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The Correlation between Gene Effects and Mid-Parent Heterosis in Selected Crops

F. Bnejdi^{1*}, N. Rassaa², M. Saadoun³ and M. El Gazzah¹

¹Laboratory of Biodiversity, Biotechnology and Climatic Change, Département des Sciences Biologiques, Faculté des Sciences de Tunis, 2092, El Manar I, Tunisie.

²Laboratory of Crop Physiology, Ecole supérieure d'Agriculture du Kef, 7100, Tunisie.

³Laboratory Plant Protection, Institut National de la Recherche Agronomique de Tunisie (INRAT), Rue Hedi Karray, 2049 Ariana, Tunis, Tunisia.

Authors' contributions

This work was carried out in collaboration between all authors. Author FB designed the study, performed the statistical analysis, wrote the protocol and wrote the first draft of the manuscript. Authors NR and MS managed the analyses of the study. Author MEG managed the literature searches. All authors read and approved the final manuscript.

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ABSTRACT

This study was conducted to investigate the relationship between heterosis and gene effects estimated by the generation mean analysis. Nine traits with 74 cases of combinations cross-sit and cross- abiotic or biotic stress levels were assessed in three crops (durum wheat, pepper, and oat) and evaluated by lines crosses analysis. Trait performances of the F1 hybrid showed evident mid-parent heterosis varying from 0.6% to 89% for the 74 cases investigated. Results of Generation mean analysis revealed that the additive-dominance model was demonstrated adequate in 7 cases. Therefore the epistatic model was found appropriate in 67 cases. Analysis of correlations between gene effects estimated by the generation mean analysis revealed that heterosis was not correlated to additive, dominance or epistasis effects. Therefore, the majority of geneticists considered the non-additives effects as the genetic basis of heterosis. Thus, the lower correlations obtained

*Corresponding author: E-mail: fethibnejdi@yahoo.fr;

between heterosis and non-additives effects were due to the bias of the classical approach's models of genetic quantitative. In fact, many assumptions were proposed to develop this model. To conclude, non-additives results are apparently of great importance in the inheritance of quantitative traits and their roles in the heterosis expression are not to discuss. However, the quantitative genetic interpretation of mid-parent heterosis as a function of genetic effects was not possible basing on the model of line crosses analyses.

Keywords: *Inheritance; non-additive effects; heterosis.*

1. INTRODUCTION

The concept of heterosis is widely exploited systematically in plant and animal breeding. Hence no consensus exists about the genetic basis underlying this fundamental phenomenon [1,2]. Heterosis is defined as the difference between trait expression of the F₁ hybrid and the average of its homozygous parents [3] Various research groups have proposed dominance, over dominance and epistasis as the primary genetic basis of heterosis and recent advances in molecular biology have helped to confirm these findings in various crops [4-6].

Heterosis may also be due to the positive effects of the cytoplasm of the maternal parent of the nuclear component of the parental parent [7]. Selection of quantitative traits was simple to complicate depending upon the nature and the mode of gene effects governing this attribute. Under the typical condition, only additive and dominance effects were considered, and the selection was comparatively easy. Therefore, in the presence of additive and dominance gene effects and genes interactions the procedure of choice is so complicated. Determining the relationship between heterosis and gene effect can be found with the two classical approach of quantitative genetic, generation means analysis and triple test cross [8,9].

In quantitative genetics, inheritance of quantitative traits is based on a restrictive and straight forward model where several parameters such as epistatic effects are assumed negligible [10]. Generation means analysis has been extensively used for determining the inheritance of many quantitative traits in crops. Nevertheless, this method was developed in assuming many postulates that lead to the bias in the estimation of additive, dominance and epistatic genetic effects. Based on two points of reference F₂-metric and F_∞-metric [11,12] two simpler models have been developed, and each model has its characteristics. The objective of this study was to

investigate the relationship between gene effect estimated by the generation mean analysis and mid-parent heterosis for nine traits with 74 cases of combination cross-sit cross-biotic or abiotic stress.

2. MATERIALS AND METHODS

2.1 Origin of Data

Nine quantitative traits with 74 cases of combination cross-site, cross-isolate or cross-treatment of six generations (P₁, P₂, F₁, F₂, BC₁ and BC₂) for three crops (*Triticum durum*, *Capsicum annum* and *Avena sp*) were collected from different works realized in our laboratory. Crops, traits and origin of data are reported in Table 1. For each trait parents of crosses were extreme. For several traits, transformations (such as Kleckowski transforms [13] were applied to normalize the distribution of data or to make means independent of variances.

