

New Theory of the Mechanism of Heterosis

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Abstract

Heterosis is widely used in crop production to increase crop yields and is applied to more crops. Until the middle of the twentieth century, the mechanism of heterosis was due mainly to the hypotheses of domination and over domination. From the middle of the 50s of the XX century to the beginning of the 21st century, a number of hypotheses emerged in explaining the mechanism of heterosis, among which are: genetic, metabolic and bioenergetic balances. On the problem of the mechanism of heterosis, one must return to a detailed analysis of the genetics of traits. The emergence of heterosis in the hybrids of the first generation can be explained on the basis of allelic and non-allelic gene interaction, which creates a favorable combination of genes during hybridization, which causes a better manifestation of an economically valuable trait. Allelic interaction of genes is mainly manifested in the complete or incomplete dominance of the dominant gene over the recessive gene of one allelic pair, as well as in co-dominance, when the external manifestation of the trait is a mixture of the action of both alleles of one allelic pair. Intergenic interaction of genes, as a rule, is expressed in four basic forms: complementarity, epistasis, polymorphism and modifying action. In connection with the fact that practically all forms of intergenic nonallelic and allelic interaction of genes are observed in the mechanism of manifestation of heterosis, this phenomenon is still difficult to explain to nature. In the work, somatic heterosis in *Arabidopsis* was studied on the basis of the "diameter of the rosette of leaves". It was established that when the plants of different races Col-0 and La-0 cross in the generation of F₂, polymeric interaction of the genes takes place. In this case, the splitting in F₂ goes in a ratio of 15:1. In this case, hybrids of the first generation have somatic heterosis, which manifests itself in a more powerful development of the rosette of leaves compared with the original forms. In F₁, the Col-0 and La-0 genes in each pair of alleles suppress the dominant gene, which is responsible for the better expression of the "leaflet diameter" attribute, the recessive gene (Col-0 < COL-0 wt, La-0 < LA-0 wt). Hybrid plants of the first generation also have an additive polymer effect of non-allelic dominant COL-0^{wt} and LA-0^{wt} genes to increase the size of the leaf rosette. In the second generation there is a process of splitting hybrids, and their superiority in the diameter of the rosette of leaves over the parental forms is reduced. This is due to a decrease in the heterozygosity of plants in the F₂ generation. This can be explained by the assumption that the size of the rosette of leaves depends on two dominant non-allelic genes acting on this feature unambiguously. In hybrids of the second generation, the largest diameter of the rosette leaves the two dominant alleles COL-0 wt and LA-0 wt in the homo- or heterozygous state, whereas the combination of the recessive Col-0 and La-0 alleles in the homozygous state determines the small size of the leaf rosette.

Keywords: *Arabidopsis thaliana* (L.) Heynh; Heterosis; Gene; Mutation; Race

Introduction

Heterosis is widely used in crop production to increase yields and is applied to more types of crops. Until the mid-twentieth century, the mechanism of heterosis was mainly explained by the

hypotheses of dominance and overdominance. According to the hypothesis of dominance, heterosis is associated with three effects of the action of dominant genes: their suppression of harmful recessive alleles, an additive effect, and a nonallelic complementary interaction [1]. The overdominance hypothesis explains the

effect of heterosis by the interaction between the dominant and recessive alleles of the same gene, which in the heterozygote perform somewhat different functions and can therefore mutually complement each other [2].

Unfortunately, these two hypotheses cannot fully explain the nature of the phenomenon of heterosis. The theory of dominance cannot explain why, in free-growing maize and rye varieties, the removal of recessive genes harmful in the homozygous state does not lead to an increase in their yield. In fact, the adverse effect of recessive genes appears, as a rule, only when they are in a homozygous state. In the heterozygous state, most recessive genes do not adversely affect the viability of the organism [3,4]. A retrospective analysis of breeding improvement of maize showed that the elimination of harmful recessions by inbreeding does not change the relative advantage of F_1 hybrids [5]. From the standpoint of the theory of dominance, it is also difficult to explain heterosis in polyploids, which increases with the number of polyploid genomes [6].

