

## COMPONENTS OF GENETIC VARIANCE FOR SOME QUANTITATIVE CHARACTERISTICS IN CASTOR BEAN

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### Abstract

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The castor bean (*Ricinus communis* L.) cultivation emerges as a promising activity for biodiesel production. There is limited information on genetics of modern castor bean cultivars. To be able to foresee results of selection for a characteristic in a population, it is necessary to determine the values of genetic variance, environmental variance and their interaction within the total phenotypic variance. Castor bean studies have mostly been concentrated on the roles of additive and dominant gene effects in the expression of quantitative characteristics. Two two-line castor bean hybrids have been evaluated for mode of inheritance and gene action in the expression, especially epistatic one, of the number of flowers, number of filled seeds per flower head and 1000-seed mass. Epistatic gene effects have played important roles in the inheritance of the studied characteristics in both hybrids. Highly significant values of epistatic gene effects additive  $\times$  additive and dominant  $\times$  dominant have been found for all three characteristics in both crosses. Highly significant epistatic gene effect additive  $\times$  dominant has been found for the number of filled seeds per flower head in cross  $L_2 \times L_3$ .

*Key words:* additive, dominant, non-allelic interaction, scaling test, six-parameter test

### Introduction

Castor bean (*Ricinus communis* L.) is a non-food crop cultivated for its seeds, which are primarily used in industry (e.g., aviation oil), farming (as a source of high-nitrogen fertilizer) and medicine (as a purgative) (Allan et al., 2007). Nowadays, with increasing prices of the crude oil, the castor bean cultivation emerges as a promising activity for biodiesel production (Savy Filho, 2005). The castor bean seeds are highly toxic (Endo et al., 1987) and are known to be the deadliest natural poisons when administered intravenously or inhaled as fine particles. Given its potential and historical use as a bioweapon, castor bean is also a concern for bioterrorism (Allan et al., 2007). Castor bean is considered to be native to tropical Africa, but is cultivated in many tropical and subtropical regions of the world (Govaerts et al., 2000). World-wide production of seeds in 2007 was 1.2 million t, with In-

dia, China, and Brazil leading global harvests (FAOSTAT, 2007). A monotypic genus of *Euphorbiaceae*, castor bean is both self- and cross-pollinated by wind, but controlled crossing studies suggest that out crossing is a frequent mode of reproduction (Meinders and Jones, 1950; Brigham, 1967). However, there is limited information on genetics of modern castor bean cultivars.

To be able to foresee results of selection for a characteristic in a population, it is necessary to determine the values of genetic variance, environmental variance and their interaction within the total phenotypic variance. Genetic variance is the result of sum action of all genes controlling the expression of a quantitative characteristic and it comprises three components: the variance due to action of additive genes, the variance due to action of dominant genes and the variance due to interaction between these genes.

To confirm the presence and to assess the magnitude of genetic effects on the expression of a quantitative trait, methods that are capable of providing information on mean effects of individual genes, interactions among genes in the same locus and interactions among loci are needed. It is also necessary to take into account the environmental effects, i.e., non-genetic parameters, as well as the genotype  $\times$  environment interaction.

Although the first paper dealing with components of genetic variance (additive, dominant, epistatic) had been published long ago (Fisher, 1918), many subsequent papers dealt only with the role of additive and dominant gene effects in the expression of various quantitative characteristics because epistatic gene effects were considered as negligible (Mather, 1949; Comstock et al., 1952; Jinks, 1954). Later studies, however, have shown that epistatic gene effects play an important role in the expression of quantitative characteristics (Anderson and Kempthorne, 1954; Hayman, 1960; Munns et al., 2003).

Castor bean studies have mostly been concentrated on the roles of additive and dominant gene effects in the expression of quantitative characteristics (Singh et al., 1981; Patel et al., 1985; Pathak et al., 1989; Marinković and Marjanović-Jeromela, 1995; Laureti, 1995).

The research reported in this paper was carried out in order to determine the modes of inheritance of the number of flowers per plant, the number of filled seeds per plant and 1 000-seed mass, as well as to obtain information about the action of genes, especially epistatic ones, associated with the expression of the mentioned characteristics in castor bean.

## Materials and Methods

Four castor bean lines were used to create two two-line hybrids,  $L_1 \times L_5$  and  $L_2 \times L_3$ . During inbred lines, crossing and backcrossing, anthers were manually removed from female plants in order to prevent self-pollination.

Parents ( $P_1$  and  $P_2$ ),  $F_1$  and  $F_2$  generation and backcrosses ( $BC_1$  and  $BC_2$ ) were tested at the Rimski Jančevi Experiment Field of the Institute of Field and Vegetable Crops, Novi Sad. Experimental materials were planted manually, after the system of random blocks in three replications, five rows per replication. Distance between rows was 70 cm, distance in the row 30 cm. The studied characteristics (number of flowers and filled seeds per flower head, 1000-seed mass) were assessed in laboratory, after harvest. The traits were measured on 120 plants from each genotype.

The studied characteristics were processed by the analysis of variance for the factorial trial, fixed Model I (Steel et al., 1960). Gene effects and mode of inheritance were processed by generation mean analysis (Mather et al., 1982).

