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Molecular basis of heterosis: A review

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Abstract
A naturally occurring phenomenon known as heterosis, also known as hybrid vigor, occurs when the offspring of genetically diverse individual (parental line) outperform their parents in terms of physical characteristics such as functional ability, growth, and development. Crossing of Parental cultivars produces offspring with higher biomass, grain yield, and growth rates than their inbred parental lines, and has been used in agriculture for many years to boost yields and yield per acre. In an F_1 hybrid, heterosis refers to the offspring's morphological and genetic superiority over the inbred parental population. Heterosis is the superiority of offspring physical and genetic features over inbred parents. In hybrid improvement, heterosis is important because it helps plant breeders to better harness the hybrid vigor of both non-inbred and inbred parental material, increasing hybrid breeding success rates. Because heterosis is used in so many crops, a variety of hybrids have emerged. The heterotic groups of inbred parental lines and their ability to merge define the inbred paternal lines and breeding aims for a healthy breeding program. In India, maize is the most significant food crop, accounting for around a quarter of total output. Its high cross-pollinated crop gives several options for increasing hybrid vigor. As a result, once heterosis, or hybrid vigour, has been achieved, it is vital in hybrid development. Several studies are presently underway to determine the molecular basis of heterosis. Molecular markers have enabled researchers to determine the genetic origin of heterosis development at the gene-expression or molecular level. It assists in identifying the genes responsible for the desired traits, as well as their chromosomal location. Molecular marker technology has been utilized to assist find desired genes in genomic regions that lead to heterosis. On the genetic and molecular basis of heterosis, as well as its contemporary advances and usage in agricultural plants, particularly those produced for human use.

Keywords: Hybrid vigor, QTL, dominant hypothesis, overdominance hypothesis, epistasis

Introduction
Heterosis, also known as hybrid vigor, is a natural phenomenon that occurs when the offspring of genetically diverse individuals (parental line) outperform their parents in functional, growth, and developmental morphological traits (Shull, 1948; Coors and Pandey 1999) [85, 17]. Crop heterosis may also be defined as a rise in yield, an increase in growth rate, stress resistance, and an increase in biomass tolerance (Kalloo *et al*., 2006) [53]. It is most obvious in adult attributes such as biological yield or yield, but it is also visible during embryo development (Meyer *et al*., 2004; 2007; Jhanke *et al*., 2010) [67, 69] and sprout development (Meyer *et al*., 2004 and 2007; Jhanke *et al*., 2010) [67, 69]. (Hoecker *et al*., 2006) [45]. This technique improves plant reproduction and adaptation to varied environmental situations. It is also critical to agricultural productivity since hybrid breeding has been proven to be one of the most successful techniques for improving grain yield in a variety of crops (Schnable and Springer, 2013) [82]. According to a recurring theme throughout the past century, the amount of heterosis varies across species and is the outcome of variation in various genomic positions and complex aspects that are often explored for heterosis, including production, and are positioned by many (hundreds of) genes. Furthermore, rather than reflecting a hybrid's entire genetic variety, heterosis is most likely a representation of the diversity of a few important genes that contribute to a certain feature.

Heterosis is currently defined as the discovery that cross-pollinated hybrids are more fit than their parents. Almost every yearly crop exhibits some degree of heterosis. When related to self-pollinating crops like rice, wheat, barley, and oats, cross-pollinated cereals like maize, bajra, rye, and other fodder grasses exhibit a high degree of heterosis. Nonetheless, they have generated remarkable cultivars as well as a large number of high-yielding hybrids (Rajendrakumar *et al*., 2015) [77]. In self-pollinating populations, hybrids have also been produced since hybrids frequently outperform line types in terms of yield stability. Several elements of heterosis may be investigated at various stages of development (Hochholdinger

and Baldauf, 2018).

The degree of heterosis may be measured by comparing the phenotypic expression of character traits in a hybrid to the average of its two independent parents. The following features may be used to identify heterosis: On begin with, heterosis is quite variable; the degree of heterosis varies depending to the genetic distance between the parents, their reproductive method, and the traits evaluated (Zhou *et al*., 2012) [105]. Plant development stages (Groszmann *et al*., 2013) [35] and the environment (soil type, geography, climate, solar radiation, temperature, and water availability) have all been shown to impact heterosis (Munaro *et al*., 2011; Griffing and Zsiros, 1971; Langridge, 1962 and Blum, 2013) [71, 33, 58].

