GENERATION MEAN ANALYSIS OF YIELD COMPONENTS AND YIELD IN TOMATO (*LYCOPERSICON ESCULENTUM* MILL.)

JASMINA ZDRAVKOVIĆ[1*], NENAD PAVLOVIĆ[1], ZDENKA GIREK[1], MILKA BRDAR-JOKANOVIĆ[1], DUBRAVKA SAVIĆ[2], MILAN ZDRAVKOVIĆ[1], AND DEJAN CVIKIĆ[1]

[1]*Institute for Vegetable Crops, Karađorđeva 71, 11420 Smederevska Palanka, Serbia*
[2]*Faculty of Agriculture, Belgrade, Nemanjina 8, 11080 Zemun, Serbia*
[*]*Corresponding author, E-mail: jzdravkovic@institut-palanka.co.rs*

Abstract

Tomato yield depends on two components viz., fruit weight and number of fruit per flower branch. These traits are quantitative and therefore influenced by multiple genes. The objective of this study was to estimate the main gene effects (additive, dominant and digenic epistasis) and to determine the mode of inheritance for yield components and yield in three tomato cross combinations by generation mean analysis. The trial included genotypes differing in morphology and yield: line DAT, cultivar SP-109 and local population KGZ. The analyzed genotypes belong to tomato germplasm collection of the Institute for Vegetable Crops, Smederevska Palanka, Serbia. Six families per hybrid, including parents, have been tested. Besides, the additive and dominance gene effects, non-allelic gene interactions have been detected for yield components and yield. Duplicate type of epistasis was confirmed for fruit weight and yield in all cases characterized by significant dominance and dominance/dominance effects, which diminishes the effect of dominant genes and makes breeding for yield increase more difficult. Therefore, number of fruits per flower branch increase would be the most efficient strategy for increasing tomato yielding ability.

Introduction

Yield is the most important agronomical trait; therefore, it is included in almost all tomato selection programs. The adequate choice of parental lines possessing the potential to produce high-yielding hybrids is essential (Koutsika-Sotiriou *et al.*, 2008). However, yield is a complex trait, influenced by genetic and environmental effects, such as numerous abiotic (Scott & Jones, 1990; Foolad & Lin, 2001) and biotic factors, applied agrotechic procedures (Kaşkavalci, 2007) and growing location (Yoltas *et al.*, 2003).

An effective selection criterion is precondition for achieving the inherent yielding ability of a species. Besides yield itself, yield components or other yield contributing agronomic characters may be utilized for breeding for yield increase. In tomato, yield per plant depends on fruit weight and number of fruits per flower branch; however, they are both determined by numerous genetic and environmental factors (Singh & Singh, 1985; Dhaliwal & Nnandpuri, 1988; Singh *et al.*, 1989; Zdravković *et al.*, 1998). Therefore, an understanding of the mode of inheritance of the yield and its components is crucial for the adequate choice of selection strategy for developing high-yielding cultivars and hybrids.

Generation mean analysis (Mather & Jinks, 1982) is a useful technique that provides the estimation of main genetic effects (additive, dominance and their digenic interactions) involved in the expression of quantitative traits such as yield components and yield. Besides for yield (Bhatt *et al.*, 2001), the method was successfully applied for research on mode of inheritance pattern of numerous tomato traits; such as time to seed germination (Scott & Jones, 1990), salt (Foolad, 1996) and cold tolerance (Foolad & Lin, 2001), vitamin C and total soluble solids (Bhatt *et al.*, 2001) and acylsugar content (Resende *et al.*, 2002). The inheritance of tomato resistance to *Phytophthora parasitica* root rot (Kozik *et al.*, 1991) and *Phytophthora infestans* late blight (Abreu *et al.*, 2008) have been also studied by generation mean analysis. The model has been used for similar research on yield inheritance pattern in other agronomical species, cotton for example (Hussain *et al.*, 2009).

The study was undertaken to estimate the main genetic effects including digenic non-allelic interactions controlling yield components and yield in three tomato cross combinations. The second aim was to determine the yield component that affects yield to a greater extent in order to define efficient selection strategy for increasing yielding ability in tomato.

