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S&T REVIEW

UTILIZATION OF HETEROSIS IN CROP IMPROVEMENT

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ABSTRACT

Heterosis is a natural phenomenon in which offspring of distinct species or offspring of species hybrids exhibit better biomass, faster rates of growth, and higher fertility than either of their parents. In comparison to either parents or their self-pollinated cousins, the offspring of two homozygous inbred lines are more robust and have bigger heights and weights. With naturally cross-pollinating species the degree of heterosis is frequently higher than in self-pollinating crop. One of the most significant advancements in agriculture was the development of hybrids. Today, heterosis is widely used without having a thorough understanding of the underlying molecular and genetic concepts. By enabling the best possible exploitation of crop yield and stability, the understanding of the genetic and epigenetic framework underlying heterosis would be a major discovery that would revolutionize current plant breeding.

KEYWORDS

Inbred; hybrids; genetic; crop

1. INTRODUCTION

Heterosis is the natural phenomenon in which offspring of different species or offspring of species hybrids exhibit improved biomass, faster rates of growth, and higher fertility than either of their parents (Birchler et al., 2010). Heterosis has been explored in the majority of eukaryotic creatures, including plants, animals, and fungi. The offspring of two homozygous inbred lines (true breeding lines formed by recurrent inbreeding) with different genetic make-ups are more robust and have larger heights and weights than either of their parents or their self-pollinated relatives. The degree of heterosis is often higher in naturally cross-pollinating species like pearl millet, rye, maize, and other grasses than in self-pollinating crop plants like rice, barley, wheat, and oats. The development of several hybrid cultivars in self-pollinating plant species is still frequent(K. Srivastava et al., 2020) . One of the key advancements in the global seed industry that harvested heterosis and led to a major improvement in crop yields as well as in the corresponding revenue from crop husbandry per se was the introduction of hybrid crops. For instance, hybrid rice has helped China raise its production of rice by 44.1% while the European market has been heavily favoring hybrids for several of its major commodities, including sugar beet, rapeseed, and rye (Hochholdinger and Hoecker, 2007; Cheng et al., 2007). When talking about heterosis models, two terminologies are frequently employed. One is the "dominance" model, which holds that interactions between various alleles in the hybrid result in an increase in vigor, and the other is the "overdominance" model, which holds that interaction between recessive alleles occurs at various loci in the hybrid. Genetic knowledge at the time was so limited that it appeared essential to assume that vigor is increased when the genes at specific loci are dissimilar—a hypothesis for which there was no supporting evidence and one that was not informative as a dynamic interpretation. This remark still holds today (Birchler et al., 2010).

In plant breeding, heterosis is frequently characterized using various terminologies and broader concepts. A hybrid's improved performance in comparison to its better-performing parents or a control cultivar is denoted by alternative terms like "Heterobeltiosis" and "Commercial Heterosis," respectively. These criteria could be a valuable tool for crop variety creation, but they are not always connected to population genetic improvement. Additionally, depending on the breeding goals, the progenies' strong phenotypic expression in comparison to their parents might be viewed as either beneficial or bad. For example, a "late" flowering plant would have a positive value for days to flowering but will have less of a positive value for the rate of development as it may mature at a slower pace. Positive heterosis for days to flowering is an alternative to negative heterosis for the rate of plant development. Therefore, depending on the phenotypic measure or characteristic being studied, the sense of heterosis may simply be an artifact of the researcher's choice (Falconer, 1996). Furthermore, heterosis can be recognized as a "system-wide" phenomenon that results in improved size, vigor, resistance to pests and diseases, or environmental variables impacting crop performance on a crop and is viewed as an overall "effect". The perspective of heterosis has not only allowed plant breeders to make use of this phenomenon to breed superior crops, but it has also sparked research on multiple scientific levels to comprehend the origins of hybrid vigor and the quest for a unified explanation.

Based on parental breeding, heterosis is divided into three groups from the viewpoints of plant breeding, i.e. (Figure 1): Three types of heterosis exist :

- Intraspecific heterosis, which involves crosses between two accessions from the same species
- Inter-subspecific heterosis, which results from hybridization between two subspecies and has been used in hybrid rice (Virk et al., 2004)

Wide hybridization, which is the result of crossing between two individuals from different species from remote gene pools and is specifically intended to increase plant biomass (Zeliang and Pattanayak, 2018).

In essence, plant science specialists from all over the world have been interested in the phenomenon of heterosis for a long time. To offer directions for future study and the expression of hybrid vigor, we extensively review the underlying processes of heterosis in plants with a focus on plant breeding in this paper.

