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Recent Advances in Perception of Crop Heterosis: A Review

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ABSTRACT: Heterosis or Hybrid Vigour is defined as the natural phenomenon in which the resulting F1 Hybrid is genetically superior to its parental inbred lines and have phenotypically and genotypically improved characteristics or traits. This phenomenon is most important in many crops using F1 hybrid cultivars. In this the progeny produced from crossing of various different cultivars have Increased biomass, higher grain yield, and better growth and development rate than their parental lines and this has been in use for production of agricultural crops for many years. Heterosis is the morphological and genetical superiority of offspring's in F1 cross over the parental population. The heterosis is very useful in hybrid development and help the plant breeders to utilize the hybrid vigour of both parental germplasm in a more precisely and efficient manner through exploitation of the heterosis and increase the outcomes of hybrid breeding program. The development of many hybrids has been done by the exploitation of heterosis in various crops. The selection of the parental lines and breeding objectives for a sound breeding program is decided by the heterotic groups of parental inbred lines and the extent of combining ability in them. Maize is most important staple cereal crop grown in India. It is highly cross-pollinated crop and there is a wide scope for the exploitation of hybrid vigour, hence it has a significant role in production of hybrids after the successful exploitation of heterosis or hybrid vigour. However there has been many researches are going on to clearly finding out the molecular mechanisms of heterosis. The availability of molecular markers has paved the way to find out the genetic basis for occurrence of heterosis phenomenon at molecular or at Gene-expression level. It helps to identify the genes contributing for those traits of interest and helps in the mapping of those genes on chromosome. Several approaches are made using molecular markers technology which helped to find out and identify the gene of interest in genome sequence contributing for heterosis. This review discusses the phenomenon of heterosis, genetic, molecular basis, its recent advances and exploitation in crop plants.

Keywords: Heterosis; Maize; Genome Sequence; QTL; Epigenetics

INTRODUCTION

Heterosis (Hybrid Vigour) is a naturally occurring phenomenon in which the F_1 hybrid produced from genetically different individuals (Parental Lines) shows superiority in morphology, Growth and development comparative to their parental population (Shull, 1948; Coors and Pandey 1999). Highly Cross-pollinated Crops like Maize, Pearl millet, Rye and other forage grasses generally tend to show high degree of heterosis compared to self-pollinating crops like wheat, rice, barley and oats. However, many high yielding hybrids and notable hybrid cultivars have been developed in them (Rajendrakumar *et al.*, 2015). Heterosis is commonly occurred in multicellular organisms like plants, animals and microorganisms like Fungi. In heterosis two parental inbred lines of diverse genetic constitution with wider adaptability are used in hybridisation and the resultant F_1 hybrid have increased height, foliage, seed formation and overall yield higher than the parental population (Darwin, 1876). Heterosis can be exploited by improvement of traits contributing for the growth, development and other important characters of species. In maize, a significant growth increase is seen between parents and hybrids and in later developmental stages F_1 hybrids exhibits relatively more vegetative growth, increase in biomass and higher grain filling than their parents. The superiority of F_1 Hybrid is solely depending upon the genetically diverse parents and their combining ability, but it is observed that hybrid vigour of progenies decreases in further generations. Heterosis is exploited in many crops like wheat, rice, maize, pearl millet and many other like Oils seeds, pulses, fruits and vegetables through development of hybrids (Rajendrakumar *et al.*, 2015).

Evolutionary History of Heterosis: During early 18th century the Darwin has performed experiments on maize through cross pollination and concluded that the cross pollination is helpful and beneficial for the crop improvement and while self-pollination as deteriorating and injurious due to its effect of narrowing of genetic base (Darwin, 1876). Heterosis has some basic principles such as high genetic variability and the effect of heterosis depends on the genetic base of parental population, mode of reproduction and the traits used for the selection (Zhou *et al.*, 2012), Plant Developmental

Stages (Groszmann *et al.,* 2011), the Environmental conditions (Duvick, 1999). The Kolreuter was first to observe the heterosis phenomenon in Tobacco Hybrids (Reed, 1943). Further many scientists have done their researches in many crops to exploit and study about the heterosis phenomenon.