Table 1. Traits assessed and origin of data

Durum Wheat (<i>Triticum durum</i>)
Two crosses/two sites
Number of head per plant , Spiklets per spike and Number of grains per spike (29)
Four crosses/ one site
Resistance to yellowberry (30)
Four crosses/ Two sites
Grain protein content (31)
Two crosses/ Five salt treatments
Resistance to salt at germination stage (27)
Two crosses/ fifteen isolates
Resistance to <i>Septoria tritici</i> (28)
Pepper (<i>Capsicum annum</i> L.)
Two crosses/ Two isolates
Resistance to <i>Phytophthora nicotianae</i> (33)
Two crosses/ Six isolates
Resistance to <i>Phytophthora nicotianae</i> (34)
Oates (<i>Avena sp.</i>)
Two crosses/ Two isolates
Resistance to <i>P. coronate</i> Cda. f. sp. <i>avenae</i> Eriks (32)

2.2 Best-fit Genetic Model

Generation mean analysis was applied to determinate the best-fit genetic model. Means and variances Calculated were used to estimate the mid-parent (m), additive (d), and dominance (h) gene effects, as described by Rowe and Alexander [14] and following the method of Mather and Jinks (15) for a three-parameter model. When the three-parameter model was inadequate (significant X^2 value), the interaction terms [additive x additive (i), additive x dominance (j), and dominance x dominance (l)] were added [15]. The genetic parameters [m, (d), (h), (i), (j), and (l)] were tested for significance using an unpaired t-test. Adequacy of the best fit model was determined by the X^2 test with three degrees of freedom and was accepted if $p > 0.05$ (non-significant X^2 value).

3. RESULTS

The results of generation mean analysis revealed that the additive-dominance model were only additive and dominance effects significant was found appropriate in 7 cases. Therefore, the epistatic models were considered necessary in 67 cases and additive, dominance and epistatic were revealed significant. With the magnitude of dominance effect when significant was more pronounced than additive and the absolute total of epistatic results for 35 cases. Therefore, the absolute sum of epistatic impacts was more pronounced than additive and dominance effects for 12 cases (Table 2). Trait performances of the F1 hybrid showed evident mid-parent heterosis varying from 0.6% to 89.2% for the 74 cases investigated. Correlations between genetics components effects revealed that heterosis was not correlated to additive, dominance or epistasis effects (Table 3).

4. DISCUSSIONS

Varying depending on the trait, in most cases, the variation in the generation means fit an epistatic model, which indicated the complexity of model inheritance of quantitative characteristics as compared to additive-dominance model applied in the development of many theoretical concepts of genetic quantitative. The presence of epistasis is with reports published by other authors [16-19]. Heterosis has been well recognized as an essential genetic phenomenon in many species, including wheat, pepper, and oat [20-22]. In our study, the hybrid exhibited a high amount of MPH in most traits investigated. It

will provide high significance to elucidate the genetic factors involved in heterosis. The expression of MPH method as a function of gene effect showed the contribution of dominance and dominance by dominance and additive by additive type interactions and the absence of additive by dominance type interaction. The lack of contribution of additive x dominance interaction in this method was not logic. In fact, based on QTL mapping Tang et al. [23] reported digenic interactions contributing to mid-parent heterosis involving all three types of interactions (additive x additive, additive x dominance, dominance x dominance) for grain yield and yield components in maize. The second point, the estimation of heterosis as percentage lead to the parameter of means (the point of reference) in this function, which complicates the genetic interpretation of this phenomenon. Lamkey and Edwards [24] reported that from a quantitative genetic point of view, percentage mid-parent heterosis is challenging to interpret because it does not refer to the genetic architecture of the parents crossed to produce the hybrids.

The absence of correlation between dominance and heterosis and between epistasis and heterosis can be due to the several assumptions proposed in the fundamental genetic quantitative model and lines cross analysis. First we assumed that we start with two populations (P1 et P2) each with loci in Hardy-Winberg and gametic phase phase equilibrium. Second, we also assumed that loci differentiating the two populations are unlinked [13] and generation mean analysis method. The preponderance of non-additive effects in the majority of cases can explain the presence of heterosis. Based on QTLs analysis several new types of research reported the contribution of epistasis in the manifestation of heterosis [2,25]. Also, a systemic property of metabolic networks has to lead to an epistasis-based model for heterosis [26]. Another point, the expression of genes or interaction between genes can be changed from parents to hybrids the new genetic background of hybrid can solicit a new genes or interaction between genes. All concepts of genetic quantitative such as narrow-sense heritability, heterosis, etc. were developed based on a simple restrictive model. Therefore, recent research revealed the complexity of the mode of inheritance of quantitative traits. Also, several works in our laboratory reported the variation of inheritance of many quantitative traits with abiotic or biotic stresses [27- 32].

