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RESEARCH ARTICLE

Functional activity of the genetic apparatus of cell during heterosis of various agricultural crops

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Abstract

The paper presents the results of a comprehensive study of functional activity of the genetic apparatus, taking into account the localization of its components in the nuclei, mitochondria and chloroplasts to determine their possible role in yield formation during heterosis in tomato, cucumber, eggplant and wheat. A clear pattern was revealed in terms of DNA content per cell in all hybrids, regardless of the species and the degree of heterosis exceeded their parents. Tomato hybrids exhibited activation of genetic material synthesis in mitochondria, while wheat hybrids showed activation in both mitochondria and chloroplasts. Establishing the pattern of DNA synthesis activity in heterotic hybrids in comparison with parental varieties allows us to recommend determining the DNA content in a somatic cell for predicting heterosis. The results of the present study indicated that in the case where the nuclear, mitochondrial and chloroplast genetic systems of a plant cell function with an increased load in a hybrid, which thereby receives more energy to enhance the processes of biosynthesis of plastic substances, one can, as a consequence, expect the manifestation of a high heterotic effect. These data are consistent with James's hypothesis that one of the causes of heterosis is the redundancy of the genetic code, and Kihara H.'s hypothesis on nuclear-cytoplasmic heterosis.

Keywords: Heterosis, DNA, RNA, cell, nucleus, mitochondria, chloroplasts

Introduction

Heterosis is a long-known and widespread general biological phenomenon, the study of which is of great practical and theoretical interest. Heterosis is evident already at the early stages of development of the hybrid organism (Meyer et al. 2004). The meristematic tissue of hybrids has the ability to actively divide, which ensures more powerful vegetative development of hybrid plants (Hochholdinger 2018; Karlberg, 2011). On the 6th day, the hybrid corn embryo is already larger than non-hybrid embryos (Hoecker et al. 2005). Hybrids show an increase in the degree of development of individual characteristics such as plant height, root mass, leaf surface, etc. So, heterosis in corn is already evident during the development of primary roots in the form of intensification of growth of both primary and lateral roots (Paschold et al. 2010). Hybrids exhibit heterosis in total mass (Shrestha et al. 2021), moreover, a positive correlation between barley yield and dry plant biomass was found (Bakhtin 2012). The high correlation between the number of grains in a panicle and the growth rate of the germinal root in rice, between the number of grains in a panicle and the growth rate of the germinal stem allows us to recommend the selection of hybrid combinations with a high growth rate at the early stages of development as a method of selection for yield (Goncharova 2010). Rapid root development gives hybrids an advantage in mineral uptake and photosynthesis rates. In many agricultural crops, a correlation is observed between plant productivity and the intensity of photosynthesis (Zhang et al. 2024; Nazari 2024).

Numerous studies have been devoted to identifying the molecular mechanisms underlying the heterosis effect. The activity of a number of enzymes was studied in tissues of hybrid organisms at different stages of development (Kamalkumar et al. 2007; Singh et al. 2010), protein synthesis

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(C Marcon, 2013), protein polymorphism (Comarova et al., 2017**),** activity of biosynthetic processes (Titok et al. 2008), and content of biologically active compounds (Karpukhin 2024). The overwhelming majority of heterosis manifestations are associated with the regulatory systems of the genome, that is, the central genetic apparatus of the cell. The plant cell's genetic program is realized not only at the nuclear genome level. Mitochondria and chloroplasts play a key role in energy supply, and changes in the genetic material of these cellular structures during hybridization allow us to assess the energy capacity of the systems under study. To date, a number of approaches have been developed for assessing the structural and functional state of the genome and plasmon of heterotic hybrids and their parental forms. Among these, assessing the effectiveness of heterosis based on DNA synthesis activity in plant vegetative organs is of particular importance. A number of studies in this area have been published (Wang et al. 2015; Mammadova and Aliyev 2016; Lauss 2018; Yadava 2021).

