

## GENETIC BASES OF HETEROSIS AND ITS CONTRIBUTION TO MODERN AGRICULTURE

### BASES GENÉTICAS DA HETEROSE E SUA CONTRIBUIÇÃO PARA A AGRICULTURA MODERNA

### BASES GENÉTICAS DE LA HETEROSIS Y SU CONTRIBUCIÓN A LA AGRICULTURA MODERNA



<https://doi.org/10.56238/sevened2026.019-046>

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#### ABSTRACT

Heterosis, or hybrid vigor, is the phenomenon in which hybrid individuals exhibit superior performance compared to their parents, particularly in traits such as growth, productivity, and physiological vigor. This phenomenon is of great importance in plant breeding and is widely used in crops such as maize and rice, where it significantly contributes to increased agricultural productivity. Studies on heterosis began in the 18th century with hybridization experiments and were later expanded by researchers such as Mendel, Darwin, and Shull, who observed greater vigor in plants derived from crosses compared to those obtained through self-fertilization. From these studies, heterosis began to be applied in the production of hybrid cultivars. Several hypotheses have been proposed to explain the genetic basis of heterosis, with the dominance, overdominance, and epistasis theories standing out, involving different forms of gene interaction. Despite scientific advances, the phenomenon is still not fully understood and remains the subject of studies in molecular genetics and genomics. The measurement of heterosis can be performed using different methods, comparing the performance of the hybrid with that of its parents or with standard cultivars. Its application provides benefits such as higher productivity, plant uniformity, and greater efficiency in genetic improvement. Thus, heterosis represents one of the most important contributions of genetics to agriculture, being essential for the development of more productive cultivars adapted to market demands.

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**Keywords:** Genetic Improvement. Gene Interactions. Hybrid Vigor.

## RESUMO

A heterose, ou vigor híbrido, é o fenômeno em que indivíduos híbridos apresentam desempenho superior em relação aos seus genitores, destacando-se em características como crescimento, produtividade e vigor fisiológico. Esse fenômeno possui grande importância no melhoramento genético de plantas, sendo amplamente utilizado em culturas como o milho e o arroz, onde contribui significativamente para o aumento da produtividade agrícola. Os estudos sobre heterose tiveram início no século XVIII, com experimentos de hibridação, sendo posteriormente aprofundados por pesquisadores como Mendel, Darwin e Shull, que observaram maior vigor em plantas provenientes de cruzamentos em comparação àquelas obtidas por autofecundação. A partir desses estudos, a heterose passou a ser aplicada na produção de cultivares híbridas. Diversas hipóteses foram propostas para explicar a base genética da heterose, destacando-se as teorias da dominância, sobredominância e epistasia, que envolvem diferentes formas de interação entre genes. Apesar dos avanços, o fenômeno ainda não é totalmente compreendido, sendo objeto de estudos em genética molecular e genômica. A mensuração da heterose pode ser realizada por diferentes métodos, comparando o desempenho do híbrido com seus genitores ou com cultivares padrão. Sua utilização proporciona benefícios como maior produtividade, uniformidade das plantas e maior eficiência no melhoramento genético. Dessa forma, a heterose representa uma das mais importantes contribuições da genética para a agricultura, sendo fundamental para o desenvolvimento de cultivares mais produtivas e adaptadas às necessidades do mercado.

**Palavras-chave:** Melhoramento Genético. Interações Gênicas. Vigor Híbrido.

## RESUMEN

La heterosis, o vigor híbrido, es el fenómeno en el que los individuos híbridos presentan un desempeño superior en relación con sus progenitores, destacándose en características como crecimiento, productividad y vigor fisiológico. Este fenómeno posee gran importancia en el mejoramiento genético de plantas, siendo ampliamente utilizado en cultivos como el maíz y el arroz, donde contribuye significativamente al aumento de la productividad agrícola. Los estudios sobre heterosis comenzaron en el siglo XVIII con experimentos de hibridación y posteriormente fueron profundizados por investigadores como Mendel, Darwin y Shull, quienes observaron un mayor vigor en plantas provenientes de cruzamientos en comparación con aquellas obtenidas por autofecundación. A partir de estos estudios, la heterosis pasó a aplicarse en la producción de cultivares híbridos. Diversas hipótesis fueron propuestas para explicar la base genética de la heterosis, destacándose las teorías de la dominancia, sobredominancia y epistasia, que involucran diferentes formas de interacción entre genes. A pesar de los avances científicos, el fenómeno aún no se comprende completamente y sigue siendo objeto de estudios en genética molecular y genómica. La medición de la heterosis puede realizarse mediante diferentes métodos, comparando el desempeño del híbrido con sus progenitores o con cultivares estándar. Su utilización proporciona beneficios como mayor productividad, uniformidad de las plantas y mayor eficiencia en el mejoramiento genético. De esta manera, la heterosis representa una de las contribuciones más importantes de la genética a la agricultura, siendo fundamental para el desarrollo de cultivares más productivos y adaptados a las necesidades del mercado.

