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Variability of meiotic recombination and cytological parameters in F1 tomato hybrids under extreme environmental conditions

Aleksey Samovol[*]**, Sergey Kondratenko and Elena Mogilnaya**

National Academy of Agrarian Sciences of Ukraine, Institute of Vegetable and Melon Growing, 62478 Selektsiyne Village of Kharkiv Region, Ukraine
[*]*Corresponding author:* ovoch.iob@gmail.com

Abstract

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This paper presents the results of the impact of the environmental conditions in the three regions of the high-mountain Western Pamirs (Vanj, Khorugh and Ishkashim) located at different altitudes above sea level (2300, 2320 and 2600 meters) on the meiotic replicating and transforming functions in the interspecies of F_1 tomato hybrids, as well as on the Mendelian segregation displacement and the variability of recombination parameters for linked and unlinked maker genes. Generally, a direct coherence between the frequency of interstitial chiasm, the variability of meiotic recombination parameters and the combined conditions within the specified ecological niche have been determined, in particular: the increased radiation on the experimental site at the soil level and the reproductive organs of F_1 hybrid plants, high intensity of solar radiation in the UV, PHAR, IR spectral bands and increased temperature fluctuations during a month and a day.

Keywords: F_1 tomato hybrids; meiotic recombination; cytological parameters; climatic conditions; Western Pamirs

Introduction

It is believed that in order to control recombination and genotypic variation, apart from the wide application of the already known artificially created basic endogenous (Wu & Burgess, 2006; Dolgin, 2008; Wu et al., 2008; Naranjo, 2015) and exopathic (Khlebova, 2010; Vranis et al., 2010; Gulfishan et al., 2012; Bilgir et al., 2013; Garvin et al., 2013; Feller et al., 2015; Samovol et al., 2017) causes, it is of high importance to search for brand new integrated approaches and ways rooted in the evolutionary past.

From this point of view, the identification of possible causes that led to the "explosive" course of evolution will provide us with an opportunity to outline innovative ways and approaches as well as to determine environmental factors, which may deem to be quite effective inducers for mutations and recombination (Zhuchenko, 2010). In this regard, according to the author, of significant interest are to be considered mountain conditions that combine a wide range of factors (high fluctuations in temperature and solar UV radiation, an increased background radiation, special humidity conditions, etc.), within which the speed of mutation and recombination processes, and in particular, speciation are being accelerated.

According to the renowned evolutionist V. A. Blagoveshchensky, plant speciation occurs in those areas where nature has created extreme conditions for their existence (mountains, deserts). We find a similar statement in the published scientific works of E.N. Sinskaya: "*The intensity of the species-forming process increases where there is a wide variety of ecological niches, as happens in mountainous countries*" (Filatenko, 2010). In confirmation of the above, it is also considered that the spontaneous processes that affect the landscapes and anthropogenic loads in the high-mountain ecosystem of Pamir-Alai rather quickly form ecological elements ("primary-forming knots"), which, having entered the self-sustaining evolutionary scene, often contribute to the creation of not only ecotypes, but also brand new ecosystems (Safarov, 2017).

It is also reported that high-mountain environmental factors in the Western Pamirs significantly influence the character of differences in chromosome morphology (the magnitude of long and short arms, the total length of chromosomes of somatic cells) in plants of local wheat species populations (Muminshoyeva, 2015). Due to this, the work at the Mexican International Wheat and Maize Breeding Center was carried out mainly in mountainous areas at an altitude of 2000 m above sea level. Of particular interest are the works performed on triticale breeding in the USA (the center is located in California, Salinas). The selected conditions increased the likelihood of genetic recombination in some cases more than 100 times compared to the conditions of the greenhouse (Bernard, 1979; Badaeva et al., 2010). Within the framework of our experiments carried out in the high-mountain areas of the Western Pamirs, the natural elements of the environment had a certain dechanneling effect not only on the development of morphological characters in the F_1 tomato heterozygote, but also on the variability of their meiotic recombination and cytological parameters.

