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Communications in Biometry and Crop Science
Vol. 5, No. 1, 2010, pp. 11–18

International Journal of the Faculty of Agriculture and Biology,
Warsaw University of Life Sciences, Poland

REGULAR ARTICLE

Inheritance of quantitative traits in opium poppy (*Papaver somniferum* L.)

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CITATION: Kumar, B., Singh, H.P., Patra, N.K. (2010). Inheritance of quantitative traits in opium poppy (*Papaver somniferum* L.). *Communications in Biometry and Crop Science* 5 (1), 11–18.

Received: 14 January 2009, Accepted: 24 March 2010, Published online: 27 April 2010

ABSTRACT

Lodging in opium poppy (*Papaver somniferum* L.) leads to seed loss and consequently loss of the economically important constituent, morphine. Enhancing lodging resistance through plant breeding is the objective of a program at the Central Institute of Medicinal and Aromatic Plants (CIMAP) in Lucknow, India. Specific objectives of the program are moderate plant height and high yield potential. Prior to finalize the breeding strategy it was necessary to gather the genetic information on selected parents. The magnitude of genetic parameters was determined from an analysis of F_1 and F_2 progenies from an eight-parent diallel. Data was collected from F_1 and F_2 generations for days to 50% flowering, plant height, peduncle length, leaves per plant, leaf length, leaf width, branches per plant, stem diameter, capsules per plant, seed yield, capsule index and percent morphine. The dominance component H_1 was significant for all the characters except for morphine content in both F_1 and F_2. The additive component (D) was not significant for 13 of the 28 tests (F_1 and F_2 generations for 14 traits). Results suggested that heterotic breeding approaches should be followed for exploiting the over-dominance effects, while recurrent selection is utilized for overall population improvement of the opium poppy.

Key Words: *genetic improvement; estimates; additive; dominance, inheritance.*

INTRODUCTION

Opium poppy (*Papaver somniferum* L.) is a diploid (2n = 2x = 22) crop of antiquity and was well known to the ancient Greek from whom it gained its modern name of opium. In a sub-tropical climate it is an annual herb. It is primarily self-pollinated (Kumar, 2007) but cross-pollination is estimated to be 10 – 37 % (Patra et al., 1992). Opium poppy is highly valued by pharmaceutical industries because it is a source of phenantherene alkaloids including morphine, thebaine and codeine. The seed contains 35-50% edible oil and high

quality protein (Nergiz and Qtles, 1994; Sharma et al., 1999). India, as the largest legitimate poppy producer is developing improved, higher yielding poppy cultivars.

Additive genetic variance is expected to result mostly from additive gene action which is fixable, whereas non-additive genetic variance is made up of dominance and epistasis. The dominance variance diminishes by half with each generation of selfing. The decrease or increase in estimate of variances due to non-additive gene action in F_2 depends primarily on its nature in segregating population. Estimates of additive variance were larger than the dominance variances or environmental variances for the majority of the studied eight economic traits (Srivastava and Sharma, 1987). Kandalkar et al. (1992), Singh et al. (1996, 2001) and Yadav et al. (2009) have also reported non-additive genetic variance for capsules/plant, capsule weight/plant, leaves/plant and seed yield/plant. However, additive genetic variance for days to 50% flowering, plant height, leaves/plant, capsule diameter, capsules/plant, capsule weight/plant, seed yield/plant, husk yield/plant and straw morphine was reported by various workers (Khanna and Shukla, 1989; Lal and Sharma, 1991; Shukla, 1992; Kandalkar et al., 1992; Kandalkar and Nigam, 1993; Kumar et al., 2008; Shukla et al., 1993; Singh et al., 1999, 2002, 2003; Yadav et al., 2009). Singh et al. (2001) reported non-additive gene action for plant height, capsule length, husk yield/plant, seed yield/plant and morphine content. Lal and Sharma (1991) reported additive component for morphine content. Shukla and Khanna (1997) reported additive gene action for plant height and capsule/plant and non-additive for seed yield/plant while both additive and non-additive genetic variances were important for stem diameter, days to flower, capsule size and morphine content. The study of the estimates of genetic components of variance for various quantitative characters is essential for formulating efficient breeding program for increasing productivity.

MATERIALS AND METHODS

An eight parent diallel with reciprocals was produced using hand crossing with emasculation for the production of F_1 generation. Parents included two released cultivars (Vivek and Sanchita) and six advanced breeding lines maintained as inbreds (Table 1). Seed for F_2 generation was produced by selfing (bagging the buds) of F_1 plants.