The genetical mechanism for expression of heterosis is greatly different across various species and also depend upon their mode of pollination (Self or Cross Pollinated) But the heterosis is more commonly seen in cross pollinated crops compared to self-pollinated crops (Chen, 2010). By this it shows that genetic mechanism of cross-pollinated species involves interaction of different alleles in F_1 Hybrid thus resulting in superior performance than self-pollinated species (Fu *et al.,* 2014). It is also to be noted that even though the F_1 hybrid is superior over the parental inbred lines, but in the successive generations due to continuous selfing results in Inbreeding depression (Charlesworth and Charlesworth 1999). Several studies have explained that the hybrid vigour is due to genomic turbulence, which is generated due to the union of two distinct genomes resulting in widening of genome genetic base and also leads to unique gene expressions in Hybrids (McClintock, 1993; Ha *et al.,* 2009).

Understanding the Genetic Basis of Heterosis: Dominance, Over-dominance and epistasis are the considerable theories for genetic basis of heterosis and to explain about the hybrid vigour in many Crops (Lamkey and Edwards, 1999; Crow, 2000; Reif *et al.*, 2006). Even though it has not been clearly stated, these genetic models forms a complex of numerous genes contributing for hybrid vigour (Hochholdinger and Hoecker 2007). Although the gene actions involved in exploitation of heterosis in superior hybrid is contributed by dominance and it is the most accepted theory (Charlesworth and Willis, 2009). These Conventional Hypotheses have initially guided the researches and paved the way to understanding the molecular level, gene expressions contributing heterosis (Birchler *et al.,* 2010). As discussed the dominance theory demonstrates heterosis by dominance effect of dominant alleles from two parental inbred at different loci to mask the expression of recessive alleles and helps in increase vigour of F_1 Hybrid over Parental Inbred (Davenport, 1908; Bruce, 1910; Keeble and Pellow, 1910; Jones, 1917). The Over-dominance theory states that heterosis is believed to be the superiority of heterozygous individual over homozygous occurring at one loci (Shull, 1908; East, 1908; Crow, 1948; Stuber, 1994). This overdominance hypothesis states that diverse alleles interact with each other and result in various allelic combinations generating the superiority in F_1 hybrid (Lippman and Zamir, 2007). However many research Studies explained that heterosis is contributed by single gene in tomato, cereals, and Arabidopsis (Gustafsson, 1946; Semel *et al.,* 2006; Krieger *et al.,* 2010). (Jones, 1917) raised a point that linkage cab be causing notable changes in identification of overdominance that gave rise to new concept Pseudo Dominance which refers to an specific genes with dominant alleles in repulsion in parental inbred lines can cause overdominance (Crow, 1999; Stuber *et al.,* 1992). The last model of epistasis in heterosis is considered to be an favourable allelic interaction at multiple loci of two inbred has shown dominant, Additive and Overdominance effects (Yu *et al.,* 1997; Li *et al.,* 2001).

Understanding the Molecular Background of Heterosis: The recognized hybrid vigour in heterotic individual than it parental inbred lines is the aggregate outcome of the genetic information coded by various gene regulation levels i.e., transcription, Translation. With the emergence of new molecular tools like single nucleotide polymorphism, next generation sequencing, large number of structural and numerical variations and many others tools that come up with diversity in plant population can be easily interpreted (Díaz *et al.,* 2012; Zmienko *et al.,* 2013; Saxena *et al.,* 2014). To decipher the underlying mechanism that regulates the extend of hybrid vigour deviation between the hybrids and parental inbreds, molecular research were reading in the play to evaluate their transcription level, protein level, epigenetic level and other gene regulatory aspects contributing for heterosis (Kaeppler, 2012).

Transcriptome: When two parental inbred lines are hybridised that results in the gene interaction between cytoplasm and nucleus and leading to the changes in the molecular and cellular level resulting in change of pattern of expression of gene these modifications of gene expression and their functioning at genome level in the hybrid through its parental inbreds have been notice in many hybrids of cereals i.e., Maize (Swanson-Wagner *et al.*, 2006; Stupar and Springer, 2006), Cotton (Flagel *et al.,* 2008), Wheat (Wang *et al.,* 2006). The Transcriptome study and its ability ion heterosis can be treated as provisional stage in between the phenotypic expression of a plant and its genetic information and particularly quantify the extent of contribution of every allele in Hybrid Progeny (Schnable and Springer 2013). To recognize the involvement of genes and its contribution in heterosis can be studied through analysis of transcriptomes many transcriptome technologies like DNA Micro Array, RNA- Sequence Based approach etc. are to be used to differentiate inbred lines with their hybrid progenies. From early studies in transcriptome on many crops it was assumed that useful gene expressions in hybrid are more important when compared o its parental inbred lines (Comings and MacMurray, 2000; Stupar *et al.,* 2008; Baranwal *et al.,* 2012; Fujimoto *et al.,* 2018). Anyhow it is important to consider that distinctive gene expression will not directly leads to the protein synthesis between inbreds and hybrids. It is necessary to study the post transcription regulations of gene that are altered (Xing *et al.,* 2016*;* Fu *et al.,* 2014).