## Results and Discussion

In hybrid  $L_1 \times L_5$ , inbred line  $L_5$  had higher values for the number of flowers and filled seeds per flower head and a lower value for 1,000-seed mass than line  $L_1$ . The  $F_1$  generation did not exceed the values of the better parent for either one of the studied characteristics (Table 1).

In hybrid  $L_2 \times L_3$ , inbred line  $L_3$  had higher values for all three characteristics than line  $L_2$ . Mean values of the  $F_1$  generation for the number of flowers per flower head and 1,000-seed mass were lower than the mean value of the better parent; however, the number of filled seeds was higher in  $F_1$  than in the better parent (Table 1).

Determination of mode of inheritance according to generation mean is based, according to Fisher et al. (1932) and Mather (1949), on parameters, which reflect mutual relationships between homozygous parents and their progenies for a particular quantitative characteristic. The method is in fact based on the existence of connections among mean generation values, which are foreseeable and dependent solely on additive and dominant gene effects.

There are several ways to test these relationships as well as the verity of the hypothesis that these relationships depend solely on additive and dominant genes. One of them is the scaling test (Mather, 1949) which implies that, if relationships among mean values of progenies are used as criteria for determining adequacy of the additive-dominant model, attention must be focused on the variances of the generation mean.

Mean values and variability parameters for the studied characteristics in the parents,  $F_1$ ,  $F_2$  and backcrosses of both hybrids are presented in Table 1. To check the additive-dominant model, the values of tests A, B and C and their dispersions were calculated. The obtained results showed that the values of tests A, B and C were significantly different from zero in both hybrids for the number of filled seeds and the number of flowers per flower head. Regarding 1,000-seed mass, values of tests A and C were significantly different from zero in hybrid  $L_1 \times L_5$ , and values of tests A and B in hybrid  $L_2 \times L_3$ . It should be noted that the variability of 1,000-seed mass was highest in hybrid  $L_2 \times L_3$ . All this indicated that the additive-dominant model was not adequate for either one of the previous instances. If the model had been adequate, the values of A, B and C would have been equal, within the limits of sampling error. In some cases (Powers, 1941), however, the model may be adequate for a certain cross but inadequate for another cross possessing the same variability range, and still less adequate for crosses with higher variability ranges.

The joint scaling test (Cavalli, 1952) is considered a more appropriate than Mather's scaling test for checking the ad-



two characteristics of hybrid  $L_2 \times L_3$ . The negative value of  $|h|$  for the number of flowers per flower head and the positive value of  $|h|$  for the number of 1,000 seed in hybrid  $L_2 \times L_3$  show that the dominant alleles decreased the value of the former characteristics but increased the value of the latter. Mean values of the characteristics presented in Table 1 confirm the above statement. However, sum contributions of all six family types of all three characteristics in both hybrids representing values  $\chi^2$  for the three degrees of freedom (6-3), were significantly different from zero. Since the obtained results are in full agreement with the conclusions drawn based on tests A, B and C, it means that the joint scaling test also testifies that the additive-dominant model is not adequate. In other words, additive and dominant genes do not exclusively control the expression of the studied characteristics, in both hybrids, i.e., non-allelic interaction is also present.

The six-parameter test (Jinks and Jones, 1958) was used to establish the presence of effects of the non-allelic interaction on the expression of the studied characteristics and their magnitude in the progenies. The six parameters were evaluated based on the mean values of the parents,  $F_1$ ,  $F_2$  and first backcrosses with both lines.

The values of the six parameters and their standard errors for the three characteristics studied in the two hybrids are given in Table 3. The obtained values of gene effects indicated that the effects of dominant genes  $|h|$  were most important for the inheritance of the three characteristics in hybrid  $L_1 \times L_5$ . These effects were highly significant (when testing the significance of individual parameters by the T test). The effects of additive genes  $|d|$  were also highly significant for the studied characteristics, but they were lower several times than the effects of dominant genes. The values of parameter  $|h|$  were positive for all three characteristics. The values of parameter  $|d|$  were positive for 1,000-seed mass and neg-

ative for the numbers of flowers and filled seed per flower head. With a single exception, the values of parameters of non-allelic interaction exceeded significantly the values of their standard errors, confirming the importance of epistatic gene effects in the expression of all three characteristics. These results were in agreement with the results of tests A, B and C and the joint scaling test ( $\chi^2_{(1)}$ ).