The application of heterosis in many agricultural plants and animals has been very successful in agriculture, and it is currently recognized as critical to meeting the world's food needs (Duvick, 1999) [24]. Furthermore, heterosis occurs almost everywhere, boosting crop productivity by 15–50% depending on the crop. To boost agricultural performance, most cereal crop varieties, as well as marketable forms of vegetable and decorative crops, are stocked with hybrid seeds (Duvick, 1999; Birchler *et al*., 2003) [24, 7]. The heterosis of most eukaryotic species, including plants, animals, and fungus, has been studied. Two homozygous inbred lines (purebred lines that have been repeatedly inbred) with differing genetic constitutions are merged. When this occurs, the hybrids exceed both parents as well as their self-pollinated counterparts in height and weight, as well as fertility, durability, and constitutional vigor (Darwin, 1876) [21].

The degree of heterosis diminishes with time. At the turn of the century, genetic gain for productivity was growing at an annual rate of 1.5–2.0 percent on average, while heterotic gain was declining (Hoisington and colleagues, 1999) [46]. Much recent genome-wide research has focused on the underlying foundation of heterosis in plants. Their results imply that significant changes in gene expression between hybrids and paternal lines might play a role in plant heterosis. Some of the writers are Swanson-Wagner *et al*. (2006) [91], Zhang *et al*. (2008) [104], Wei *et al*. (2009) [97], and Song *et al*. (2010) [86]. Maize (*Zea mays*) was the first plant studied for heterosis, followed by beet (*Beta vulgaris*), onion (*Allium cepa*), sorghum (*Sorghum bicolor*), brinjal (*Solanum melongena*), chilly (*Capsicum*), tomato (*Solanum lycopersicum*), rice (Oryza sativa), sunflower (*Helianthus annuus*) and cotton (*Gossypium hirsutum*) (Melchinger and Gumber, 1998) [66]. Recent study has shown the importance of non-additive gene expression, short RNAs, altered hormone balance, and epigenetic regulation in hybrid vigour, as well as circadian-mediated biochemical activities, which may lead to greater hybrid vigour use and exploitation (Okoh *et al*., 2007; Birchler *et al*., 2010; Chen, 2010; Osborn *et al*., 2003; Okoh *et al*., 2003) [7, 8, 14, 74]. Despite the fact that heterosis boosts crop and vegetable output, the molecular processes that cause heterosis remain unclear. Scientists have been working on this issue for a long time. This review focuses on the current status of heterosis research.

Revolutionary History of Heterosis

Charles Darwin originally described hybrid vigour in 1876, and Shull and East independently rediscovered it in 1908, showing for the first time the great agricultural potential of this phenomena. Shull adopted the word "heterosis" to simplify and shorten the phrase "stimulation of heterozygosis." In the early 1800s, Darwin performed cross pollination tests on maize and discovered that cross pollination is good and useful for crop development, but self-pollination is deteriorating and destructive owing to its influence on restricting the genetic base (Darwin, 1876) [21].

Kolreuter identified the heterosis phenomena in tobacco hybrids, which he named after himself (Reed, 1943). Furthermore, numerous scientists have carried out research on a broad variety of crops in order to better understand and use the heterosis phenomena in agriculture (Bruce, 1910; Jones, 1917; East, 1936) [11, 51, 26]. Over the course of more than a century, the scientific community has been fascinated by the genetic processes that create heterosis, primarily because of the well-known medical and economic ramifications of these systems. The genetic processes that induce heterosis vary widely from species to species and are very dependent on the kind of pollination that occurs, whether it is spontaneous self-pollination or out-crossing, to be effective.