The nature of heterosis, which is determined at the genetic level but manifests through the physiology of hybrid plants, remains largely unknown. Despite the fact that this phenomenon has received much attention in recent years, the biochemical and genetic mechanisms of heterosis in hybrid offspring have not been fully elucidated. There is currently no single theory explaining the phenomenon of heterosis. The absence of well-substantiated genetic hypotheses capable of explaining this unique phenomenon hinders the development of effective technologies aimed at increasing plant productivity. One consistent feature of the heterosis effect is that hybrids do not exhibit entirely new traits; rather, they display modified characteristics derived from the parental lines. For this reason, it is widely believed that genes associated with quantitative traits – QTLs – play a central role in the manifestation of hybrid vigor (Asins 2002; Gepts 2002; Dongdong et al. 2021), many of which have been identified through molecular genetic approaches.

This work is devoted to a comprehensive assessment of the genetic apparatus of the cell, taking into account the localization of its components in various cell structures (nuclei, mitochondria and chloroplasts) to clarify their role in the formation of crop yield during heterosis and to clarify their role in the formation of crop yield during heterosis.

Materials and methods

The study used heterotic hybrids of cucumber (*Cucumis sativus* L.), eggplant (*Solanum melongena* L.), tomato (*Solanum lycopersicum* L.), wheat (*Triticum aestivum* L.) and their parental forms obtained in various variants of crossing varieties and samples. Vegetable hybrids were obtained at the Azerbaijan Scientific Research Institute of Vegetable Growing, and wheat hybrids were obtained at the Institute of Genetic Resources of Azerbaijan. Samples for analysis of wheat plants were taken in the ear emerging phase, and vegetable crops in the flowering phase (second leaf from the top). The leaves of hybrid and parental forms were determined for the mass of one cell, the content of nucleic acids, the content of RNA and DNA in mitochondria and chloroplasts. To account for the number of cells in the samples, a modified Brown method was used (Ali et al. 1979). The essence of the method consists of maceration of a piece of tissue with chromic acid and subsequent counting of the number of cells in a drop of suspension in a Fuchs-Rosenthal counting chamber under a microscope. The counting was carried out in four large squares taken diagonally across the counting chamber. We counted 24 squares for each sample, obtaining 24 numbers. Taking into account biological replicates, this gives 72 measurements in each variant. The obtained figures for the number of cells in one large square were recalculated for the volume of cell suspension present in the test tube and the number of cells in the disk taken from the leaf blade was calculated. Having thus determined the number of cells in the disk and knowing the mass of the substance, we calculated the number of cells per unit of substance. Knowing the relative content of nucleic acids, we can convert these results to a single cell.

To ensure statistical significance of the results, five plants were collected for each study variant. Laboratory analyses to determine the amount of nucleic acids in plant leaves were performed in triplicate, to determine the DNA content in plant cell nuclei, 50-100 nuclei were photometered in preparations for each experimental variant. This allows for reliable analysis and identification of patterns in the obtained results.

Cytophotometric determination of DNA in nuclei was carried out using the Feulgen reaction. The material was fixed in Carnoy's mixture (3 parts rectified ethanol: 1 part glacial acetic acid). The fixed material was washed with 96% alcohol several times for 25 minutes until the acetic acid smell disappeared, and then transferred to 70% alcohol for storage. Unlike the generally accepted object for cytophotometry– the root tip, we conducted experiments on leaves. To determine the optimal hydrolysis period based on the intensity of the Felgen reaction, we carried out special methodological work. It was established that the optimal hydrolysis time for an intensive reaction of Felgen in wheat leaves is 12 min (1 NHCl at t=60°C), and for tomato leaves, 1 hour (5 NHCl at t=22°C). After hydrolysis, the leaves were stained with Schiff's solution for 1.5-2 hours, washed 3 times with sulfurous acid, and then with running water. Pressed preparations were prepared in glycerin-gelatin. The content of the DNA complex in the poisons was determined by the wavelength λ= 530 nm.

The DNA content in plant cell nuclei on the preparations was measured in such a way that the nuclei fit into the

measuring probe. The DNA content was expressed in relative units. The average of the minimum values of the obtained indicators was used as the ethanol of the DNA quantity corresponding to the diploid chromosome set.

