

## GENE EFFECTS INVOLVED IN THE MANIFESTATION OF GROWTH CHARACTERISTICS AND RESISTANCE TO THERMAL STRESS

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### Abstract

*Data are presented on the response of tomato plant growth characters in hybrid combinations  $F_1$ ,  $F_2$ ,  $BC_1$ ,  $BC_2$  and parental forms to stress temperatures (40, 42, 10°C). The reaction of seedlings to high temperatures (40, 42°C) and low positive (10°C) was differentiated depending on the combination, character and temperature level. The calculation of the degree of dominance ( $h_p$ ) of the growth characters (radicle, stem, whole seedling) of tomatoes demonstrated the significant influence of positive (+), negative (-) dominance factors on their phenotype. By researching the genetic effects involved in the phenotype and the inheritance of the radicle and stem length character, it was found that for each combination, in the control (25°C) and thermal stress (40°C, 42° and 10°C) variants, effects with positive values (increasing) and, with negative values (which decrease) the character. The combinations under study showed duplicated epistasis, which reveals the need for long individual selections in order to obtain tomato genotypes resistant to high temperatures.*

**Key words:** tomatoes, varieties, hybrids, gene effects.

### INTRODUCTION

Temperature is one of the main environmental factors influencing plant growth, development and productivity. Global average temperatures are continuously increasing, and this change has negative effects on crop productivity. Thermal stress (TS) is a major abiotic factor that globally causes fruit decline in many agricultural crops, including tomatoes, thus presenting a problem for food security (Tripathi et al., 2016; Bisbis et al., 2018). The challenges generated by climate change will thus require the implementation of new strategies to adapt the newly created varieties in a timely manner to local conditions to reduce the effect of stress temperatures (Porter et al., 2014; Bisbis et al., 2018).

TS has negative effects on physiological processes in the plant (disruption of photosynthesis, increase in respiration), which leads to decrease in plant productivity (Prasad et al., 2017). Another effect of TS is the negative impact on the root system, which provides support for the plant, nutrient absorption and transport to other plant organs (Valdés-López et al., 2016). These phenomena lead to poor root

development, disruption of growth stages, pollination and flowering (Sehgal et al., 2017). In many species, including tomato, in both cool and hot seasons, productivity decreases as a result of the reduced rate of fruit set. In general, the reproductive period is more sensitive to heat stress than the vegetative period (Mittler & Blumwald, 2010; Ruan et al., 2010; Zinn et al., 2010). Increasing the temperature even by 2-4°C above the optimal level of 25-30°C/20°C - day/night (Camejo et al., 2005), can strongly affect the reproductive organs, especially the viability of the pollen and the development of the gametes (Ayenan et al., 2019; Raja et al., 2019), pollination capacity, causing flower drop and fruit firmness reduction (Firon et al., 2006; Ozores-Hampton et al., 2012). It was found that resistant tomato genotypes have the ability to form a much higher number of fruits than sensitive ones under stress conditions (Comlekcioglu et al., 2010).

The environmental conditions of recent years, presenting a major risk for agricultural crops, require the creation of tomato genotypes with complex resistance to extreme environmental factors (Hazra et al., 2007; Mihnea, 2022).

The quantitative characters of living organisms, including plants, are influenced by several genes, with the participation of additive gene actions and epistatic interactions (Ardiarini et al., 2022), the study of the number of genes and gene actions being necessary for the efficiency of breeding programs (Samak et al., 2011). Characters, for which the proportion of duplicated epistasis with a minus sign is significant, can be improved only in advanced generations, and positive epistatic interactions indicate the existence of complementary gene actions and the need for intensive selection from early to advanced generations (Jayaramachandran et al., 2010).

Higher-order gene interactions frequently influence the genetic bases of complex characters and contribute to their evolution (Dwivedi et al., 2024). The purpose of the research consisted in establishing the influence of high temperatures on some tomato varieties, lines of perspective and the particularities of actions, gene interactions involved in the response reaction of the growth organs at the early ontogenetic stage.

