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FEATURE OF HETEROSIS IN *Capsicum annuum* L. IN CONNECTION WITH DEGREE OF IDENTITY OF KEY ALLELES OF ECONOMIC VALUABLE DETERMINANTS

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S u m m a r y

With the use of parental forms of Capsicum annuum L. (Dobrynya Nikitich, Kolobok, Prometei varieties and also L 48 and L 49 lines) by the regression-cluster analysis the authors revealed the correlation between degree of identity of key alleles of economic valuable determinants and effect of heterosis. It was shown, that for the prognosis of heterosis in the conditions of the film nonheated greenhouse on module of marketable crop the degree of identity alleles in three clusters: fruit's length—fruit's index, fruit's rot and duration of I phenophase—number of cameras in fruit; in the conditions of open ground — identity in the clusters: fruit's length—fruit's index, average fruit's mass—marketable fruit's mass have key significance. For the forecast of heterosis on mentioned module for both variants of growing the correlation between character and degree of identity of alleles in clusters: fruit's length—fruit's index and duration of II phenophase—duration of III phenophase is important.

Keywords: quantitative traits, regression cluster analysis, gene net, heterosis, vegetable pepper.

Genetic mechanisms of heterosis are still discussed. Today, there are two hypotheses explaining this phenomenon (1-3): one of them shows heterosis as the result of interactions of non-allelic dominant genes, and another one – heterosis occurs due to the overdominance of a heterozygote during the intraloci interaction of alleles. The study of genetic basics of heterosis sets a primary task of identification the key alleles for commercially valuable traits. Currently, QTL is considered as the most promising method for detection of polygenic characters (4, 5). This method is used in studies of pepper (6): the first complete genetic map of pepper genome was developed by the US company "DNA LandMarks" in collaboration with scientists of Cornell University (http://www.sign.cornell.edu/cview / map.pl? map_version_id = 58). This map is based on a series of common genes detected in both the *Solanaceae* family (tomato, potato, eggplant) and in the model plant *Arabidopsis thaliana* (L.) Heynh (7, 8). However, this map hasn't been tested in practice yet and requires clarification and validation of specific polygenes (at least due to non-desirable linkage in a number of polygenes) (6). At the same time, it is assumed that biological nature of quantitative traits isn't completely clear yet (9-12), which highlights using different approaches in studying polygenes. The theory of ecology-genetic control of quantitative traits (9-11, 13) was the basis for introducing the concept of a module – the basic unit describing the structure of a quantitative trait. The module includes three interrelated characters: one resultant and two component traits. According to this theory, it is impossible to identify quantitative traits due to their environmental mobility. At the same time, it is possible to detect dominant alleles responsible for expression of specific characters by their norm of reaction using the regression-cluster analysis of genotypes developed by the authors (14-16).

The purpose of this study was to assess heterosis manifestation in vegetable pepper depending on nature and extent of identity of effects provided by re-determined alleles for commercially valuable traits in order to clarify regularities and mechanisms of heterosis.

Technique. Five genotypes of sweet pepper (the cultivars Dobrynya Nikitich, Kolobok, Prometei, the lines L 48 and L 49) were subjected to diallel crosses according to the scheme [×p(p+1)] (non-heated greenhouse, center of the Transnistrian region, 2004). During the following season (2005), parental plants and F_1 hybrids were grown according to a common technique for this crop. Using the scheme of randomized blocks, 50-days-old seedlings were planted (two replicates, 10 plants in each variant) in open ground and in non-heated film greenhouses. Regression-cluster analysis and assessment of identity of re-determined alleles were performed as described (16).

Heterosis effects (compared with mean values of parental lines) for each character were estimated according to Kh. Daskalov et al. (1). The software Correlation matrices Statistica 6.0 was used to assess correlations between heterosis effects and levels of identity of re-determined alleles manifested in particular environmental conditions, and to perform partial visualization of these processes. The complete visualization was performed using the graph of gene network describing the genes whose interactions varied within 20% of extreme values in the entire matrix. The matrix – the table of correlations between heterosis effects of quantitative traits and degrees of identity of effects provided by re-determined alleles in both variants of cultivation (protected ground, open ground). The graph was designed using Graphviz software package the "dot" algorithm (http://www.graphviz.org/) (solid lines show positive correlations, dashed lines - negative values).

Results. Protected ground. The nature of heterosis manifestation was assessed upon the module of marketable yield in tested genotypes (Table 1).

