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Generation mean analyses for flowering and maturity in Indian mustard (*Brassica junces* (L.) Czern & Coss) *

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Summary. Components of generation means were partitioned for days to flower initiation and maturity in three crosses of Indian mustard (*Brassica juncea* (L.) Czern and Coss) cultivars. A linked digenics model was adequate for flowering in cross II and maturity in Cross I. All three types of digenic interactions among the linked pairs of genes, additive×additive (i), additive×dominance (j) and dominance×dominance (1), contributed significantly in the inheritance of flowering in cross II and maturity in cross I. A complete association among the genes of greater effects in higher mean parent was detected for flowering in cross II and maturity in Cross I. Duplicate epistasis was evident for flowering in Crosses I and II and maturity in Crosses I and III.

Inadequacy of all the fitted models for days to flowering in Cross III and maturity in Cross II indicated the presence of higher order interactions.

Key words: *Brassica juncea* – Joint scaling test – Linked epistasis – Generation means

Introduction

Information on the amount and nature of variation in any breeding population is of fundamental importance in designing a suitable breeding method. Such information that is available, in Indian mustard (*Brassica juncea* (L.) Czern & Coss) is inadequate and inconclusive. Diallel, line×tester, and partial diallel techniques have usually been used for estimating gene effects with the assumption that epistatic effects are negligible. Consequently, the results pertain to the relative importance of additive and/or nonadditive gene effects. A review of pertinent literature on Indian mustard revealed that very few studies have been made allowing the partitioning of epistatic effects that include only digenic interactions. The present study was undertaken to estimate gene effects, including digenic and trigenic interactions, among unlinked genes and interactions among linked pairs of genes, for days-to-flowering and maturity in three crosses of Indian mustard cultivars.

Materials and methods

The material for the study included 21 generations (P_1, P_2, F_1, F_2, F_3, B_1, B_2, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, $B_1 \times F_1$, $B_2 \times F_1$, B_{1bip}, B_{2bip}, $F_2 \times P_1$, $F_2 \times P_2$, $F_2 \times F_1$ and F_{2bip}) of three crosses: 'Varuna×PR-5' (Cross I): 'Varuna×YRT-4' (Cross II); and 'BRR63×YR-4' (Cross III). Notations for generations are according to Jinks and Perkins (1969). The parents are homozygous and homogeneous varieties of Indian mustard. Generations were grown in a compact family block design with three replications at the Crop Research Centre, G. B. Pant University of Agriculture and Technology, Pantnagar, during 1980–81. The crosses were randomized among the main plots within replication, and the generations were randomized within these family main plots. The number of rows (2 to 10) was different for different generations depending upon the expected variances of generations. Each plot thus consisted of different numbers of rows, each of 3 m in length with a spacing of 30 cm between rows and 15 cm between plants. The two border rows on either side of main plots were sown with an early strain of mustard (Pant Rai 1D) and were treated as nonexperimental. Depending upon the expected variances of generations, 5 to 30 plants were selected randomly from each plot for recording the observations on days-to-flower initiation and maturity from the planting.

The joint scaling test suggested by Cavalli (1952) was applied to test the adequacy of genetic models as well as for

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Table 1. Generation means averaged over replications for days to flowering and maturity in three crosses of Indian mustard cultivars

Generation	Days to flower initiation			Days to maturity		
	No.			No		
	Cross I	Cross II	Cross III	Cross I	Cross II	Cross III
P_1	46.4	49.5	48.5	118.8	121.2	119.4
P_2	46.3	65.6	65.6	118.3	144.5	141.9
F_1	43.0	50.4	51.3	118.3	129.5	125.4
F_2	47.1	46.4	50.8	123.3	119.5	124.1
F_3	46.0	49.5	54.0	121.3	129.3	127.5
B_1	44.4	46.5	47.9	122.0	124.5	124.2
B_2	44.4	47.7	50.7	119.0	126.9	127.2
B_{11}	46.1	48.5	45.5	122.0	127.9	122.7
B_{12}	43.7	49.2	49.0	120.3	128.9	126.3
B_{21}	46.0	47.2	50.6	121.0	124.4	122.3
B_{22}	43.8	53.4	50.5	119.9	127.8	124.6
B_{1s}	47.6	50.2	49.7	121.1	129.4	123.9
B_{2s}	44.9	55.1	48.3	117.3	128.5	121.7
$B_1 \times F_1$	47.0	46.5	47.7	121.3	127.8	123.0
$B_2 \times F_1$	45.8	46.7	47.3	120.7	126.9	123.1
B_{1bip}	47.4	50.2	49.5	123.3	128.5	127.8
B_{2bip}	47.2	53.0	53.0	122.1	125.5	123.3
$F_2 \times P_1$	45.8	49.9	49.7	122.5	126.3	124.2
$F_2 \times P_2$	44.5	49.8	51.2	120.8	128.5	126.2
$F_2 \times F_1$	47.1	46.6	48.3	121.4	125.3	125.1
F_{2bip}	46.8	53.2	52.6	121.8	125.3	125.3
SEM±	0.35	0.58	0.58	0.31	0.64	0.72
CD (at 5%)	0.98	1.62	1.62	0.85	1.76	2.00

estimating the parameters of the models. Four genetic models (Viz., additive-dominance, digenic interactions, trigenic interactions, and linked digenics) were fitted successively for both characters according to Jinks and Perkins (1969). Degree of dispersion (rd) was computed following Jinks and Jones (1958).

