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Linked epistasis for six quantitative traits in Indian mustard (*Brassica juncea* (L.) Czern & Coss)

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Summary. Gene effects, and interactions, and associations between days-to-flower initiation and maturity, number of secondary branches and siliquae per plant, and 1,000-seed weight and yield per plant were studied in a cross of Indian mustard (*Brassica juncea* (L.) Czern & Coss) using the parents and F_1, F_2, F_3, B_1, B_2, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, B_1F_1, B_2F_1, B_{1bip}, B_{2bip}, F_2P_1, F_2F_1, and F_{2bip} generations. A linked digenic model was adequate for all characters studied. According to this model, the main effects, additive and interactions between linked pairs of genes, were present in varying proportions for days-to-flower initiation and maturity and number of siliquae per plant. The contribution of linked epistatic effects, however, was much greater than that of additive effects. Dominance effects contributed significantly to the inheritance of days-to-flower initiation. Duplicate epistasis was observed for all traits except 1,000-seed weight where epistasis was of the complementary type. A complete association among the genes of similar effect (increasing or decreasing) was observed for number of secondary branches and siliquae, and yield per plant. Coupling phase linkage was observed for days-to-flower initiation whereas repulsion phase linkage was observed for days-to-maturity and 1,000-seed weight.

Key words: *Brassica juncea* – Gene effects – Joint scaling test

Introduction

An understanding of the mode of inheritance of complex quantitative traits is essential in choosing an efficient breeding methodology for improving these characters. In mustard (*Brassica juncea* (L.) Czern & Coss), diallel (Rehman et al. 1977; Anand and Rawat 1978; Govil et al. 1981), line × tester (Badwal et al. 1976; Labana et al. 1978; Yadava et al. 1979) and partial diallel techniques (Singh et al. 1970; Kashi Ram et al. 1976; Chauhan and Singh 1979) usually have been used for estimating gene effects. Consequently, the results pertain to the relative importance of additive and/or nonadditive gene effects but because of epistatic effects, the reported estimates would be biased. A review of the literature on Indian mustard revealed that very few studies have been made allowing the partitioning of epistatic effects so as to include only digenic interactions. The objective of the study was to estimate the gene effects, including the interactions of linked pairs of genes, for six quantitative characters related to productivity in Indian mustard.

Materials and methods

The material included 20 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_1F_1, B_2F_1, B_{1bip}, B_{2bip}, F_2P_1, F_2F_1 and F_{2bip}) of a cross of 'Pant Rai-5' × 'BRR-63'. Notations for generations used are according to Jinks and Perkins (1969). Twenty generations were evaluated in a randomized complete block design with three replications at the Crop Research Centre, G. B. Pant University of Agriculture and Technology, Pantnagar, during 1980–81. Plot size was 10-rows spaced 30 cm apart, with an approximate spacing of 15 cm between plants maintained by thinning. Depending upon the expected variances of generations, 5 to 30 plants were selected randomly from each plot for recording observations on days-to-flower initiation and maturity, number of secondary branches per plant, number of siliquae per plant, 1,000-seed weight (g), and seed yield per plant (g).

The joint scaling test suggested by Cavalli (1952) was applied to test the adequacy of genetic models as well as for estimating the parameters of the models. Four genetic models (additive-dominance, digenic interactions, trigenic interactions, and linked digenics) were fitted successively for all the characters (Jinks and Perkins 1969). Degree of dispersion (rd) was computed following Jinks and Jones (1958).

Results

The means of different generations for various quantitative characters are presented in Table 1. F_1 means were higher than those of both the parents for secondary branches, number of siliquae, and seed yield but lower for flower initiation. F_1 means tended towards mid-parental values for maturity and seed weight. Backcross (B_1 and B_2) means were higher than those of both the parents for secondary branches and siliquae per plant and yield. The mean of B_1 was closer to P_1 for flower initiation, but tended towards P_2 means for maturity and seed weight. Further, the means of B_2 tended towards P_2 for flower initiation, maturity, and seed weight.

The χ^2 tests of goodness-of-fit of various models fitted to the generation means for different characters (Table 2) revealed that additive-dominance, digenic

Table 1. Generation means averaged over replications for six quantitative characters in a cross of two Indian mustard cultivars