Materials and Methods

We studied the influence of extreme factors of three ecological niches of the high-mountain areas of the Western Pamirs (Vanj, Khorugh and Ishkashim) located at different altitudes above sea level (2300, 2320 and 2600 m) on the reproducing and transforming functions of maturation in F_1 interspecies tomato hybrids, as well as on the displacement of Mendelian segregation and the variability of recombination parameters within linked and unlinked maker genes. Three mutation forms were used in the testing as a maternal component (♀): two of them with four marker genes – Mo 628 (*hl* – hairless, *a* – anthocyaninless, *ful* – yellow leaves at growing point, *e* – entire), Mo 656 (*a*, *c* – potato leaf type, *m-2* – mottled-2, *d* – dwarf); and one with two of them – Mo 638 (*a*, *c* – potato leaf) (Chetelat & Rick, 2005). As a comparison, two marker-free plant varieties were also used in the study– *Maryushka* and *Slava Moldavii.* The paternal components (♂) represented distant and ancestral species and varieties of the genus of the *Lycopersicon species,* Tourn. – L. *esc*. var. *pimpinellifolium*, L. *esc*. var. *cerasiforme*, L. *cheesmanii typicus* Riley and L. *hirsutum* var. *glabratum*, as well as the AZHM 15 with a compound trusses. For the cytological evaluation, buds were taken from five F_1 plants. The buds' fixation as well as squash aceto-carmine specimen was carried out following the standard practice (Zhunchenko et al., 1980). The frequency of total,, terminal and interstitial chiasms was determined at the diplonema stage, i.e. early diakinesis. According to the measurements taken, these stages of meiosis provided for the buds' growth (2.1–2.7 mm). Each option covered 50 meiocytes under study.

Solar radiation intensity within the spectrum bands (UV, PHAR and IR) was measured through the Kozyrev phytopyranometer equipped with BS-8 and KS-19 filters (Toming & Gulyaev, 1967).

The marker genes were identified in the plants cultivated in the result of the second generation (F_2) seeding in total of 500 for each hybrid combination. Further, the digital identification results obtained and entered into the matrix were calculated according to the generally accepted method (Immer, 1930). Statistical processing of data and their reliability were determined on the basis of the Student's χ^2 and Student's t – test (Rokitskyi, 1978).

Results and Discussion

According to our observations, the extreme conditions in the selected ecological niches of the Western Pamirs have left a peculiar imprint on the growth and development of plants. Thus, the F_1 hybrid plants with *L. hirsutum* var. *glabratum* and a variety of cultivated species var. *cerasiforme* in situ of the Ukrainian vegeculture area demonstrated the variability towards the anomalous growth, while in the Pamirs ecological niches they were affected by a severe vegetative depression, which led to the "stockiness" of the bush mien to the level of determinant type and leaf microphilia.

As specified below, within the framework of our research carried out, in the ecological niches of the Western Pamirs, natural environmental conditions have had a certain influence not only on the variability of morphological characters in F_1 tomato heterozygous plants, but also on their meiotic reproducing and transforming functions, as well as on the reliable variability of meiotic recombination ratio.

Meiotic replicating function (formation of pollen fertility factors and the number of seeds in the F_1 hybrid fruits)

The research has shown that the majority of the studied interspecies hybrids handled in Khorugh had a reduced percentage of pollen fertility. This was especially observed in plants with hybrid combinations of Mo 628 / *L. hirsutum* var. *glabratum* and Maryushka / *L. esc*. var. *pimpinellifolium* – 65.5 ± 4.6 and 57.9 ± 6.3 % respectively (Figure 1). The lowest fertility was found in plants of the F_1 intraspecific hybrid (*Slava Moldavii* / AZHM 15) – up to 54.8 ± 4.8 %. It should be highlighted that in the conditions of the high-monition ecological niche of Ishkashim, the low percentage of pollen