Heterosis is more common in cross-pollinated crops than in self-pollinated crops due to the genetic pathways involved in its expression, which differ greatly across species and also depending on the kind of pollination used (self or cross-pollinated) (Chen, 2010) [14]. This demonstrates that cross-pollinated species' genetic processes involve interactions between distinct alleles in F1 hybrids, resulting in superior performance than self-pollinated species (Fu *et al*., 2014) [28]. However, aside from the fact that F_1 heterogeneous hybrids outperform their inbred parental homozygous lines in terms of yield, self-pollination of such hybrids over a few of generations results in inbred depression (Charlesworth and Charlesworth, 1999) [12]. According to certain studies, genomic turbulence induced by the union of two separate genomes creates hybrid vigour, which results in an expansion of the genome's genetic basis and distinctive gene expressions in hybrids (McClintock, 1993 and Ha *et al*., 2009) [65, 40].

Genetic model of Heterosis

For understanding the genetic foundation of heterosis as well as the hybrid vigor of distinct crops, concepts like as dominance, over-dominance, and epistasis are essential (Lamkey and Edwards, 1999; Crow, 2000; Reif *et al*., 2006) [57, 19, 79]. The fact that these genetic models are made up of a complex of multiple genes that contribute to hybrid vigor has not been directly stated, but it is implied by the fact that they are not (Hochholdinger and Hoecker, 2007) [43]. However, despite the fact that the most widely accepted explanation is that dominance influences gene activities in superior hybrids that exploit heterosis (Charlesworth and Willis, 2009) [13], these popular hypotheses influenced early research and paved the way for a better understanding of how gene expression contributes to heterosis at the molecular level (Birchler *et al*., 2010) [8].