In hybrid  $L_1 \times L_5$ , all three interaction effects, ( $|i|$ ,  $|j|$ ,  $|l|$ ), played important roles in the inheritance of the number of filled seeds and 1000-seed mass, while interaction effects  $|i|$  and  $|l|$  were important for the inheritance of the number of flowers per flower head. The interaction effect  $|j|$  evidently did not contribute to the expression of the last characteristics since its value was not significantly different from zero. The values of parameters  $|h|$  and  $|l|$  had opposite signs for the three characteristics - the former were positive and the latter negative. Thus, it could be concluded that the interactions on balance were mainly of the duplicate, dominant epistatic or recessive suppressor kind. To distinguish these interactions, however, knowledge is required of the relative magnitudes and signs of the individual  $d$ s and  $h$ s of the interacting genes (Mather et al., 1982). Duplicate epistasis is not desirable because it diminishes the effects of dominant genes, reducing the phenotypic expression of the characteristics under study. Complementary epistasis is more desirable

In hybrid  $L_2 \times L_3$ , the effects of dominant genes  $|h|$  were most important for the inheritance of the studied characteristics. The values of parameter  $|h|$  were positive and the values of parameter  $|d|$  negative for all three characteristics. In this hybrid too, the values of the former parameter were several times higher than the values of the latter parameter. Epistatic gene effects were again found to play important roles in the inheritance of the studied characteristics. Highly significant values of the interaction effects additive  $\times$  additive  $|i|$

**Table 3**  
Estimate of the values of gene effects using the six-parameter model

Gene effects	Hybrid					
	$L_1 \times L_5$			$L_2 \times L_3$		
	Characteristic			Characteristic		
	No. of flowers per flower head	No. of filled seeds per flower head	1,000-seed mass, g	No. of flowers per flower head	No. of filled seeds per flower head	1000-seed mass, g
$m+S_\epsilon$	-23.96±2.01	-48.89±14.32	260.87±12.92	33.10±7.43	72.94±8.30	239.75±14.33
$ d +S_\epsilon$	-25.21±0.69	-78.46±2.98	13.84±1.82	-3.61±1.39	-0.61±2.101	-12.14±2.61
$ h +S_\epsilon$	278.01±6.03	684.18±38.67	137.11±34.27	121.91±21.24	298.95±20.73	437.47±37.95
$ i +S_\epsilon$	104.17±1.89	241.79±14.01	76.97±12.79	50.94±7.30	103.19±8.03	140.55±14.09
$ j +S_\epsilon$	-0.95±2.32	-40.06±12.70	-22.92±10.52	3.10±7.19	42.04±6.63	5.29±11.79
$ l +S_\epsilon$	-180.79±4.13	-438.43±24.81	-52.66±22.01	-78.85±14.02	-188.42±12.85	-291.76±25.78

**Table 4**  
**Estimate of the values of gene effects using the five-parameter model**

Gene effects	Hybrid					
	$L_1 \times L_5$			$L_2 \times L_3$		
	Characteristic			Characteristic		
	No. of flowers per flower head	No. of filled seeds per flower head	1.000-seed mass, g	No. of flowers per flower head	No. of filled seeds per flower head	1.000-seed mass, g
$m \pm S_{\sigma_e}$	-23.86±2.00	-16.94±10.14	289.26±4.34	30.50±6.76	73.51±8.06	239.06±14.25
$ d  \pm S_{\sigma_e}$	-25.36±0.56	-82.87±2.63	13.17±1.65	-	-	-11.62±2.34
$ h  \pm S_{\sigma_e}$	277.70±5.98	588.36±23.95	56.70±5.60	129.71±19.13	297.24±19.89	439.52±37.67
$ i  \pm S_{\sigma_e}$	103.93±1.78	213.98±10.89	48.73±4.80	52.85±6.62	103.19±8.03	141.32±13.98
$ j  \pm S_{\sigma_e}$	-	-	-	-	40.81±5.12	-
$ l  \pm S_{\sigma_e}$	-180.58±4.10	-374.57±14.34	-	-84.06±12.59	-187.28±12.24	-293.12±25.60
$\chi^2_{(1)}$	0.176	9.95	7.39	7.14	0.09	0.20
P	0.75-0.5	0.005		0.01-0.005	0.90-0.75	0.75-0.50

and dominant  $\times$  dominant  $|l|$  were established for all three characteristics. The interaction effects additive  $\times$  dominant  $|j|$  were highly significant for the number of filled seeds per flower head, but they were not significantly different from zero for the other two characteristics.

The test of adequacy of the five-parameter model, as can be seen on the basis of  $\chi^2$  values calculated for one and two degrees of freedom, showed, quite expectedly, that the model was adequate (Table 4). Five parameters model was adequate for explanation of mode of inheritance for number of flowers per flower head for combination  $L_1 \times L_5$ , 1000-seed mass of combination  $L_2 \times L_3$  and number of filled seeds per flower head for combinations  $L_1 \times L_5$  and  $L_2 \times L_3$ . For other traits, four parameters were suitable. Presence of duplicate epistasis in inheritance of all estimated traits in both hybrid combinations was detected.

## Conclusion

The results obtained in this investigation are partially in accordance with Hallauer and Miranda (1988), who emphasised that dominance effects for traits showing expression of heterosis phenomenon are often more important than additive ones. High estimates of dominance effects compared to the additives are due to heterozygosity of those genes for which the parents are differing (Karsey and Pooni, 1996).

From the breeders "point of view" having dominance as the major type of gene action for the most important traits suggests that selection for these traits would be quite difficult and a long-term process (Zdunic et al., 2008). Regarding epistatic effects, additive  $\times$  additive effects are more favourable than other interaction effects due to a greater chance of breeding success (Novoselovic et al., 2004).

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