Materials and Methods

Three tomato genotypes of local origin, differing in yield and morphology (line DAT-indeterminate type, cultivar SP-109-determinate type and local population KGZ-indeterminate type), were chosen from tomato germplasm collection of the Institute for Vegetable Crops, Smederevska Palanka, Serbia. The genotypes have been intercrossed during the tomato growing season of 2005 in order to produce F_1 hybrids. In the next year F_2 generation has been obtained and the backcrosses (BC_1 and BC_2) have been performed. Comparative field trial including six basic populations of each hybrid (parents, F_1, F_2 and backcross populations) has been conducted in 2007, in complete random block design with three replications. Standard agronomical procedures have been applied. The main plot size was 10 m^2, with 45 cm within-row spacing and 1 m between-row spacing.

Tomato yield and yield components (number of fruits per flower branch and fruit weight) have been examined. The yield analyses had been limited to the first three flower branches due to segregation of determinate tomato type that may occur in F_2 generation. 30 fruits for parents, F_1, BC_1 and BC_2 generations and 40 fruits for segregating F_1 generation have been included in the analyses.

Mean values, standard errors of mean, as well as coefficients of variation have been calculated. The data concerning F_1 generation and parental mean have been included in the calculation of heterosis value (%).

The mode of inheritance of the tomato yield components and yield was estimated for each cross combination by generation mean analysis (P_1, P_2, F_1, F_2, BC_1, and BC_2), using additive/dominance model, three parameter model (Mather & Jinks 1982). The effects of genes were calculated as:

$$(m) = 0.5P_1 + 0.5P_2 + 4F_2 - 2BC_1 - 2BC_2$$
$$(d) = 0.5P_1 - 0.5P_2$$
$$SE^2_{(d)} = 0.25SE^2_{P1} + 0.25SE^2_{P2}$$
$$(h) = 6BC_1 + 6BC_2 - 8F_2 - F_1 - 1.5P_1 - 1.5P_2$$
$$SE^2_{(h)} = 36SE^2_{BC1} + 36SE^2_{BC2} + 64SE^2_{F2} + SE^2_{F1} + 2.25SE^2_{P1} + 2.25SE^2_{P2};$$

with (m) representing mean, (d) additive and (h) dominance effect.

The estimated (m), (d) and (h) values were tested by t-test at the 0.05 and 0.01 levels of probability. The gene effects were calculated and tested by inversion of matrix system, on the basis of the expected model. The adequacy of the model was tested according to individual scaling and joint chi square tests. Individual scaling tests were based on mean generation values, for six generations (P_1, P_2, F_1, F_2, BC_1, and BC_2):

$$A = 2BC_1 - P_1 - F_1$$
$$SE^2_{(A)} = 4SE^2_{BC1} + SE^2_{P1} + SE^2_{F1}$$
$$B = 2BC_2 - P_2 - F_1$$
$$SE^2_{(B)} = 4SE^2_{BC2} + SE^2_{P2} + SE^2_{F1}$$
$$C = 4F_2 - 2F_1 - P_1 - P_2$$
$$SE^2_{(C)} = 16SE^2_{F2} + 4SE^2_{F1} + SE^2_{P1} + SE^2_{P2}$$

The joint chi square test was based on comparison of experimental mean generation values and the expected generation values that indicate epistatic effects. If at least one value from the C, A, B set and the calculated chi square turn out statistically significant, three parameter model is declared inadequate and the effects of epistasis were calculated using six parameter model:

$$(i) = 2BC_1 + 2BC_2 - 4F_2$$
$$SE^2_{(i)} = 4SE^2_{BC1} + 4SE^2_{BC2} + 16SE^2_{F2}$$
$$(j) = 2BC_1 - P_1 - 2BC_2 + P_2$$
$$SE^2_{(j)} = 4SE^2_{BC1} + SE^2_{P1} + 4SE^2_{BC2} + SE^2_{P1}$$
$$(l) = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2$$
$$SE^2_{(l)} = SE^2_{P1} + SE^2_{P2} + 4SE^2_{F1} + 16SE^2_{F2} + 16SE^2_{BC1} + 16SE^2_{BC2};$$

where (i) represents additive/additive, (j) additive/dominance and (l) dominance/ dominance effects.