**Palabras clave:** Mejoramiento Genético. Interacciones Gênicas. Vigor Híbrido.

## 1 INTRODUCTION

One of the greatest events in the history of plant breeding was the discovery of the phenomenon of heterosis, also known as hybrid vigor. Heterosis represents the superiority of the hybrid over its parents. According to FEHR, 1987, heterosis is the increase in vigor, plant height, carbohydrate content, productivity and intensity of physiological phenomena among contrasting individuals.

The heterosis value can be quantified using the difference between the mean values of generation F1 and of parents father 1 (P1) and father 2 (P2), with the result expressed as a percentage, considering the average value of the parents equals 100. However, for practical and commercial purposes, heterosis is measured in relation to the superior parent (heterobeltiosis) or of greater economic importance (standard heterosis) (PATERNIANI, 1974).

Growth rate, fertility, biomass and productivity are among the traits where heterosis, or hybrid vigor, is often evaluated in plants. In no other cultivated species, heterosis had, and continues to have, as much impact as in maize, responsible for a continuous increase in productivity in the last century. But heterosis is also observed in autogamous species, such as rice. The impact of the use of hybrid vigor in rice is responsible for the large increase in crop productivity in China, and now in other countries. This result, again, is due to the combination of classical breeding methods based on extensive phenotypic analysis (FERREIRA ; FALEIRO, UNDATED).

For the breeder of vegetable or fruit species, the visual aspect and the size of the fruit are often more important than the productivity itself. For example, the Hawaii papaya market values fruits with an average weight of 200 to 250 grams. In this case, heterosis will become undesirable if its manifestation results in fruits with weight above these values (BORÉM; MIRANDA, 2009).

Several hypotheses have been elaborated in an attempt to explain the phenomenon of heterosis, highlighting the theses of dominance, overdominance and epistasis. All these hypotheses suggest that the contribution of many genes is responsible for the greater vigor of hybrids in relation to inbred lines.

## 2 HISTORY OF HETEROISIS

Heterosis began to be studied by Koelreuter (1761-1766), who observed in an experiment with tobacco crossing that the F1 hybrids had more vigor and that such hybrids received the characteristics of their parents. After Koelreuter's experiments, Mendel and Darwin

in experiments carried out with crossbreeding, they also realized that plants were larger than plants from self-fertilization (MOTA, 2011).

Gregor Mendel, in 1865, crossed peas with a length of 0.30m x 1.80m and obtained in the F1 generation plants between 1.80m and 2.25m, observing the superiority of the descendants.

Charles Darwin (1876) made detailed observations of various characteristics (height, weight, number of grains, color, fertility, etc.) in a wide and varied set of plants, comparing plants that were self-fertilized with plants of the same species crossed. Among the observations carried out, sterility and lower vigor in the self-fertilized offspring of some species stand out. Although this study has great repercussion due to the volume of information collected regarding the effects of inbreeding and heterosis, it does not delve into the mechanisms of inheritance.

The hybridization work began with BEAL using intervarietal hybrids (BEAL, 1876), EAST (1908) and SHULL (1908, 1909) who established the inbreeding-hybridization system and JONES (1918), who suggested the use of double hybrids to enable the commercialization of the hybrid seed, these being the major initial contributions to the success of hybrid maize.

According to Goldman (1999), Darwin's work (1876) was inspired by botanist Asa Gray, mentor of William James Beal, who pioneered the modern concept of heterosis. Beal has focused his career on the production of intervarietal hybrids and the control of corn pollination.

The work developed by Beal and his students was repeated, conducted by George Espy Morrow and Frank Duane Gardner in 1890. The results indicated that individuals from controlled crosses showed wide variation in ear dimensions and higher productivity than the average of the parents (Morrow and Gardner, 1893), data that corroborate the results previously obtained by Beal.

In 1909, the American botanist and geneticist Shull showed that by fertilizing the plant with its own pollen, less vigorous offspring were produced. By repeating the process over the next seven or ten generations, the descendants fixed important agronomic characteristics. Plants that generated genetically similar offspring came to be called pure lines. SHULL noticed that two different pure lines, when crossed with each other, produced offspring with great vigor, called hybrid vigor or heterosis, giving rise to hybrid maize (CIB, 2006).