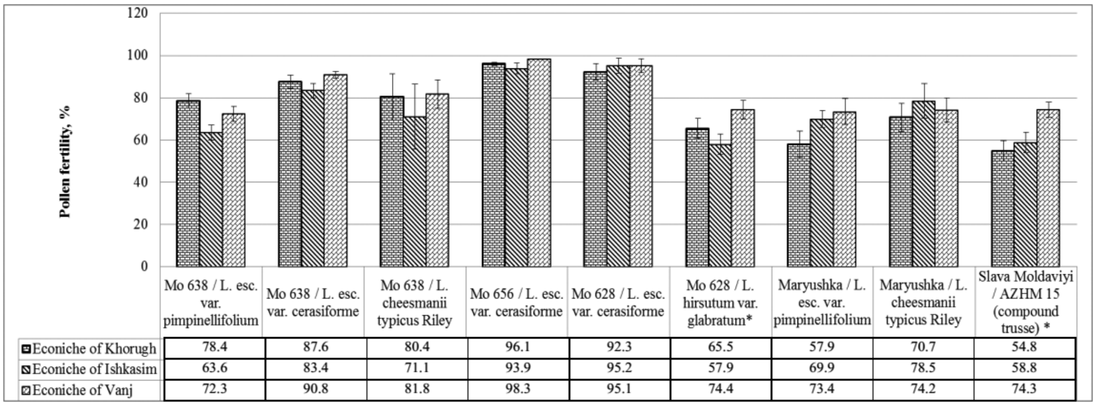


Fig. 1. Influence of extreme factors of the mountain climate of the Western Pamirs (the ecological niches of Khorugh, Ishkashim and Vanj) on pollen fertility of 8 interspecific and 1 intraspecific F_1 tomato hybrids

Note * – in comparison with the Vanj ecological niche (control variant) for the noted combinations of the Ishkashim ecological niches crossing, a statistically significant decrease in pollen fertility was revealed at the level of 2.22 and 2.51 values of the t-criterion of Student (at $p < 0.01$)

fertility remains at the level of the above-mentioned cross-combinations.

Alternatively, within the Vanj ecological niche (check option), pollen fertility in plants of the same hybrid combinations increased up to 74.4 ± 4.5; 73.4 ± 6.1 and 74.3 ± 3.6 % respectively (see Figure 1). A drop or boost in the F_1 plant fertility may occur due to natural radioactivity measured at the reproductive organ level. Thus, in the Khorugh ecological niche, its level varied from 17.8 to 21.6 mR/h., within the Ishkashim area it ranged from 17.8 to 23.0 mR/h. Meanwhile, in the Vanj ecological niche, the lower point of the accepted value decreased 12.3 mR/h. Other influencing factors shall not be excluded as well. In particular, such factors may include both a different intensity of solar radiation covering the spectrum bands observed in the ecological niches: Khorugh (UV – 0.63 cal/cm^{2}min, PAR – 19.98 cal/cm^{2}min, IR – 28.3 cal/cm^{2}min), Ishkashim (UV – 2.07 cal/cm^{2}min, PAR – 18.5 cal/cm^{2}min, IR – 19.6 cal/cm^{2}min) and Vanj (UV – 0.43 cal/cm^{2}min; PAR – 19.88 cal/cm^{2}min, IR – 37.8 cal/cm^{2}min), and temperature variability. For instance, within the period of the reproductive organs' formation as well as blossoming, the monthly positive temperature in June, July and August was as follows: in the Khorugh ecological niche: 18.9, 22.4 and 22.6°C; in the Ishkashim ecological niche: 16.7, 19.5 and 19.5°C; in the Vanj ecological niche: 19.8, 23.0 and 22.5°C respectively. Notably, the temperatures dropped to 14.4, 15.0 and 12.8°C during several days in August in the Vanj, Khorugh and Ishkashim ecological niches, and rose to 30.7, 30.2 and 26.2°C respectively.

It is deemed to be logical to believe that the degree of fruit saturation with the seeds of the hybrid plants under research should be preceded by the level of pollen fertility, however, the current situation is somewhat different. For example, in the Ishkashim and Khorugh ecological niches the plants of four hybrid cross-combinations (No. No. 1, 3, 7 and 11), despite the drop in pollen fertility in relation to the check option (the Vanj ecological niche) by 8.7–16.5 % and 1.4-19.5%, the number of seeds in the Ishkashim ecological niche increased by an average of 5.6-43.6 pcs/fruit. In addition, provided all the combinations initially used in the testing are analyzed, only ten out of eleven grown under the aforementioned Ishkashim environmental conditions have an average of 5.6 seeds per fruit to 53.6 seeds per fruit (when compared to similar hybrid combinations grown in the Khorugh ecological niche). It can be assumed that in this case, the multidirectional influence of extreme environmental factors at the meiosis and post-meiosis stages contributed to the alteration of the vector of the initial direction within the ecological niche of Ishkashim, which is distinguished by the eliminating effect of natural gametic and zygotic selections.