1. Heterosis effects (%) **for characters in the module of marketable yield in vegetable pepper *Capsicum annuum* L. under the conditions of protected ground and open ground** (upon the results of diallel crosses, Tiraspol, 2005)

Cultivars and lines used in crosses	Protected ground								Open ground							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
L 48 × Prometei	125	122	97	99	108	113	88	125	151	90	78	95	105	110	84	133
Kolobok × Prometei	97	84	111	108	92	85	95	98	87	121	86	100	77	79	82	90
L 49 × Prometei	159	124	128	105	108	100	95	112	77	95	99	97	100	101	84	97
Dobrynya Nikitich ×	148	88	128	106	114	108	101	110	131	96	102	97	98	102	91	121

Prometei																
Kolobok × L 48	127	104	105	114	85	77	93	106	127	91	111	112	96	83	82	106
L 49 × L 48	213	173	107	107	104	101	99	141	195	113	111	102	117	115	87	120
L 49 × Kolobok	217	131	161	123	86	67	108	113	81	90	96	105	84	77	98	100
Dobrynya Nikitich × Kolobok	228	116	166	129	110	85	109	131	95	73	106	109	90	82	85	126
Dobrynya Nikitich × L 49	337	206	136	117	108	91	112	154	88	86	78	92	103	110	83	160
Dobrynya Nikitich × L 48	168	121	118	105	115	114	96	109	115	71	112	103	121	116	97	101

Note. 1 – marketable yield, 2 – number of fruits per plant, 3 – weight of a marketable fruit, 4 – fruit diameter , 5 – fruit length, 6 – fruit index, 7 – thickness of a fruit wall, 8 – plant height..

According to literature data, *Capsicum annuum* exhibits pronounced heterosis effects for a number of characters – duration of vegetation period, yield, pathogen resistance, number of fruits and seeds, plant height, etc. (1, 17). The earlier findings of the authors (Table 1) agree with these facts – firstly, for a marketable yield, as well as for number of fruits per plant, plant height and fruit weight. However, a marketable yield should be considered as the result determined by contributions of other traits (9-11); in vegetable pepper, this is formed by the number of marketable fruits per plant multiplied by the weight of one fruit. In turn, fruit weight is the result of multiplying the specific effective mass to the weight of one fruit, while a fruit volume is associated with thickness of the pericarp wall, fruit length, diameter, etc. Therefore, it is possible the presence of a small number of key genes providing the resulting trait. However, specific genes for yield and fruit weight can be virtual and unidentified. For the module of yield, the most important real characters are fruit wall thickness, fruit length and diameter, number and specific weight of marketable fruits (and, respectively, the encoding alleles). The analysis of heterosis manifestation in the studied characters revealed significant positive correlation between fruit length and fruit index with fruit diameter (r = 0,83) and negative - with fruit wall thickness (r = –0,77). This resulted in a positive correlation between heterosis for marketable yield, fruit diameter and weight, number of fruits and plant height. The data for non-heated greenhouse indicate the presence of both direct and indirect interactions between characters, which combine to give the final effect.

2. Identity (%) **of effects provided by key alleles for a number of commercially valuable characters in vegetable pepper *Capsicum annuum* L. depending on growing conditions** (upon the results of diallel crosses, Tiraspol, 2005).

Cultivars and lines used in crosses	Protected ground									Open ground								
	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
L 48 × Prometei	50	0	0	0	0	0	0	0	100	50	0	0	0	100	0	0	50	0
Kolobok × Prometei	0	66,6	0	0	0	0	50	50	100	0	0	0	100	0	100	0	50	0
L 49 × Prometei	50	33,3	0	0	0	0	0	0	100	50	0	0	0	0	100	0	100	100
Dobrynya Nikitich × Prometei	0	100	100	0	0	50	0	50	50	0	0	0	0	0	100	0	100	100
Kolobok × L 48	0	33,3	0	0	0	100	0	0	100	0	0	100	0	0	0	0	0	100
L 49 × L 48	100	66,6	0	0	0	100	100	0	100	100	0	0	0	0	0	0	50	0
L 49 × Kolobok	0	66,6	0	0	0	0	50	50	100	0	0	0	100	0	100	0	50	0
L 49 × L 48	100	66,6	0	0	0	100	100	0	100	100	0	0	0	0	0	0	50	0
L 49 × Kolobok	0	66,6	0	0	0	0	50	50	100	0	0	0	100	0	100	0	50	0
Dobrynya Nikitich × Kolobok	0	66,6	0	0	100	50	0	0	50	0	0	0	0	0	100	50	50	0
Dobrynya Nikitich × L 49	50	33,3	0	0	0	50	0	0	50	0	100	100	0	0	100	50	100	100

Note. 1-9 — respectively, the clusters: fruit length– fruit index; total yield – marketable yield – number of fruits per plant; fruit diameter; plant height; fruit rot; average fruit weight– marketable fruit weight; duration of II phenophase – duration of III phenophase; fruit wall thickness – Verticillium wilt; duration of I phenophase – number of segments in a fruit.

The authors compared the identity of effects provided by re-determined alleles for commercially valuable characters (Table 2) and heterosis effects (Table 1) in both growing conditions. It was observed a significant positive correlation (r = 0,67) between identity in the cluster “fruit length - fruit index” and heterosis for number of fruits per plant, as well as between identity in the cluster “fruit rot” and heterosis for fruit diameter; the negative correlation was found between identity in the cluster “duration of I phenophase – number of segments in a fruit” and heterosis for fruit length (Table 3). The rest of studied identity indices were indirectly associated with heterosis (through other characters). Considering both direct and indirect interconnections, it can be concluded that increasing the identity of effects provided by re-determined alleles in the cluster “fruit length – fruit index” promotes to raise of heterosis for number of fruits, plant height, marketable yield, fruit length and index, but it reduces heterosis for diameter, wall thickness and fruit weight.