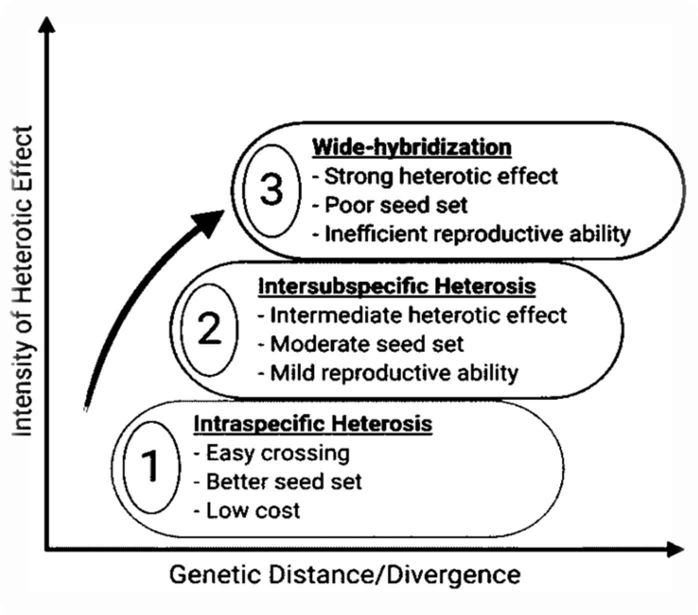

Figure 1

2. Methodology

The review paper addresses the different aspects of heterosis, including its molecular basis, genetic model and its utilization for agricultural purposes. It is based on a survey of several pieces of literature related to heterosis. This article takes use of recently available knowledge and facts. In order to learn more about the unique issues and potential for heterosis breeding in crop improvement in the future, these considerations were taken into account in the review.

2.1 Molecular Basis of Heterosis

Heterosis is the term used to describe how heterozygous hybrid plants perform better than their homozygous inbred parental lines. Even though heterosis was identified a century ago and despite its crucial agronomic significance, its genetic and molecular foundations are still unknown. Recent pioneer research has revealed variations in the genome structure and gene expression between hybrids and their inbred parental lines. Different inbred lines of maize were shown to exhibit a considerable loss of collinearity at multiple loci at the genomic level. In maize (*Zea mays*), rice (*Oryza sativa),* and Arabidopsis, complex transcriptional networks specialized for various developmental phases and tissues were seen at the level of gene expression (Arabidopsis thaliana). Our understanding of the molecular basis of heterosis may be improved by integrating this complicated expression data(Hochholdinger and Hoecker, 2007).

There are several techniques to investigate heterosis at the molecular level, including transcriptome-wide gene expression profiling, genome organization studies, and examining allele-specific contributions to gene expression (Hochholdinger and Hoecker, 2007). The most fundamental and commonly accepted models of heterosis, which incorporate combined allelic expression and diversified allelic interactions in a hybrid, are the result of several of these molecular techniques (Birchler et al., 2003).

2.2 Genetic Model of Heterosis

The most common and widely used technique to understanding the rational components of heterosis is through the use of genetic models. A variety of hypothesis have developed throughout time to account for the occurrence of heterosis, but none of them can account for the whole basis of this phenomenon on their own. The Dominance, Over-Dominance, and Pseudo-Overdominance models are the three most crucial ones (Figure 2). Additionally, epistasis has also been discussed as a potential causative factor for crop heterosis (Figure 2, iv) (Rehman et al., 2021).

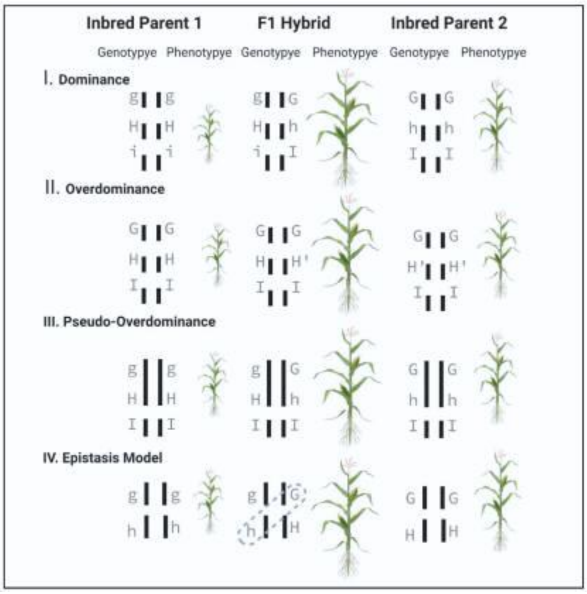

Figure 2

In diagrams, numerous linked or unlinked loci (for example, 'g', 'h', and I are shown to influence the hypothesized phenotypic or trait.