Mitochondria and chloroplasts were isolated by differential centrifugation in the cold at +4°C: mitochondria in a medium containing 0.5 M sucrose; EDET 0.005 M; potassium phosphate buffer 1/15 M pH 7.4, chloroplasts – in a medium containing 0.4 M sucrose; 0.05 M Tris-HCl buffer (pH 7.4); 0.01 M HCl and 0.03 M MgCl2. Nucleic acids were isolated by stepwise centrifugation. The nucleic acid content was determined by the spectrophotometric method described in the work of Konarev and Tyuterev (1970). The data obtained as a result of the study are presented as an arithmetic mean with an error (Dospekhov 1985).

Results

Study of nucleic acid content and quantitative leaf parameters in vegetable crops in connection with heterosis

In the first series of studies, the total content of nucleic acids per somatic cell in parental and hybrid forms of vegetable crops was studied, the results of which are presented in Table 1. In the highly heterotic hybrid Din-zo-sn × Iva, the amount of RNA was intermediate compared to the parent varieties. The less productive reverse hybrid had a slightly higher RNA content per cell. But it should be noted that the Din-zo-sn and Iva varieties and their direct and reverse hybrids had approximately the same RNA content per cell.

Table 1. Heterosis index, nucleic acid content in leaf cells and its quantitative parameters in hybrids and parental forms of vegetable crops

Variety, hybrid	Heterosis index, %	RNA	DNA	Cell mass, $\times 10^{-9}$ g	Number of cells, $\times 10^{6}$
		$\times 10^{-12}$ g			
Cucumis sativus L.					
Din-zo-sn		26.70	1.21	1.73	57.2
Iva		24.50	1.13	1.58	64.7
Anshansky		29.90	0.99	1.98	43.4
Din-zo-sn×Iva	35.2	25.60	1.97	2.24	39.5
Iva×Din-zo-sn	12.0	27.50	1.77	2.05	46.0
Iva × Anshansky	5.8	38.89	1.69	2.93	40.2
Solanum melongena L.					
Yerevanskiy 3		29.60	2.26	5.24	25.65
G-10		34.10	1.83	5.60	22.19
Yerevanskiy 3 ×G-10	63,.	34.20	2.43	6.15	20.45
Solanum lycopersicum L.					
Kiev139		73.97	4.67	6.66	18.7
Leningradsky		89.96	3.53	6.90	17.2
Kiev139×Leningradsky	29.4	95.93	6.61	6.63	17.9
Valiant		63.32	3.36	6.12	21.7
Leningradsky		89.96	3.53	6.90	17.2
Valiant ×Leningradsky	11.5	97.36	4.75	8.36	15.2
Whitenaliv		102.8	5.86	7.18	17.4
Resista		108.3	5.34	7.58	18.5
White naliv × Resista	51.8	105.1	6.42	8.00	17.2
Cavalier		64.90	5.25	6.00	20.7
Fanal		111.7	5.34	10.74	14.9
Cavalier×Fanal	63.8	100.8	6.64	9.66	18.34

The research revealed a clear pattern with regard to all hybrid cucumber combinations had a higher DNA content per cell than the parent varieties. Moreover, for the highly heterotic hybrid Din-zo-sn × Iva, it was approximately 63% of the form fixed for this parameter – the Din-zo-sn variety, and for the other two hybrids (Iva × Din-zo-sn and Iva × Anshansky) with a smaller heterotic effect, approximately 50% of the value of the parental form best for this parameter for each crossing combination. In this case, the number of cells per unit leaf area in hybrids decreased, while the size of the cells themselves increased. A study of all the above indicators in tomato and eggplant hybrids revealed similar patterns**.**

Cytophotometric evaluation of DNA-fuchsin content in the nuclei of leaf cells of hybrids in connection with heterosis

Table 2 presents the results of a comparative study of the amount of DNA per nucleus in the cells of young apical leaves of parental forms and heterotic tomato hybrids. All tomato hybrids exceeded the parental forms in fruit yield from one bush by 38 to 64%. The content of DNA fuchsin in the nuclei of hybrids was also higher than in the original forms. For example, the Kiev 139 × Leningradsky hybrid differed in the average value of this parameter from its parental forms by 65%. The same sharp difference between hybrids and parental forms was observed in other hybrid combinations.