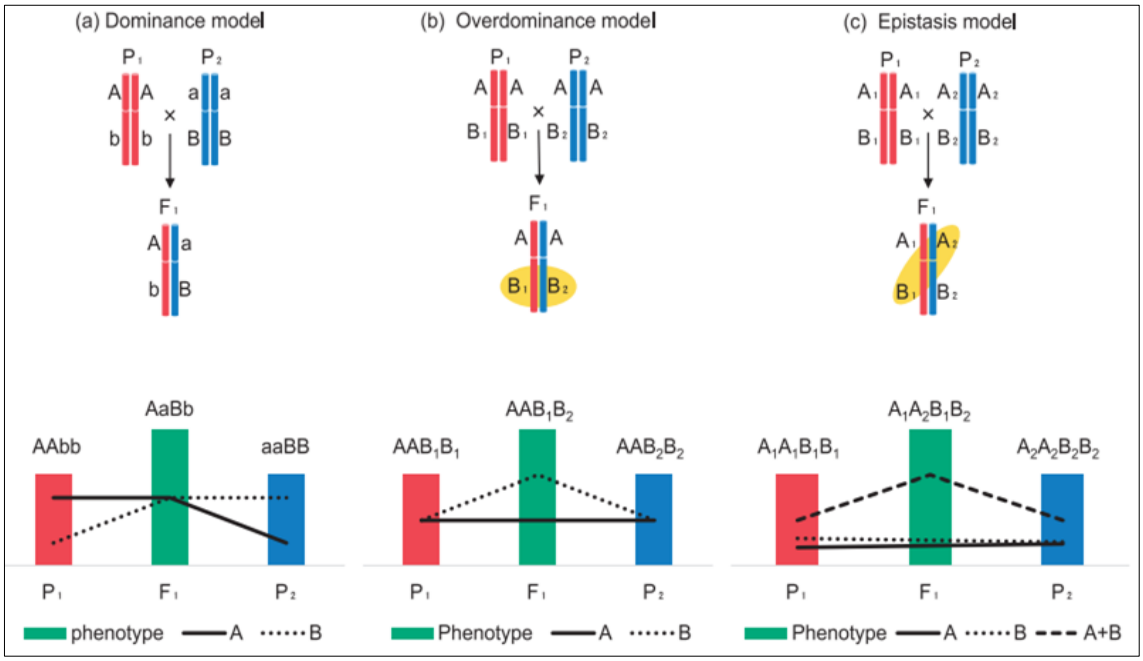


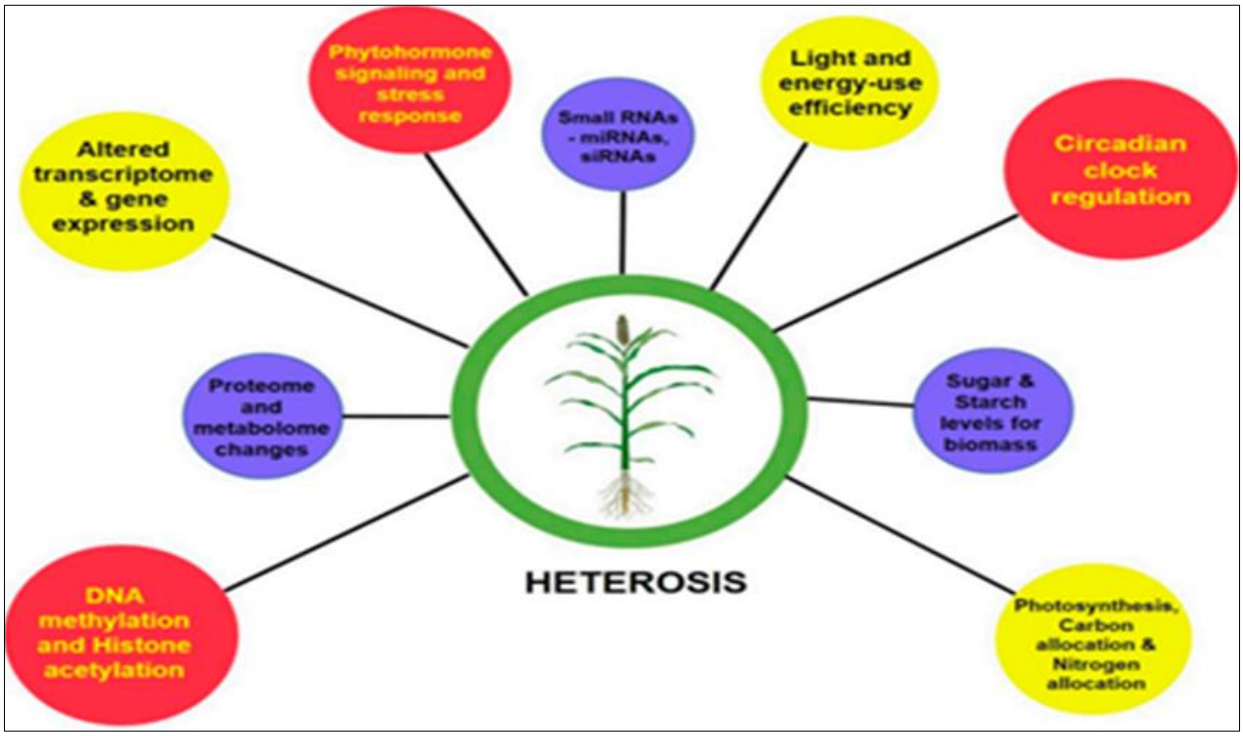
Fig 1: Three hypotheses on the genetic basis of heterosis. The total of gene effects (A, B, A + B) is a phenotype. (a) The dominant and recessive alleles (A and B) may either block or complement each other, according to the dominance paradigm (a and b). (b) The overdominance model, in which heterozygosity (B1/B2) at a key locus causes heterosis, leading in improved performance. In the epistasis theory, non-allelic genes (A2 and B1) inherited from paternal lines interact and cause heterosis (Fujimoto *et al*., 2018) [29]

Researchers started to comprehend the genetic etiology of heterosis in the 1990s, and numerous theories were presented to explain the process. The research was all about the levels of gene activity. The dominant hypothesis highlights the completely overwhelming complementarity of helpful alleles in hybrid varieties; this theory holds that the detrimental genes of one parent may be veiled by the positive dominant genes of the further parent (Bruce 1910, Crow 1998, Davenport 1908, Jones 1917) [11, 18, 51]. An inbred line with performance equal to that of the F1 hybrid cultivar is expected to be developed by deleting all unfavourable alleles and/or introducing favourable alleles, it is predicted. The overdominance theory, on the other hand, contends that heterozygozity at a single locus leads to heterosis (Crow, 1998; East, 1936 and Shull, 1908) [18, 26, 8] Different alleles interact with one another, resulting in an abundance of allelic combinations that contribute to superiority in F1 hybrids, according to the overdominance theory (Lippman and Zamir, 2007) [62]. However, many studies have shown that heterosis in tomatoes, grains, and Arabidopsis is mediated by a single gene (Gustafsson, 1946; Semel *et al*., 2006; Krieger *et al*., 2010) [39, 83, 56].

