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Investigating the molecular mechanisms of heterosis in plant breeding

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Abstract

The past century or more have seen extensive inbreeding of plant species, leading to the development of numerous new hybrid plant kinds. In agriculture, hybrids are typically superior to their inbred parents, both in terms of productivity and disease resistance. These hybrids have improved yields and disease resistance in agriculture compared to their inbred parents. Studies of this kind are being conducted to comprehend the heterotic impacts of heterotic loci. The enormous amounts of data and information that will be produced by molecular studies of heterotic loci and genes will be utilized by hybrid breeding that is based on molecular design in the future. This will be achievable because hybrid breeding will be able to benefit from the fact that heterotic loci and genes will be the subject of molecular investigations. This will allow for the creation of hybrids with desirable characteristics of both their parent species. These investigations will function as an important source of information. The purpose of this study is to investigate current developments in our knowledge of the genetic and molecular pathways that are accountable for heterosis in plant populations. In addition, the unanswered scientific problems regarding the molecular basis of heterosisare discussed here, as are the prospective uses in breeding.

Keywords: Heterosis, loci, hybridization, hybrid, moleculars

1. Introduction

The phenomenon of heterosis, which is often referred to as hybrid vigor, has interested researchers and breeders for more than a century. It is a comparison between the improved performance of hybrid offspring and the inbred performance of their parental lines concerning a variety of characteristics, including yield, growth rate, disease resistance, and stress tolerance. The utilization of heterosis has substantially enhanced both the quantity and quality of crop production, which has led to a revolution in agricultural practices

(Pansare*et al.,* 2023). MS is a condition that affects plants that occurs when the male reproductive organs of the plant develop irregularly and do not engage in the sexual process. Multiple sclerosis can be generated by nuclear genes by themselves or by mitochondrial genes that are related to nuclear genes. Both types of multiple sclerosis are referred to as cytoplasmic-nuclear multiple sclerosis (CMS) (Li *et al.,* 2019). As plants naturally anchor themselves in the soil, they inherently encounter a diverse array of both biotic and abiotic stresses throughout their life cycles. One of the most important environmental stress factors that can have an effect on plant growth, development, and even crop production is salt (mostly NaCl) stress. A significant amount of information suggested that at least 20% of the farmed area is severely impacted by salt stress. To guarantee adequate food production, it is necessary to increase the resistance of plants to the adverse effects of salt stress (Cheng *et al.,* 2022). Since ancient times, heterosishas been observed and documented and it is known to exist in a large variety of species.These works were able to improve the quality of the animals they were breeding. Extensive studies on heterosishave also been conducted in a number of other countries (Yu *et al.,* 2021). Heterosis, also known as hybrid vigour, occurs when an F1 hybrid outperforms both of its parents in terms of biomass production, yield, rate of growth, and resistance to abiotic stress. The term heterosiscan also be used to describe the situation in which an F1 hybrid outperforms both of its biological parents. Heterosiscan also be used to describe when an F1 hybrid outperforms both of its parent species. This is due to the fact that babies bred through hybridization are genetically indistinguishable from their parents but have a better chance of survival because to the hybridization process. Since Darwin first noticed this pattern, it has remained unabated (Fu *et al.,* 2023). Heterosis, sometimes called hybrid vigour, occurs spontaneously when the progeny of two or more genetically diverse people exhibit enhanced functional, growth, and developmental physical characteristics beyond those of either parent. Hybrid superiority is another term for this phenomenon. Heterosis occurs in a wide range of organisms, from plants and animals to bacteria and fungi. Increased yield, faster growth rate, stress resistance, and biomass tolerance are a few other characteristics of crops with heterosis (Rao*etal.,* 2023). When an F1 hybrid has greater success than its inbred parents, this phenomenon is known as heterosis or hybrid vigour. Charles Darwin made this finding, and it has piqued the interest of scientists and breeders alike. Heterosis can be demonstrated not only by straightforward quantitative aspects like increased growth rate, increased plant height, and increased organ size, but also by more nuanced and complex composite features like increased biomass (Ye *et al.,* 2023). Breeding animals using hybrid ancestry is a cutting-edge method that is revolutionizing agricultural productivity and improving the safety of the food supply. Hybrids have surpassed inbreeds as the most significant and even primary variety type for agricultural plants and animals because of the dramatic increase in yield, which can be measured in tens of percent or even twice that of inbreds (Xie *et al.,* 2022).