(I) Dominance Model: Homozygous minor-detrimental alleles are present in parents' 1 and 2 of an inbred population (g and I in parent 1; h in parent 2). When superior alleles (G, H, and I) complement each other in an F1 hybrid, the resulting phenotype is superior.

(II) Overdominance Model: The homozygous alleles at locus 'h' are distinct for both of the inbred parents (HH and H'H'). When compared to both homozygous parents in an F1 hybrid, the interaction H and H' results in a better phenotype.

(III) Pseudo-Overdominance Model: The better performance of F1 hybrids is attributable to a small region of the chromosome that contains two or more loci (for example, g and h) connected in repulsion, where the complementation of G and H is simulating overdominance.

(IV) Epistasis Model: The interplay between two separate loci is what gives F1 hybrids their enhanced performance.

2.3 Heterosis in Self-Pollinated and Apomictic Plant Species

The dominance theory may be taken into account as a potential contributor to heterosis in several crops, according to current molecular genetics. In reality, many genetic and epistatic factors may need to be taken into consideration to have a better knowledge of the hybrid vigor.(Cowling et al., 2020; Moll et al., 1964). On vegetable crops, some crude deductions about hybrid vigor were made (Mulualem and Abate, 2016). Farmers opted for hybrid cultivars as soon as diverse firms made seeds available (Moll et al., 1964). In contrast to cross-pollinated vegetable species, hybrid cultivars are used more frequently in self-pollinated vegetable species (Mulualem and Abate, 2016). In some self-pollinated crops, such as *Solanum melongena* L., *Capsicum annuum* L., *Solanum lycopersicum*, and *Lactuca sativa*, extreme hybrid vigor has been shown. These crops expressed stronger heterosis (33-97%) than the parents. Because of the discovery and use of cytoplasmic male sterility in bulb and root crops, hybrid breeding has been successful in these crops as well (CMS). When CMS was first applied to *Allium cepa*, the yield rose by 14-67% in comparison to open-pollinated cultivars. The hybrid breeding approach is now widely employed for numerous root and bulb crops, and this accomplishment completely changed the onion industry (Mulualem and Abate, 2016). The outstanding floral morphologies and a low incidence of out-crossing in onions are two potential causes of this self-pollinated heterotic occurrence. According to a prior study on heterosis, this condition is just the reemergence of inbreeding depression caused by important genes (Moll et al., 1964). Quantitative genetics, however, suggests that hybrid vigor may happen whenever there is genetic diversity between the parents, which can also be seen in self-pollinated species itself (Mulualem and Abate, 2016).

Although higher biomass, rapid development, viable fertility, and uniform progeny are well-known characteristics of heterotic hybrids, these desirable qualities can also be seen in self-pollinated species. Even more intriguingly, cross-pollinated crops were found to have more inbreeding depression than their self-pollinated counterparts. In terms of environmental endurance, self-pollinated crops are very resistant to inbreeding. Crop performance varies so much, and genetic balance is thought to be related to this. Heterozygous balancing results in decreased fitness in crop species that have undergone cross-pollination. As opposed to heterozygous species, self-pollinated species exhibit a strong homozygous balance that increases overall progeny fitness (Mulualem and Abate, 2016).

Even though apomixis has numerous opportunities to take advantage of hybrid vigor, the phenomenon of heterosis is not well understood in the case of apomictic plant species. However, a classical selection from natural ecotypes is the basic basis for genetic improvement in such plant species. Because features in apomictic hybrids remain stable over generations and parental lines do not need to be maintained, apomictic plants provide a compelling argument for focusing on heterosis (Hanna and Bashaw, 1987). In addition to these benefits, F1 hybrid seed from apomictic plants can be replicated directly for advanced studies because creating parental inbred lines is not strictly necessary. This increases productivity and may hasten the release of novel cultivars (Moser et al., 2004). Therefore, the study and use of the heterosis phenomenon in apomictic plant species is a desirable objective for the field of plant breeding research.