Heterosis only became important in plant genetic improvement after the studies of George Shull (1908), as he was the first to suggest how heterosis could be used to develop new cultivars, interpreting that heterosis is the opposite of depression by inbreeding. Shull believed that hybrid vigor was correlated with the degree of dissimilarity between gametes.

According to him, the greatest difference in the union of the gametes, up to a certain limit, increases the stimulus or vigor. (JOSÉ, 1992; CARBONERA, 1990).

The main expected effect of heterosis is related to a substantial increase in productivity and, without a doubt, the greatest impact produced by its use was on the production of hybrid corn, which, from the 20s onwards, began to be widely used in the United States and, later, in numerous other countries, and is therefore natural. that broader data are more available for maize than for another crop (PATERNIANI, 1975).

### **3 GENETIC AND MOLECULAR BASIS OF HETEROSIS**

Since its beginnings, modern genetics and plant breeding programs have tried to explain why, in certain crosses, the F1 hybrid is superior to the performance of homozygous parental lines, or the most vigorous of parental lines. There is great expectation about the unveiling of the molecular and physiological principles that are behind the phenomenon of heterosis. Molecular biology and genomics have recently contributed to shed light on the issue and potentially offer new strategies to capitalize on the hybrid increase in force by genetic improvement programs (FERREIRA ; FALEIRO, UNDATED).

Quantitative characters are influenced by allelic interactions. It can be of the additive type, complete or partial dominance, or overdominance. It is observed that in the additive interaction, the mean of F1 is equal to the mean of the parents, does not explore heterosis and symmetrical distribution is found in the F2 generation. In the dominance and/or overdominance interaction, the average of F1 is different from the average of the parents, and can explore heterosis. In this case, there is an asymmetric distribution in the F2 generation.

Several hypotheses have been suggested to explain the genetic basis of heterosis, including the dominance, overdominance, and epistasis hypotheses.

#### **3.1 THE DOMINANCE HYPOTHESIS**

The hypotheses to explain heterosis propose that hybrid vigor is the result of non-additive effects on the phenotype. The Dominance Theory was proposed by Bruce (1910). According to this theory, heterosis is a function of the accumulation of favorable dominant loci of different loci.

Model:  $AA = Aa > aa$

$AA=10 \ Aa=10 \ e \ aa=0$

Parental 1  
 $aaBBccDDee = 20$

x

Parental 2  
 $AAbbCCddEE = 30$

F1

$AaBbCcDdEe = 50$

$AABBCCDDEE = 50$

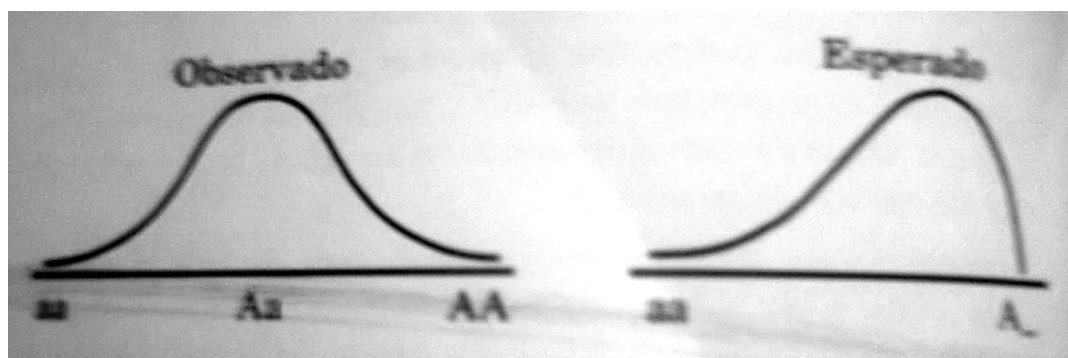
(1)

The main objection to this theory is that, theoretically, it would be possible to find inbred lines (homozygous) as productive as hybrids, which has never been observed in practice. Proponents of this theory respond to this objection by stating that the probability of this occurring is very small, due to the large number of genes involved.

According to Borém and Miranda (2009), in the first years after the proposition of the main hypotheses explaining heterosis, these were much questioned in several specialized journals. The dominance hypothesis was objected to four times in the debate forums. The first is that some researchers considered it too simplistic and non-explanatory. The second refers to the distribution in the F2 generation, which should be asymmetric, of the type  $(3A_+ + 1aa)^n$ , for n genes that affect the trait in question.

### Figure 1

*Expected and observed distributions of heterosis in the F2 generation*



Source: Google, 2026.