The experimental design for progeny evaluation was a randomized complete block design (r = 3) in the 2003-04 and 2004-05 rabi (spring) cropping seasons at the Research Farm of Central Institute of Medicinal and Aromatic Plants, Lucknow located at 26.50°N and 80.50°E and 120 m above mean sea levels. Soil of the experimental plot was sandy loam having moderate fertility and pH 6.5. Plots were three meters long and the five rows were spaced 30 cm apart and the plants were 10 cm apart within the row. Only the center three rows were harvested. The crop was managed using standard agronomic practices for opium production. Five plants per plot were randomly selected for measurement of mature plant height (cm), peduncle length (cm), leaves per plant, leaf length (cm) at fifth internode, leaf width (cm), branches per plant, stem diameter at 10 cm from the soil line, capsules per plant, stigmatic rays (notches) on main capsule, seed yield per plant (gm), straw yield per plant (gm), capsule index (CI = Capsule Width / Capsule Length), and morphine content (percent of capsule dry weight). Days to 50% flowering plants was also recorded.

Mean plot data was subjected to the genetic analysis (Hayman, 1954 a,b) to estimate $D = 4uvd^2$ = measure of variation due to additive effect of the genes, $H_1 = 4uvh^2$ = measure of component of variations due to dominance effect of the genes, $H_2 = 16uvh^2$ = measure the proportion of dominance variance due to the positive (u) and negative (v) effects of the genes, if the distribution of dominant and recessive alleles among the parents are equal then the relationship of estimate of H_1, H_2 and h^2 will be: $H_1 = H_2 = h^2$; if $H_1 > H_2$ means that $u_i \neq v_2$ positive and negative alleles at these loci are not in equal proportion in the parents. However, it is not possible whether positive or negative are in

excess. Where u and v, are the proportion of positive and negative genes in the parents while d and h are the additive and dominance effects caused by them, h^2 measures the net dominance effect (expressed as the algebraic sum over all loci as heterozygous phase in all the crosses). $Fr = 2 \Sigma di\ hi\ Ø\ ri\ (1 - wi^2)$ or $2\ (Vo\ Lo - Wo\ Lo_1 + V_1\ L_1 - Wr - Vr)$ -2 $(n - 2)\ \hat{E}/n$ (Hayman, 1954b). Usually in case of non-homologous if $hi\ Ø\ ri$ is positive means abundance of dominant homozygotes and if negative means recessive. The greater the value of Fr, the more parents are with dominant alleles and *vice-versa*. The F measures the mean of Fr over the arrays which indicates the relative frequency of dominant and recessive alleles in the parents. It may take the negative (-) sign if there is an excess of recessive allele or the positive (+) sign indicating an excess of dominant alleles. E is the measure of expected environmental component of variation which is observed from the analysis of variance. Analysis was executed using computer program SPAR-1 of IASRI, New Delhi SPAR1 (Release1.1, 1991).

Table 1. Brief description and origin of the inbred/hybrid parents.

No.	Parents	Pedigree	Salient features
1	Vivek	Induced mutant, obtained in mutagen treated material of the cv. Shweta (mutagen doses: 5kR γ rays) (Patra and Chauhan, 1990).	Broad leaves, big capsule size, high seed yielder, high morphine in straw, tall and white petal color.
2	Sanchita	Half sib family selection (Patra and Kumar, 2005).	Broad leaves, leaves are highly serrated, medium capsule size, medium morphine content in straw, tall and white petal color.
3	SG35II	Mutant strain derived from cv. Sanchita upon irradiation with γ- rays (15kR). (Satpute, 2000; Kumar, 2007).	Broad leaves, big capsule size, high seed yielder, less morphine content in straw, tall and white petal color.
4	VE01	Chemical mutant strain developed from cv. Vivek upon treatment with EMS (0.4%) (Satpute, 2000; Kumar, 2007).	Broad and medium sized leaves, small capsule size, elongated capsule shape, less seed yielder, high morphine content in straw, dwarf and white petal color.
5	VG26	Mutant derived from cv. Vivek upon irradiation with γ rays (15kR) (Satpute , 2000; Kumar, 2007).	Broad leaves, big capsule size non-waxy capsule surface ('telia'), high seed yielder, medium morphine content in straw, tall and white petal color.
6	VG20	Induced mutant derived from cv. Vivek upon irradiation with γ rays (15kR) (Satpute, 2000; Kumar, 2007).	Broad leaves, medium capsule size, early flowering, high morphine content in straw, tall and white petal color.
7	VN35I	Chemical mutant strain developed from cv. Vivek upon treatment with sodium azide (0.001M) (Satpute,2000; Kumar, 2007).	Fringed leaves, hairy trichomed peduncle, medium capsule size, high morphine content in straw, tall and white petal color.
8	VN23	Chemical mutant strain developed from cv. Vivek upon treatment with sodium azide (0.001M) (Satpute, 2000; Kumar, 2007).	Broad leaves, flat and big capsule size, less morphine content in straw, tall and white petal color.