Shiraki *et al.,* (2023) analyzed previous studies on the epigenetic aspects of heterosis in horticulture crops. Molecular approaches are currently being applied in researching the molecular foundation of heterosis in horticultural crops. Xiong*et al.* (2022) looked at the leaf transcriptomes of both strong hybrids and weak hybrids, in addition to the hybrids' parents, throughout two distinct time periods. The transcriptome analysis revealed that the number of genes with varying levels of expression between the parents was the largest. These genes are called DEGs. Liu *et al.,*(2022) investigated the ways in which omics approaches, such as genomic, transcriptomic, and population genetics methodologies, including genome-wide association analyses, can shed light on the mechanisms by which hybrid genomes in plant species outperform their parental genomes. These omics approaches include genomics and

transcriptomics. The availability of the knowledge paves the way for new avenues of genomic investigation and the management of heterosis in crop breeding .To gain a better understanding of the underlying basis of heterosis, the research gathered information from a wide variety of sources, spanning from traditional genetic studies and field trials to diverse high-throughput omics and computational modeling investigations. Wang and Wang, (2022)was a presentation of non-additive expression non-coding RNAs, as well as ncRNAs connected to allele-specific expression genes. This led to the finding of unique sets of ncRNA regulatory networks that are intimately tied with heterosis. During the same period of time, research came to light that showed the presence of heterosis-related regulatory networks that included ceRNA and miRNA.Saxena*et al.,* (2021) showed the use of WGRS data and heterosis in crops where hybrid breeding is predicted to boost selection gain to assure worldwide availability of food. Sinha *et al.,* (2020) showed that microRNAs might play significant roles in hybrid vigor in both hybrids by regulating the genes that they target. The discovery mentioned above sheds light on the molecular workings of the heterosis process that occurs in pigeonpea.

2. Materials and methods

Dissection of Heterotic Loci and Genes Using Genetic Methods

It is essential to employ quantitative genetics approaches in order to discover the gene loci that are responsible for heterosis to achieve a comprehending the molecular mechanisms that control plant heterosis. This will allow one to gain an understanding of the molecular underpinnings that govern heterosis. This will allow for the identification of the gene loci responsible for heterosis. This contrasts the traditional method of identifying quantitative trait loci (QTL), which uses single-parent lines. This is necessary to facilitate both of these processes. This would allow for the identification of heterotic loci with greater ease. To identify representations of a wide variety of unique heterotic population types (**Table 1**). As a result, the F2 population has heterozygous genotypes in addition to both homozygous and homozygous genotypes. There is a uniform distribution of allelic combinations across several loci, which enables exact estimates of the influence that genetic variation has.

Table 1: Contrasting various populations for heterotic investigations

Populations suitable for heterotic research	**Ideal genotypic ratio**	**Genotyped once, phenotyped repeatedly**	**Considering hybridization works, pop**
RH-F_2	Yes,at target regions	Yes	High
CSSL backcrossing	Yes,at target regions	Yes	Modest
Diverse F_1	No	Yes	Modest
Immortalized F_2	Yes	Yes	Modest
F_2	Yes	No	Very high

The three genotypes are frequently found in the proportion of 1:2:1, and there is also an even distribution of the genotypes. Recent developments in high-throughput sequencing technology have made it possible to genotype large F2 populations at a price that is more reasonable in comparison to what it used to be. Similar numbers of genes were expressed both additively and nonadditivly, as seen in (**Table 2**).

Table 2: Research on gene expression in heterosis

Plant organ	**Genetic background**	**Global expression trend**	**Developmental stage**	**Approach**
Rice				
Panicle	G protein γ subunit	Additivity	Stage III, IV, V	8K cDNA microarrays
Maize				
Endosperm	8 Pioneer inbred lines	Non-additivity	11,15,22 DAP	GeneCalling
Seedling	B74		12 DAG	
Embryo	UH006 UH302	Additivity	7 DAP	12K cDNA microarrays SSH qRT-PCR
Embryo	Mo18	Additivity	17 DAP	13.5K microarrays
Endosperm	B74 BSSS54	Non-additivity	19 DAP	RT-PCR
Immature ear				
Diasporic and triploid plants'	Mo18	Non-additivity		Quantitative blotting

adult leaves				
Immature ear	B74 18 Poineer inbred lines	Additivity-Non-additivity		GeneCalling
Shoot apical meristem	UH003 UH006 UH251 UH302	Non-additivity	21-23 DAP	13K cDNA microarrays qRT-PCR
Seedling	Mo18 B74	Additivity	15 DAG	15K cDNA microarrays qRT-PCR
Arabidopsis thaliana				
First leaves	Col Ler Cvi	Non-additivity	22, 25 DAG	7K cDNA microarrays