Proteomics: There is a important role of proteins in detecting heterosis, as changes at primary transcript level will always does not yield protein of altered gene expression and it depends upon post transcriptional regulation and translation mechanisms (Xing *et al.,* 2016*).* In generally, the parent inbred lines has higher protein metabolism due to lack of stable protein levels that requires lot of energy to supress ultimately there will be a lack of energy for its biomass production, vegetative growth and its yield. The genetic background for this circumstance in parental inbred lines due to absence of intra allelic interaction in their homozygous state but in case of hybrids they will have many alleles and generate more allelic combination and this able to express higher growth due to accelerated cell division leading to hybrid vigour (Goff *et al.,* 2010). A Number of studies has revealed that heterosis can be determine using the differentially expressed proteins additionally mass spectrometry helps in detection and quantifying the altered protein based on isobaric labelling reagents *i.e*., Tandem Mass Bags (TMT) and Isobaric tags for Relative and Absolute Quantification (ITRAQ) in heterotic individuals (Xing *et al.,* 2016; Wang *et al.,* 2016). Till dater there are many DEP's that determine heterosis has been recognised in many cereals like Maize, Wheat, Rice From Plant Tissues like Leaf, Embryo, root (Guo *et al.,* 2013; Song *et al.,*2007; Zhang *et al.,* 2012). There are many evidences showing that most of the recognised DEP's between Parental inbreds and hybrids have non additive effects in nature and also stated that these DEP's belong to many plant metabolic pathways like Photosynthesis, Glycolysis, signal Transduction, Protein Metabolism, etc. (Marcon *et al.,* 2010). Hence these conclusions shows that the extent or level of heterosis expressed is based upon the protein incidence and the protein modifications (Kaeppler, 2012).

Epigenomes: The hybrid vigour resulted from crossing of two diverse parental inbred lines is frequently associated with the epigenetic changes *viz.,* Histone Acetylation (Tanabata *et al.,* 2010), DNA Methylation (Parisod *et al.,* 2009), Chromatin Remodelling (Moghaddam *et al.,* 2007) and Small RNAi Regulations (Groszmann *et al.,* 2011). In any crop species the cellular development and genome activity are actually regulated by DNA methylation. The DNA methylation in many crops is due to accumulation of methyl groups at 5^l Position of cytosine with the help of DNA Methyl transferases (Law *et al.,* 2010; Fernie *et al.,* 2013). The level of DNA Methylation alters in hybrids depending upon the genetic diversity among the parental inbred lines (Chen, 2013). The demonstration of heterosis through DNA Methylation is Primarily initiated by the repressin's the process of transcription by supressing the regulatory genes responsible to induce inbreeding depression or through stimulating the gene expression for heterosis (Nakamura *et al.,* 2010). The Sites of DNA Methylation in hybrids were often correlated with the regions that are methylated in parental inbreds. In specific methylated sequence in parental inbreds are covered by siRNA levels and this indicates that DNA methylation is associated with RNA (RNA-directed DNA Methylation) may cause the remodelling in the sites which are DNA Methylated in Hybrids to exploit the heterosis (Greaves *et al.,* 2012; Greaves *et al.,* 2016). Histone Modifications also occur after translational level for amino acids at N-Terminal Tails in Histones in the form of Acetylation, Methylation and Phosphorylation (Berger, 2007). Generally these modification will takes place in histones like H3K4me3 and H3K9ac that are found in actively expressing Euchromatic regions (Roudier *et al.,* 2009). In Hybrid Maize the Transcriptome derived from endosperm and the histone HTA112 has shown significantly variably in expression of genes more than their parental inbred lines (Jhanke *et al.,* 2009).

Energy Efficiency Model for Heterosis: In Recent Years the turning up theory proposed by Goff, an energy model demonstrating the multigenic heterosis which explains the differences in yield, growth and development between hybrids and inbreds. According to this theory, the allele specific gene expression is related to the stability and protein folding and helps in energy conservation of the cell and accelerates cell division (Goff, 2010).