Broad sense heritability was calculated by Mather & Jinks (1982):

$$h^2 = \frac{VF2 - (VP1 + VP2 + VF1)/3}{VF2}$$

with V representing corresponding variances.

Results

The mean values of yield per plant, fruit weight and number of fruits per flower branch for six basic generations of three biparental tomato crosses, together with the corresponding coefficients of variation, are listed in Table 1. Among the parents, the highest yield on the first three flower branches was noted for line KGZ (1528.6 g) and the lowest for the line SP-109 (730.5 g). Significant yield increase in comparison to parental genotypes was registered for all generations obtained after crossing. The highest yield increase was observed for F_1 generation, with the best performance of cross combination DAT × SP-109 (2090.5 g). Among the F_2 genotypes, the highest yield was measured for KGZ × SP-109 (1534.0 g) and the lowest for DAT × KGZ (1204.2 g). Comparing genotypes of backcross generations, the highest yield was noted for DAT × SP-109 BC_1 (1800.8 g) and the lowest for DAT × KGZ BC_2 (1010.0 g). Coefficient of yield variation ranged from 3.8 (KGZ) to 7.0% (DAT) for parents. As expected, F_1 was the most uniform generation, with an average coefficient of yield variation of 3.7, whereas the greatest variability was registered for F_2 generation (14%). For backcross generations, coefficient of yield variability ranged from 0.9 (DAT × SP-109 BC_2) to 19.2 (KGZ × SP-109 BC_1). (Table 1).

Heterosis values for yield varied in wide range, from 39.7 (DAT × KGZ) to 93.6% (DAT × SP-109); whereas values concerning broad sense heritability were fairly high for all three studied cross combinations and ranged from 87.5 for DAT × KGZ to 93.3% for DAT × SP-109 (Table 2).

According to individual scaling and joint chi square tests, three parameter additive/dominance model was adequate for fruit yield of DAT × SP-109 cross combination only, confirming significant additive and dominance gene effects. The estimated values of additive genes were higher than the values of dominant genes, indicating additive as decisive type of gene action. In the remaining two cases, additive/dominance model failed; therefore, six parameter model was used for estimation of gene effects. For DAT × KGZ and KGZ × SP-109 cross combinations, individual scaling and joint chi square tests confirmed the effect of digenic non-allelic interactions. For DAT × KGZ cross combination, the effects of both dominant and additive genes were significant. The estimated dominance effect was higher than additive. Additive/ additive, additive/ dominance and dominance/ dominance gene effects were noted. The applied model confirmed duplicate epistasis; the estimated value of dominance/ dominance interaction was characterized by opposite sign comparing to the value of the dominance effect. Significant additive and dominance effects, additive/additive and dominance/ dominance gene interactions, as well as duplicate type of epistasis were confirmed for KGZ × SP-109 cross combination (Table 2).

Among parents, the heaviest fruits (145.7 g) with the lowest coefficient of variation (9.5%) were measured for KGZ. Line SP-109 was characterized by the lightest fruits (55.5 g) with coefficient of variation of 12.4% (Table 1). The estimated heterosis values for fruit weight of cross combinations DAT × KGZ and DAT × SP-109 were low (8.9 and 13.8%, respectively), whereas KGZ × SP-109 exhibited negative heterotic effect. Broad sense heritability varied between 71.7 for DAT × KGZ to 90.9% for DAT × SP-109 (Table 3).

As well as for yield, the adequacy of three parameter model was confirmed for fruit weight of DAT × SP-109 only. Fruit weight of the combination is determined by both additive and dominance gene effects, with higher values for dominant genes. For the remaining two cross combinations six parameter model was applied. In the case of DAT × KGZ, additive gene effects and additive/dominance interaction were significant. The estimated additive/dominance effects were negative and higher than the additive effects, implying additive/dominance gene interaction as predominant type of gene action. Six parameter model confirmed the significance of main and additive genetic effects, as well as additive/dominance and dominance/dominance gene interactions for KGZ × SP-109 cross combination (Table 3).