The F2 population is notoriously difficult to maintain, which is why the immortalized F2 population was created using the Design III. Finally, in the final phase, immortalized F2 is derived from immortalized F2. Because of this, the immortalized F2 population is a particularly powerful population for heterosis investigations. In contrast to the widely utilized F2 populations, which can only be genotyped once, this can be done multiple times. This topic will be covered in further depth later on below in this section. The rice lines that were utilized in the cross were PA64s and 93-11. After conducting several tests with the RIL populations as well as the backcross population, researchers were able to identify several key QTLs that were responsible for yield heterosis. One of the methods that can be applied in the process of producing test populations is known as backcrossing. These loci were found in the genetic population that was used to produce the genetic population. This was done by utilizing a maize inbred line as a reference. In heterosis analysis, there is also the option of using the residual heterozygosity, abbreviated as RH.

For heterotic studies and experimentation with test crossing, the RH-F2 lines are as useful as the CSSL test populations. Heterotic loci can also be studied through the population of offspring from various hybrid crosses (F1 lines). In order to learn more about the genetics

underlying biomass heterosis, GWAS were performed on the model plant Arabidopsis thaliana. Using 200 hybrids, researchers were able to identify many potential genes involved in heterosis, such as WUSCHEL and ARGOS. The goal of this study was to gain insight into the processes that give hybrid maize its distinctive qualities.

The presence of rare alleles in the population may account for the discrepancy in the genotype distribution. Additionally, since there is no recombination between inbred parental lines and heterotic groups in F1 lines, the allelic combinations in these lines stay stable. This is because inbred lines do not produce heterotic offspring. This is because F1 lines do not contain any heterotic groups. After the heterotic loci have been identified, the genes responsible for the disorder need to be unearthed. This is because the heterotic loci themselves have dominant or recessive effects. This is a result of the fact that between two homozygous genotypes, there could be only a minute difference in phenotypic expression. On the other hand, we can speculate that the functionally relevant causal genes will, in the vast majority of instances, regulate many features simultaneously while exhibiting a wide range of heterotic effects.

3. Results

The genetic underpinnings of heterosis

The genetic causes of heterosis are presently explained by three fundamental ideas. These hypotheses are based on the traditional genetics model, which is depicted in (**Figure 1**). The dominant complementation hypothesis is the first of these hypotheses. (A) One sort of hypothesis is referred to as the prevailing complementation hypothesis. Positive alleles found in the dominant state in the F1 hybrid will balance out any negative alleles found in the recessive state in the maternal and paternal inbred line, leading to an improvement in performance due to the combination of these two types of alleles. These alleles are A_2 and B_1, respectively. (B) The hypothesis of the single locus's overpowering influence. A superior characteristic is produced in the F1 hybrid line ("A_1 A_2") due to the combination of the A_1 and A_2 alleles from the paternal and maternal inbred lines, respectively. This is in contrast to the situation in which both parents have homozygous genotypes ("A_1A_1" and "A2 A_2"). (C) Epistasis. Because of the way that the A and B loci interact with one another, the effect of " A_1 A_2 B_1B_2" is enhanced when it is considered as a whole. This is the case when it is assumed that the two loci do not interact with each other.