The wheat hybrids also differed in DNA-fuchsin content from the parental forms. Thus, if the K-47091 × K-51647 and K-47091 × K-53215 hybrids had a noticeable increase in DNA content in the nuclei, then in the K-47091 × K-51549 hybrid, this increase was insignificant. These data are consistent with the magnitude of the heterosis effect. For example, in the K-47091 × K-53215 hybrid, the grain weight per plant exceeded the average values of the parental forms by 16.7% respectively, and the DNA-fuchsin content in the cell nucleus of the same hybrid increased by 21.6%. A slightly lower heterosis effect was observed in the hybrid K-47091 × K-51647. The same pattern was observed in the amount of fuchsin DNA in the nuclei of cells of this hybrid. The content of fuchsin DNA in the nuclei of cells of the hybrid K-47091 × K-51647 increased by 19.5% of the average value of the parental forms. The heterosis effect in grain yield was 14.6%. The hybrid K-47091 × K-51549 occupied an intermediate position between the parental forms in grain yield. In the nuclei of this hybrid, the amount of fuchsin DNA compared to the parental samples increased slightly by 6.65.

Table 2. Content of DNA-fuchsin in the nuclei of leaf cells of heterotic hybrids and their original forms

Crossbreeding combination	Average density of DNA fuchsin per leaf cell nucleus, conventional units			Increase in the amount of DNA in hybrids compared to parents, %
	P_1	F_1	P_2	
Solanum lycopersicum L.				
Kiev139×Leningradsky	0.077 ± 0.005	0.125 ± 0.009	0.075 ± 0.005	64.5
Valiant ×Leningradsky	0.106 ± 0.010	0.151 ± 0.009	0.075 ± 0.005	67.8
Whitenaliv×Resista	0.098 ± 0.005	0.191 ± 0.010	0.148 ± 0.009	56.1
Cavalier × Fanal	0.092 ± 0.005	0.150 ± 0.009	0.102 ± 0.005	55.7
Triticum aestivum L				
K-47091× K-51647	0.356 ± 0,010	0.408 ± 0,009	0.327 ± 0.009	19.5
K-47091 × K-53215	0.356 ± 0,010	0.473 ± 0,009	0.422 ± 0.009	21.6
K-47091× K-51549	0.356 ± 0,010	0.369 ± 0,010	0.338 ± 0.010	6.3
erythrospermum Gyurgyan ×*erythrospermum* Zardabi	0.500 ± 0,009	0.548 ± 0,012	0.457 ± 0.013	14.5
Erythrospermum Zardabi×*erythrospermum* Gyurgyan	0.457 ± 0,013	0.527 ± 0,015	0.500 ± 0.009	10.1
erythrospermum Zardabi×*lutescens*10	0.457 ± 0,013	0.543 ± 0,011	0.523 ± 0.010	10.8
lutescens 10 ×*erythrospermum* Zardabi	0.523 ± 0,010	0.528 ± 0.014	0.457 ± 0,013	7.8
erythrospermum Zardabi ×*erythrospermum* 9	0.457 ± 0,013	0.542 ± 0,010	0.480 ± 0.012	15.7
erythrospermum 9 ×*erythrospermum* Zardabi	0.480 ± 0,012	0.528 ± 0,012	0.457 ± 0.013	12.7
Erythrospermum Zardabi×*provincial* Karabakh	0.457 ± 0,013	0.524 ± 0,009	0.524 ± 0.010	6.8
provincial Karabakh×*erythrospermum* Zardabi	0.524 ± 0,010	0.528 ± 0,010	0.457 ± 0.013	7.6

An increase in the quantity of DNA-fuchsin in comparison with the parental samples is also noticed in the other hybrid combinations of wheat.