3. Correlations (*r*) between heterosis effects and degrees of identity of key alleles providing a number of commercially valuable characters in vegetable pepper *Capsicum annuum* L. 10 hybrid descendants F_1 grown under the conditions of protected ground and open ground (upon the results of diallel crosses, Tiraspol, 2005)

V	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1	1	–0,39	–0,30	–0,30	–0,30	0,00	0,56	–0,45	0,12	0,41	–0,48	0,56	–0,18	0,28	0,67*	–0,42	0,57	0,82*	0,20	–0,08	–0,30	0,20	–0,49	–0,26	0,20	–0,12	0,80*	–0,41	0,83*	–0,05	0,56	0,13	–0,08	0,29
2	–0,39	1	0,58	0,22	0,22	0,28	–0,14	0,60	–0,09	–0,15	0,37	–0,36	0,45	0,05	–0,22	0,41	–0,07	–0,10	–0,15	–0,22	0,22	–0,51	0,58	0,19	0,22	0,09	–0,49	0,13	–0,43	0,07	–0,01	0,43	0,37	–0,10
3	–0,30	0,58	1	–0,11	–0,11	0,00	–0,21	0,67*	–0,41	0,35	–0,20	0,31	0,06	–0,17	–0,37	0,03	–0,20	–0,20	–0,11	–0,17	–0,11	–0,11	0,27	–0,22	0,44	0,41	–0,03	–0,23	0,10	0,22	0,15	0,08	0,13	0,09
4	–0,30	0,22	–0,11	1	–0,11	0,43	–0,21	–0,17	0,27	–0,53	0,44	–0,60	0,38	0,18	0,04	0,53	–0,14	–0,20	–0,11	–0,17	–0,11	–0,11	0,27	0,51	–0,11	–0,27	–0,39	0,21	–0,46	0,63	–0,32	–0,06	0,02	–0,26
5	–0,30	0,22	–0,11	–0,11	1	0,00	–0,21	–0,17	–0,41	0,22	0,67*	–0,20	0,42	0,23	–0,10	0,61	0,22	–0,20	–0,11	–0,17	–0,11	–0,11	0,27	0,51	–0,11	–0,27	–0,24	0,44	–0,35	–0,13	–0,18	–0,45	0,20	0,18
6	–0,00	0,28	0,00	0,43	0,00	1	0,16	–0,32	–0,00	–0,40	0,47	–0,46	0,38	0,34	0,29	0,22	0,19	0,00	0,00	0,32	–0,43	–0,43	–0,26	0,28	–0,43	–0,00	0,15	0,58	–0,13	0,39	0,32	–0,11	0,58	0,04
7	0,56	–0,14	–0,21	–0,21	–0,21	0,16	1	–0,00	0,00	0,18	–0,34	0,37	–0,22	–0,09	0,13	–0,38	–0,01	0,37	–0,21	–0,31	0,21	–0,21	–0,51	–0,41	–0,21	–0,51	0,55	0,08	0,45	0,29	0,47	0,22	0,38	–0,28
8	–0,45	0,60	0,67*	–0,17	–0,17	–0,32	0,00	1	–0,10	0,00	–0,24	0,08	–0,11	–0,45	–0,58	–0,14	–0,48	–0,30	–0,17	–0,25	0,67*	–0,17	0,41	–0,33	0,25	0,10	–0,45	–0,23	–0,24	–0,07	–0,08	0,54	–0,02	–0,25
9	0,12	–0,09	–0,41	0,27	–0,41	0,00	0,00	–0,10	1	–0,67*	–0,27	–0,30	–0,54	–0,47	–0,14	–0,42	–0,30	0,49	–0,41	–0,10	0,27	0,27	–0,25	–0,36	–0,41	–0,17	–0,25	0,13	–0,27	–0,24	0,17	0,62	–0,20	–0,47
10	0,41	–0,15	0,35	–0,53	0,22	–0,40	0,18	–0,00	–0,67*	1	–0,31	0,83*	0,06	0,22	0,17	0,02	0,35	0,17	0,16	–0,31	–0,35	0,16	–0,00	–0,10	0,61	0,06	0,60	–0,50	0,72*	0,10	0,17	–0,39	–0,07	0,42