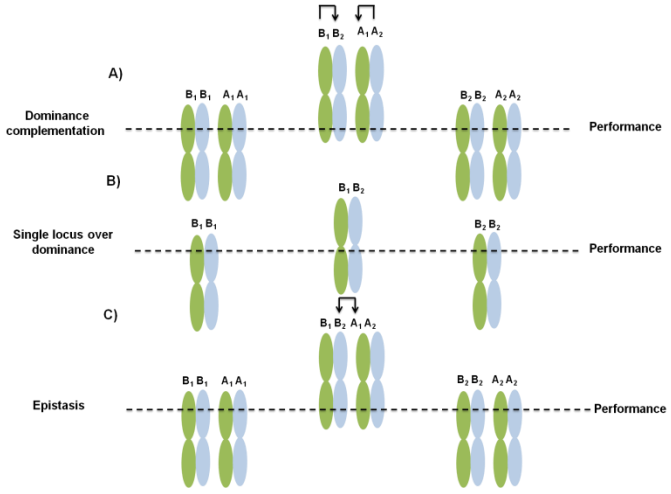

Figure 1: Heterosis's genetic foundation

In addition, the dominance complementation theory and the pseudo-overdominance hypothesis refer to the same thing in practice. The only difference between the two is that pseudo-overdominance occurs when two loci are closely linked on the same chromosome.

This is the only difference between the two. The single locus over dominance hypothesis is the name given to the second hypothesis in this set. According to this theory, the heterozygous genotype "A1 A_2" is superior to both homozygous genotypes for the overall performance of yield or a particular trait.

Florigen, also known as the floral stimulus, is produced by Arabidopsis plants that have the blooming Locus T (FT) gene. This was possible because of the high level of genetic similarity between the two lines. The third hypothesis that attempts to explain heterosis in plants is the epistatic model. That is to say; there is a chance that two different loci, A and B, will interact with one another, which will lead to the effect of "A1 A_2 B_1B_2" is amplified. This is a possibility. Epistasis is proven to play a large role in heterosis for numerous traits in Arabidopsis, rice, and maize, according to a body of evidence that is considered to be very robust. It is crucial to state unequivocally that the 3 model of overdominance, epistasis are all involved in the process of plant heterosis and do not exclude one another. This is because heterosis is a process that plants go through to create new varieties. This is because it is of the utmost importance that this point be made crystal plain. (**Figure 2**) illustrates correlation between gene expression levels in hybrids and the genetic principles of dominance and over dominance is not precisely straightforward. (**Table 3**) displays the hybrid exhibits altered levels of gene expression.

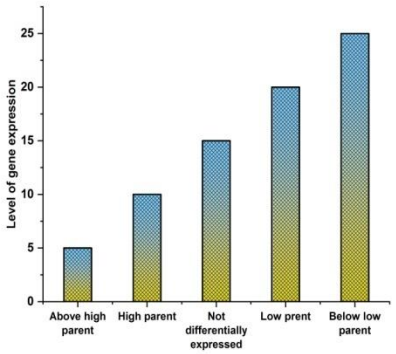

Figure 2: *Levels of gene expressions in hybrid*

Table 3: Expression levels of genes in hybrid

	Level of gene expression
Above high parent	5
High parent	10
Not differentially expressed	15
Low parent	20
Below low parent	25

It is exceedingly difficult to separate heterosis into three independent variables because the phenomenon of heterosis in agricultural output is the nonlinear effect of a large number of

heterozygous genes functioning simultaneously. This is because of the fact that heterosis is caused by the simultaneous action of heterozygous genes. In light of this, for us to achieve progress, we need to make use of genetic techniques to (i) It is strongly proposed that research on the heterotic consequences of heterozygous genotypes be done based on statistical analysis and (ii) increase the visibility of the regulatory networks that are related with heterosis genes. A condition in the classical model in which the effect of "A1 A_2 " is comparable to that of " A_1A_1," where " A_1A_1" is the homozygous superior allele, is referred to as a "complete dominance effect," and the term "complete dominance effect" is used to characterize the circumstance. Complete recessive means that the "A1 A_2" allele is the same as the "A2A2" allele, whereas complete additive means that the "A1 A_2" allele is the same as the "average" of the "A1 A_2 " and " A_2A_2 "alleles. The condition known as "complete dominance" describes the circumstance in which a damaging recessive gene that is nonfunctional has been "covered" by a dominant allele that is functional. The expression "complete dominance" is used to describe this kind of circumstance. A recent study on the genetics of rice revealed that the majority of heterotic genes have "partial dominance" or "partial recessive" effects. These conclusions were reached as a result of the study's findings. When "A1 A_2" has the same effect as "A1A1," where "A1A1" is the homozygous superior allele, this situation is known as the "complete dominance effect" in the classical paradigm. In this circumstance the effect of "A1 A_2" is similar to that of "A1A1." Our comprehension of heterosis will deepen if additional study on the genetic relationships in plants is conducted. This could be the case because functional genomics data and omics data are both increasing in quantity. In (Figure 3), the allelic involvement to gene appearance in hybrid reflected expression levels of the parental genes in comparison and inbred lines for genes that undergo complete cis regulation.