Activity of genetic material synthesis in cytoplasmic organelles of plant cells in connection with heterosis

The content of nucleic acids in mitochondria and chloroplasts of heterotic tomato hybrids

Table 3 presents the results of the activity of nucleic acid synthesis in the cytoplasmic organelles of tomato in connection with heterosis. The RNA content in the mitochondria of all hybrid tomato forms, with the exception of Valiant × Leningradsky, was slightly higher than that of their parents. The best hybrid according to this indicator was White Naliv × Resista. In terms of mitochondrial DNA content, all hybrid combinations exceeded their parents: Valiant × Leningradsky and Cavalier × Fanal by approximately 30-35%, and Kyiv 139 × Leningradsky and Bely Naliv × Rezista by almost 10%. Among hybrids, Valiant x Leningradskiy stands out for its mitochondrial DNA content. Then the value of this indicator decreases in the following order: White naliv × Resista, Cavalier x Fanal, Kiev 139 × Leningradsky. However, the RNA/DNA ratio in the last hybrid was the highest and decreased in the reverse order compared to the DNA content in the mitochondria. The nature of the RNA and DNA content and their ratio may indicate a high synthesis of functional components of mitochondria in the hybrids Kiev 139 × Leningradsky and Cavalier × Fanal. Obviously, in these forms, the mitochondrial energy production system makes a significant contribution to the energy potential of the cell.

A study of the genetic material of chloroplasts of heterotic tomato hybrids showed that although the White naliv × Resista hybrid has the highest RNA level; its value does not exceed that of the parent varieties. The remaining

Table 3. Content of nucleic acids in mitochondria and chloroplasts of tomato hybrids and their parental forms (mg% of dry matter of organelles)

Varieties, hybrids	Mitochondria			Chloroplasts		
	RNA	DNA	RNA / DNA	RNA	DNA	RNA / DNA
Solanum lycopersicum L.						
Kiev 139	2728.5 ± 16.8	128.9 ± 0.2	21.2	1174.7 ± 5.3	233.6 ± 1.1	5.0
Leningradskiy	2603.7 ± 23.7	129.2 ± 0.3	20.2	1025.6 ± 6.3	237.6 ± 1.2	3.7
Kiev 139 × Leningradskiy	3186.7 ± 81.7	142.7 ± 2.6	22.3	1814.2 ± 2.2	271.5 ± 3.6	6.7
Valiant	3181.0 ± 7.0	171.3 ± 1.0	18.6	1288.9 ± 9.3	135.2 ± 0.6	9.5
Leningradskiy	2603.7 ± 23.7	129.2 ± 0.3	20.2	1025.6 ± 6.3	273.6 ± 1.2	3.7
Valiant × Leningradskiy	3132.1 ± 113.3	232.2 ± 3,0	13.5	1481.1 ± 6.8	154.8 ± 1.4	9.6
Belyi naliv	3019.9 ± 12.2	188.7 ± 1.0	16.0	2382.9 ± 8.0	121.4 ± 1.6	19.6
Resista	3016.5 ± 13.3	154.6 ± 1.2	19.5	3215.5 ± 8.9	256.4 ± 1.5	12.5
Belyi naliv × Resista	3337.5 ± 23.8	206.4 ± 2.7	16.2	2388.4 ± 9.1	187.5 ± 1.9	12.7
Cavalier	1918.0 ± 12.0	92.4 ± 0.2	20.8	1558.5 ± 15	111.1 ± 2,5	14.0
Fanal	1887.5 ± 7.8	126.2 ± 1.5	15.0	1572.0 ± 8,7	129.9 ± 1,2	12.1
Cavalier × Fanal	3210.1 ± 55.4	166.1 ± 3.1	19.3	2052.8 ± 17	214.5 ± 0,8	9.6
Triticum aestivum L						
lutescens FRG	1070.4 ± 7.8	509.7 ± 6.0	2.1	1426.2 ± 6.9	306.9 ± 1.2	4.7
lutescens Birlik	1009.8 ± 8.9	556.3 ± 5.8	1.8	910.5 ± 7.5	267.2 ± 1.7	3.4
lutescens FRG × *lutescens*Birlik	1948 ± 14.2	750.1 ± 4.1	2.6	2495.2 ± 5.0	416.4 ± 3.0	3.6
lutesces Birlik × *lutescens* FRG	1617.3 ± 8.7	910.9 ± 6.8	1.8	1146.1 ± 8.8	371.4 ± 5.6	3.1
lutescens KSI	1324.4 ± 9.7	318.9 ± 1.2	4.2	1297.5 ± 13.1	138.9 ± 1.8	9.3
lutescens FRG × *lutescens* KSI	1134.1 ± 8.1	779.6 ± 5.8	1.5	1856.8 ± 12.9	529.1 ± 2.5	3.5
lutescens KSI × *lutescens* FRG	1565.2 ± 10.4	554.1 ± 7.0	2.8	1419.2 ± 14.1	315.8 ± 1.6	4.5
Besostaya 1	880.6 ± 6.2	662.9 ± 3.1	1.3	1149.5 ± 6.8	236.3 ± 1.2	4.7
lutescens Birlik × Besostaya 1	1415.0 ± 11.5	800.0 ± 8.7	1.8	1138.8 ± 5.6	305.1 ± 1.5	3.7
Besostaya 1× *lutescens* Birlik	1245.9 ± 9.1	604.2 ± 7.3	2.1	870.7 ± 7.2	289.3 ± 7.2	3.0