Among parents, number of fruits per flower branch ranged from 3.7 (KGZ) to 6.7 (SP-109), with coefficients of variations in the range from 8.5 for SP-109 to 14.8% for DAT (Table 1). Differences between parental lines DAT and KGZ concerning number of fruits per flower branch were insignificant; therefore, the estimation of mode of inheritance of the trait failed for cross combination DAT × KGZ (Table 4).

The estimated heterosis values for number of fruits per flower branch varied from 21.1 to 26.9% for DAT × SP-109 and KGZ × SP-109, respectively. Broad sense heritability ranged from 64.1 (KGZ × SP-109) to 89.7% (DAT × SP-109). Additive gene effects were significant for both DAT × SP-109 and KGZ × SP-109 cross combinations. Additive/dominance was the only type of non-allelic gene interaction (Table 5).

Summary of main genetic effects and mode of inheritance for yield, fruit weight and number of fruits per flower branch for three studied tomato cross combinations is given in Table 5. Higher number of epistatic effects of genes was noted for fruit weight comparing to number of fruits per flower branch. The highest number of non-allelic gene interactions was determined for yield.

Table 1. Mean values and coefficients of variation for yield per plant, fruit weight and number of fruits per flower branch in six generations of three tomato crosses.

Parents	Yield per plant (g)		Fruit weight (g)		Number of fruits per f. b.	
	Mean ± SE	CV	Mean ± SE	CV	Mean ± SE	CV
DAT	907.4 ± 36.8	7.0	95.3 ± 5.2	9.7	4.2 ± 0.4	14.8
KGZ	1528.6 ± 15.8	3.8	145.7 ± 8.0	9.5	3.7 ± 0.2	9.6
SP-109	730.5 ± 35.9	4.1	55.5 ± 4.0	12.4	6.7 ± 0.3	8.5
Generations	**Mean ± SE**	**CV**	**Mean ± SE**	**CV**	**Mean ± SE**	**CV**
DAT × KGZ						
F_1	1585.3 ± 39.6	4.3	131.2 ± 2.7	3.6	5.6 ± 0.2	7.6
F_2	1204.2 ± 123.3	17.7	103.8 ± 10.7	17.9	4.8 ± 0.5	18.6
BC_1	1188.7 ± 33.3	4.8	104.6 ± 6.0	10.0	5.6 ± 0.1	3.9
BC_2	1010.0 ± 62.7	10.7	127.4 ± 12.0	16.3	4.7 ± 0.2	8.7
DAT × SP-109						
F_1	2090.5 ± 45.6	3.8	85.3 ± 1.1	2.2	6.6 ± 0.2	5.4
F_2	1494.0 ± 112.2	13.0	70.0 ± 5.5	13.6	5.7 ± 0.9	28.9
BC_1	1800.8 ± 10.9	1.0	71.5 ± 3.0	7.2	5.6 ± 0.2	6.7
BC_2	1783.6 ± 10.0	0.9	69.6 ± 6.8	17.0	5.5 ± 0.3	11.1
KGZ × SP-109						
F_1	1654.0 ± 29.7	3.1	89.8 ± 2.5	4.9	6.6 ± 0.2	6.1
F_2	1534.0 ± 99.9	11.3	88.9 ± 11.2	21.8	5.6 ± 0.5	15.2
BC_1	1303.7 ± 14.4	19.2	75.4 ± 4.4	10.1	5.6 ± 0.1	4.3
BC_2	1078.3 ± 34.2	5.5	71.8 ± 3.2	7.8	5.7 ± 0.3	9.4
LSD 0.05	77.1		19.2		1.1	
0.01	109.8		27.3		1.5	

SE = Standard error of mean

CV = Coefficient of variation (%)

F_1, F_2 and BC_1, BC_2 = first and second filial and backcross generation, respectively

Table 2. Generation mean analysis for yield of six generations in three tomato crosses.