Another popular genetics-based method is the epistatic hypothesis. Powers (1944) [76] argued that heterosis is caused by the interaction of nonalleles in hybrids at separate loci; this idea was supported by heterosis research in maize and rice (Yu *et al*., 1997; Tang *et al*., 2010) [102, 94], especially in terms of paddy seed weight per panicle and seeds per panicle (Li *et al*., 1997; Zhang *et al*., 2021) [61, 103]. Furthermore, via epistasis, negative alleles may disrupt other positive QTLs during the maize floral transition (Xiao *et al*., 2021) [98]. From diverse views, the aforementioned theories explain the genetic foundation of heterosis. These arguments highlight the most fundamental genetic foundation for heterosis: hybrid parents must be genetically distinct. The three dominance, overdominance, and epistasis theories, on the other hand, are all related to plant heterosis but are not mutually exclusive. Furthermore, since heterosis is a nonlinear effect of multiple heterozygous gene combinations on agricultural production, it is difficult to split heterosis into three distinct components (dominance, overdominance, and epistasis) (Liu *et al*., 2020) [63].

Molecular Mechanism of Heterosis: The genetic evidence coded by diverse gene regulation levels, such as central of dogma, is the overall output of the genetic information expressed by numerous gene regulation levels in heterotic individuals relative to parental inbred lines. Significant structural and quantitative variety in plant populations may now be readily quantified because to the development of modern molecular tools such as single-nucleotide polymorphisms and next-generation sequencing (Daz *et al*., 2012; Zmienko *et al*., 2013 and Saxena *et al*., 2014) [28]. Molecular analysis was performed to assess protein, epigenetic, transcription, and other gene regulatory components that contribute to heterosis to investigate the underlying structure that impacts the degree of hybrid vigour divergence between hybrids and parental inbreds (Kaeppler, 2012) [52].

Transcriptome studies: The transcriptome analysis of successful parental inbred lines and hybrids has been carried out in order to categorize diverse gene expression designs into types of gene activity in a hybrid combination as opposed to its parental inbred lines, as well as to link those alterations to improvements in biological yield and yield production (Kollipara *et al*., 2002; Guo *et al*., 2003, 2004, 2006; Bao *et al*., 2005; Auger *et al*., 2005; Swanson-Wagner *et al*., 2006; Huang *et al*., 2006a, b; Meyer *et al*., 2007; Hochholdinger and Hoecker, 2007; Springer and Stupar, 2007; Song *et al*., 2007[l]) [54, 36, 38, 37, 3, 1, 91, 47, 48, 69, 43, 88, 87]. To determine if there were any correlations between different gene expression patterns in many inbred parental lines and yield-related features of hybrids created by factorial crosses, transcriptomes from large parental populations were studied separately.



Gene interaction between the nucleus and the cytoplasm happens during the hybridization of two inbred parental lines, resulting in cellular and molecular changes as well as a shift in gene expression pattern. These alterations in gene expression and genome function in the F1 hybrid via its inbred parental lines have been seen in a number of cereal hybrid crops, including maize (Swanson-Wagner *et al*., 2006; Stupar and Springer, 2006) [91, 89], wheat (Wang *et al*., 2006) [96], and cotton (Wang *et al*., 2006) [96]. (Flagel *et al*., 2008) [27]. Transcriptome analysis, and its capacity to quantify the degree of contribution of each allele in hybrid progeny, might be seen as a transitional phase between phenotypic expression and genetic information in plants (Schnable and Springer, 2013) [82]. Many transcriptome technologies, such as RNA-Sequence and DNA Micro-Array-Based Approaches, will be used to differentiate parental inbred lines from their hybrid offspring in order to find gene involvement and impact in heterosis. Early transcriptome investigations on a range of crops revealed that hybrids outperformed parental inbred lines in terms of gene expression patterns (Comings and MacMurray, 2000; Stupar *et al*., 2008; Baranwal *et al*., 2012; Fujimoto *et al*., 2018) [16, 90, 4, 29]. Although transcriptomic investigations in reciprocal hybrids were enhanced in order to discover allele-specific expression, the value of maternal or paternal influences on gene expression patterns could not be identified (Guo *et al*., 2004; Stupar and Springer, 2006) [38, 89]. Maize and Arabidopsis have recently shown increased biomass as a result of epigenetic modifications in circadian clock genes and variances in gene expression patterns caused by differentially generated short RNAs (Ni *et al*., 2009; Groszmann *et al*., 2011) [72, 34]. Surprisingly, it has been shown that a single blossoming gene's over-dominant manner of gene activity generates yield heterosis (Krieger *et al*., 2010) [56]. In any case, it is crucial to recognize that distinct gene expression patterns in inbred lines and hybrids do not necessarily result in varied protein production. It is essential to investigate the post-transcriptional regulation of changed genes (Xing *et al*., 2016; Fu *et al*., 2014) [99, 28].