hybrids showed an increase in RNA content compared to their parent varieties, with the Kyiv 139 × Leningradsky hybrid exhibiting the highest percentage increase at 54.4%. Only when crossing the varieties Cavalier and Fanal, the hybrid showed a significant increase in chloroplast DNA content compared to the parent varieties.

Calculation of the chloroplast RNA/DNA ratio of tomato shows a decrease in this indicator in chloroplasts compared to the mitochondrial and total cellular pool. Probably, in chloroplasts at the studied stage of ontogenesis, all active biosynthetic processes fade; all biosynthesis is aimed at maintaining the already existing balance. The Kyiv 139 variety has a low RNA/DNA ratio in its chloroplasts, while the Kyiv 139 x Leningradsky hybrid has an increased ratio due to a more than 50% increase in RNA content in its chloroplasts.

This may indicate a more active chloroplast system in the hybrid at this stage of development. The Cavalier x Fanal hybrid may not have yet reached the maximum level of biosynthetic processes, as this hybrid has significantly increased both RNA and DNA content in its chloroplasts compared to the original parent varieties. However, at this stage of development, the RNA/DNA ratio in its chloroplasts is lower than in its parents. Thus, it should be noted that if in the hybrids Valint x Leningradsky and Belyi Naliv × Rezista the genetic system of mitochondria operates with a high degree of load, then in the chloroplasts, the processes proceed most actively in other hybrids: Kiev139 × Leningradskiy and Cavalier × Fanal. That is, both the mitochondrial and chloroplast systems can contribute to the overall increased energy supply of the cell in different hybrids. This may be explained by the complementary interaction of the genetic systems of mitochondria and chloroplasts.

The content of nucleic acids in the mitochondria and chloroplasts of a heterotic wheat hybrid

The study of the activity of nucleic acid synthesis in connection with heterosis in the cytoplasmic organelles of wheat showed that in most cases the hybrids were characterized by an increase in the content of RNA and DNA in comparison with the original varieties. Thus, the hybrids *lutescens* FRG × *lutescens* Birlik by 87%, *lutescens* Birlik × *lutescens* FRG by 55%, and *lutescens* KSI on *lutescens* FRG by 31% exceeded the average indicator of the parents for RNA synthesis in mitochondria. The same sharp difference between the hybrids (*lutescens* FRG × *lutescens* Birlik, *lutescens* Birlik × *lutescens* FRG, *lutescens* FRG × *lutescens* KSI, *lutescens* Birlik × Bezostaya 1, etc.) and the parental forms was also observed in the content of mitochondrial DNA. The only exception was the hybrid Bezostaya 1 × Birlik, which took an average position compared to the original forms.