2.4 Utilization of Heterosis for Agricultural Purposes

One of the major advancements in modern agriculture, and one of exceptional economic significance, is the use of heterosis in agricultural plants. All hybrid varieties of maize are grown in the major corn-producing nations, where it produces the biggest annual worldwide production of kernels of any crop species. In addition to maize, hybrid varieties of other crops have significant market shares in various parts of the world. For instance, in Europe, 100% of the sugar beet, > 90% of the rapeseed, and > 70% of the rye varieties, as well as > 70% of the rice in China and > 80% of the cotton in India, are hybrids. The separate rediscovery of heterosis in maize by George Shull and Edward East, which was documented in their seminal articles in 1908, forms the basis for the agronomic exploitation of hybrid vigor.

Shull and East created unique, nearly homozygous lines that were then crossed to produce hybrid plants, going beyond Darwin's tests. To achieve homozygosity in nearly all genes, homozygous lines are typically created by performing several (more than seven) cycles of self-pollination. This process, known as inbreeding depression, results in a steady decline in heterozygosity as well as a loss of vigor in these plants. The so-called "double haploid" technique used in modern breeding enables the creation of fully homozygous inbred lines within two generations by producing haploid embryos whose chromosomes are then doubled to produce diploid offspring(Hochholdinger and Baldauf, 2018).

3. Discussion

Heterosis is a widespread phenomenon that reflects global variations in gene and protein expression levels, in contrast to existing models based on classical genetics, which are still widely used by plant breeders. For diploid genomes, the dominance model explains the hybrid vigor very convincingly, but for polyploid species, it must be taken into account in the context of genome dynamics (cis, trans, and chromatin/epigenomic interactions) (Virk et al., 2004). The use of molecular markers, allozymes, and plant genome sequencing has been recommended as a way to better understand hybrid vigor and the effects of self-pollination on this phenomenon. Innovations and the creation of various supporting ideas that show elements other than heterozygosity, such as genetic diversity levels and causes of variations leading to hybrid vigor, can result from the employment of current methodologies (Charlesworth, 2003). The most popular dominance model of heterosis postulates that genetic divergence causes hybrid vigor, a phenomenon where the effects of superior alleles outweigh those of recessive alleles. The phenomenon that leads to improved agricultural output, fertility, and weight cannot be attributed only to heterozygosity, though. It is frequently even more important to use the heterotic effect in an economically efficient manner than it is to comprehend the chemical mechanisms underlying it. By maximizing breeding schemes in various crops and ornamental species, the knowledge gained from the research of the underlying basis of heterosis can be employed in crop breeding, genetic improvement of parents, and generation of superior performing hybrids. In the case of conventional hybrid breeding, the typical method is to examine features of the breeder's interest in a wide group of individuals generated through many crosses. After years of field testing, only a very small percentage of tested individuals progress to elite hybrid types. Artificial emasculation is labor- and time-intensive in the case of self-pollinated crop species, making the dependence on the emergence of male sterility clear. Understanding the genes and molecular processes involved in CMS could help overcome this barrier and offer up new opportunities for hybrid breeding in crops where it hasn't been done before. Utilizing the genetic variety of the parental lines and the buildup of unfavorable loci in the F1 generation are two practical concerns that still need to be resolved to take use of heterosis (Fu et al., 2014). Similar to extensive hybridization, genetic admixtures present obstacles for plant scientists to investigate. Wide hybridization may cause chromosomal abnormalities and activation of transposons (Nicolas et al., 2007).

4. Conclusion

To summarize, one of the most significant advancements in contemporary agriculture was the development of hybrids. One of the pillars of global food security is the utilization of heterosis via continuous enhancement of hybrid production and environmental resilience. Despite the agronomic and therefore financial success of hybrids, no overall genetic or molecular hypothesis has been able to fully explain hybrid vigor to this point. The fact that no one principle explains this phenomenon is one reason for this. Today, heterosis is widely used without having a thorough understanding of the underlying molecular concepts. By enabling the best possible exploitation of crop yield and stability, the understanding of the genetic and epigenetic framework underlying heterosis would be a major discovery that would revolutionize current plant breeding. Further, it has previously been suggested that with improved knowledge and understanding of heterosis, it may one day be able to create inbred lines that perform similarly to elite hybrids without the need for inter-individual crossing. We concur that this may be feasible but that it will be exceedingly difficult to accomplish given the intricacy of heterosis' genetic and molecular underpinnings. However, more study is required to not only unravel the mysteries of hybrid vigor but also create fresh approaches to handle intricate interactions and control breeding platforms to satisfy the demands of global food security.

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