Proteomics studies: Although changes in primary transcriptional activity may not always result in proteins with altered gene expression, and detecting heterosis is reliant on post-transcriptional regulation and translation processes, proteins play an vital role in heterosis detection (Xing *et al*., 2016) [99]. As a consequence of the lack of stable protein levels, parental inbred lines have enhanced protein metabolism, which requires a significant amount of energy to suppress, resulting in a lack of liveliness for biological synthesis, vegetative growth, and production. Inbred parental lines' genetic makeup is primarily due to a lack of intra-allelic interaction in their own homozygous state, whereas F_1 hybrids will have multiple alleles and produce many more allelic combinations, allowing for higher development caused by rapid cell division and resulting in hybrid vigour (Goff *et al*., 2010) [30]. Several investigations have shown that heterosis may be detected using proteins that express in distinct ways. By combining Tandem Mass Bags (TMT) with isobaric labels for Relative and Absolute Quantification (ITRAQ), mass spectrometry may assist detect and quantify altered proteins in heterozygotes (Xing *et al*., 2016; Wang *et al*., 2016) [99, 95]. The majority of the DEPs responsible for heterosis have been found in tissue samples from major cereal crop species such as rice, maize, and wheat leaves, embryos, and roots (Guo *et al*., 2013; Song *et al*., 2007; Zhang *et al*., 2012) [87]. The majority of DEPs found in parental inbred lines and their hybrids are due to non-additive gene effects, and these DEPs are linked to a variety of plant metabolic pathways, including photosynthesis, transcriptional regulation, disease resistance, glycolysis, carbon metabolism, protein, amino acid metabolism, and others (Marcon *et al*., 2010) [64]. As a result of these findings, protein modification and protein occurrence influence the amount or degree of heterosis expressed (Kaeppler, 2012) [52].

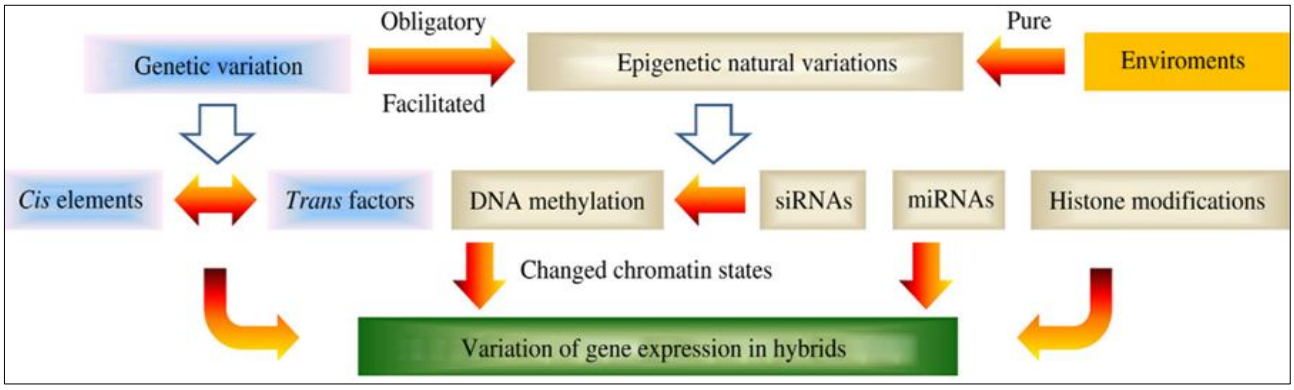


Fig 2: Epigenetic and Genetic Regulation of gene expression pattern in hybrid plants (He, *et al*., 2013)

