C.H. (Eds.), Quantitative Inheritance. HMSO, London, pp. 135–144.

Doshi, S.P., Gupta, K.C., 1991. SPAR-1 Software. Indian Agricultural Statistical Research, New Delhi, India.

Facchini, P.J., Park, S.U., 2003. Developmental and inducible accumulation of gene transcripts involved in alkaloid biosynthesis in opium poppy. Phytochemistry 64, 177–186.

Griffing, B., 1956. Concept of general and specific combining ability in relation to diallel crossing system. Aust. J. Biol. Sci. 9, 463–493.

Hayman, B.I., 1954. The theory and analysis of diallel crosses. Genetics 39, 789–809.

Hayman, B.I., Mather, K., 1955. The description of genetic interaction in continuous variation. Biometrics 11, 69–82.

Kandalkar, V.S., Patidar, H., Nigam, K.B., 1992. Combining ability analysis for harvest index, seed yield and important component characters in opium poppy (*Papaver somniferum* L.). Indian J. Genet. Plant. Breed. 52, 275–279.

Kempthorne, O., Curnow, R.N., 1961. The partial diallel cross. Biometrics 17, 229–250.

Kumar, B., 2007. Study on genetic architecture of opium poppy (*Papaver somniferum* L.) in relevance to yield improvement. Ph.D. Thesis, Lucknow University, Lucknow, India.

Kumar, B., Patra, N.K., 2010. Genetic analysis of capsule and its associated economic traits in opium poppy (*Papaver somniferum* L.). J. Hered. 101, 657–660.

Kumar, B., Singh, H.P., Verma, A.K., Misra, H.O., Patra, N.K., 2008. Combining ability analysis in relation to heterosis in opium poppy (*Papaver sominferum* L.). J. Med. Aromat. Plant Sci. 30, 83–87.

Lal, R.K., Sharma, J.R., 1991. Genetics of alkaloids in *Papaver somniferum*. Planta Med. 57, 271–274.

Mather, K., Jinks, J.L., 1971. Biometrical Genetics. The Study of Continuous Variation. Chapman and Hall Ltd., London.

Narain, V., Singh, P.K., Kumar, N., Singh, V.S., 2007. Gene effects for grain yield and related traits in sorghum [*Sorghum bicolor* (L.) Moench.]. Indian J. Genet. Plant Breed. 67, 34–36.

Pawar, I.S., Singh, S., Paroda, R.S., Singh, I., 1988. An analysis of generation means for yield and its component traits in bread wheat. Indian J. Genet. Plant Breed. 48, 317–319.

Satpute, G.K., 2000. Mutation breeding for genetic enhancement of desirable alkaloids in opium poppy (*Papaver somniferum* L.). Ph.D. Thesis, Lucknow University, Lucknow, India.

Singh, S.P., Shukla, S., Khanna, K.R., 1996. Diallel analysis for seed yield and its components in opium poppy (*P. somniferum*). J. Med. Aromat. Plant Sci. 18, 259–263.

Singh, S.P., Shukla, S., Yadav, H.K., 2004. Genetic studies and their implication to breed desired plant type in opium poppy (*Papaver somniferum* L.). Genetika 36, 69–81.

Singh, S.P., Singh, H.P., Singh, A.K., Verma, R.K., 2001. Identification of parents and hybrids through line × tester analysis in opium poppy (*Papaver somniferum* L.). J. Med. Aromat. Plant Sci. 22, 327–330.

Tefera, H., Peat, W.E., 1997. Genetics of grain yield and other agronomic characters in t'ef (*Eragrostis tef* Zucc. Trotter). I. Generation means and variances analysis. Euphytica 96, 185–191.

Weid, M., Ziegler, J., Kutchan, T.M., 2004. The roles of latex and the vascular bundle in morphine biosynthesis in the opium poppy, *Papaver somniferum*. Proc. Natl. Acad. Sci. U.S.A. 101, 13957–13962.

Yadav, H.K., Shukla, S., Singh, S.P., 2007. Genetic divergence in parental genotypes and its relation with heterosis, F_1 performance and general combining ability (GCA) in opium poppy (*Papaver somniferum* L.). Euphytica 157, 123–130.

Yadav, H.K., Shukla, S., Singh, S.P., 2009. Genetic combining ability estimates in the F_1 and F_2 generations for yield, its component traits and alkaloid content in opium poppy (*Papaver somniferum* L.). Euphytica 168, 23–32.