Results

Generation means of different crosses for days-to-flowering and maturity are presented in Table 1. F_1 means were lower than the midparent value and tended towards early parent (P_1) for flowering and maturity in all three crosses. F_1 means were higher than the F_2 means in crosses II and III for flowering and maturity. However, the F_2 mean was higher than the F_1 mean and midparent value for days-to-flowering and maturity in Cross I. Means for backcross (B_1 and B_2) tended towards the early parent (P_1) in Crosses II and III for both characters. However, in Cross I, backcross (B_1 and B_2) means were lower than those of both parents for flowering but higher than both parents for maturity.

The χ^2 tests of goodness-of-fit of various models fitted to the generation means for days-to-flowering and maturity are given in Table 2. The χ^2 values for the additive-dominance and digenic interactions model were significant ($P < 0.001$) for flowering and maturity in three crosses. For days-to-flowering, nonsignificant ($P > 0.01$) χ^2 values were observed for the trigenic interactions model in Cross I and linked digenics model in Cross II. However, in Cross III, χ^2 values for trigenic interactions as well as for the linked digenics model were significant. Nonsignificant χ^2 values for days-to-maturity were observed for the trigenic interactions model in Cross III and linked digenics model in Cross I. However, significant χ^2 values for trigenic interactions and linked digenics model were observed for maturity in Cross II.

The estimates of gene effects under an adequate model for days-to-flowering and maturity are given in Table 3. The main effects, additive (d) and dominance (h), were important for flowering and maturity in Cross I, additive (d) effects were important for flowering in Cross II, and dominance (h) effects contributed significantly in the inheritance of maturity in Cross III.

Among the digenic interactions, additive × additive (iab/) and dominance × dominance (l/ab) were important for flowering in Cross I, whereas dominance × dominance (l/ab) for days-to-maturity in Cross III. Digenic interactions among linked pairs of genes were

Table 2. χ^2 test of the goodness-of-fit of various models for flowering and maturity in three crosses of Indian mustard cultivars

Model	No. of parameters	χ^2-degrees of freedom	χ^2 values					
			No.					
			Days to flower initiation			Days to maturity		
			Cross I	Cross II	Cross III	Cross I	Cross II	Cross III
Additive-dominance	3	18	135.0*	1,505.5*	1,311.6*	152.8*	949.6*	130.2*
Digenic interactions	6	15	58.9*	121.3*	210.3*	62.2*	226.1*	93.7*
Trigenic interactions	10	11	23.0 (0.020)	335.3*	446.5*	43.6*	62.0*	24.1 (0.014)
Linked digenics	12	9	–	20.8 (0.014)	56.9*	13.7 (0.098)	182.5*	–

* χ^2, $P < 0.001$ (Figures in parenthesis indicate the probability)

Table 3. Estimates of parameters with standard errors under adequate model for days to flowering and maturity in three crosses of Indian mustard cultivars

Parameters	No.					
	Days to flower initiation			Days to maturity		
	Cross I	Cross II	Cross III[a]	Cross I	Cross II[a]	Cross III
m	41.3** ± 2.1	–	–	–	–	132.6** ± 4.9
(d)	7.4** ± 2.1	8.0** ± 0.3	8.5** ± 0.3	0.3** ± 0.1	7.6** ± 0.4	2.4 ± 4.9
(h)	33.8** ± 11.8	–3.0 ± 2.4	–0.9 ± 3.2	–3.3** ± 1.1	3.0* ± 1.4	–54.3* ± 27.5
(iab/)	4.3* ± 2.0	–	–	–	–	–2.5 ± 5.0
(ja/b)	–8.6 ± 6.6	–	–	–	–	–28.8 ± 15.2
(l/ab)	–55.3** ± 20.2	–	–	–	–	104.9* ± 46.1
(iabc/)	–6.7** ± 2.0	–	–	–	–	13.2** ± 4.8
(jab/c)	–27.1** ± 6.0	–	–	–	–	5.6 ± 14.8
(ja/bc)	–1.9 ± 7.6	–	–	–	–	62.5** ± 17.0
(l/abc)	23.0* ± 10.8	–	–	–	–	–56.9* ± 23.8
m + (i)		57.5** ± 2.3	57.0** ± 3.3	118.6** ± 1.0	136.8** ± 1.2	
(pi)		1.2 ± 1.5	9.0** ± 1.0	2.9* ± 0.9	4.4** ± 1.6	
(p^2i)		7.5** ± 1.2	0.7 ± 1.0	0.1 ± 1.2	1.4 ± 1.9	
(pj)		–6.3** ± 0.7	–6.2** ± 0.5	3.3** ± 0.7	–6.9** ± 0.9	
(p^2j)		–2.3 ± 1.5	–3.1** ± 0.9	4.3** ± 1.6	2.7 ± 1.6	
(pl)		12.9** ± 1.9	1.5 ± 1.2	–6.7** ± 1.2	7.8** ± 2.0	
(p^2l)		6.6** ± 0.8	6.5** ± 0.9	0.2 ± 1.0	2.1 ± 1.9	
(p^3l)		6.2** ± 1.9	8.7** ± 1.6	3.4** ± 1.3	–3.5 ± 2.8	
(p^4l)		0.9 ± 1.7	21.8** ± 2.4	7.5** ± 1.5	–1.7 ± 3.5	
rd		1.0	–	1.0	–	