11	–0,48	0,37	–0,20	0,44	0,67*	0,47	–0,34	–0,24	–0,27	–0,31	1	–0,77*	0,80*	0,55	0,16	0,84*	0,25	–0,46	0,22	0,24	–0,12	–0,46	0,47	0,87*	–0,16	–0,07	–0,47	0,52	–0,62	0,09	–0,45	–0,36	0,31	0,15
12	0,56	–0,36	0,31	–0,60	–0,20	–0,46	0,37	0,08	–0,30	0,83*	–0,77*	1	–0,45	–0,19	0,01	–0,50	0,10	0,39	–0,07	–0,34	–0,20	0,42	–0,39	–0,57	0,38	–0,01	0,72*	–0,54	0,85*	0,05	0,47	–0,11	–0,21	0,21
13	–0,18	0,45	0,06	0,38	0,42	0,38	–0,22	–0,11	–0,54	0,06	0,80*	–0,45	1	0,85*	0,49	0,84*	0,53	–0,35	0,56	0,20	–0,21	–0,52	0,62	0,89*	0,36	0,07	–0,22	0,01	-0,19	0,23	–0,39	–0,29	0,22	0,43
14	0,28	0,05	–0,17	0,18	0,23	0,34	–0,09	–0,45	–0,47	0,22	0,55	–0,19	0,85*	1	0,86*	0,56	0,84*	–0,04	0,78*	0,38	–0,43	–0,29	0,29	0,78*	0,39	0,13	0,19	–0,21	0,23	0,09	–0,16	–0,35	0,03	0,69*
15	0,67*	–0,22	–0,37	0,04	–0,10	0,29	0,13	–0,58	–0,14	0,17	0,16	0,01	0,49	0,86*	1	0,11	0,89*	0,36	0,75*	0,40	–0,41	–0,05	–0,07	0,45	0,28	0,08	0,46	–0,36	0,51	–0,06	0,15	–0,11	–0,13	0,67*
16	–0,42	0,41	0,03	0,53	0,61	0,22	–0,38	–0,14	–0,42	0,02	0,84*	–0,50	0,84*	0,56	0,11	1	0,18	–0,44	0,16	–0,12	–0,22	–0,43	0,70*	0,85*	0,27	–0,05	–0,40	0,21	–0,44	0,36	–0,60	–0,45	0,25	0,09
17	0,57	–0,07	–0,20	–0,14	0,22	0,19	–0,01	–0,48	–0,30	0,35	0,25	0,10	0,53	0,84*	0,89*	0,18	1	0,36	0,68*	0,30	–0,44	0,10	–0,02	0,50	0,30	0,03	0,39	–0,34	0,47	–0,21	0,26	–0,17	–0,22	0,86*
18	0,82*	–0,10	–0,20	–0,20	–0,20	0,00	0,37	–0,30	0,49	0,17	–0,46	0,39	–0,35	–0,04	0,36	–0,44	0,36	1	–0,20	–0,30	–0,20	0,30	–0,43	–0,39	0,05	–0,18	0,50	–0,22	0,52	–0,19	0,68*	0,42	–0,08	0,06
19	0,20	–0,15	–0,11	–0,11	–0,11	0,00	–0,21	–0,17	–0,41	0,16	0,22	–0,07	0,56	0,78*	0,75*	0,16	0,68*	–0,20	1	0,67*	–0,11	–0,11	0,27	0,51	0,44	0,41	0,10	–0,51	0,28	–0,25	–0,25	–0,15	–0,30	0,75*
20	–0,08	–0,22	–0,17	–0,17	–0,17	0,32	–0,31	–0,25	–0,10	–0,31	0,24	–0,34	0,20	0,38	0,40	–0,12	0,30	–0,30	0,67*	1	–0,17	–0,17	–0,10	0,22	–0,17	0,61	0,02	0,07	–0,03	–0,42	–0,10	–0,14	–0,01	0,44
21	–0,30	0,22	–0,11	–0,11	–0,11	–0,43	0,21	0,67*	0,27	–0,35	–0,12	–0,20	–0,21	–0,43	–0,41	–0,22	–0,44	–0,20	–0,11	–0,17	1	–0,11	0,27	–0,22	–0,11	–0,27	–0,57	–0,07	–0,42	–0,31	–0,26	0,65*	–0,16	–0,42
22	0,20	–0,51	–0,11	–0,11	–0,11	–0,43	–0,21	–0,17	0,27	0,16	–0,46	0,42	–0,52	–0,29	–0,05	–0,43	0,10	0,30	–0,11	–0,17	–0,11	1	–0,41	–0,22	–0,11	–0,27	0,15	–0,35	0,28	–0,19	0,34	–0,06	–0,83*	0,29