RESULTS AND DISCUSSION

Analysis of variance showed that variation within parents, F_1s and F_2s was statistically significant for all traits (Table 2). The estimates of genetic components of traits for F_1 and F_2 generations with standard errors appear in Table 3.

Estimates of the *D* effect (additive component) were significant for days to 50% flowering, plant height, peduncle length, leaves/plant, leaf length and width and stigmatic rays (notches) in F_1 and F_2 generations and stem diameter in F_1 generation. The magnitude of the estimates was intermediate in F_1 and F_2 analysis.

Table 2. Analysis of variance for 14 quantitative traits for F_1 and F_2 progeny from an 8-parent diallel in opium poppy.

Source of variation	Treat-ments	Parents	F_1	Parents vs F_1	F_2	Parents vs F_2	Block	Error
df	119	7	55	1	55	1	2	238
Days to 50% flowering	15.779 **	43.025 **	14.415 **	0.258	14.118 **	0.659	1.878	0.965
Plant height	357.739 **	1430.737 **	344.396 **	119.866 **	237.267 **	0.371	7.382	5.305
Peduncle length	11.760 **	29.947 **	11.693 **	15.604 **	9.109 **	37.328 **	0.812	1.578
Leaves / plant	31.412 **	14.487 **	4.845 **	71.457 **	1.028 **	9.873 **	0.345	0.127
Leaf length	26.685 **	54.114 **	20.822 **	6.668 *	28.761 **	2.504 **	0.756	1.626
Leaf width	7.225 **	11.233 **	5.592 **	3.709 **	8.353 **	0.015 **	0.770	0.470
Branches / plant	0.530 **	0.108 **	0.566 **	1.540 **	0.534 **	1.716 **	0.060	0.037
Stem diameter	1.096 **	0.535 **	1.016 **	4.915 **	1.153 **	7.314 **	0.052	0.089
Capsules / plant	0.535 **	0.108 **	0.572 **	1.630 **	0.541 **	1.646 **	0.079	0.042
Stigmatic rays on main capsule	8.111 **	66.297 **	5.311 **	124.645 **	0.426 **	183.636 **	0.230	0.094
Seed yield / plant	4.361 **	0.968 **	5.063 **	24.732 **	3.795 **	21.166 **	0.961	0.374
Straw yield / plant	2.231 **	0.380 **	2.216 **	7.822 **	2.145 **	3.041 **	0.776	0.204
Capsule index	0.088 **	0.063 **	0.118 **	0.046 *	0.062 **	0.003	0.499	0.007
Morphine content	0.005 **	0.006 **	0.004 **	0.010 **	0.005 **	0.006 **	0.000	0.000

*, ** significant at $P = 0.05$ and $P = 0.01$, respectively.

The H_1 dominance component was highly significant for all of the characters in both F_1 and F_2 except for morphine content. The estimates of H_2 dominance component were highly significant ($P < 0.01$) for plant height (F_1 and F_2), peduncle length (F_1), leaves/plant (F_2), leaf length and width (F_1), branches/plant (F_2), stem diameter (F_1 and F_2), capsules/plant (F_1 and F_2), stigmatic rays (F_1 and F_2), seed yield (F_1 and F_2) and straw yield (F_1 and F_2) and significant ($P < 0.05$) for days to 50% flowering (F_1 and F_2), peduncle length (F_2), leaves/plant (F_1), leaf length and width (F_2), branches/plant (F_1) and capsule index (F_1 and F_2). The magnitude of H_1 and H_2 were higher for all characters in F_2 than the F_1. The estimates of H_1 were consistently higher than for H_2. This indicates that unequal distribution of dominant and recessive genes among the parents.

The significant positive estimates of h^2 which is a measure of net dominance effect were observed only for leaves/plant, branches/plant, stem diameter, capsules/plant stigmatic rays, seed yield and straw yield only in F_1 analysis while in F_2 analysis, peduncle length, leaves/plant, branches/plant, stem diameter, capsules/plant, stigmatic rays (notches) on main capsule and seed yield/plant (Table 3).