## MATERIALS AND METHODS

Dolgonosic, Mary Gratefully, Rufina, Flacara and L 10B, hybrid combinations F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub>, BC<sub>2</sub> were used as study material. Varieties and hybrids were tested at 4 temperature levels: optimal - 25°C and thermal stress: 41, 43 and 10°C. The assessment of the resistance of the tomato samples to high and low temperatures was carried out according to the growth capacity of the embryonic radicle, stem and intact seedling for 7 days after maintaining them on day 4 at temperatures of 42° and 43°C within 6 hours, and at the temperature of 10°C - 21 days (Mihnea, 2016). Seedlings kept constant at 25°C served as a control.

The degree of dominance was established based on the formula proposed by Brübeiker (1966):  $h_p = F_1 - 0.5 (P_1 + P_2) / H_p - 0.5 (P_1 + P_2)$ , where F<sub>1</sub> - the average value of the character in the F<sub>1</sub> generation;

P<sub>1</sub>, P<sub>2</sub> - the average value of the character in the parental forms;

H<sub>p</sub> - the average value of the character in the best parental form.

The analysis of gene effects (actions *a* - *additive*, *d* - *dominant*, epistatic interactions: *aa*, *ad*, *dd*) was performed based on the Gamble model (1962). The obtained data were statistically processed in the STATISTICA 7 software package.

## RESULTS AND DISCUSSIONS

In the hybrid combinations F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub>, BC<sub>2</sub>, it was found that the reaction of the seedlings to high (40, 42°C) and low positive temperature (10°C) (Figure 1) was differentiated both in the parental forms and in the hybrid combinations and they recorded a inhibition of the radicle length within the limits of 8.1-51.5% in the parental forms at a temperature of 40°C; 13.6-42.9% at 42°C and at 10°C - 87.5-98.9%. A 2.2% stimulation was recorded in the Mary Gratefully variety at the temperature of 42°C. Decreased growth was attested to L 10 B which was 40.9 and 42.9% at the temperature of 40 and 42°C, respectively.

In the case of hybrid combinations, the decrease in radicle length (R.I.) compared to the control varied in the F<sub>1</sub> generation within the limits of 4.8-31.5% at 40°C, 18.1-55.9% - 42°C, 87.5-94.3% - 10°C; F<sub>2</sub> - 5.0-26.7% at 40°C, 11.8-27.2% - 42°C, 84.1-92.5% - 10°C; BC<sub>1</sub> - 12.2-43.6 - 40°C, 23.2-29.5% - 42°C, 88.8-90.0% - 10°C; BC<sub>2</sub> - 14.2-31.3 - 40°C, 2.3-42.2% - 42°C, 81.1-90.9% - 10°C. Mild stimulation (2.2%) was recorded in Mary Gratefully at 42°C. The temperature of 40°C most strongly influenced the hybrids F<sub>1</sub> L 10B x Rufina (31.5%), BC<sub>1</sub> (F<sub>1</sub> Dolgonosic x Mary Gratefully) x Dolgonosic (43.6%), BC<sub>2</sub> (F<sub>1</sub> Dolgonosic x Mary Gratefully) x Mary Gratefully (31.3%). A weaker influence at the temperature of 42°C was recorded in F<sub>1</sub> Rufina x Flacara (18.1%), F<sub>2</sub> Dolgonosic x Mary Gratefully (11.8%), BC<sub>2</sub> (F<sub>1</sub> L 10B x Rufina) x Rufina (12.3%) and BC<sub>2</sub> (F<sub>1</sub> Rufina x Flacara x Flacara) (2.3%).