The Mendelian segregation displacement and the variability of meiotic recombination parameters in tomatoes

Within the framework of the further analysis of the performed researched, it is established that in the majority of the cases concerning induced segregation displacement throughout all three ecological niches, the factors are observed following the advantage of elimination of the recessive class (Table 1). In terms of the number of segregation displacements emerged towards the abovementioned direction, the actual deficiency to the recession excess ratio as well as the tendency to the latter can be expressed as 26: 12. Besides,

Table 1. Dependence of the segregation of markers 2, 4, 6, and 11 of tomato chromosomes on the environmental conditions of the highlands of the Western Pamirs

Altitude under sea level, m (econishe)	Marker (chromosome)	Number of plants F_2, pcs.	Ratio splitting	χ^2 (3:1)	P
Mo 628/*L. esc.* var. *cerasiforme*					
2300 (Control No. 1)	*ful*(4)	330	1.9	17.5	0.001
	a(11)	330	2.5		
	e(4)	330	4.7	9.7	0.01
	hl(11)	330	6.8	26.5	0.001
2320 (Khorugh)	*ful*(4)	334	2.8		
	a(11)	334	2.3	4.4	0.05
	e(4)	334	4.7	9.6	0.01
	hl(11)	334	9.8	44.3	0.001
2600 (Ishkashim)	*ful*(4)	377	1.7	30.6	0.001
	a(11)	377	2.1	16.0	0.001
	e(4)	377	3.9	4.7	0.05
	hl(11)	377	4.0	6.0	0.05
Mo 638/*L. cheesmanii typicus* Riley					
2300 (Control No. 1)	*a*(11)	442	2.9		
	c(6)	442	2.9		
2320 (Khorugh)	*a*(11)	227	2.6	1.48	
	c(6)	227	3.8	2.44	
2600 (Ishkashim)	*a*(11)	323	4.0	4.6	0.05
	c(6)	323	3.7	2.28	
Mo 638/*L. esc.* var. *cerasiforme*					
2300 (Control No. 1)	*a*(11)	110	3.8		
	c(6)	110	3.6		
2320 (Khorugh)	*a*(11)	434	3.7	3.35	
	c(6)	434	4.3	8.63	0.05
2600 (Ishkashim)	*a*(11)	449	3.7	3.53	
	c(6)	449	3.8	3.96	0.05
Mo 638/*L. esc.* var. *pimpinellifolium*					
2300 (Control No. 1)	*a*(11)	298	3.9	3.27	
	c(6)	298	2.7		
2320 (Khorugh)	*a*(11)	191	3.1		
	c(6)	191	3.7	1.27	
2600 (Ishkashim)	*a*(11)	379	2.9		
	c(6)	379	3.4		
Mo 656/*L. esc.* var. *cerasiforme*					
2320 (Control No. 2)	*a*(11)	331	4.5	8.4	0.05
	c(6)	331	2.5	2.1	
	d(2)	331	5.4	16.3	0.001
	m-2(6)	331	8.4	36.7	0.001
2600 (Ishkashim)	*a*(11)	342	7.0	28.2	0.001
	c(*6*)	342	3.3		
	d(2)	342	7.0	28.2	0.001
	m-2(6)	342	5.6	17.5	0.001

Note: In this and the following tables: 1) control No. 1 (Vanj econiche 2300 m above sea level) was used for experiments that were conducted in the econiches of Khorugh (2320 m above sea level) and Ishkashim (2600 m above sea level); 2) control No. 2 (Khorugh econiche of 2320 m above sea level) was used for an experiment that was conducted in the Ishkashim econiche (2600 m above sea level); 3) deviations from the expected splitting ratio are significant, respectively, at $P < 0.05$; 0.01; 0.001

regarding the first and the second effect, in 15 and 4 cases the segregation displacement in the studied marker genes appeared to be relevant (Table 1, see "χ^2 3: 1" column). Probably, it is due to the fact that at the increase of the altitude above sea level, the spectrum of the incoming total solar radiation changes. More importantly, as the altitude of the terrain increases, the spectral composition of light also changes significantly (the intensity of ultraviolet radiation and the proportion of infrared rays increase as well).

Among the heterozygotes under study, the hybrid combination (Mo 628/*L. esc.* var. *cerasiforme*) possesses the most "reactive" genome, demonstrating within all ecological niches specificity following the displacement of the alternative marker genes ratio, i.e., in the direction of *ful* genes, *a* – In the direction of excess of recessions, while in the direction of *e* genes, *hl* – of the deficiency.