Crosses	DAT × KGZ		DAT × SP-109		KGZ × SP-109			
Gene effects estimated from three parameter model								
		t		t		t	$t_{0.05}$	$t_{0.01}$
(m)	1291.8**	57.03	798.0**	48.27	1125.4**	61.02	2.23	3.17
(d)	-62.2**	4.92	70.2*	4.32	399.8**	21.64	2.78	4.60
(h)	970.2**	21.44	23.6**	17.21	495.68**	14.70	2.18	3.05
H (%)	39.7		93.6		40.9			
h^2	87.5		93.3		92.3			
Individual scaling and joint chi square test								
		t		t		t	$t_{0.05}$	$t_{0.01}$
C	-641.1[ns]	1.39	8.3[ns]	0.02	568.9[ns]	1.40	2.18	3.06
A	603.7**	9.74	-115.3[ns]	1.46	-575.7[ns]	1.97	2.26	3.25
B	-51.9[ns]	0.84	-295.7[ns]	1.26	-228.4*	2.99	2.26	3.25
chi square	150.1**		6.6[ns]		14.9**			
Epistasis effects estimated from six parameter model								
		t				t	$t_{0.05}$	$t_{0.01}$
(m)	2587.0[ns]	0.06			2501.6**	5.05	2.23	3.17
(d)	-313.3**	12.12			399.1**	21.39	2.78	4.60
(h)	3807.0**	4.21			-3023.0*	2.55	2.18	3.05
(i)	1191.5*	2.66			-1371.9*	2.77	2.45	3.71
(j)	658.7**	11.11			-347.3[ns]	1.18	2.31	3.35
(l)	-1744.0**	3.77			2176.3**	3.06	2.18	3.06

H = Heterosis value

h^2 = Broad sense heritability

t, $t_{0.05}$, $t_{0.01}$ = t-distribution table values, estimated t values at the 0.05 and 0.01 levels of probability, respectively

ns, *, ** = Insignificant, significant at the 0.05 and 0.01 levels of probability, respectively

Discussion

Yield per plant is one of the most important tomato traits, especially in genotypes intended for processing. Yield, as well as yield components, is determined by numerous genes, with specific interactions that make breeding for yield increase more difficult. Both additive and dominance gene effects on yield have been confirmed in this study, with prevalence of dominance gene action, which is in accordance to the results reported by Chandrasekhar & Rao (1989). On the contrary,

according to Christakis & Fasoulas (2001) and Salem *et al.*, (2009) additive genetic variation predominates. The prevailing type of non-allelic gene interactions was dominance/dominance, similar to the results of Singh & Singh (1985), who reported additive/dominance and dominance/dominance gene interactions as more important than additive/additive for yield inheritance in tomato. However, duplicate epistasis has been confirmed in our study in both cross combinations with significant dominance and dominance/dominance gene effects, implying the stability of this type of epistasis in tomato yield

inheritance. The phenomenon of duplicate epistasis is unfavorable from the breeder's point of view because of its decreasing effect on the analyzed trait (Zdravković *et al.*, 2000). Duplicate epistasis in yield inheritance has been found in the study involving three tomato hybrid combinations and

performed by Dhaliwal & Nandpuri (1988). Furthermore, the results of the trials including 21 (Khalf-Allah & Kassem, 1985) and 2 cross combinations (Khattra *et al.*, 1990) confirmed significant additive, dominance and epistatic effects in tomato yield inheritance.

Table 3. Generation mean analysis for fruit weight of six generations in three tomato crosses.