23	–0,49	0,58	0,27	0,27	0,27	–0,26	–0,51	0,41	–0,25	0,00	0,47	–0,39	0,62	0,29	–0,07	0,70*	–0,02	–0,43	0,27	–0,10	0,27	–0,41	1,	0,53	0,61	0,25	–0,67*	–0,25	–0,47	–0,03	–0,74*	0,08	–0,03	0,02
24	–0,26	0,19	–0,22	0,51	0,51	0,28	–0,41	–0,33	–0,36	–0,10	0,87*	–0,57	0,89*	0,78*	0,45	0,85*	0,50	–0,39	0,51	0,22	–0,22	–0,22	0,53	1	0,15	–0,09	–0,34	0,09	–0,35	0,16	–0,49	–0,43	–0,05	0,44
25	0,20	0,22	0,44	–0,11	–0,11	–0,43	–0,21	0,25	–0,41	0,61	–0,16	0,38	0,36	0,39	0,28	0,27	0,30	0,05	0,44	–0,17	–0,11	–0,11	0,61	0,15	1	0,41	0,09	–0,79*	0,39	0,04	–0,28	0,01	–0,19	0,34
26	–0,12	0,09	0,41	–0,27	–0,27	0,00	–0,51	0,10	–0,17	0,06	–0,07	–0,01	0,07	0,13	0,08	–0,05	0,03	–0,18	0,41	0,61	–0,27	–0,27	0,25	–0,09	0,41	1	0,01	–0,23	0,08	–0,33	–0,21	–0,03	0,11	0,23
27	0,80*	–0,49	–0,03	–0,39	–0,24	0,15	0,55	–0,45	–0,25	0,60	–0,47	0,72*	–0,22	0,19	0,46	–0,40	0,39	0,50	0,10	0,02	–0,57	0,15	–0,67*	–0,34	0,09	0,01	1	–0,20	0,91*	0,21	0,60	–0,29	0,14	0,29
28	–0,41	0,13	–0,23	0,21	0,44	0,58	0,08	–0,23	0,13	–0,50	0,52	–0,54	0,01	–0,21	–0,36	0,21	–0,34	–0,22	–0,51	0,07	–0,07	–0,35	–0,25	0,09	–0,79*	–0,23	–0,20	1	–0,58	0,14	0,03	–0,21	0,64*	–0,45
29	0,83*	–0,43	0,10	–0,46	–0,35	–0,13	0,45	–0,24	–0,27	0,72*	–0,62	0,85*	–0,19	0,23	0,51	–0,44	0,47	0,52	0,28	–0,03	–0,42	0,28	–0,47	–0,35	0,39	0,08	0,91*	–0,58	1	0,09	0,53	–0,13	–0,15	0,44
30	–0,05	0,07	0,22	0,63	–0,13	0,39	0,29	–0,07	–0,24	0,10	0,09	0,05	0,23	0,09	–0,06	0,36	–0,21	–0,19	–0,25	–0,42	–0,31	–0,19	–0,03	0,16	0,04	–0,33	0,21	0,14	0,09	1	–0,04	–0,36	0,32	–0,28
31	0,56	–0,01	0,15	–0,32	–0,18	0,32	0,47	–0,08	0,17	0,17	–0,45	0,47	–0,39	–0,16	0,15	–0,60	0,26	0,68*	–0,25	–0,10	–0,26	0,34	–0,74*	–0,49	–0,28	–0,21	0,60	0,03	0,53	–0,04	1	0,26	0,03	0,21
32	0,13	0,43	0,08	–0,06	–0,45	–0,11	0,22	0,54	0,62	–0,39	–0,36	–0,11	–0,29	–0,35	–0,11	–0,45	–0,17	0,42	–0,15	–0,14	0,65*	–0,06	0,08	–0,43	0,01	–0,03	–0,29	–0,21	–0,13	–0,36	0,26	1	–0,10	–0,29
33	–0,08	0,37	0,13	0,02	0,20	0,58	0,38	–0,02	–0,20	–0,07	0,31	–0,21	0,22	0,03	–0,13	0,25	–0,22	–0,08	–0,30	–0,01	–0,16	–0,83*	–0,03	–0,05	–0,19	0,11	0,14	0,64*	–0,15	0,32	0,03	–0,10	1	–0,43
34	0,29	–0,10	0,09	–0,26	0,18	0,04	–0,28	–0,25	–0,47	0,42	0,15	0,21	0,43	0,69*	0,67*	0,09	0,86*	0,06	0,75*	0,44	–0,42	0,29	0,02	0,44	0,34	0,23	0,29	–0,45	0,44	–0,28	0,21	–0,29	–0,43	1