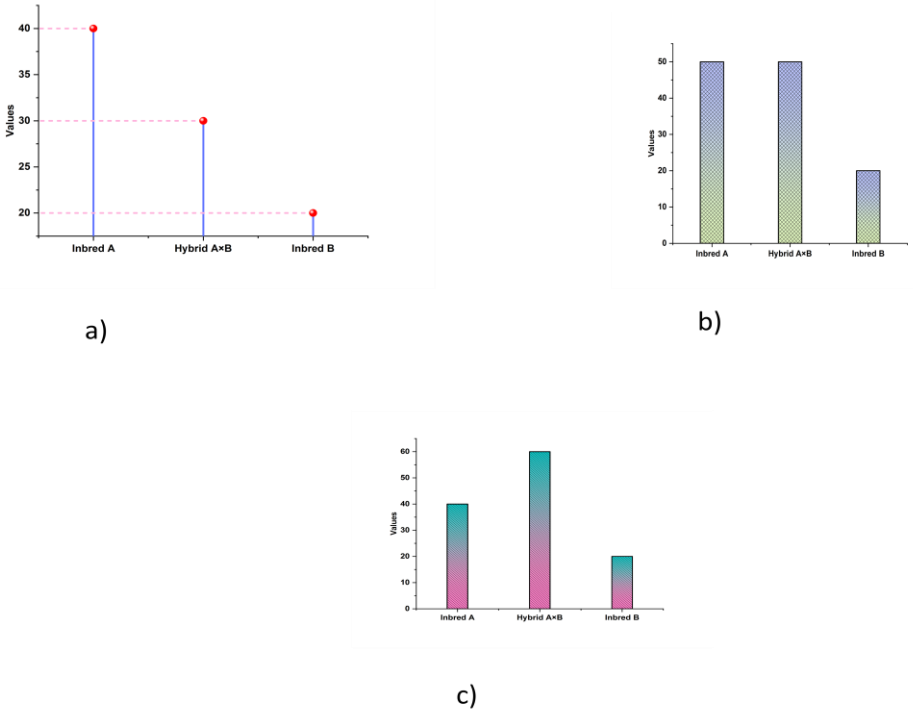

Figure 3: *A ratio of allelic gene expression*

This might help us understand the genetic factors that contribute to the disease better. On the other hand, deciphering the regulatory networks that contain heterosis genes might bring some additional challenges. To gain a comprehensive insight into the developmental mechanisms governing the impact of heterozygous gene states on gene regulation, one must either employ near-isogenic lines containing multiple key heterosis genes or advance

genome editing technology to mimic natural allele replication. To properly comprehend the developmental principles that control how genes can exist in heterozygous situations, it is imperative to do this. This is essential in order to achieve a comprehensive comprehension of the function played by genes in heterozygous situations during the control of gene expression.

Epigenetic regulation in heterosis

Plant development and adaptation are significantly influenced by epigenetic factors, including DNA methylation, short RNAs, and modified histones. In addition, there is mounting evidence that epigenetics is one of the missing pieces to the puzzle when it comes to comprehending the regulation of heterosis. There are two distinct processes that are involved in DNA methylation. It was important to make use of isogenic epigenetic recombinant inbred lines, also known as epiRILs, in order to get rid of the confusing effect that was caused by genetic differences that were inherited from both parents. The probable impact of DNA methylation on complex features was shown using the epiRILs. It was revealed that the accumulation of short RNAs with a length of 24 nucleotides was diminished in F1 hybrids of Arabidopsis, rice, or maize. This lends credence to the notion that siRNAs could potentially play a part in heterosis. It was shown that the Arabidopsisheterosis process did not involve RNA polymerase IV, a crucial enzyme in the production of 24-nt siRNAs. In addition, alterations occur in the expression of miRNA as well as the modification of histones in F1 hybrids. However, it is not always simple to determine whether the alterations in epigenetic modifications that have occurred are the effects or the causes of heterosis.