The theory of overdominance is associated with contradictions in the fact that this model implies a complementary effect in the interaction between alleles within one locus, and while most agronomic signs have a polygenic character of manifestation [7]. It is assumed that the effect of heterosis in one or a small number of loci is associated with a change in regulatory networks [8].

Theories of overdominance and dominance also cannot explain why heterosis often does not occur in F_1 hybrids. Far from any crossing in plants F_1 is manifested heterosis, and also not always its manifestation is discrete: it can manifest itself in one productivity element, in another it is not [9]. If heterosis was due to a simple set of dominant alleles or allelic interaction of genes in the heterozygous state that are present in the population, then this set would be easy to make up by a series of crosses and get heterotic combinations.

Bircler JA., *et al.* [10] believe that heterosis is due to the selection of alleles over the years in the "correct" set of loci that create the best combinations during hybridization.

From the mid-50s of the twentieth century to the beginning of the twenty-first century, a number of hypotheses emerged in explaining the mechanism of heterosis, among which there

are: genetic, metabolic and bioenergetic balances. According to the hypothesis of the genetic balance of heterosis, it should be considered as the cumulative effect of the phenotypically similar action of heterogeneous genetic processes. From the point of view of the hypothesis of the metabolic balance of heterosis, the result is a result of biochemical reactions, each of which is controlled by one or more specific enzymes. In this case, the heterosis effect is manifested in the coordination of all reactions and systems for efficient growth in the medium. From the standpoint of the bioenergy concept, heterosis is due to the bioenergy balance arising in the heterozygous state when genetic blocking is lifted due to the compensatory action of the genomes of the parental forms carrying segregated loci of bottlenecks of metabolic metabolism [11].

In order to solve the problem of the mechanism of heterosis, the use of *Arabidopsis thaliana* (L.) Heynh is successful. as a model plant. Studies on model objects are always considered to be leading. They allow the development of new genetic approaches that can later be used on other objects.

Within a large species range of *Arabidopsis*, a large number of races differing in morphophysiological indicators: winter and spring, early and late, with the presence or absence of a period of deep dormancy in seeds, etc., have been settled [12]. Currently, the world collection of *A. thaliana* contains about 750 different ecotypes from around the world.

In the world centers of the genetic resources of *Arabidopsis* there are many races, usually named after settlements, near which the seeds were first collected in natural conditions. Two of these races are Landsberg from Germany and Columbia from the USA, which are abbreviated respectively as La-0 and Col-0 [13].

Now the race Col-0, through sequencing in 2000, of its genome has become a popular subject for genetic, molecular, biological and other studies. In particular, it is also actively used in studies on induced mutagenesis [14]. On the genetic basis of the race Col-0, a large number of mutations and mutant lines have already been obtained.

Externally, the aerial parts of plants of the races Col-0 and La-0 do not differ in principle between themselves. However, compared to La-0, the race Col-0 is characterized by a longer developmental period of about 3.5 months, a more powerful habit, and a higher yield [12].

Given the vagueness of the question about the nature of the heterosis phenomenon, the purpose of this work was to study the heterosis effect from the point of view of allelic and nonallelic gene interaction in F1 hybrids from crossing the ecotypes Col-0 and La-0.

Materials and Methods

The material for research was the plants *Arabidopsis thaliana* (L.) Heynh. ecotype (race) of Columbia (Col-0) and Landsberg (La-0). The seeds of the races were obtained from the Nottingham *Arabidopsis* Stock Center (NASC), UK.

Plants were grown in the laboratory in soil culture in a mixture of soil, sand and peat in the ratio of 4: 2: 1 [15]. As vessels for the cultivation of plants, used plastic pots with a capacity of 100 - 1253 cm.

Seeds for sowing were prepared by vernalization for 5 days at a temperature of 4 - 60°C and subsequent one-day germination at room temperature. Tubes to protect from heat and light on the roots of plants wrapped with two layers of paper. Plants were cultivated at a temperature of 18 - 20°C, illumination around the clock within 4000 - 7000 lx.

Castration and forced hybridization were performed under a microscope of the type MBS-9. Genetic analysis of the inheritance of traits in plants was performed in F₁, F₂. The sample size in the second generation was 186 plants. When observing the plants, they were guided by generally accepted methods of vegetative and comparative morphological studies [16]. Mathematical processing of the results was performed according to the methods described by BA Dospikhov [16] and GF Lakin [17].