Table 2. Estimates of additive (A), dominance(D), absolute total epistatic effect (ATE), absolute total of non-additive effects (ATN) and heterosis (Htero) of nine traits with 74 cases of combinations cross-sit or cross-abiotic or biotic stress

TR	1	2	3	4	5	6	7	8	9	10
A	1.21	1.88	1.85	2.46	5.7	6.7	7.4	5.02	2.32	1.51
D	0.15	0.36	10.28	3.63	12.75	29.28	-32.23	-10.76	-4.97	-3.12
ATE	0	5.07	9.9	6.12	14.77	38.37	39.36	11.27	4.43	4.61
TNA	0.15	5.43	10.94	4.39	16.24	16.87	6.13	0.51	3.76	3.53
hetro	9.0	11	6.0	3.5	2.53	8.92	5.29	2.93	7.11	7.30
TR	11	12	13	14	15	16	17	18	19	20
A	1.48	1.65	2.60	2.04	1.83	1.19	1.81	1.71	2.56	1.75
D	-6.28	6.01	10.76	1.08	1.26	0.12	10.39	6.29	6.52	3.81
ATE	6.93	6.65	11.53	0	0	0	10.99	3.58	3.54	4.45
TNA	6,19	5.98	22.29	1.08	1.26	1.12	21.38	9.87	10.06	3.46
hetro	0.88	1.14	18.42	19.56	9.96	0.09	24.81	26.88	21.17	14.28
TR	21	22	23	24	25	26	27	28	29	30
A	28.68	20.02	15.53	43.07	-0.21	-0.33	-0.28	-0.32	0.33	0.30
D	108	-144.48	-12.45	-98.20	0	-0.95	-0.7	1.01	2.14	3.43
ATE	190.72	221.1	84.91	130.34	0.58	0.77	0.89	1.26	2.26	3.91
TNA	161.9	62.23	72,64	228,54	0.58	1.08	0.19	0.85	4.4	7.34
hetro	28.50	52.12	43.54	36.03	75.13	42.94	26.87	75.62	48.00	36.00
TR	31	32	33	34	35	36	37	38	39	40
A	0.49	0.52	-2.97	-3.24	-2.37	-2.94	-2.67	-2.36	-2.63	-2.31
D	4.95	3.39	-12.95	-17.24	-14.79	-21.49	-15.23	-8.46	-14.31	-9.18
ATE	5.54	3.54	14.24	18.93	14.44	23.26	15.57	7.2	12.99	8.71
TNA	94.43	6.93	8.71	13.41	10.67	11.49	9.56	9.78	12.58	7.705
hetro	55.00	3.61	30.51	28.95	21.30	64.73	34.97	30.86	78.40	11.19
TR	41	42	43	44	45	46	47	48	49	50
A	-2.48	-2.23	-1.90	-2.16	-1.96	-1.93	-1.71	-3.02	-3.2	-2.22
D	-10.84	-6.20	-6.59	-6.26	-0.93	-0.05	0.44	-11.03	-17.37	-8.76
ATE	10.65	5.87	6.57	6.30	2.11	0	0	12.70	19.09	10.18
TNA	9.83	5.75	6.54	4.88	3.04	0.05	0.44	6.25	13.74	4.9
hetro	4.93	9.16	9.92	1.44	4.48	2.53	13.67	6.54	2.83	22.62
TR	51	52	53	54	55	56	57	58	59	60
A	-2.87	-2.42	-2.10	-2.7	-2.08	-2.50	-1.78	-1.57	-1.62	-1.52
D	-21.38	-9.14	-7.99	-10.52	-9.96	-8.77	5.98	-2.73	-1.36	-1.28
ATE	23.66	9.58	6.88	9.04	8.82	8.04	6.85	3.16	2.25	2.71
TNA	10.52	5.22	8.47	10.89	9.46	9.33	2.41	5.89	3.61	3.99
hetro	15.15	35.02	25.58	33,71	25.58	19.72	21.72	24.89	10.06	2.93
TR	61	62	63	64	65	66	67	68	69	70
A	-1.51	-1.36	-1.36	-1.08	-2.05	-2.0	-1.0	-1.7	-1.36	-1.31
D	0.02	0.36	-1.25	-0.14	-2.46	-9.7	0.03	-0.08	-0.93	0.13
ATE	0	0	0	0	3.03	11.54	0	2.60	0	0
TNA	0.02	0.36	1.25	0.14	0.57	6.16	0.03	0.08	0.93	0.13
hetro	0.69	11.21	68.42	6.03	22.79	29.41	1.81	72.53	89.20	30,68
TR	71	72	73	74						
A	-1.80	-1.80	-1.41	-1.79						
D	-8.13	-5.92	0.21	-3.16						
ATE	10.81	8.62	0	4.06						
TNA	3.1	2.4	0.21	2.88						
hetro	45.57	29.97	13.24	60.82						

Table 3. Correlation between additive, dominance, absolute total of epistatic effect, total of non-additives effect and heterosis

	Additive	Dominance	Absolute total epistasis	Non additives effects
Heterosis	0.08	0.12	0.14	0.15

5. CONCLUSION

To conclude, the contribution of dominance and epistasis in the manifestation of heterosis is a reality not to discuss. Therefore, the estimation of genetic effect with generation means analysis should be reconsidered.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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