Crosses	DAT × KGZ		DAT × SP-109		KGZ × SP-109		$t_{0.05}$	$t_{0.01}$
Gene effects estimated from three parameter model								
		t		t		t	$t_{0.05}$	$t_{0.01}$
(m)	109.9^{**}	26.67	61.0^{**}	44.14	82.8^{**}	23.89	2.23	3.17
(d)	14.1^{*}	3.39	8.7^{**}	6.32	26.7^{ns}	1.89	2.78	4.60
(h)	18.9^{**}	3.64	18.4^{**}	7.33	3.5^{ns}	0.74	2.18	3.05
H (%)	8.9		13.8		-10.7			
H^2	71.7		90.9		77.4			
Individual scaling and joint chi square test								
		t		t		t	$t_{0.05}$	$t_{0.01}$
C	-56.1^{ns}	-1.73	-4.4^{ns}	-0.15	-20.5^{ns}	-1.58	2.18	3.06
A	18.0^{**}	4.28	-9.1^{ns}	-1.53	-79.6^{**}	7.57	2.26	3.25
B	-20.1^{**}	4.51	7.1^{ns}	0.79	11.5^{ns}	1.71	2.26	3.25
chi square	25.2^{**}		3.1^{ns}		49.4^{**}			
Epistasis effects estimated from six parameter model								
		t		t		t	$t_{0.05}$	$t_{0.01}$
(m)	71.7^{ns}	1.41			161.0^{**}	3.48	2.23	3.17
(d)	25.2^{**}	5.31			45.1^{**}	10.18	2.78	4.60
(h)	68.8^{ns}	0.58			-218.0^{ns}	0.26	2.18	3.05
(i)	48.8^{ns}	0.96			-60.4^{ns}	1.31	2.45	3.71
(j)	-96.0^{**}	3.36			-83.0^{**}	5.91	2.31	3.35
(l)	-9.3^{ns}	0.13			146.8^{*}	2.89	2.18	3.05

H = Heterosis value
h^2 = Broad sense heritability
t, $t_{0.05}$, $t_{0.01}$ = t-distribution table values, estimated t values at the 0.05 and 0.01 levels of probability, respectively
ns, *, ** = Insignificant, significant at the 0.05 and 0.01 levels of probability, respectively

Table 4. Generation mean analysis for number of fruits per flower branch of six generations in three tomato crosses.

Crosses	DAT × KGZ		DAT × SP-109		KGZ × SP-109		$t_{0.05}$	$t_{0.01}$
Gene effects estimated from three parameter model								
		t		t		t	$t_{0.05}$	$t_{0.01}$
(m)			5.3^{**}	25.44	5.1^{**}	28.42	2.23	3.17
(d)			-0.9^{ns}	2.64	-1.1^{ns}	2.76	2.78	4.60
(h)			1.2^{ns}	1.67	1.7^{ns}	2.00	2.18	3.05
H (%)			21.1		26.9			
H^2			89.7		64.1			
Individual scaling and joint chi square test								
		t		t		t	$t_{0.05}$	$t_{0.01}$
C			-1.3^{ns}	-0.95	-1.2^{ns}	0.41	2.18	3.06
A			0.4^{ns}	0.44	0.9^{ns}	2.14	2.26	3.25
B			-2.3^{*}	-2.85	-1.9^{*}	2.57	2.26	3.25
chi square			9.0^{*}		13.8^{**}			
Epistasis effects estimated from six parameter model								
		t		t		t	$t_{0.05}$	$t_{0.01}$
(m)			6.0^{ns}	1.54	5.0^{*}	2.39	2.23	3.17
(d)			-1.25^{**}	5.12	-1.5^{**}	7.70	2.78	4.60
(h)			-1.9^{ns}	0.24	0.8^{ns}	0.17	2.18	3.05
(i)			-0.6^{ns}	0.15	1.2^{ns}	0.09	2.45	3.71
(j)			2.7^{*}	2.80	2.8^{**}	3.57	2.31	3.35
(l)			2.5^{ns}	0.59	0.8^{ns}	0.31	2.18	3.05

H = Heterosis value
h^2 = Broad sense heritability
t, $t_{0.05}$, $t_{0.01}$ = t-distribution table values, estimated t values at the 0.05 and 0.01 levels of probability, respectively
ns, *, ** = Insignificant, significant at the 0.05 and 0.01 levels of probability, respectively

Table 5. Summary of main genetic effects and mode of inheritance for yield, fruit weight and number of fruits per flower branch in three tomato crosses.