Results

When two plants of different races Col-0 and La-0 were crossed, all F₁ hybrids (genotype COL-0 wt Col-0 LA-0 wt La-0) had a larger leaf rosette size than the parental forms. Like the wild type, the rosette leaves of the first generation hybrids had an oval shape. From self-pollination of such plants in F₂ 15/16 of all plants were with a large diameter of the rosette of leaves and 1/16 with a small size of the rosette of leaves (Table 1).

Designation	COL-0 ^{wt} LA-0 ^{wt} COL-0 ^{wt} La-0 La-0 Col-0 Col-0 LA-0 ^{wt}	Col-0 Col-0 La-0 La-0	Total
f	170	16	186
f ¹	174	12	186
d	-4	4	
d ²	16	16	
χ ²	0,09	1,25	1,34

Table 1: Splitting in the F₂ generation by the Col-0 and La-0 genes.

A more powerful development in F₁ hybrids of the diameter of the rosette of leaves in comparison with the initial forms can be explained by somatic heterosis, which increases the linear dimensions of the hybrid plant and its mass. The manifestation of heterosis in hybrid plants of the first generation is associated with allelic interaction of genes (suppression of recessive alleles by dominant genes) and additive polymeric intergenic interaction.

In F₁, the genes Col-0 and La-0 in each pair of alleles are suppressed by the dominant gene, which is responsible for the best expression of the sign "diameter of the rosette of leaves", the recessive gene (Col-0 < COL-0 wt, La-0 < LA-0 wt). In addition, in hybrid plants of the first generation, an additive polymer effect of nonallelic dominant genes COL-0 wt and LA-0 wt appears on the increase in the size of the rosette of leaves. In the second generation, the process of splitting hybrids occurs, and their superiority in the diameter of the rosette of leaves over the parental forms is reduced. This is due to a decrease in plant heterozygosity in the F₂ generation.

This can be explained by assuming that the size of the rosette of leaves depends on the two dominant nonallelic genes uniquely acting on this trait. In this case, in hybrids of the second generation, the largest diameter of the rosette of leaves is determined by two dominant alleles COL-0 wt and LA-0 wt in the homozygous or heterozygous state, whereas the combination of the recessive alleles Col-0 and La-0 in the homozygous state determines the small size rosettes of leaves. The value of the diameter of the rosette of leaves depends on the number of dominant and

recessive genes in the genotype. The presence of dominant alleles of two different genes COL-0 wt and LA-0 wt in the homozygous or heterozygous state (COL-0 wt _ LA-0 wt _) determines in 9/16 plants the maximum size of the rosette of leaves. The presence of only one La-0 recessive allele in the homozygous state (COL-0 wt _ La-0 La-0) or only another recessive allele Col-0 also in the homozygous state (Col-0 Col-0 LA-0 wt _) determines 6/16 plants have different intermediate values of the diameter of the rosette of leaves. The homozygous state of both recessive genes Col-0 Col-0 La-0 La-0 results in a small size of a rosette of leaves in 1/16 of the plants. These results can be explained by the polymeric effect of two different genes Col-0 and La-0 on the development of the same sign "rosette diameter of leaves".

In the considered crossing, a stronger development of the diameter of the rosette of leaves is associated with the action of two pairs of genes. At the same time, the additive polymer effect of nonallelic dominant genes on the development of the trait "diameter of the rosette of leaves" can also manifest itself under the action of three or more pairs of alleles. The more pairs of additive polymeric nonallelic genes favorably influence the development of the diameter of the rosette of leaves, the more powerful the manifestation of this trait in first generation hybrid plants will be.

To determine the genotypes of the F₂ plants, analyzing crosses with a recessive homozygote for the trait under study were carried out. When plants with the largest diameter of the rosette leaves are crossed with plants with a small rosette size, the offspring was obtained in the first case only with a large diameter of rosette leaves, while in the second - 1/4 of it was from the large rosette size of the leaves, 2 / 4 - with an average diameter of rosette leaves (typical for the wild type), and 1/4 - with small rosette leaves.