We do not exclude a sufficiently active effect of natural UV radiation on the processes of the meiotic transforming function, which led to an increase or decrease in the percentage of crossing-over for linked marker genes. The above is confirmed by the presence of the special linked marker genes in plants of F_2 progeny cultivated from F_1 (Mo 628/*L. esc.* var. *cerasiforme*) (Table 2). For instance, the Ishkarim mountain conditions, including the core factor, UV radiation, contributed to the reliable ($P < 0.05$) inducing of the crossing-over frequency in the linked *e*, *ful* marker genes, chromosome 4, as well as to its increase being compared with the map data (see Table 2, Mo 628/*L. esc.* var. *cerasiforme* combination). Whereas other linked marker genes (*c*, *m-2*) a reverse effect is being registered: a significant decrease in the *rf* value used in the testing compared to the accepted map value (see Mo 656/*L. esc.* var. *cerasiforme* combination). It is worth noticing that there is the direct dependence of the crossing-over frequency on the marker zone of the chromosome, genotype as well as the height of the cultivation of the F_1 heterozyhotes above sea level.

According to the results of the implemented studies, high-altitude conditions proved to be effective factors able to change the degree of recombination between unlinked marker genes. Data on the reliable difference between *rf* and 50% for unlinked marker genes are presented in Table 3 (< 50% "quasilinkage" effect (see Khorugh and Ishkasjhim's ecological niches, check No.2, *hl e*, *a m-2* and *hl e* genes); > 50% "quasirepulsion" effect (see Vanj's ecological niches (check No. 1), *hl ful* genes, Khorugh's– *c a* and Ishkashim's area – *hl ful*, *d m-2* genes). Thus, the dependence of the emergence of unlinked marker genes on the height above sea level of cultivation of heterozyhotes, in several combinations, is close to the behavior of linked genes. This is especially evident in the hybrid combination (Mo 628/*L. esc.* var. *cerasiforme*).

Based on the above, it can be concluded that the "vertical" disruptive selection stemming from the UV exposure combined with other environmental factors may deem to be an effective additional feature for the exogenous induction of recombination.

Meiotic transforming function

It is acknowledged that the calculation of the average frequency of chiasmas per cell, and especially their qualitative component, allows us to predict, at an early stage of ontogenesis of F_1 hybrid plants (meiosis), the direction vector of high or low recombination variability in F_2 heterogeneous segregating population (Phillips et al., 2012). The reason for that is that currently the causal relationship between chiasms and

Table 2. Influence of environmental conditions in the highlands of the Western Pamirs on the frequency of crossing over between linked marker genes

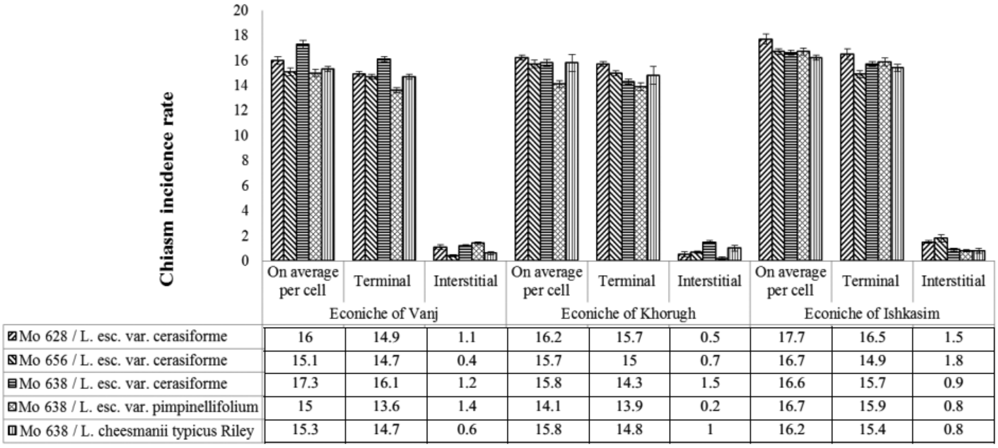
Altitude under sea level, m (econishe)	Marker (chromosome)	Number of plants F_2, pcs.	Genotype F_1	*rf* (%) fact.	*t*-test		*rf* (%) according to the chromosome map
					experiment	chromosome map	
Mo 628/*L. esc.* var. *cerasiforme*							
2300 (Control No. 1)	*e*(4). *ful*(4)	330	*e ful*/++	41.0±2.5	-	6.86***	22±1.2
	hl (11). *a*(11)	330	*hl a*/++	19.5±1.7	-	0.23	20±1.4
2320 (Khorugh)	*e*(4). *ful*(4)	334	*e ful*/++	47.5±2.7	1.62	8.64***	22±1.2
	hl(11). *a*(11)	334	*hl a*/++	22.0±1.8	1.0	0.88	20±1.4
2600 (Ishkashim)	*e*(4). *ful*(4)	377	*e ful*/++	49.0±2.8	2.11*	8.85***	22±1.2
	hl(11). *a*(11)	377	*hl a*/++	20.5±1.6	0.43	0.23	20±1.4
Mo 656 / *L. esc.* var. *cerasiforme*							
2320 (Control No. 2)	*c*(6). *m–2*(6)	331	*c m-2*/++	21.1±1.1	-	2.68*	27±1.9
2600 (Ishkashim)	*c*(6). *m–2*(6)	342	*c m-2*/++	20.0±1.7	0.55	2.80**	27±1.9