In the case of stem length (St.I.), a wide range of variability was also recorded in response to stress temperatures. The inhibition of the stem in relation to the control was reported within the limits of 8.4-46.9% at 40°C, 4.9-55.5% - 42°C, 76.3-97.0% - 10°C. Stimulation was attested in 4 cases at 40°C and 3 cases at 42°C. As with the radicle, genotypes were most strongly influenced by 10°C heat stress. Greater than

70.0% inhibition was noted in all genotypes (Figure 1).

Regarding the *length of the seedling* (Sd.l.), its reduction in relation to the control varied between 3.0-51.5% at the temperature 40°C, 2.9-47.0% - 42°C, 80.2-98.5% - 10°C. At the same time, the temperature of 40°C most

strongly influenced the genotypes Flacara (51.5%), L 10 B (43.0%), BC<sub>1</sub> (F<sub>1</sub> Dolgonosic x Mary Gratefully) x Dolgonosic (43.9%), and at temperature of 42°C, inhibition was greater than 40.0% in F<sub>1</sub> Dolgonosic x Mary Gratefully, L 10 B, F<sub>1</sub> L 10B x Rufina, (Figure 1).

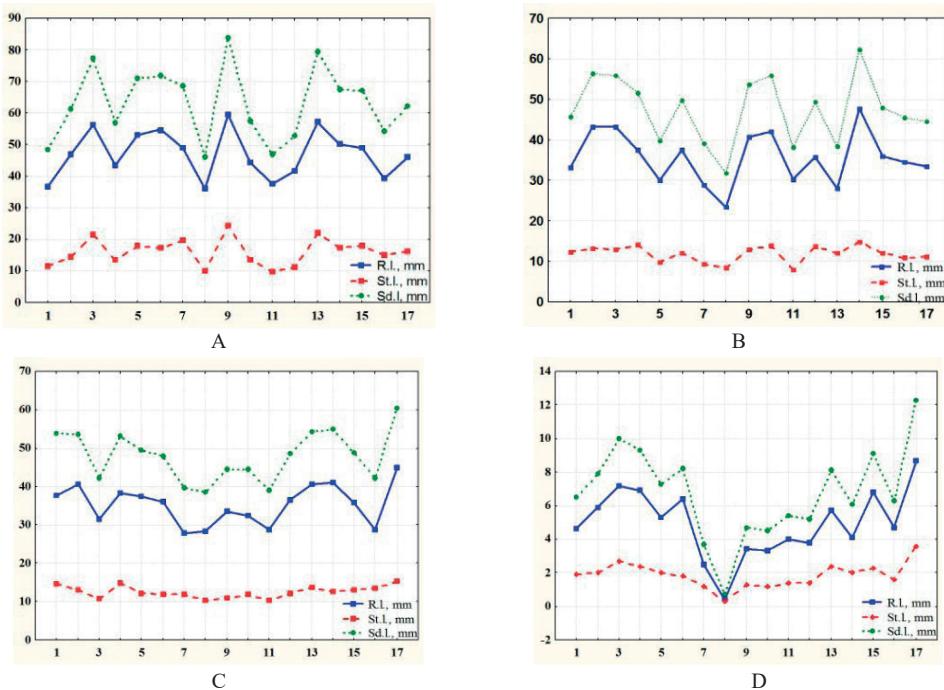


Fig. 1. The influence of optimal temperature:  
A - 25°C and thermal stress B - 40°C, C - 42°C, D - 10°C on growth characteristics in tomato

1– Dolgonosic, 2 – Mary Gratefully, 3 – F<sub>1</sub> Dolgonosic x Mary Gratefully, 4 – F<sub>2</sub> Dolgonosic x Mary Gratefully, 5 – BC<sub>1</sub> (F<sub>1</sub> Dolgonosic x Mary Gratefully) x Dolgonosic, 6 – BC<sub>2</sub>(F<sub>1</sub> Dolgonosic x Mary Gratefully) x Mary Gratefully, 7 – L 10 B, 8 – Rufina, 9 – F<sub>1</sub>L 10B x Rufina, 10 – F<sub>2</sub>L 10B x Rufina, 11 – BC<sub>1</sub>(F<sub>1</sub> L 10B x Rufina) x L 10B, 12 – BC<sub>2</sub>(F<sub>1</sub> L 10B x Rufina) x Rufina, 13 – Flacara, 14 – F<sub>1</sub>Rufina x Flacara, 15 F<sub>2</sub> Rufina x Flacara , 16 – BC<sub>1</sub> (F<sub>1</sub> Rufina x Flacara) x Rufina, 17 – BC<sub>2</sub> (F<sub>1</sub> Rufina x Flacara) x Flacara