The third objection questioned the need for heterozygosity for the expression of vigor. It was argued that, if this hypothesis were correct, it would be possible to obtain an individual equally vigorous as an F1 hybrid and homozygous with respect to favorable dominant genes. However, an individual as vigorous as F1 has never been found that did not segregate.

In 1917, Jones introduced the concept of factorial linkage in the debates on heterosis and stated that hybrid vigor was a function of the interaction of dominant or partially dominant favorable alleles, coming from both parents. He also argued that if large numbers of alleles were involved in the manifestation of vigor, they would be linked and it would be extremely difficult to obtain all favorable alleles in a single homozygous individual.

The fourth objection to this hypothesis is based on the lack of evidence of dominance in the expression of quantitative traits. This criticism was immediately removed from the discussions, due to the experimental results that indicate partial or complete dominance as the main mode of inheritance of quantitative traits.

### 3.2 HYPOTHESIS OF OVERDOMINANCE

Theory that believes that the vigor presented by the F1 plants is due to high heterozygosity, that the union of the two allelic forms of the heterozygote is superior to the separate action of any of the alleles in homozygosis; the variability of protein forms in heterozygous plants would make them more efficient in the face of varying environmental conditions (CROW, 1948).

$$\begin{array}{l} \text{AA BB CC dd} \quad + \quad \text{aa bb cc DD} \\ \text{Value} \quad 10+12+10+5 = 37 \quad \quad 5 + 7 + 8 + 10 = 30 \end{array}$$

$$\begin{array}{l} \text{F1} \quad \quad \quad \text{Aa Bb Cc Dd} \\ \text{Value} \quad \quad \quad 11+13+11+11 = 46 \end{array}$$

(2)

There are many cases in which the gene action of dominance has been detected, and very few cases of the occurrence of overdominance.

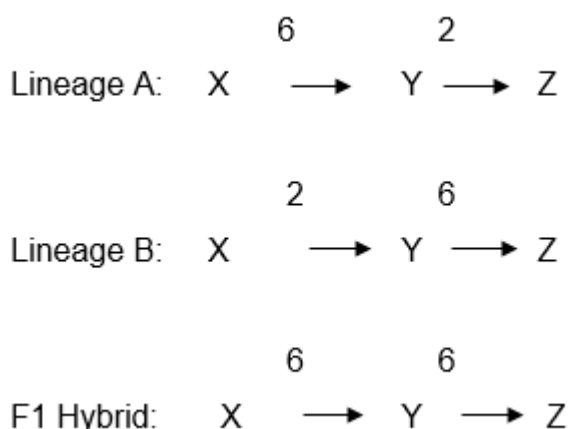
### 3.3 HYPOTHESIS OF EPISTASIS

The epistasis hypothesis considers the interallelic epistatic interactions of two or more loci as the main factor of superiority in the phenotypic expression of a trait in hybrids and involves the epistatic effects additive x additive, additive x dominant and dominant x dominant (POWERS, 1945; BETRÁN et al., 2004).

Epistasis was also investigated by PATERNIANI (1974) as to its possible effect on heterosis. For corn, it proved to be important in terms of days for flowering, ear height and productivity.

According to Borém and Miranda, 2009, epistasis can explain heterosis in the following situations:

- **Complementary gene action.** Considering that the  $A\_bb$  and  $aaB\_$  parents have a relative value equal to zero, the hybrid  $AaBb$  of the cross of these parents may express heterosis with a relative value equal to 2. The gene segregation of two complementary genes, such as those previously described, is 9:7 in the F2 generation. This same idea is extended to quantitative characters, that is, there is a need for favorable alleles from all *loci* for the manifestation of heterosis.
- **Limiting reaction.** Considering that vigor occurs due to a series of reactions that can be limiting



(3)

In lines A and B, only two units of product Z are produced, due to the limitation imposed in one of the stages of the reaction, while in the hybrid, because of the epistatic action of the genes, six units of Z are produced. This hypothesis was presented by Hegeman, Leng and Dudley, in 1967, in the article "A biochemical approach to corn breeding".

- **Multiplicative sum.** Considering the total production of maize seeds with the result of the number of rows of seeds and the number of seeds per row on the cob, also considering that the number of rows and the number of seeds/row are complementarily additive characteristics, the hybrid F1 will present intermediate values to the parents for the number of rows and seeds/row, but it will manifest heterosis as to the total number

of seeds. This explanation of heterosis based on the multiplicative sum between additive traits was presented by Mayo (1980).