In the first case, splitting was not observed as a result of the analyzing cross, and all plants in F₁ had a large diameter of rosette leaves. Therefore, the maternal form, which was taken for analyzing crosses, was homozygous for two pairs of genes (COL-0 wt COL-0 wt LA-0 wt LA-0wt). In the second case, analyzing crosses in F₁, splitting by phenotype occurred in a ratio of 1 : 2: 1. In this regard, the maternal form was heterozygous for two pairs of genes (COL-0 wt Col-0 LA-0 wt La-0).

COL-0 wt COL-0 wt LA-0 wt LA-0 wt (large diameter of the rosette leaves) x Col-0 Col-0 La-0 La-0 (small size of the rosette leaves) → COL-0 wt Col-0 LA-0 wt La-0 (large diameter rosette leaves).

COL-0 wt Col-0 LA-0 wt La-0 (large diameter of the socket leaves) x Col-0 Col-0 La-0 La-0 (small size of the socket leaves) → 1/4 COL-0 wt Col-0 LA-0 wt La-0 (large diameter of rosette leaves): 2/4 COL-0 wt Col-0 La-0 La-0; Col-0 Col-0 LA-0 wt La-0 (average size of rosette leaves, typical of the wild type): 1/4 Col-0 Col-0 La-0 La-0 (small leaves of the rosette).

At the same time, when plants with an average diameter of a rosette of leaves were crossed with plants that had small sizes of a rosette of leaves, progeny were obtained in the first case only with an average size of a rosette of leaves, whereas in the second case half of it was with an average size of a rosette. and half - with small leaves rosettes.

In the first case, splitting was not observed as a result of the analyzing crossing and all plants in the first generation had an average diameter of the rosette leaves, typical of the wild type. In this regard, the mother form can be in one embodiment a dominant homozygous for the first pair of genes, in the second - a recessive homozygote (COL-0 wt COL-0 wt La-0 La-0), while in another, on the contrary, a recessive homozygote on the first pair of genes, on the second - the dominant homozygote (Col-0 Col-0 LA-0 wt LA-0wt).

COL-0 wt COL-0 wt La-0 La-0 (average diameter of the rosette leaves) x Col-0 Col-0 La-0 La-0 (small size of the rosette leaves) → COL-0wt Col-0 La-0 La-0 (average diameter of rosette leaves).

Col-0 Col-0 LA-0 wt LA-0 wt (average outlet diameter of the leaves) x Col-0 Col-0 La-0 La-0 (small size of the outlet leaves) → Col-0 Col-0 LA-0 wt La-0 (average diameter of rosette leaves).

In the second case, the analyzing crossing in F₁ was split by phenotype in the ratio of 1: 1. In this regard, the maternal form may be in one embodiment a heterozygote for the first gene, for the second - a recessive homozygote (COL-0 wt Col-0 La-0 La-0), and in another embodiment, on the contrary, a recessive homozygote for the first gene, the second is heterozygous (Col-0 Col-0 LA-0 wt La-0).

COL-0 wt Col-0 La-0 La-0 (average diameter of the rosette leaves) x Col-0 Col-0 La-0 La-0 (small size of the rosette leaves) → 1/2 COL-0 wt Col-0 La-0 La-0 (average diameter of rosette leaves): 1/2 Col-0 Col-0 La-0 La-0 (small rosette leaves).

Col-0 Col-0 LA-0 wt La-0 (average outlet diameter of the leaves)
 x Col-0 Col-0 La-0 La-0 (small size of the outlet leaves) → 1/2 Col-0
 Col-0 LA-0 wt La-0 (average diameter of rosette leaves): 1/2 Col-0
 Col-0 La-0 La-0 (small rosette leaves).

It is well known that the polymer interaction of genes is characteristic of all quantitative traits. Conditionally distinguish non-cumulative and cumulative polymers. A non-cumulative polymer is characterized by the fact that for the full manifestation of the trait of a sufficiently dominant allele of one of the polymeric genes. In this case, the splitting in F_2 according to the phenotype during dihybrid crossing occurs in the ratio of 15: 1. In cumulative polymers, the degree of expression of a trait depends on the number of dominant alleles of both the same and different polymeric genes. In this case, with hybrid crossing, splitting in F_2 according to the phenotype occurs either in the ratio 1: 4: 6: 4: 1 with incomplete dominance of the trait, or 9: 6: 1 with complete dominance. Typically, quantitative traits are inherited by the type of cumulative polymers [18].