Activation of mitochondrial nucleic acid synthesis indicates that energy supply due to the mitochondrial system in heterotic wheat hybrids is higher than in the parent varieties. No specific pattern in the content of chloroplast RNA in wheat hybrids was noted. In some cases, the hybrids were characterized by activation of synthesis *(lutescens* FRG x *lutescens* Birlik, *lutescens* FRG x *lutescens* KSI), in others, they were inferior to the original components (*lutescens* Birlik x *lutescens* FRG, *lutescens* KSI x *lutescens* FRG, *lutescens* Birlik x Bezostaya1, Bezostaya 1 x *lutescens* Birlik). However, all the studied hybrid wheat combinations exceeded the parent varieties in the amount of chloroplast DNA.

Discussion

The literature reveals an opinion that heterosis is based on interallelic, intergenic and plasmatic interactions, which in functional terms can be represented as processes of stimulation of gene function, complementation and gene dosage effect (Konarev et al. 1981). Analysis of the functions of genes with increased expression showed that these are mainly genes involved in the regulation of transcription or initiation of replication, protein and RNA synthesis, as well as cell division. (Meyer et al., 2007). Currently, many genes are known whose expression determines the development of economically valuable traits in plants (Dicks et al. 2000). In *Vicia faba* L., of the 5,500 loci studied, about 9% showed a change in expression in heterotic hybrids, including genes involved in the control of carbon and nitrogen metabolism, stress resistance, cell division, hormonal regulation, and the manifestation of mitochondrial activity (Meitzel et al. 2009). Altmann and co-authors believe that in *Arabidopsis,* a cluster of 23 genes is localized on chromosome 4, the dominance, over-dominance, or additive effect of which at different stages of development determines the heterosis of biomass (dry mass of shoots) (Altmann et al. 2009). A study of gene expression during heterosis in rice showed that immediately after fertilization, hybrids show increased gene expression compared to the parental forms (Bao et al., 2005). In our studies, in plant hybrids, regardless of their species and degree of heterosis, we observed activation of DNA synthesis in one cell compared to the parental forms, which is consistent with the hypothesis of K. James (James, 1961) about the redundancy of the genetic code in hybrids during heterosis. The activation of the synthesis of the genetic apparatus of mitochondria and chloroplasts that we established during the study is consistent with the information described in the literature on the so-called plastid or chloroplast and mitochondrial heterosis (Fujimoto et al. 2012; Ovchinnikova 1976; McDaniel and Sen 1981; Scotti et al. 1981; Dahal 2012). Among the numerous hypotheses explaining the phenomenon of heterosis, the hypothesis of nuclear-cytoplasmic heterosis is also considered within the framework of the theory of genetic equilibrium. Our research and literature data (Kihara 1979) allow us to assume that in the case where the nuclear, mitochondrial and chloroplast genetic systems of a plant cell function with an increased load in a hybrid, which thereby receives more energy to

enhance the processes of biosynthesis of plastic substances, one can, as a consequence, expect the manifestation of a high heterotic effect.

Conclusively, an integrated approach to assessing the state of the cellular genetic apparatus in hybrid forms, in comparison with parental varieties, made it possible to create a more complete understanding of the implementation of the activity of both the nuclear genome and the genetic elements of mitochondria and chloroplasts in the manifestation of the heterotic effect. A study of the nucleic acid content in somatic cells and leaf cell nuclei showed that all heterotic plant hybrids, regardless of plant species, exceed the parent varieties in DNA content, which may have general biological significance. Counting the number of cells per unit area showed that hybrids exhibit an increase in cell size and, as a consequence, a decrease in their number per unit area. In heterotic hybrids, both the mitochondrial and chloroplast systems can contribute to the overall increased energy supply of the cell, which is perhaps where their complementary interaction lies. Apparently, the manifestation of heterosis is ensured due to a more favorable nuclear-cytoplasmic interaction of genetic systems.

Authors' contribution

Conceptualization of research (RA); Designing of the experiments (RA); Contribution of experimental materials (RA); Execution of field/lab experiments and data collection (RA, ADM); Analysis of data and interpretation (RA, ADM); Preparation of the manuscript (RA, ADM).

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