Based on the evaluation of tomato genotypes according to three test parameters, it can be concluded that the varieties Dolgonosic, Mary Gratefully, F<sub>2</sub> Dolgonosic x Mary Gratefully, BC<sub>1</sub> (F<sub>1</sub> L 10B x Rufina) x L 10B, BC<sub>2</sub> (F<sub>1</sub> L 10B x Rufina) x Rufina, F<sub>1</sub> Rufina x Flacara, showed complex resistance to high temperatures, and the variety Mary Gratefully and the combination FDolgonosic x Mary Gratefully they are highly resistant, showing interest in tomato breeding.

In order to establish the inheritance pattern of tomato resistance to the mentioned stress

temperatures, the degree of dominance was estimated. It was found that according to the level (high/low) and orientation (+/-) the parameter was different and depended on the combination, character and temperature level. In optimal conditions, F<sub>1</sub> hybrids showed positive overdominance, intermediate dominance of radicle, stem and seedling length characters (Table 1).

Stress temperature also influenced the degree of dominance ( $h_p$ ) of growth characters in terms of degree of expression as well as orientation.

Table 1. Dominance degree of tomato seedling growth characters

The character	F <sub>1</sub> Dolgonosic x Mary Gratefully	F <sub>1</sub> L 10B x Rufina	F <sub>1</sub> Rufina x Flacāra
25°C			
The length of the radicle	+2.8	+2.64	+0.33
The length of the stem	+6.0	+1.98	+0.23
Seedling length	+3.49	+2.37	+0.29
40°C			
The length of the radicle	+1.0	+5.2	+9.61
The length of the stem	+0.5	+8.4	+2.61
Seedling length	+0.93	+4.92	+8.03
42°C			
The length of the radicle	-5.13	+27.5	+1.06
The length of the stem	-3.44	+0.00	+1.00
Seedling length	-116.0	+8.00	+2.16
10°C			
The length of the radicle	+2.86	+1.82	+0.41
The length of the stem	+8.00	+1.20	+0.64
Seedling length	+4.00	+1.67	+0.46

Notes:  $-0.0 < h_p < -1$  – negative overdominance;  $-1 < h_p < -0.5$  – negative dominance;  $-0.5 < h_p < +0.5$  – intermediate dominance;  $+0.5 < h_p < +1$  – positive dominance;  $+1 < h_p < +0.0$  – positive overdominance [Bryubeyker, 1966].

For example, in the control variant  $h_p$  for the *radicle length* varied within the limits of  $+0.33...+2.80$ , and in the variants with temperatures of 40, 42 and 10°C – within the limits of  $+1.0...+9.61$ ,  $-5.13...+27.5$  and  $+0.41...+2.86$ , i.e. between the overdominance of the parent with the highest radicle growth values to the overdominance to the parent with the lowest values, which denotes the existence of specific interactions of the alleles of the two genomes, function of character, combination and temperature level. In the control variant, the degree of dominance of the *stem length* character varied within  $+0.23...+6.0$ . In the variants with temperature 40 and 10°C, the hybrid combinations differed only based on the values of the degree of dominance, which were  $+0.5...+8.4$  and  $+0.64...+8.0$ . At the temperature of 42°C, the F<sub>1</sub> Dolgonosic x Mary Gratefully combination recorded negative overdominance (-3.44), the F<sub>1</sub> Rufina x Flacara combination (+1.00) – positive dominance, and the F<sub>1</sub> L 10B x Rufina ( $h_p=0, 00$ ).