As a rule, the division of signs into qualitative and quantitative is conditional. Any quantitative trait can be reduced to a qualitative trait. Then the interaction of genes in the inheritance of such a feature occurs in a non-cumulative polymer in the ratio of 15: 1. This we observe in our study when crossing plants of the races Col-0 and La-0.

Discussion and Conclusion

In recent years, it has become increasingly clear that the problem of the mechanism of heterosis requires a return to a detailed analysis of the genetics of characters. The emergence of heterosis in hybrids of the first generation can be explained on the basis of the allelic and nonallelic interaction of genes, which creates a favorable combination of genes during hybridization, causing the best manifestation of an economically valuable trait. Allelic interaction of genes is mainly manifested in the complete or incomplete dominance of the dominant gene over the recessive gene of one allelic pair, as well as in codominance, when the external manifestation of a trait is a mixture of the action of both alleles of the same allelic pair. The intergenic interaction of genes is usually expressed in four basic forms: complementarity, epistasis, polymers, and modifying action. Due to the fact that practically all forms of intergenic nonallelic and allelic interaction of genes are observed in the mechanism of manifestation of heterosis, this phenomenon has so far been difficult to explain.

The emergence of heterosis in F_1 hybrids is usually due to the six effects of genes. Of which, two effects are associated with allelic interaction of genes: suppression of recessive alleles by dominant genes, codominance (a mixture of the action of both alleles of one allelic pair). The other four effects are caused by intergenic interaction of genes: additive polymer action, nonallelic complementary interaction, epistasis, and modifying action.

At the same time, allelic and nonallelic interaction of genes, in particular, incomplete dominance, epistasis and the modifying effect of genes, can have a negative impact on the direction of heterosis. For example, with incomplete dominance, an intermediate variant of the manifestation of the trait is observed.

For the emergence of a heterosis usually requires the following requirements: 1. heterozygosity of the hybrids of the first generation; 2. suppression in F_1 for each allelic pair by dominant genes of recessive alleles; 3. the interaction between the dominant and recessive alleles of one gene in the form of codominance; 4. additive polymeric intergenic interaction of genes; 5. nonallelic complementary gene action; 6. modifying interaction of genes.

Let us consider in detail each of these phenomena. Heterosis occurs in first-generation hybrids that are in a heterozygous state. At the same time, the rule of uniformity of F_1 hybrids is observed, that is, the First Law of Mendel. In the homozygous dominant and recessive state of genes, heterosis usually does not occur. In the second generation, with mono-, di-, and polyhybrid crossing, the process of splitting hybrids is underway, and their superiority in terms of economically valuable traits over parental forms is reduced. Complied with the second and third laws of Mendel. This is due to a decrease in plant heterozygosity in the F_2 generation. Therefore, it is not possible to consolidate the advantage of heterozygotes in the second and subsequent generations. The development of methods of fixing heterosis is an important task of selection, since the use of this phenomenon is possible only in F_1 hybrids. In this regard, many crops, in particular sunflower, corn, have to conduct complex seed farming. The solution of the fixation of heterosis would simplify and cheapen its practical use in crop production.

According to the American geneticist V. Shell, the grain yield of heterotic maize hybrids decreases on average in F_2 by 35%, and in F_3 by 50% compared with the yield of F_1 hybrids. These data are confirmed by the works of other researchers [3].

In hybrids of the first generation in heterozygote for each allelic pair, the recessive alleles are suppressed by dominant genes. Usually, one self-pollinating line for each allelic pair carries a recessive gene, and the second is the dominant gene (aaBB x AaBB). When two self-pollinating lines are crossed in F1 hybrids (AaBB) in each pair of alleles, as a rule, the wild type dominant gene is suppressed, which is responsible for the best expression of the economically useful trait, the recessive gene ($a < A, B < B$).