Note. V – variable (denotations of variable values – see Fig. 1).
*Significant at p < 0,05.

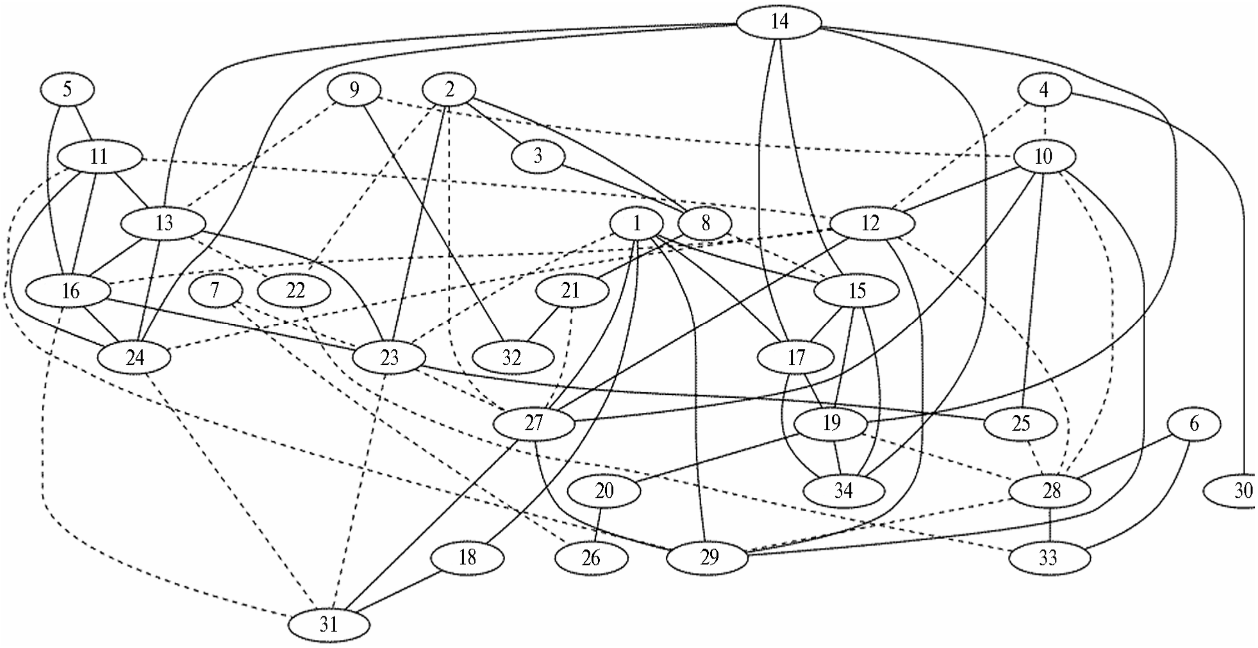

Fig. 1.Visualization of interactions between heterosis effects and key alleles for commercially valuable characters of vegetable pepper *Capsicum annuum* L. (upon the results of diallel crosses, Tiraspol, 2005).

Degrees of identity in clusters for cultivation in protected ground (1-9) and in open ground (18-26): 1, 18 — fruit length – fruit index; 2, 19 — total yield – marketable yield – number of fruits per plant; 3, 20 — fruit diameter; 4, 21 — plant height; 5, 22 — fruit rot; 6, 23 — average fruit weight – marketable fruit weight; 7, 24 — duration of II phenophase – duration of III phenophase; 8, 25 — thickness of fruit wall – Verticillium wilt; 9, 26 — duration of I phenophase – number of segments in a fruit.

Heterosis effects in protected ground (10-17) and in open ground (27-34) for the following criteria: 10, 27 — fruit lenght; 11, 28 — fruit diameter; 12, 29 — fruit index; 13, 30 — thickness of fruit wall; 14, 31 — marketable yield; 15, 32 — number of fruits per plant; 16, 33 — fruit weight; 17, 34 — plant height.

At the same time, the higher was identity in the cluster "duration of I phenophase – number of segments in a fruit", the lower was heterosis for yield component characters (fruit length, wall thickness, marketable yield, fruit weight, diameter and index, number of fruits and plant height). The decrease of identity in the cluster "fruit rot" reduced heterosis for fruit diameter, weight, length and wall thickness, as well as the marketable yield, while there was a trend towards the growth in fruit index and number of fruits.

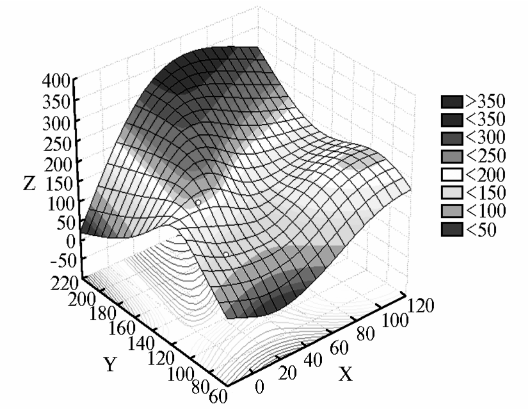

Fig. 2. Visualization of correlation between heterosis effects by the criteria of marketable yield (Z) **and number of fruits per plant** (Y) **and identity of alleles in the cluster "fruit length – fruit index"** (X) **in *Capsicum annuum* L. hybrids grown in protected ground** (upon the results of diallel crosses, Tiraspol, 2005).