Regarding *seedling length*, in the control variant the degree of dominance varied within the limits of  $+0.29...+3.49$ , and in the variant with stress temperatures:  $+0.93...+8.03$ ;  $-116.0...+8.00$  and  $+0.46...4.00$ , respectively, at temperatures of 40, 42 and 10°C (Table 1), which once again

demonstrates the influence of stress temperatures on the radicle, stem phenotype and tomato seedlings.

By researching the genetic effects involved in the phenotype and the inheritance of the radicle and stem length character, it was found that for each combination, in the control (25°C) and thermal stress (40°C, 42° and 10°C) variants, effects with positive values and negative values were manifested, that increase or decrease, respectively, the character.

Positive additive actions (*a*) with statistical support for which, compared to other effects, are chosen a lot in the selection process, were attested in the control version only for the combination Dolgonosic x Mary Gratefully for the length of the stem (0.61), and for  $t = 40^\circ\text{C}$  – for the combination Rufina x Flacara for the length of the radicle (1.36) and at 42°C they recorded for the combination – Dolgonosic x Mary Gratefully for both variants.

It should be noted that in the variant with a temperature of 10°C the combination Dolgonosic x Mary Gratefully recorded positive values for the stem length (Table 2).

Epistases *ad*, always contributed to the growth of the radicle and the stem in optimal conditions and to the thermal stress of 40°, 42°C.

Table 2. Gene actions and interactions, involved in the inheritance of tomato growth characters under optimal conditions and thermal stress

	Combination	<i>m F<sub>2</sub></i>	<i>a</i>	<i>d</i>	<i>aa</i>	<i>ad</i>	<i>dd</i>
		25°C					
		The length of the radicle					
1	Dolgonosic x Mary Gratefully	43,49±1,70*	-1,78±2,14	55,98±1,84*	41,78±1,83*	40,36±2,04*	-60,57±1,99
2	L 10B x Rufina	44,19±1,79*	-4,94±1,80*	-3,51±1,82*	-20,0±1,79*	38,02±1,81*	68,06±1,86
3	Rufina x Flacara	49,04±2,04*	-7,38±2,21*	-	-26,52±2,09*	39,44±2,14	50,78±2,14
		The length of the stem					
1	Dolgonosic x Mary Gratefully	13,35±0,80*	0,61±0,72	25,20±0,79*	16,69±0,78	13,57±0,71	-17,90±0,78
2	L 10B x Rufina	13,37±0,83*	-1,65±0,91*	-2,91±0,90*	-12,51±0,85	13,30±0,93	50,51±0,97
3	Rufina x Flacara	18,10±1,46*	-1,60±1,26	-9,69±1,41*	-10,80±1,41	14,52±1,21	15,93±1,34
		40°C					
		The length of the radicle					
1	Dolgonosic x Mary Gratefully	37,53±1,78*	-7,42±1,55*	-9,70±1,74*	-14,87±1,72	30,85±1,56	42,86±1,69
2	L 10B x Rufina	41,65±1,76*	-5,21±1,96*	-	-35,03±1,82	20,88±1,87	36,94±1,87
3	Rufina x Flacara	36,09±1,72*	1,36±1,87	17,07±1,78*	-5,75±1,76	27,22±1,82	16,25±1,85
		The length of the stem					
1	Dolgonosic x Mary Gratefully	14,23±0,70*	-2,28±0,55*	-	-12,88±0,66	10,61±0,56	20,45±0,63
2	L 10B x Rufina	13,76±0,66*	-6,0±0,75*	-7,68±0,68*	-11,81±0,68	2,87±0,71	12,33±0,70
3	Rufina x Flacara	12,01±0,58*	-0,12±0,68	2,10±0,64*	-2,86±0,61	10,09±0,70	8,46±0,69
		42°C					
		The length of the radicle					
1	Dolgonosic x Mary Gratefully	38,30±1,93*	0,55±2,10	-	-3,64±1,97	39,54±2,04	-4,84±2,03
2	L 10B x Rufina	32,32±1,78*	-7,77±1,81*	7,20±1,81*	1,88±1,79	20,57±1,81	-9,04±1,84
3	Rufina x Flacara	35,83±1,72*	-15,58±2,04*	11,50±1,83*	5,33±1,81	19,17±2,02	-2,60±1,94
		The length of the stem					
1	Dolgonosic x Mary Gratefully	14,97±0,79*	0,17±0,65	-	-11,79±0,75	14,00±0,65	12,79±0,70
2	L 10B x Rufina	11,67±0,66*	-1,78±0,52*	-1,15±0,63*	-1,86±0,63	8,44±0,56	-0,67±0,59
	Rufina x Flacara	13,01±0,64*	-1,70±0,86*	8,24±0,71*	6,35±0,70	10,21±0,83	-13,30±0,78
		10°C					
		The length of the radicle					
1	Dolgonosic x Mary Gratefully	7,07±0,53*	-1,08±0,39*	-3,17±0,49	-4,71±0,49	4,62±0,40	7,00±0,45
2	L 10B x Rufina	3,22±0,50*	-0,55±0,52	5,33±0,50	3,74±0,50	1,28±0,50	-9,86±0,51
3	Rufina x Flacara	6,97±0,65*	-4,50±0,67*	0,12±0,65	-0,92±0,65	-1,16±0,64	-10,56±0,66
		The length of the stem					
1	Dolgonosic x Mary Gratefully	2,5±0,15*	0,27±0,12*	-1,51±0,14	-2,20±0,14	2,31±0,11	3,89±0,13
2	L 10B x Rufina	1,22±0,11*	0,03±0,10	1,12±0,11	0,67±0,10	1,0±0,10	-1,49±0,10
3	Rufina x Flacara	2,35±0,18*	-2,22±0,35*	2,02±0,25	1,50±0,25	-0,69±0,34	-5,25±0,30