In hybrids of the first generation in heterozygote for each allelic pair, the recessive alleles are suppressed by dominant genes. Usually, one self-pollinating line for each allelic pair carries a recessive gene, and the second is the dominant gene (aaBB x AA \overline{bb}). When two self-pollinating lines are crossed in F1 hybrids (AaBB) in each pair of alleles, as a rule, the wild type dominant gene is suppressed, which is responsible for the best expression of the economically useful trait, the recessive gene ($a < A, B < B$).

The manifestation of the dominance of the trait is conditional and depends on the selection of parental pairs and many other factors. In this regard, breeders have to carry out difficult work to create inbred lines and assess their combination value. The dependence between the yield of self-pollinated lines and hybrids obtained from their crossing was studied by many scientists. At the same time, there is no clear connection between the productivity of hybrids and their component lines [19].

In some cases, when heterosis occurs, hybrids of the first generation will interact between the dominant and recessive alleles of the same gene in the form of codominance. At the same time, the external manifestation of a trait is a mixture of the action of both alleles. For example, people who are heterozygous for the blood hemoglobin gene that causes sickle cell anemia are more resistant to tropical malaria than homozygous for both the dominant and the recessive genes of this allelic pair [20]. In flax lines, a specific gene from a series of multiple alleles confers resistance to one specific race of rust, and heterozygotes for these genes show resistance to two races [21].

In the main, when heterosis occurs in F₁ hybrids, an additive polymer intergenic interaction of genes is observed. Heterosis is manifested by the stronger, than self-pollinated lines, by their hereditary features, better complement each other in terms of additive polymer intergenic interaction of genes.

For example, when crossing two varieties of peas in F1 hybrids, heterosis was observed in plant height compared to parental forms. This is due to the effect on the stem length of two different dominant genes. One gene caused lengthening of internodes, another - increased their number. Dominant genes can have a summing effect in all cases where they determine the components of a complex quantitative trait. Thus, the mass of grain per corn cob is determined by the number of grains in a row and a mass of 1000 grains [3].

The polymeric nature of the action of genes is widely used in breeding and is directly related to heterosis. Typically, the type of polymer interaction of genes in plants inherits many economically useful traits, such as the amount of protein in the endosperm of maize and wheat grain, the sugar content of beet roots, ear length, corn cob size, the content of vitamins in fruits, and many others, including and the length of the roots. Knowing the patterns of inheritance of these traits in the interaction of genes, it is possible by crossing with the correct selection of parental pairs as a result of genetic recombination to obtain plants with a positive transgressive combination of polymer genes of additive action in one genotype, which determine a stronger degree of economic trait compared to both parental forms.

Sometimes, when heterosis occurs, hybrids of the first generation will have a nonallelic complementary interaction of genes that may have a stronger influence on the development of a trait or condition the development of a new trait. For example, heterosis caused by the interaction of complementary genes was observed in an increase in the rate of root growth in nutrient solutions in a hybrid obtained by crossing two varieties of tomato Red Karent and Johannesfeir. Due to the interaction of two nonallelic complementary dominant genes, the hybrid manifested heterosis, manifested in a more powerful root development, since difficulties in biosynthesis at both loci controlling the formation of vitamins necessary for good development of the tomato root system were overcome [18].

Thus, the basis of the mechanism of heterosis is the allelic and nonallelic interaction of genes, which creates a favorable combination of genes, causing the best manifestation of an economically valuable trait. At the same time, the occurrence of heterosis in F1 hybrids is due to a variety of gene effects. Of which, some of the effects are associated with the allelic interaction of

genes: the suppression of recessive alleles by dominant genes, codominance (a mixture of the action of both alleles of one allelic pair). Other effects are determined by intergenic interaction of genes: additive polymeric action, nonallelic complementary interaction, epistasis and modifying action. The nature of the phenomenon of heterosis can be explained by the hypothesis proposed by us of the allelic and nonallelic mechanism of heterosis, according to which the advantage of F_1 hybrids over parental forms is due to different types of allelic and nonallelic interaction of genes, which creates the best combination of genes that determine the optimal expression of an economically valuable trait.

Compliance with Ethical Standards

The authors declare no conflict of interest. This article does not contain any studies with human participants or animals performed by any of the authors.

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