Generation	No.				g	
	Days to flower initiation	Days to maturity	Secondary branches/plant	Siliquae/plant	1,000-seed weight	Yield/plant
P_1	47.0	118.3	9.2	167.8	2.2	2.8
P_2	52.5	129.9	9.0	234.8	2.0	3.6
F_1	45.5	123.7	9.6	300.8	2.1	5.9
F_2	50.1	125.2	7.9	242.1	1.9	3.4
F_3	50.6	123.5	7.7	213.7	1.9	3.2
B_1	45.0	124.7	9.8	275.4	2.1	4.9
B_2	50.1	127.7	9.7	255.8	2.0	4.6
B_{11}	44.5	124.1	9.5	275.7	2.0	4.7
B_{12}	47.8	126.0	8.3	237.1	2.3	4.4
B_{21}	46.1	125.3	12.0	324.4	2.2	5.7
B_{22}	48.2	125.6	8.4	222.5	2.1	4.3
B_{1S}	47.4	125.2	6.4	217.1	2.3	3.3
B_{2S}	49.0	125.9	6.8	187.8	2.2	2.5
B_1F_1	46.0	124.3	9.2	239.1	2.1	3.9
B_2F_1	48.3	125.8	7.7	226.7	2.1	3.5
B_{1bip}	47.7	126.9	13.7	375.0	2.3	5.8
B_{2bip}	50.6	130.4	11.6	288.9	2.1	5.0
F_2P_1	45.1	123.8	12.8	353.7	2.1	6.0
F_2F_1	48.5	125.1	8.6	255.2	2.1	4.0
F_{2bip}	52.0	128.8	17.3	442.3	1.8	8.2
SEM±	0.70	1.02	1.35	33.53	0.05	0.78
C D (at 5%)	2.01	2.93	3.85	95.83	0.05	2.24

Table 2. χ^2 tests of the goodness-of-fit of various genetic models for six quantitative characters in a cross of two Indian mustard cultivars

Model	No. of parameters	Degrees of freedom	χ^2 values No.				g	
			Days to flower initiation	Days to maturity	Secondary branches/ plant	Siliquae/ plant	1,000-seed weight	Yield/ plant
Additive-dominance	3	17	162.1*	45.5*	98.5*	195.3*	76.3*	123.2*
Digenic interactions	6	14	108.0*	38.5*	77.5*	109.0*	73.2*	65.0*
Trigenic interactions	10	10	91.2*	35.7*	74.9*	78.4*	61.2*	45.2*
Linked digenics	12	8	14.7 (0.060)	26.1 (0.001)	6.5 (0.650)	20.2 (0.010)	26.3 (0.001)	9.5 (0.320)

* χ^2, $P<0.001$

Figures in parenthesis indicate the probability

Table 3. Estimates of parameters of linked digenic model and degree of dispersion (rd) for six quantitative characters in a cross of two Indian mustard cultivars

Parameters	No.				g	
	Days to flower initiation	Days to maturity	Secondary branches/ plant	Siliquae/ plant	1,000-seed weight	Yield/plant
(d)	2.5** ±0.6	2.7** ±0.8	0.1 ±0.9	34.9** ±12.1	0.1 ±0.1	0.5 ±0.3
(h)	– 5.7** ±0.9	–	–	–	–	–
m + (h) + (l)	–	124.7** ±1.6	9.2** ±1.9	273.4** ±42.5	2.2** ±0.1	5.1** ±1.6
m + (i)	49.2** ±0.7	125.4** ±1.6	9.4** ±1.9	208.5** ±35.8	2.1** ±0.1	3.3* ±1.5
(pi)	0.1 ±1.0	1.7 ±1.7	8.5** ±1.6	204.6** ±28.8	0.1 ±0.1	3.8** ±0.6
(p^2i)	– 5.5** ±1.6	– 0.9 ±1.3	3.6 ±2.1	204.9** ±53.1	0.4** ±0.1	3.1** ±1.1
(pj)	2.5* ±1.0	– 0.3 ±1.2	0.3 ±1.6	– 82.2** ±25.7	0.1 ±0.1	– 1.9** ±0.6
(P^2j)	3.8* ±1.8	– 0.1 ±1.7	– 4.3 ±2.9	153.8** ±57.1	0.2 ±0.1	– 0.3 ±1.1
(Pl)	0.5 ±1.6	– 4.6 ±2.3	– 9.2** ±2.1	–230.6** ±50.5	0.1 ±0.1	– 5.8** ±1.0
(P^2l)	2.6* ±1.2	– 3.1* ±1.4	– 2.1 ±1.5	– 46.7 ±43.9	– 0.1 ±0.1	– 3.4** ±0.8
(P^3l)	1.0 ±1.5	– 3.4* ±1.6	– 1.9 ±2.0	23.4 ±55.1	– 0.4** ±0.1	– 2.6* ±1.2
(P^4l)	5.3** ±1.8	– 1.9 ±2.3	3.3 ±2.3	109.3* ±51.0	– 0.5** ±0.2	– 0.2 ±1.2
rd	– 0.9	– 0.5	1.0	1.0	0.5	– 1.0

* Significant at 5% level of probability; ** Significant at 1% level of probability

and trigenic interactions models were inadequate for all characters. However, the nonsignificant χ^2 values ($P > 0.001$) for the linked digenic model indicated its adequacy for all the traits.