* $P = 0.05$; ** $P = 0.01$

[a] Parameters of complex model, as none of the model is adequate

significant for flowering in Cross II and for maturity in Cross I. Trigenic interactions, additive × additive × additive (iabc/), additive × additive × dominance (jab/c), and dominance × dominance × dominance (l/abc), contributed significantly to the inheritance of flowering in Cross I, while additive × additive × additive (iabc/), additive × dominance × dominance (ja/bc) and dominance × dominance × dominance (l/abc) contributed significantly to maturity in Cross III.

The estimates of the degree of dispersion presented in Table 3 indicates a complete association of genes with increasing effects (rd = 1) in one parent for flowering and maturity in Crosses II and I, respectively.

Discussion

Deviation of F_1 means from the midparent values indicated the presence of dominance and/or epistasis for days-to-flowering and maturity in all crosses. Lower values of F_1 means as compared with midparent values indicated the existence of heterosis for early flowering and maturity in all cases except for maturity in Cross I. However, the observed higher values of F_2 means over F_1 means in Cross I for flowering and maturity may be because of sampling variance. Still, the higher values of F_2 means than the midparent values in Cross I for flowering and maturity period indicated the existence of residual heterosis.

Significant ($P < 0.001$) χ^2 values for the additive-dominance model for flowering and maturity in all crosses revealed its inadequacy and indicated the presence of epistasis for both characters in all crosses. Further, the significant χ^2 for the digenic interactions model for both characters in all crosses indicated that digenic interactions among unlinked genes were not adequate to describe the epistasis.

Nonsignificant χ^2 ($P > 0.01$) of the trigenic interactions model for days-to-flowering in Cross I and days-to-maturity in Cross III indicated its adequacy in these cases and revealed that trigenic interactions among unlinked genes were adequate to describe the variation in generation means for flowering in Cross I and for maturity in Cross III. Similarly, nonsignificant chi-squares of the linked digenics model for flowering in Cross II and maturity in Cross I revealed its adequacy and indicated the significant contribution of linked pairs of genes showing digenic interactions in the inheritance of flowering in Cross II and maturity in Cross I.

The χ^2 test for days-to-flowering in Cross III indicated that digenic interactions between unlinked genes were not satisfactory but they accounted for a highly significant portion of variation among the generation means. The addition of trigenic interactions leads to no improvement over digenic interactions alone, but there is substantial improvement when the linked digenics model is fitted. Since the addition of the trigenic interactions model brought about no significant improvement, it is perhaps not surprising that a model combining linked digenic interactions and trigenic interactions also proved unsatisfactory. The results might be expected if the linked pairs of genes showing digenic interactions were involved in the trigenic interactions. Hence, no model could be expected to be adequate which does not allow for linkage among the genes showing trigenic interactions. Therefore, there can be little doubt that a model allowing for trigenic interactions among linked genes is required for flowering in Cross III. The present experiment provides insufficient statistics to fit and test the adequacy of such a model.

The χ^2 analysis for days-to-maturity in Cross II indicated that digenic interactions between unlinked genes were not a satisfactory model, but they accounted for a high portion of variation among the generation means. The addition of trigenic interactions leads to a significant improvement, but there is no further improvement when the linked digenics model is fitted. It is, therefore, possible that tetragenic or higher-order interactions involving unlinked genes may be involved in the inheritance of maturity in Cross II.

The importance of fixable effects in the forms of additive effects (d), additive × additive (iab/) and additive × additive × additive (iabc/) for flowering in Crosses I and II and maturity in Cross I indicated the potential for improvement in these traits through selection. A positive sign of (h) for flowering in Cross I indicated that late flowering is dominant over early flowering. On the other hand, the negative sign of (h) for maturity in Crosses I and III revealed that early maturity is dominant over the late maturity. Because earliness is desirable, dominance is in the desirable direction. Considering the sign of (h) and (1), duplicate epistasis was evident for flowering in Crosses I and II and maturity in Crosses I and III. Sachan and Singh (1986) also reported duplicate epistasis for flowering and maturity. Chaudhary and Sharma (1982) reported duplicate epistasis for flowering, but Rahman et al. (1977) reported that epistasis was not important for flowering and maturity.

The presence of marked epistatic effects for flowering and maturity emphasizes the need for maintaining heterozygosis in breeding populations. This is possible and practicable in Indian mustard where a considerable amount of cross pollination does occur.

The results of degree of dispersion revealed that the higher mean parent (P_1 = YRT 3) contains all the genes of greater effects for flowering in Cross II and 'Varuna' (P_1 = higher mean parent) for maturity in Cross I.

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