Crosses	Yield									Fruit weight									Number of fruits per f. b.								
	3 p. m.			6 p. m.						3 p. m.			6 p. m.						3 p. m.			6 p. m.					
	m	d	h	m	d	h	i	j	l	m	d	h	m	d	h	i	j	l	m	d	h	m	d	h	i	j	l
DAT×KGZ				*	*	*	*	*					*			*											
DAT×SP-109	*	*	*							*	*	*												*		*	
KGZ×SP-109				*	*	*	*		*				*	*		*	*		*	*				*			

3 p. m. = Three parameter model
6 p. m. = Six parameter model
* = Significant at the 0.05 level of probability

Additive gene effects played decisive role in fruit weight inheritance for all three studied tomato cross combinations, however, both additive and dominance gene effects were noted in the case of DAT × SP-109, with dominance effects being more significant. Mean generation analysis performed by Conti *et al.,* (1984) confirmed the significance of additive and dominance gene effects in tomato fruit weight inheritance, with the prevalence of estimated additive effects. Significant action of dominant genes in tomato fruit weight inheritance has been reported by Singh *et al.,* (1989).

Non-allelic gene interactions that have been found for tomato fruit weight inheritance in our study are in accordance to the results of Singh & Singh (1985) and Singh *et al.,* (1989). Similarly, the extended digenic model performed on three tomato crosses (Dhaliwal & Nandpuri 1988) confirmed epistasis in two cases, whereas three parameter additive/dominance model was adequate for only one cross combination (Cold Set x Punjab). In our study, the most important effects were additive/dominance and dominance/dominance. In the research of Singh & Singh (1985), the significant additive/additive epistatic effects have been confirmed in only one out of two tomato growing seasons, implying strong environmental impact on the expression of the trait. Therefore, there is a probability for additive/additive epistatic effect occurrence in our material if analyzed in different environmental conditions. Duplicate epistatis noted for KGZ × SP-109 cross combination diminished the effect of dominant genes and therefore decreases the expression of the analyzed trait, which is unfavorable for breeding for fruit weight increase. Vice versa, there is a probability that crossing different parental lines would lead to complementary epistasis that would increase fruit weight (Causse *et al.,* 2007).

Additive gene effects and additive/ dominance epistasis that have been confirmed for number of fruits per flower branch of DAT × SP-109 and KGZ × SP-109 cross combinations are in accordance to the results of Singh & Singh (1985), Dhalliwal & Nandpuri (1988) and Zdravković *et al.,* (1998). According to Hidayatuulah *et al.,* (2008), number of fruits per flower branch is the most important yield component in tomato.

Conclusions

The selection of high-yielding tomato genotypes is complicated by often occurrence of duplicate epistasis. Higher number of epistatic gene effects estimated for tomato fruit weight comparing to number of fruits per flower branch, duplicate type of epistasis confirmed for fruit weight, as well as additive gene effects and stable additive/dominance epistatic effects noted for number of fruits per flower branch, imply number of fruits per flower branch increase as the most efficient strategy for increasing tomato yielding ability. However, fruit weight has to meet the standards proposed by growers and market.

References

Abreu, F.B., D.J.H. Da Silva, C.D. Cruz and E.S.G. Mizubuti. 2008. Inheritance of resistance to *Phytophthora infestans* (Peronosporales, Pythiaceae) in a new source of resistance in tomato (*Solanum* sp., (formerly *Lycopersicon* sp.), Solanales, Solanaceae. *Genet. Mol. Biol.*, 31: 493-497.

Bhatt, R.P., B.R. Biswas and N. Kumar. 2001. Heterosis, combining ability and genetics for vitamin C, total soluble solids and yield in tomato (*Lycopersicon esculentum*) at 1700 m altitude. *J. Agric. Sci.*, 137: 71-75.

Causse, M., J. Chaib, L. Lecomte, M. Buret and F. Hospital. 2007. Both additivity and epistasis control the genetic variation for fruit quality traits in tomato. *Theor. Appl. Genet.*, 115: 429-442.

Chandrasekhar, P. and M.P. Rao. 1989. Studies on combining ability of certain characters in tomato. *South India Hortic.*, 37: 10-12.

Christakis, P.A. and A.C. Fasoulas. 2001. The recovery of recombinant inbreds outyielding the hybrid in tomato. *J. Agric. Sci.*, 137: 179-183.

Conti, S., M. Candilo and P. Franssoldati. 1984. Analysis of fruit uniformity in two processing tomato. *Genet. Agrar.*, 38: 327-328.

Dhaliwal, M.S. and K.S. Nandpuri. 1988. Genetics of yield and its components in tomato. *Ann. Biol.*, 4: 75-80.