The performed analysis reveals very complex gene interactions underlying the final result - yield. This fact suggests defying the quantitative trait module as a representative functional unit. This indicator is much more convenient to study using the gene network reflecting co-operating groups of genes responsible for performing a particular function (18, 19). Figure 1 shows the gene network (nodes - correlated quantitative traits) and degree of identity of effects provided by re-determined alleles; it allows easily trace interrelations between structural and temporal modules of quantitative traits (9, 10) that promote a particular function. Interestingly, that there wasn't revealed any significant direct interactions between identity indices of alleles in the clusters "total yield – marketable yield – number of fruits", "average fruit weight – marketable fruit weight" and heterosis effects. This fact can be explained by the complex structure of yield and fruit weight characters defined by negative and of positive interrelations that stabilize some level the gene network parameters or, on the contrary, decline them from the initial point to provide the shift to a new functional state. The analysis of contributions of gene network elements under both growing conditions allows to highlight the importance in forecasting heterosis for yield from the presence of alleles and degree of their identity in the clusters "fruit length - fruit index", "fruit rot", "duration of I phenophase - number of segments in a fruit" (visualization of interrelations in the gene network, see Fig. 2). The increase of identity of alleles in the cluster "fruit length – fruit index" is accompanied with rising heterosis effects: the curvilinear (up to a certain extent) - for marketable yield and number of fruits per plant, straightforward – for plant height. The curvilinearity indicates a significant contribution of genotypic background in heterosis effects for marketable yield and confirms the presence of gene interactions.

Open ground. The transition to less comfortable growing conditions in most cases contributed to differentiated heterosis manifestations in hybrid combinations of studied characters (Table 2). In a number of traits, these effects were stable, significant and positive: for example, the positively correlated heterosis was established for fruit length and fruit index (r = 0,91), fruit diameter and weight (r = 0,64), while the absolute values of these characters had changed).

The authors' findings are consistent with the theory of ecology-genetic control of quantitative traits (9-11), which postulates that environmental conditions can change expression of traits and re-determine them by changing the gene set providing these traits (activation of new genes and switching off the previously operated genes). In the module of yield, the change of growing conditions contributed to correlation shifts in its component characters. It was observed weakening the correlation between heterosis in yield and number of fruits (r = 0,26), fruit diameter and wall thickness (r = 0,14), wall thickness and fruit weight (r = 0,32), yield and plant height (r = 0,21). Along with it, correlation between some characters was inversed: yield from a plant and wall thickness (r = –0,04), plant height and number of fruits per plant (r = –0,29). The lower manifestation of traits and activation of new dominant groups instead of the earlier ones were the factors inducing coordinated modifications of complex characters (fruit weight) and changes (direct and backward relations) in the gene network of yield module, which resulted in functional re-determination of the organism response adequately to environmental impacts. Severe conditions of the open ground clarified interrelations between the identity of alleles for some characters and heterosis effects. For example, the negatively correlated heterosis was established for fruit length and identity of alleles in the cluster "average fruit weight – marketable fruit weight (*r* = – 0,67), as well as fruit diameter and identity of alleles in the cluster "Verticillium wilt in monoculture – fruit wall thickness (*r* = –0,79). Positively correlated heterosis was found for number of fruits and identity of alleles in the cluster "plant height" (*r* = 0,65), as well as for plant height and identity of alleles in the cluster "total yield – marketable yield – number of fruits" (*r* = 0,75). Heterosis for a marketable yield was positively correlated with identity of alleles in the cluster "fruit length – fruit index" (r = 0,68) and negatively - with identity of alleles in the cluster "average fruit weight – marketable fruit weight" (*r* = – 0,74).

Thus, the change of growing conditions (from greenhouse to the open ground) affected heterosis manifestation for certain characters (significant increase or decrease from a significant level up to a trend) and redirected the effect from positive values to negative or vice versa. Therefore, prognostication of results should consider a whole function rather than individual characters, which is possible using the analysis of quantitative traits based on the functional module approach. Gene network visualizes negative and positive correlations; it demonstrates the possible resulting manifestation of heterosis effects, as well as the expected shifts of traits from initial levels and transition to the modified functional state (Fig. 2, 3).

These findings raise the question – is it possible to forecast heterosis for yield under both growing conditions and create the equally efficient hybrid on the basis of the analyzed genotypes.