\*- p≤0,05.

In the case of the thermal regime 10°C at a single combination – Rufina x Flacara, *ad* effects with negative values were manifested. The most important in character control were the *dominance* effects, the *additive x additive* (*aa*) and *dominant x dominant* (*dd*) epistases.

It should be noted that in most combinations, duplicated epistasis was manifested (opposite orientation of the *d* and *dd* effects), which presents a serious impediment to the improvement process, but also reveals the need for individual, respectively, and long selections in order to obtain tomato genotypes resistant to stress temperatures.

In the Rufina x Flacara combination, complementary epistasis was recorded for radicle length at 40°C, and in Dolgonosic x Mary Gratefully – for stem length at 10°C, which offers chances of success in creating resistant genotypes in limited terms.

## CONCLUSIONS

The study of five tomato parents – Dolgonosic, Mary Gratefully, Rufina, Flacara, L 10B, and hybrid combinations F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub>, BC<sub>2</sub> in order to see the reaction of growth organs to stress temperatures of 40, 42 and 10°C demonstrated

the differential sensitivity of them which depended on the combination, the growth organ (radicle, stem, whole seedling) and the thermal level.

The degree of dominance of the parents in the F<sub>1</sub> hybrid offspring was of different intensity – from intermediate dominance to overdominance, in most cases being positive.

Different gene actions (*a, d*) and interactions (*aa, ad, dd*) oriented towards increasing (+) or decreasing (-) character were involved in the growth organ phenotype, the most important being *dd* epistases. In most cases, duplicated epistasis was manifested, which creates impediments in the improvement process, however, in the combinations Rufina x Flacara and Dolgonosic x Mary Gratefully, complementary epistasis was recorded in the variants of temperatures 40 and 10°C, which creates premises for selection in narrow terms of resistant genotypes.

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