Note: The value of Student's *t*-test reflects the significance of differences at $P < 0.05$ (*). 0.01 (**) and 0.001 (***)

Table 3. The influence of the environmental conditions of the highlands of the Western Pamirs on the level of recombination between unlinked marker genes

Altitude under sea level, m (econishe)	Marker (chromosome)	Number of plants F_2, pcs.	Genotype F_1	*rf* (%) fact.	χ^2	P
			Mo 628 / *L. esc.* var. *cerasiforme*			
2300 (Control No. 1)	*e*(4), *a*(11)	330	*ea*/++	48.0±2.8	0.20	
	hl(11), *e*(4)	330	*hle*/++	51.5±2.7	0.10	
	hl(11), *ful*(4)	330	*hlful*/++	60.6±2.5	10.20	0,001
2320 (Khorugh)	*e*(4), *a*(11)	334	*ea*/++	44.5±2.9	1.30	
	hl(11), *e*(4)	334	*hle*/++	39.5±3.1	6.50	0,01
	hl(11), *ful*(4)	334	*hlful*/++	56.5±2.6	1.50	
2600 (Ishkashim)	*e*(4), *a*(11)	377	*ea*/++	40.0±2.9	5.40	0,05
	hl(11), *e*(4)	377	*hle*/++	35.0±3.0	7.40	0,01
	hl(11), *ful*(4)	377	*hlful*/++	60.2±2.5	10.20	0,001
			Mo 638 / *L. cheesmanii typicus* Riley			
2300 (Control No. 1)	*c*(6), *a*(11)	442	*ca*/++	58.5±2.2	1.27	
2320 (Khorugh)	*c*(6), *a*(11)	227	*ca*/++	51.0±3.0	0.05	
2600 (Ishkashim)	*c*(6), *a*(11)	323	*ca*/++	49.0±2.8	0.10	
			Mo 638 / *L. esc.* var. *cerasiforme*			
2300 (Control No. 1)	*c*(6), *a* (11)	110	*ca*/++	58.5±4.3	1.27	
2320 (Khorugh)	*c*(6), *a* (11)	434	*ca*/++	60.0±2.1	12.2	0,001
2600 (Ishkashim)	*c*(6), *a* (11)	449	*ca*/++	52.5±2.3		
			Mo 638 / *L. esc. var.* p*impinellifolium*			
2300 (Control No. 1)	*c*(6), *a* (11)	298	*ca*/++	55.0±2.8	2.73	
2320 (Khorugh)	*c*(6), *a* (11)	191	*ca*/++	58.5±3.3	2.56	
2600 (Ishkashim)	*c*(6), *a* (11)	379	*ca*/++	49.0±2.1	0.10	
			Mo 656 / *L. esc.* var. *cerasiforme*			
2320 (Control No. 2)	*c*(6), *a* (11)	331	*ca*/++	47.0±2.9	0.40	
	a(11), *m–2*(6)	331	*am–2*/++	36.5±3.2	3.84	0,05
	d(2), *m–2* (6)	331	*dm–2*/++	40.0±3.1	1.40	
2600 (Ishkashim)	*a*(11), *m–2*(6)	342	*am–2*/++	51.5±2.7	0.10	
	d(2), *m–2* (6)	342	*dm–2*/++	60.1±2.5	7.00	0,01

Note. Deviations from independent cleavage are significant, respectively, at $P < 0.05$; 0.01; 0.001