Foolad, M. R. 1996. Genetic analysis of salt tolerance during vegetative growth in tomato, *Lycopersicon esculentum* Mill. *Plant Breeding*, 115: 245-250.

Foolad, M.R. and G.Y. Lin. 2001. Genetic analysis of cold tolerance during vegetative growth in tomato, *Lycopersicon esculentum* Mill. *Euphytica*, 122: 105-111.

Hidayatullh, S.A. Jatoi, A. Ghafoor and T. Mahmood. 2008. Path coefficient of yield component in tomato (*Lycpersicon esculentum* Mill). *Pak. J. Bot.*, 40(2): 627-635.

Hussain, M., F.M. Azhar and A.A. Khan. 2009. Genetic inheritance and correlations of sane morphological and yield contributing traits in upland cotton. *Pak. J. Bot.*, 41(6): 2975-2986.

Kaşkavalci, G. 2007. Effects of soil solarization and organic amendment treatments for controlling *Meloidogyne incognita* in tomato cultivars in Western Anatolia. *Turk. J. Agric. For.*, 31: 159-167.

Khalf-Allah, A.M. and E. Kassem. 1985. A diallel analysis of quantitative characters in tomato. *Egypt. J. Genet. Cytol.*, 14: 251-257.

Khattra, A.S., K.S. Nandpuri and I.C. Thakur. 1990. Inheritance of some economic characters in tomato. *Indian J. Hort.*, 47: 210-215.

Koutsika-Sotiriou, M.S., E.A. Traka-Mavrona and G. L. Evgenidis. 2008. Assessment of tomato source breeding material through mating designs. *J. Agric. Sci.*, 146: 301-310.

Kozik, E., M.R .Foolad and R.A. Jones. 1991. Genetic analysis of resistance to *Phytophthora* root rot in tomato (*Lycopersicon esculentim* Mill.) *Plant Breeding*, 106: 27-32.

Mather, K. and I.L. Jinks. 1982. Biometrical Genetics. Third Edition. Champan and Hall, London.

Resende, J.T.V., W.R .Maluf, C.M. Das Graças, D.L. Nelson and M.V. Faria. 2002. Inheritance of acylsugar contents in tomatoes derived from an interspecific cross with the wild tomato *Lycopersicon pennellii* and their effect on spider mite repellence. *Genet. Mol. Res.*, 1: 106-116.

Saleem, M.Y., M. Asghar., M.A. Haq, T. Rafique, A. Kamran and A.A. Khan. 2009. Genetic analysis to indentify suitable parents for hybrid seed production in tomato (*Lycpersicon esculentim* Mill). *Pak. J. Bot.*, 41(3): 1107-1116.

Scott, S.J. and R.A. Jones. 1990. Generation means analysis of right-censored response time traits: low temperature seed germination in tomato. *Euphytica*, 48: 239-244.

Singh, R.P. and S. Singh. 1985. Detection and estimation of components of genetic variation for some metric traits in tomato (*Lycopersicon esculentum* Mill.). *Theor. Appl. Genet.*, 70: 80-84.

Singh, U.P., I. Tanki and R.K. Singh. 1989. Studies on order effect and epistatic components for yield in double-cross hybrids of tomato. *Haryana J. Hort. Sci.*, 18: 265-271.

Yoltas, T., T. Bas, N. Topcu, I. Vural, O. Serdaroglu and A.C. Aydin. 2003. The determination of agronomical and technological properties of processing tomato varieties to be introduced to the production in Marmara region (Turkey) and reactions to infections by the agents of diseases. *Acta Hort.*, 613: 345-350.

Zdravković, J., Ž. Marković, M. Kraljević-Balalić, M. Zdravković and T. Sretenović-Rajičić. 1998. Gene effects on number of fruits per flower branch in tomato. *Acta Hort.*, 487: 361-366.

Zdravković, J., Ž.Marković, M.Mijatović, M. Zečević and M. Zdravković. 2000. Epistatic gene effects on the yield of the parents of F_1, F_2, BC_1 and BC_2 progeny. *Acta Physiol. Plant.*, 22: 261-265.