The estimates of directional component *F* were positive and significant for days to 50% flowering, plant height, peduncle length, leaves/plant, leaf length and width, number of stigmatic rays on main capsule in both generation and for capsule index in F_2 generation, suggesting a preponderance of genes with positive effects (increasing the mean) determines these characters. The error component (*E*) was non-significant for all traits in F_1 and F_2.

Table 3. Estimates of genetic components of variance in F_1 and F_2 diallel progeny for 14 traits in opium poppy.

Trait		t^2	*D*		H_1		H_2		h^2		*F*		Error	
			Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
Days to 50% flowering	F_1	1.38	14.01 **	1.72	15.49 **	3.95	10.48 *	3.44	-0.11	2.31	15.70 **	4.06	0.34	0.57
	F_2	0.14	14.02 **	1.37	58.29 **	12.59	39.16 **	10.95	-0.04	1.84	30.32 **	6.47	0.32	0.46
Plant height	F_1	5.19 *	475.35 **	19.58	334.43 **	45.02	173.26 **	39.17	16.76	26.77	498.10 **	46.28	1.57	6.53
	F_2	4.61 *	474.98 **	20.34	1285.21 **	187.05	626.74 **	162.74	-0.79	27.28	1042.05 **	96.13	1.93	6.78
Peduncle length	F_1	0.62	9.98 **	0.83	14.85 **	1.90	8.56 **	1.65	2.06	1.11	13.70 **	1.95	0.50	0.28
	F_2	2.18	9.42 **	1.26	42.54 *	11.59	26.64 *	10.09	5.20 *	1.69	23.87 **	5.96	0.56	0.42
Leaves /plant	F_1	1.47	4.81 **	1.00	9.52 **	2.30	5.69 *	2.00	10.41 **	1.34	1.42 **	0.34	0.02	0.33
	F_2	0.03	4.77 **	0.25	19.76 **	2.33	9.84 **	2.02	1.42 **	0.34	13.60 **	1.20	0.06	0.08
Leaf length	F_1	1.58	17.39 **	1.83	27.22 **	4.22	18.54 **	3.67	0.69	2.46	22.39 **	4.33	0.65	0.61
	F_2	2.40	17.57 **	3.11	130.14 **	28.63	74.81 *	24.90	0.16	4.18	59.34 **	14.71	0.47	1.04
Leaf width	F_1	0.42	3.62 **	0.59	7.15 **	1.37	4.49 **	1.19	0.49	0.80	5.66 **	1.41	0.12	0.20
	F_2	0.01	3.55 **	0.70	32.83 **	6.40	20.47 **	5.57	-0.08	0.93	11.17 *	3.29	0.20	0.23
Branches /plant	F_1	14.50 **	0.02	0.05	0.38 *	0.11	0.36 *	0.10	0.22 *	0.07	0.01	0.12	0.01	0.02
	F_2	8.76 *	0.02	0.03	1.36 **	0.30	1.32 **	0.26	0.24 **	0.04	0.04	0.15	0.01	0.01
Stem diameter	F_1	1.54	0.15 *	0.06	0.79 **	0.14	0.78 **	0.12	0.70 **	0.08	0.08	0.14	0.03	0.02
	F_2	0.05	0.15	0.07	3.12 **	0.60	2.72 **	0.53	1.06 **	0.09	0.47	0.31	0.03	0.02
Capsules /plant	F_1	10.63 **	0.02	0.04	0.36 *	0.10	0.34 **	0.09	0.23 **	0.06	0.01	0.10	0.01	0.01
	F_2	14.29 **	0.02	0.03	1.31 **	0.31	1.28 **	0.27	0.23 **	0.04	0.02	0.16	0.01	0.01
Stigmatic rays (notches)	F_1	0.15	22.07 **	1.62	31.55 **	3.73	16.09 **	3.24	18.17 **	2.18	36.68 **	3.83	0.03	0.54
	F_2	17.56 **	22.07 **	0.95	100.19 **	8.74	50.98 **	7.61	26.77 **	1.28	65.77 **	4.49	0.03	0.32
Seed yield/ plant	F_1	3.40	0.19	0.37	3.06 *	0.85	2.92 **	0.74	3.55 **	0.50	0.01	0.87	0.14	0.12
	F_2	4.68	0.21	0.26	11.99 **	2.43	11.39 **	2.11	3.04 **	0.35	0.47	1.25	0.12	0.09
Straw yield/ plant	F_1	5.17	0.06	0.17	1.39 *	0.38	1.31 **	0.33	1.11 **	0.22	0.03	0.39	0.06	0.06
	F_2	3.07	0.05	0.13	4.31 **	1.16	4.45 **	1.01	0.41	0.17	-0.13	0.60	0.08	0.04
Capsule index	F_1	2.23	0.02	0.01	0.09 **	0.02	0.07 *	0.02	0.01	0.01	0.03	0.03	0.00	0.00
	F_2	0.08	0.02	0.01	0.19	0.05 **	0.11 *	0.04	0.00	0.01	0.07 *	0.02	0.00	0.00
Morphine content	F_1	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	F_2	0.03	0.00	0.00	0.02	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00