#### **4 GENETIC COLLINEARITY AND HETEROSIS**

Conclusions about the genetic causes of heterosis are difficult, because the quantitative genes involved in the control of traits are still poorly known (BERNARDO, 2002). Two areas of genomics have recently been used to understand heterosis: the analysis of the structural genome, on the one hand, through the re-sequencing of genomic regions that contain QTLs associated with the control of heterosis; and the analysis of global gene expression, in general, through DNA microarrays. The contribution of the analysis of the structural genome of some maize gene regions reveals that, at least in this species, heterosis and depression by inbreeding can be explained by the numerous deletions/insertions of genes and retrotransposons identified in regions that, theoretically, should be collinear in the genome of the species (FU; DOONER, 2002).

The model of complementation of non-collinear regions is compatible with the dominance hypothesis, and explains both the observed vigor and the depression by inbreeding. The model may also explain why genetic distance, by itself, is not a good indicator of hybrid vigor. In other words, if several lineages of a species are analyzed based on polymorphism of molecular markers and the data used to estimate genetic distance, the hybrids between the genetically most distant lineages are not necessarily the ones with the greatest heterosis. However, this may be true when lineages are derived from common ancestors that have undergone insertions/deletions over time, characterizing different complementary groups that, in essence, would be the basis of heterotic groups. Skeptics of the structural genomics explanation for hybrid vigor suggest that the evaluation is adequate for maize, but other mechanisms must be acting on the expression of heterosis, since differences in microcollinearity would not be as significant in other species as observed in maize (FERREIRA ; FALEIRO, UNDATED).

**Figure 2**

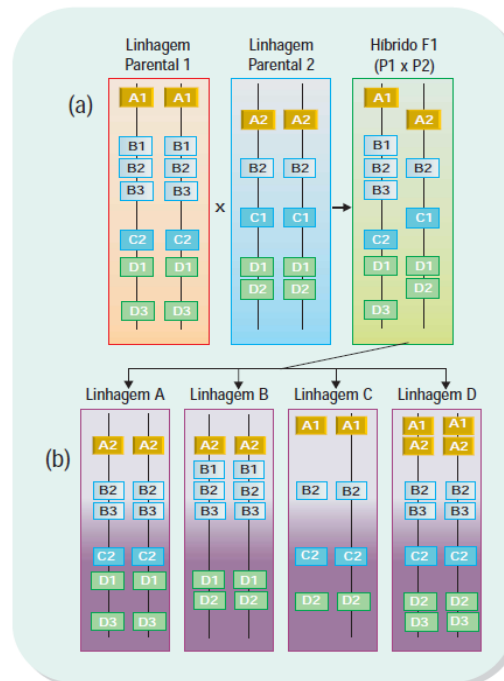


Fig. 5. O re-seqüenciamento de regiões do genoma associadas ao controle de heterose em linhagens de diferentes grupos heteróticos de milho (*Zea mays* L.) indica que a alteração de microcolinearidade nestas regiões do genoma é responsável pela heterose em híbridos F1 e por depressão por endogamia. O vigor híbrido é explicado por complementação de genes de diferentes famílias gênicas (A, B, C e D) nas regiões seqüenciadas (a). A depressão por endogamia é explicada pela ausência de genes na região seqüenciada em linhagens puras derivadas do híbrido F1 depois de repetidas gerações de recombinação e autofecundação (b).

Source: Google, 2026.

## 5 MEASURING HETEROSIS

Different concepts can be used to measure the degree of heterosis of a cross. Traditional heterosis is calculated by the difference between the value of the hybrid (F1) and the average of its parents (P1 and P2).

Traditional heterosis:

$$h (\%) = F1 - (P1 + P2 / 2) \times 100 \quad (4)$$

Another concept that can be used is that of heterobiosis, which estimates the degree of heterosis in relation to the best parent (PM).

$$3 \text{ Heterobiosis } (\%) = F1 - MP \times 100 \quad (5)$$

In standard heterosis, heterosis is estimated in relation to a standard cultivar (CP).

$$\text{Standard Heterosis (\%)} = F1 - CP \times 100 \quad (6)$$

## 6 IMPORTANCE OF HETEROSIS FOR AGRICULTURE

Heterosis is one of the greatest contributions of Genetics to world agriculture. According to PATERNIANI (1978) the advantages of using hybrid or heterosis vigor are:

- Associate characteristics of different parents in the shortest possible time;
- Obtain superior genotypes in a relatively short timeframe;
- Use gene interactions in hybrid generation;
- Produce uniform genotypes;
- Achieve less interaction with the environment in the F1 generation;
- To produce hybrid corn seeds commercially, with favorable effects on the region's economy.

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