	Econiche of Vanj			Econiche of Khorugh			Econiche of Ishkasim		
	On average per cell	Terminal	Interstitial	On average per cell	Terminal	Interstitial	On average per cell	Terminal	Interstitial
▨ Mo 628 / L. esc. var. cerasiforme	16	14.9	1.1	16.2	15.7	0.5	17.7	16.5	1.5
▧ Mo 656 / L. esc. var. cerasiforme	15.1	14.7	0.4	15.7	15	0.7	16.7	14.9	1.8
▤ Mo 638 / L. esc. var. cerasiforme	17.3	16.1	1.2	15.8	14.3	1.5	16.6	15.7	0.9
▩ Mo 638 / L. esc. var. pimpinellifolium	15	13.6	1.4	14.1	13.9	0.2	16.7	15.9	0.8
▥ Mo 638 / L. cheesmanii typicus Riley	15.3	14.7	0.6	15.8	14.8	1	16.2	15.4	0.8

Fig. 2. Dynamics of variability of cytological parameters of meiosis (total frequency of chiasm, frequency of terminal and interstitial chiasm)

genetic crossing-over is being reliably confirmed. This entails interstitial chiasms (Figure 2), which are essential to the release of additional genotypic variability, as well as increasing the recombination ratio. Thus, for example, even a slight increase in interstitial crossing-over in hybrid combination plants (Mo 628/*L. esc.* var. *cerasiforme* and Mo 656/*L. esc.* var. *cerasiforme*), place of handling: – Ishkashim ecological niche (2600 m above sea level), had a significant impact on the recombination ratio between unlinked *hl*, *e* and *d*, *m-2* marker genes, causing, respectively, the "quasilinkage" and "quasirepulsion" effects as well (Table 3).

Conclusion

According to the analysis of the results of the researches carried out it is established that environmental conditions covering three high-mountain areas of the Western Pamirs, i.e. Vanj, Khorugh and Ishkashin, (2300, 2320 and 2600 m above sea level respectively) in fact influenced meiotic and postmeiotic processes of the interspecific F_1 hybrids under research. Consequently, the change in the direction of displacements of marker genes depending on the altitude (see Table 1) can be clearly traced. For instance, throughout the Vanj ecological niche (check option) in the combination of Mo 638/*L. cheesmanii typicus* Riley, *a* and *c* genes, a typical Mendelian segregation is being observed. In the Khorugh ecological niche, on the contrary, there is a tendency towards a displacement in both genes (in *a* gene towards an excess of the recession class; in *c* gene, towards their deficiency). But in the Ishkashim ecological niche there is an excess of the dominant class for both genes (Table 1).

With regard to linked and unlinked marker genes, in the specified ecological niches, the "vertical" disruptive selection based on the effect of combined exposure to high-mountain heterogeneous conditions may prove to be quite effective exogenous inducing factor for the type of genes studied. Thus, for the *e* and *ful* linked genes, within the Ishkashim ecological niche a reliable increase of *rf* (%) was found in terms of the testing of the check No. 1 as well as a high level of reliability regarding the decrease of its value in *c* and *m-2* genes (*t*-criterion is equal to 2.68 and 2.80) according to the chromosome map (Table 2). Concerning the recombination ratio between unlinked *hl*, *ful* marker genes (11 and 4 chromosomes), there was also a reliable deference reflecting the "quasirepulsion" phase ($rf = 60.6 \pm 2.5$ for the Vanj ecological niche (check No.1) and $rf = 60.2 \pm 2.5$ for the Ishkashim ecological niche) (Table 3). The data obtained and relative to the *hl*, *e* maker genes indicate a significant drop in the recombination ratio in relation to 50% at the level $rf = 39.5 \pm 3.1$ for the Khorugh ecological niche, and $rf = 35.0 \pm 3.0$ for the Ishkashim ecological niche, which corresponds to the "quasilinkage" phase.

The above mentioned is also confirmed by the fact that the variability vector of the core parameters of the meiotic transforming function (the percentage of crossing-over, recombination ratio, chiasm frequency and their qualitative features), extra elements of the replicating function (pollen fertility, seed saturation), as well as the processes of elimination of the non-traditional recombinant gametes and zygotes are, mostly, in a direct dependence on the altitude above sea level, where the testing of F_1 hybrid tomato plants were carried out.

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