The estimates of gene effects under the linked digenic model are given in Table 3. Additive effects (d) were important for flower initiation, maturity and siliquae per plant. Dominance effects (h) were significant and negative for flower initiation. Parameters, [m + (h) + (l)] and [m + (i)] were significant for maturity, secondary branches, siliquae per plant, 1,000-seed weight and seed yield.

Among the epistatic effects between linked pairs of genes, additive × additive (i), additive × dominance (j), and dominance × dominance (l) effects were important for flower initiation, siliquae per plant, and seed yield, whereas (i) and (l) interactions among linked pairs of genes showed significant contributions in the inheritance of secondary branches per plant and 1,000-seed weight. However, interactions (l) among linked pairs of genes were involved in the inheritance of days-to-maturity.

The estimates of degree of dispersion (Table 3) indicated a complete association (red = 1 or –1) of genes with similar effects (increasing or decreasing) in one parent for secondary branches, siliquae per plant and yield per plant. Coupling phase linkage was observed for days-to-flower initiation, whereas repulsion phase linkage was evident for maturity and seed weight.

Discussion

A comparison of F_1 means with parental means indicated the presence of dominance and/or epistasis for all characters except maturity and seed weight. However, the inadequacy of the additive-dominance model and the adequacy of the linked digenic model revealed the role of epistasis in the inheritance of all characters studied. This was further confirmed by significant estimates of one or more of linked epistatic effects (s) for all characters. Overdominance was evident from the higher or lower values of F_1 over the corresponding better parents for flower initiation, secondary branches, siliquae per plant and seed yield.

Significant χ^2 values for digenic and trigenic interactions models indicated that neither digenic nor trigenic interactions among unlinked genes are adequate to describe the epistasis. On the other hand, adequacy of linked digenic model revealed the existence of linked epistasis. Rehman et al. (1977), however, did not find epistasis to be important for flower initiation and maturity. This could be due to differences in materials used in the study.

The importance of additive effects for flower initiation, maturity and siliquae per plant indicated the potential for improvement in these traits through selection. However, dominance effects contributed significantly to the inheritance of flower initiation. The negative sign of (h) indicated dominance for earliness. Because earliness is desirable, dominance is in the desirable direction. Such a situation emphasizes the need for controlled selfing to allow for selection of the desirable segregants. Since the sign of (l) type of interactions is negative for maturity, secondary branches, siliquae per plant, 1,000-seed weight and yield per plant, there are no direct estimates of sign and magnitude of (h) because it is confounded with those of the mean (m) and (l) interactions. Considering the sign of (h) and (l), duplicate epistasis was evident for all traits, except 1,000-seed weight which was of the complementary type. Chaudhary and Sharma (1982) also observed duplicate epistasis for flower initiation.

The presence of fixable effects in the form of (d) and/or (i) and with the coupling phase linkage for flower initiation, siliquae per plant and yield per plant suggested that fixable genetic variation could be exploited in the early segregating generations as no increase in such variation is expected in succeeding generations. However, the evidence for the repulsion phase of linkage indicated that the fixable genetic variability present in the form of (d) for maturity and (i) for 1,000-seed weight might become, available through recombinations in the succeeding generations. This suggested that the rate of improvement for maturity and 1,000-seed weight could be enhanced by deferring the selection to the advanced generations. Further, the interactions (i) coupled with duplicate epistasis for flower initiation, secondary branches, siliquae per plant, and yield per plant indicated the possibility of obtaining transgressive segregates of desired types.

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

The results of degree of dispersion revealed that P_1 (PR-5) contains all the genes of greater effect (rd = 1) for secondary branches per plant whereas P_2 (BRR-63) contains all the genes of greater effects (red = −1) for siliquae per plant and yield per plant. For flower initiation, BRR-63 contains about nine times (rd = −0.92) more genes of positive effects, whereas PR-5 contains nine times more genes of negative effects, on the expression of characters in the desired direction. Almost equal number of genes with positive and negative effects were present in PR-5 and BRR-63 for 1,000-seed weight and maturity.

The importance of fixable as well as nonfixable effects for different yield contributing characters suggested that the selection programme to improve yield in this population should accumulate favourable genes and simultaneously maintain heterozygosity in the population for manifestation of nonadditive effects. Reciprocal recurrent selection (Comstock et al. 1949) and the diallel selective mating system (Jensen 1970) for autogamous crops, appear to be the best available methods to meet the requirements. The method proposed by Singh et al. (1981), in which selections in early generations may be intermated in biparental fashion, and ultimately the best families may be bulked to produce phenotypically uniform but genetically buffered population, may also be used with success.

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