Epigenomic studies

When two distinct parental inbred lines are crossed, epigenetic changes such as histone acetylation (Tanabata *et al*., 2010) [92], chromatin remodeling (Moghaddam *et al*., 2007) [70], modest RNAi regulation (Groszmann *et al*., 2011) [34], and DNA methylation occur (Tanabata *et al*., 2010) [92]. (Parisod *et al*., 2009) [75] In most crop species, DNA methylation is the most essential regulator of genome-related activity and cellular development. Most crops have their DNA methylated as a consequence of the deposition of DNA methyl transferase at the 5th position of cytosine (Law *et al*., 2010; Fernie *et al*., 2013). The overall frequency of DNA methylation in hybrids varies according to the genetic variety of the parental inbred lines (Chen, 2013) [15]. The repressin-initiated transcription pathway, which either blocks the regulatory genetic causes of inbreeding depression or promotes gene expression for heterosis, is primarily responsible for the appearance of heterosis through DNA methylation (Nakamura *et al*., 2010). The methylation sites of inbred parental lines are often connected to methylation sites in hybrid progenies. Certain methylated regions in parental inbred lines are covered by siRNA levels, suggesting that DNA methylation is connected to RNA (RNA-directed DNA Methylation), which may promote remodeling in DNA methylated regions of hybrid progenies to exploit heterosis (Greaves *et al*., 2012 and Greaves *et al*., 2016) [32, 31]. Histones undergo post-translational changes such acetylation, methylation, and phosphorylation for amino acids at N-Terminal Tails (Berger, 2007) [5]. The majority of these changes take place in histone proteins like H3K9ac and H3K4me3, which are present in actively expressed euchromatic sites (Roudier *et al*., 2009) [80]. Histones are in charge of the transcriptome of a maize hybrid. Endosperm transcriptome and histone HTA112 endosperm transcriptome revealed much higher gene expression variety than inbred parental lines (Jhanke *et al*., 2010).

Energy Efficiency Model for Heterosis: Goff previously established the turning up hypothesis, an energy model that establishes polygenic heterosis and explains differences in yield, growth, and evolution across hybrids and inbred parental lines. According to this theory, allele-specific gene expression is linked to protein stability and folding, which assists in cell energy conservation and speeds up cell division (Goff, 2010) [30].

$$\text{Energy}_{\text{Biomass}} = \text{Energy}_{\text{Input}} - \text{Energy}_{\text{Consumed}}$$

(Baranwal *et al*., 2012) [4]

This was shown experimentally and scientifically in Brassica napus, resulting in a 5% increase in overall yield above parental inbred plants (Hauben *et al*., 2009) [41]. A second experiment was carried out to test this energy model, which revealed an increase in photosynthetic efficiency as well as increased hybrid vigour and output (Ni *et al*., 2009) [72]. Arabidopsis hybrids outperformed parental inbred lines in terms of metabolic activity and effective energy usage efficiency in the early stages of development. Positive energy management may be used to boost vigour and biomass in any biological system (Meyer *et al*., 2012) [68].