$\text{Energy}_{\text{Biomass}} = \text{Energy}_{\text{Input}} - \text{Energy}_{\text{Consumed}}$ (Baranwal *et al.,* 2012)

This was experimentally proved in the hybrids of *Brassica napus* and resulted in Around 5%

Increase in overall yield than Inbred (Hauben *et al.,* 2009). The further experiment tested this energy model which has shown increase in the photosynthesis efficiency and also for increased hybrid vigour and biomass (Ni *et al.,* 2009). The Hybrids produced from Arabidopsis in early stages of development has shown a high metabolic activity and effective energy-use efficiency than parental inbred this positive regulation of energy in any biological system can be exploited for biomass and vigour (Meyer *et al.,* 2012).

Heterosis and Quantitive Trait Loci (QTL): The core concept which made the molecular understanding of heterosis easy by the available of molecular markers, which helped in precisive initiative to map genes and identify them in complex traits. These molecular markers technology helpful in identification of genomic sequence that are contributing for heterosis. The quantitative trait loci concerning for specific trait which are involved in manifestation of heterosis for favourable traits in parental inbred lines by Marker Assisted Selection But it is very complex concept and difficult to achieve exactly (Korn *et al.,* 2008; Li *et al.,* 2008). The marker assisted – QTL studies are not accurate for finding the epistasis and level of epistasis (Lippman and Zamir, 2007). Challenges in determining the specific heterotic phenotypes and specific loci that control them gives rise to predominantly from epistasis effect among different segregating loci of the total genome when RIL (Recombinant Inbred Line), backcross, and F_2 Populations are utilised (Li *et al.,*2001).QTL will not always control specific agronomic trait but regulates it in nature and mediate by multiple genes at different loci (Birchler and Veitia, 2010). Advancements in QTL and genomics led to Identification of expression Quantitive Trait Loci(eQTL) has given predominant progress in understanding genetic level interaction among the genes that are involving heterosis (Brem *et al.,* 2005). The Future is with eQTL Analysis and has significant effect to Conventional techniques in QTL Analysis for genetic dissection and alteration of different Traits. By Various genome tools it will be easy to study, understand and interpret the better understanding of heterosis.

Utilisation of Crop Heterosis in Cereals: The heterosis exploitation in agriculture is regarded as innovation, that lead to the sudden and huge increase and tonnage in crop production. The yield of cereals has been increased around 5 times compared to the yield obtained from the varieties or cultivars used before hybrids. The maize is one of the major cereal crops achieved a huge production by the manifestation of heterosis and make full use of it. Many numerous hybrids of maize are showing extraordinary performance compared to parental inbred lines (Mulualem and Abate 2016). There has been an significant increase in yield and vigour of kernels in maize while inbred lines of maize exhibit a low potential of kernel yield and vigour. Around 70% of maize grown in the world comprises of hybrid seeds and there is four times increase in maize yield through hybrid seed than the conventional maize varieties (Shull, 1908). Apart from maize, the majorly grown staple cereal like rice is also extensively grown as hybrid rice by exploitation of heterosis. Around 55% of Rice grown in the world comprises of hybrid rice and it has been serving major staple cereal for majority of population. it has been observed that hybrid rice has improved around 10-20 % compared to early inbred varieties (Mulualem and Abate 2016).

CONCLUSION

The plant breeders have done noble achievements and the heterosis also has a significant role in these achievements for about 90 years. Even though, due to an increase in population and climate changes in world have created check for food surplus and the chances for increasing food supply is being deployed day by day. But in the past decades the molecular level understanding of heterosis is not clear but in recent years it has been studied through genome sequencing, gene expression in parental inbreds and hybrids and study of metabolic pathways in hybrids helped out to understand molecular mechanism of heterosis.

FUTURE SCOPE

The plant breeders have done noble achievements and the heterosis also has an significant role in these achievements for about a 90 years. Even though, due to an increase in population and climate changes in world have created check for food surplus and the chances for increasing food supply is being deployed day by day. But in the past decades the molecular level understanding of heterosis is not clear but in recent years it has been studied through genome sequencing, gene expression in parental inbreds and hybrids and study of metabolic pathways in hybrids helped out to understand molecular mechanism of heterosis. The exploitation of heterosis in various aspects like Stress tolerance, yield and other economically important traits in plants would be rewarding. The researches on heterosis is a continuous process as new concepts are known day by day and several works are being done to fix heterosis and to stabilize food production in world.

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Conflict of Interest. Nil.

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