*, ** significant at $P = 0.05$ and $P = 0.01$, respectively.

The ratios of significant genetic components for the F_1 and F_2 (Table 4) show degree of dominance (H_1/D) were higher than the unity for all the characters except plant height in F_1. This suggests that a breeding strategy used to improve these seven or eight characters should attempt to exploit heterosis.

The degree of dominance for plant height in F_1 was less than unity, suggesting incomplete dominance. The magnitude of the estimates of dominance for all the characters was greater in the F_2 than the F_1 generation, suggesting an increase in the dominance effects

and decrease in the additive effects with selfing. In normal instances successive leads to increase in additivity no doubt but when F_1s expressing with more than unity dominance ratio are selfed in resulting F_2 estimates of dominance may inflate upwardly, if epistasis or linkage etc. is present.

In the remaining cases the H_1 and H_2 estimates increased from F_1 to F_2 for days to 50% flowering, plant height, peduncle length, leaves/plant, leaf length and width, stigmatic rays and morphine content in both the generations, it was far from the expected value revealing an asymmetrical distribution of positive and negative alleles among the parents. The ratio $(4DH_1)^{1/2} + F/(4DH1)^{1/2} - F$ or KD/KR, which gives the relative value of dominant and recessive genes was greater than unity for all the characters in both the analyses, except for straw yield/plant in F_2. The ratio h^2/H_2 denotes an approximate number of genes or groups of genes controlling the character exhibiting dominance. The estimates ranged from 0.07 to 1.83 except days to 50% flowering in both generation, and plant height, leaf length and width and capsule index in F_2 generations indicating that at least one to four genes or groups of genes showing dominance were present for the different characters.

Table 4. Proportion of the genetic components of variance in F_1 and F_2 diallel progeny for 14 traits in opium poppy.

	H_1/D		$H_2/4H_1$		KD/KR		h^2/H_2	
Trait	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Days to 50% flowering	1.05	2.04	0.17	0.17	3.28	3.26	-	-
Plant height	0.84	1.64	0.13	0.12	4.33	5.00	-	-
Peduncle length	1.25	2.12	0.14	0.16	3.73	3.95	-	0.20
Leaves/ plant	1.41	2.03	0.15	0.12	3.83	5.67	1.83	0.14
Leaf length	1.25	2.72	0.17	0.14	3.12	4.27	-	-
Leaf width	1.40	3.04	0.16	0.16	3.50	3.15	-	-
Branches/ plant	-	-	0.24	0.24	-	-	0.61	0.19
Stem diameter	2.32	-	0.25	0.22	1.25	-	0.90	0.39
Capsules/ plant	-	-	0.24	0.24	-	-	0.68	0.18
Stigmatic rays	1.20	2.13	0.13	0.13	5.56	5.65	1.13	0.53
Seed yield/ plant	-	-	0.24	0.24	-	-	1.22	0.27
Straw yield/ plant	-	-	0.24	0.26	-	-	0.85	-
Capsule index	-	-	0.22	0.15	-	-	-	-
Morphine content	-	-	-	-	-	-	-	-

CONCLUSIONS

A comparison of the dominance estimates H_1 and H_2 to additive D indicates that for many characters dominance genetic variance was very important for inheritance of these traits. Similar results were found by Saini et al., 1985, Saini 1988, 1992, Saini and Kaicker, 1983, Srivastava and Sharma, 1987 and Singh et al., 1999. Thus, taking an overview of the results of this study it can be suggested that heterotic breeding approaches should be followed for exploiting the over-dominance effects, while recurrent diallel selective mating (Jensen, 1976; Redden and Jensen, 1974) exploits heterosis through breeding strategies.

ACKNOWLEDGEMENTS

Authors are highly thankful to Dr. S.P.S. Khanuja, Ex. Director, CIMAP (CSIR), Lucknow for providing necessary help during the investigation and upgrading the manuscript.

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