Quantitive Trait Loci (QTL) and Heterosis: The essential concept that aided molecular understanding of heterosis by making molecular markers accessible, allowing for a more precise method to mapping genes and detecting them in complicated phenotypes. These molecular markers aid in the identification of genomic sequences involved in heterosis. The quantitative trait loci (QTL) for specific variables associated in the formation of heterosis in parental inbred lines were found using Marker Assisted Selection. However, it is a complicated concept that is difficult to apply well (Korn *et al*., 2008; Li *et al*., 2008) [55, 59]. Several marker-assisted QTL investigations have failed to detect epistasis or the degree of epistasis (Lippman and Zamir, 2007) [62]. The difficulties in identifying specific heterotic traits and the loci that regulate them when employing RIL (Recombinant Inbred Line), backcross, and F2 populations are mostly due to epistasis effects across several segregating loci of the whole genome (Li *et al*., 2001) [60]. Although QTL does not generally rule a single agronomic trait, in nature it controls all of them and is mediated by a number of genes at several loci (Birchler and Veitia, 2010) [8]. Advances in QTL and genetics enabled the identification of the expression. Brem *et al*. (2005) [10] made great strides in finding genetic connections between heterosis-related genes. QTL Analysis is the future, and it will have a significant influence on current approaches in QTL analysis for genetic dissection and trait manipulation. Several genetic techniques will be employed to aid in the research, appraisal, and interpretation of heterosis in order to get a better understanding of it.

Utilizations of Crop Heterosis in Cereals: In agriculture, heterosis exploitation is regarded as a breakthrough that has resulted in a significant increase in crop output and tonnage. Grain yields have increased almost fivefold when compared to yields produced from types or cultivars used before to hybridization. Maize, one of the most important cereal crops, has attained tremendous production thanks to the

manifestation and full usage of heterosis. In compared to parental inbred lines, a considerable number of maize hybrids perform well (Mulualem and Abate, 2016). Inbred parental maize lines have poor kernel yield and vigour potential, while inbred lines have good kernel growth, kernel yield, and vigour potential. 70 percent of the maize grown worldwide is hybrid seed, which produces four times more corn than ordinary maize types (Shul, 1908) [84]. Aside from maize, rice is the most frequently produced staple crop, and it is also widely planted as hybrid rice through heterosis. Hybrid rice accounts for around 55% of all rice farmed in the globe, yet it is a basic diet for the majority of people worldwide. Hybrid rice has been demonstrated to improve by 10–20 percent when compared to early inbred line kinds (Mulualem and Abate, 2016). Researchers from the International Rice Research Institute (IRRI) identified 73 percent heterosis, 59 percent heterobeltiosis, and 34 percent conventional heterosis in rice production in 1980 and 1981. The genetic source of heterosis has been investigated in a "immortalized F_2" population of Shanyou 63, an exceptional Indica rice hybrid. According to the findings, heterosis is produced by over-dominance, which results in increased tillers, grain weight, and yield components (Zhou *et al*. 2012) [106].

Conclusion

In the preceding 90 years, plant breeders have accomplished a great deal, and heterosis has played a vital role in this accomplishment. The world's population has increased, and the environment has changed, while food surpluses have diminished, and new chances to enhance food supply are being discovered on a regular basis. Even still, scientists were completely baffled as to how heterosis functioned at the molecular level in the past. A greater knowledge of the process has been gained from genome sequencing, gene expression studies in parent in breds and hybrids, and metabolic pathway research in hybrids in recent years.

Future scope: Gene expression profiles of hybrids and parental lines have been compared recently using current biology and molecular technology, which is a first for the field. DEGs associated with photosynthesis, energy metabolism, and carbohydrate metabolism were discovered in these investigations. These pathways do not entirely explain the chemistry of heterosis production, which is still being investigated. Genes, climate, and environment, as well as the expression of many genes involved in physiological metabolism, all have a role in determining how effectively it works. A variety of environmental factors influence the spatiotemporal pattern of gene expression in a cell. Heterosis is a complicated characteristic that is controlled by a number of genes. Transcriptional profiling, as well as metabolomics, ionomics, and phenomics, may be used to identify potentially useful genes. Multi-omics and high-throughput approaches have the potential to alter plant biology by providing readings of genes, metabolites, proteins, and ions at different developmental stages and environmental conditions. This could pave the way for advancements in the molecular concept of heterosis breeding, as well as other fields. It is rare to locate parents who exhibit general heterosis, midparent heterosis, and outstanding parenting skills. The purpose of heterosis research is to find genetic or QTL variants that are crucial for metabolic function. Researchers working on bacterial defense heterosis (Yang *et al*., 2021) [100], gene editing systems sterile lines, MiMe (Cas9) systems, stock heterosis (Asaf *et al*., 2021), and even novel technological techniques have all been drawn to the topic in recent years (Yu *et al*., 2021) [101].

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