The molecular process underlies a number of different heterotic effects

There are still a few fundamental concerns regarding heterosis in plants that have not been answered, according to the perspective of modern molecular genetics. This is still the case despite the fact that the gene loci that control heterosis are becoming more apparent and that several examples of particular genes confirm the conventional views. Regardless of the fact that these things are taking place, the situation has not changed. We are aware that the partial or complete (-1d/a1) occurrences of dominant and recessive effects are understandable due to gene dosage effects (GDEs). This is the case regardless of whether the effects are partial or complete. Nevertheless, the question that remains is why a few genes that are in the heterozygous state display overdominance effects.

5. Discussion

The findings of the overdominance instance IPA1 suggest that the gene with overdominant effects may have the ability to influence numerous aspects of yield. It's possible that the superior alleles for various components won't be identical to one another. The gene has partial dominant effects for each factor that contributes to yield, as well as each subfactor. The composite characteristic known as grain yield per unit area or grain yield per plant is made up of numerous elements and subfactors, each of which adds to the feature's overall value, which results in the overdominance effect. However, a strong argument might be made that the heterotic effects are the result of the genes' optimal level of expression for a certain component or sub-factor. Additional dissections that try to address this question could have to rely on the identification of additional molecular pathways by making use of techniques from physiological and developmental biology. This would be necessary if the goal is to find an answer. Another question that has to be addressed is the reason why there are so many more gene loci that show partial dominant effects than partial recessive effects. This is crucial for the QTLs that affect plant biomass and height. There must be an answer to

this query. The dominant complementation theory predicts that the wild type allele will be dominant and the mutant allele will be recessive. The majority of the time, having one copy of the wild-type allele when the gene is in the heterozygous form is almost adequate for it to carry out its biological responsibilities.

On the other hand, it is possible for the mutant allele to become the dominant one depending on the set of conditions that are present. One example of a recessive mutation for dwarfism but a semi-dominant mutation for twisted growth is the twisted dwarf1-1 mutation in rice. Despite the fact that it is believed that having just one copy of the wild-type allele is sufficient to take over a function, the partial dominance effect still requires the additional assumption that the relevant genes should be positive regulators. There are a few instances where QTL genes are "negative regulators," despite the fact that many of the genes involved in the gibberellin pathway or the flowering time pathway are "positive regulators" that affect plant height and grain production. Conversely, the vast majority of QTL genes that affect plant height and grain yield are referred to as "positive regulators."

Perspectives on the breeding of animals in the future

When genotype-based predictions reach a pretty high level of accuracy, hybrid breeding will be much more efficient, which will result in a significant reduction in the amount of time and effort required. The intricate genetic interactions that take place between heterotic loci and the influence exerted by a large number of genes with just a modest effect scattered over the genome are anticipated to be the hardest components of hybrid crop breeding using molecular design. Without a doubt, these are likely to be the most difficult aspects of hybrid crop breeding. It has been demonstrated that it is possible to make accurate predictions of complex heterotic traits in maize by utilizing data from the entire genome and metabolome. These predictions have been used in hybrid breeding. A widespread application of deep learning techniques, together with enormous amounts of well-planned genetic data and detailed knowledge of the biological processes underlying heterotic genes, is one possible path that could be taken in the near future with the goal of improving prediction accuracy.

Gene pyramiding is another possibility that can be taken advantage of in hybrid breeding. This method involves searching for superior alleles across various heterotic groupings. There are a large number of well-known heterotic groups in maize. Very recently, it was discovered that an agricultural fantasy of retaining heterosisthrough the use of a one-line hybrid rice system is actually attainable. The MiMe technique was applied in these two separate investigations to substitute meiosis for mitosis, which led to the production of diploid gametes without the involvement of recombination. In order to replicate the effects of having a heterozygous genotype, it is possible to create new alleles for dominant genes that are more advantageous than the ones that are currently available. The remaining obstacle is the complication of epistatic relationships.

6. Conclusion

This study's examination of the molecular mechanisms behind heterosis in plant breeding has given us an important new understanding of the phenomena of hybrid vigor. The genetic and biochemical underpinnings of this significant phenomenon have been clarified by the identification of several essential molecular processes through several studies and research initiatives. According to the research, heterosis is the outcome of different genetic components from the two parental lines interacting, which enhances performance in the hybrid offspring. These techniques include the use of heterozygosity, differentiating gene expression, altering the epigenome, and controlling metabolic pathways.

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