A B

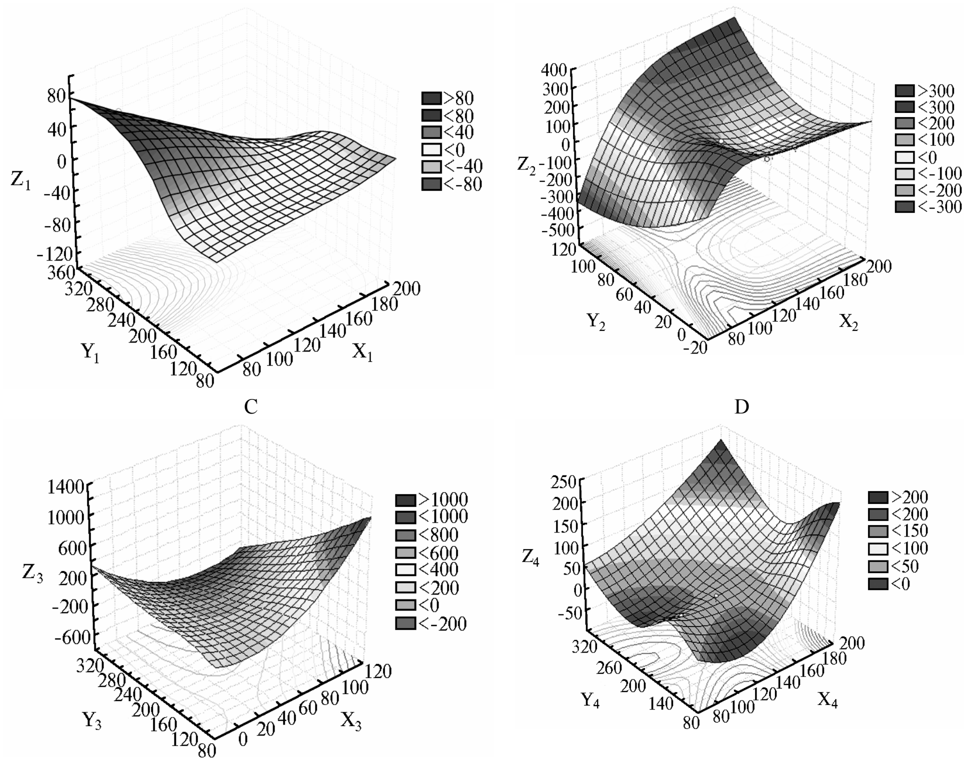

Fig. 3. The expected heterosis effect in marketable yield per plant under the conditions of open ground (A, X_1; B, X_2; C, Z_3; D, X_4) **and protected ground** (A, Y_1; B, Z_1; C, Y_3; D, Y_4) **considering identity of alleles in the clusters "duration of II phenophase-duration of II phenophase" in open ground** (A, Z_1) **and in protected ground** (B, Y_2)**, "fruit length – fruit index" in open ground** (C, X_3) **and in protected ground** (C, Z_4) **in vegetable pepper *Capsicum annuum* L. hybrids** (upon the results of diallel crosses, Tiraspol, 2005).

The analysis of these genotypes (Fig. 1, 3) revealed the close correlative sequence of characters capable to provide heterosis for yield in both growing conditions: heterosis for marketable yield in open ground → identity of alleles in the cluster "fruit length – fruit index" in open ground → identity of alleles in the cluster "fruit length – fruit index" in protected ground → heterosis for number of fruits per plant in protected ground → heterosis for a marketable yield in protected ground → identity of alleles in the cluster "duration of II phenophase – duration of III phenophase" → heterosis for a marketable yield in open ground. Owing to chain structure of this correlated sequence of characters (and their alleles), the final result depends on nature of changes (strengthening or weakening) in its any component. Such composition of gene chain suggests the increased heterosis for a marketable yield in both growing conditions positively and significantly correlated with identity of alleles in the cluster " fruit length – fruit index" and the one-direction correlation tending to higher absolute value in open ground - with identity of alleles in the cluster "duration of II phenophase – duration of III phenophase". Some elements of this sequence are shown on Figure 3 reflecting the expected heterosis for a marketable yield considering its curvilinear and straight-line interrelations with identity of alleles in the clusters "fruit length – fruit index" and "duration of II phenophase – duration of III phenophase" under both growing conditions. These data indicate that heterosis for the marketable yield module in both variants has like-directed correlation with degree of identity of effects provided by re-determined marker alleles, therefore, it is possible to predict obtaining the universal hybrid for both open and protected ground

The authors believe that these findings indicate the key role in heterosis of interactions of alleles within one locus, while the change of external environment activates new alleles and gene chains via feedback and mediated gene interactions thereby providing the resulting re-determined effect. Thus, heterosis is a complex functional response of the genotype to differentiating impact of environment based on intraloci interactions of alleles and the modifying role of cooperated gene effects.

It should be noted that re-determination of genes exhibited at changes of environmental conditions occurs at presence of gene regulators (possibly triggers or switch genes). Such model of regulation of quantitative genes was proposed for the lower fungi (12). Polygenic regulation operates via the regulators that activate or switch off individual genes or sets of genes for commercially important characters (10, 12). Along with this function, the authors assume that regulator genes trigger or block the coordinated sequence of genes determining a particular function under specific conditions. It is possible, that this type of regulation of polygenic functioning is trivial in plants. For example, in *C. annuum,* such trigger control is performed by four regulator genes during the transition from gametophyte to sporophytic development (14). The presence of such regulators (possibly triggers) can explain the fact of 12 constantly detected quantitative trait loci revealed during molecular investigations of rice under in different environmental conditions (cited from 10).

So, this study revealed the alleles providing the marketable yield module, as well as the nature and extent of their redetermination during the change of environmental conditions. It has been shown the presence and nature of correlations between variability of heterosis effects for yield and the level of functional identity of gene alleles encoding corresponding characters. The obtained results confirm and refine the hypothesis of modular structure of quantitative traits in plants, which completes the existing concepts about the possible regulation of polygenic systems. According to these data, heterosis is considered as the particular effect of gene networks' functions.

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