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Evolution of Inbreeding Depression and Genetic Bases Study on Heterosis in Cross Pollinated Species

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SUMMARY

Heterosis is the phenomena in which hybrids created by crossing members of the same or closely related species are more robust or vigorous than their parents. As a result, heterosis and hybrid vigour are frequently interchanged. The mechanisms producing heterosis are divided into two categories: dominance and overdominance. According to the dominance hypothesis, during inbreeding, harmful recessive alleles accumulate in the homozygous state, resulting in a decrease in vigour, or inbreeding depression. When inbred individuals are mated, their progeny become heterozygous at these loci, with dominant alleles covering the deleterious alleles, alleviating inbreeding depression and restoring vigour. According to the overdominance hypothesis, heterozygous loci produce more robust products than homozygous loci. As a result, greater homozygosity diminishes vigour, while outbreeding introduces heterozygozygosity, which increases robustness. These two hypotheses offer similar genetic predictions, but coupled molecular and genetic studies can help separate them. Both systems may be active and relevant in heterosis in different organisms under different situations; they are not mutually exclusive..

INTRODUCTION

The term heterosis was first used by Shull in 1914. **Heterosis** may be defined as the superiority of an F, hybrid over both its parents in terms of yield or some other character. Generally, heterosis is manifested as an increase in vigour, size, growth rate, yield or some other characteristic. But in some cases, the hybrid may be inferior to the weaker parent. This is also regarded as heterosis; Often the superiority of F, is estimated over the average of the two parents, or the mid -parent. If the hybrid is superior to the mid -parent, it is regarded as heterosis (average heterosis or relative heterosis). However, in practical plant breeding, the superiority of F, over mid-parent is of no use since it does not offer the hybrid any advantage over the better parent. Therefore, average heterosis is of little or no use to the plant breeder. More generally, heterosis is estimated over the superior parent; such an estimate is sometimes referred to as **heterobeltiosis.**

The term heterobeltiosis is not commonly used since most breeders regard this to be the only case of heterosis and refer to it as such i.e., heterosis. In 1944, Powers suggested that the term heterosis should be used only when the hybrid is either superior or inferior to both the parents. Other situations should be regarded as partial or complete dominance. However, the commercial usefulness of a hybrid would primarily depend on its performance in comparison to the best commercial variety of the concerned crop species. In many cases, the superior parent of the hybrid may be inferior to the best commercial variety. In such cases, it will be desirable to estimate heterosis in relation to the best commercial variety of the crop; such an estimate is known as economic, standard or useful heterosis. Economic heterosis is the only estimate of heterosis, which is of commercial or practical value (Fig 01).

Heterosis and Hybrid Vigour

Hybrid vigour has been used as a synonym of heterosis. It is generally agreed that hybrid vigour describes only the superiority of hybrids over their parents, while heterosis describes other situations as well. But a vast majority of the cases of heterosis are cases of superiority of hybrids over their parents. The few cases where F_1 hybrids are inferior to their parents may also be regarded as cases of hybrid vigour in the negative directions. For example, many F_1 hybrids in tomato are earlier than their parents. Earliness in many crops is agriculturally desirable. It may be argued that the earliness of F_1 hybrids exhibits a faster development in them so that their vegetative phase is replaced by the reproductive phase more quickly than in their parents. Therefore, the use of heterosis and hybrid vigous as synonym seems to be reasonably justified.

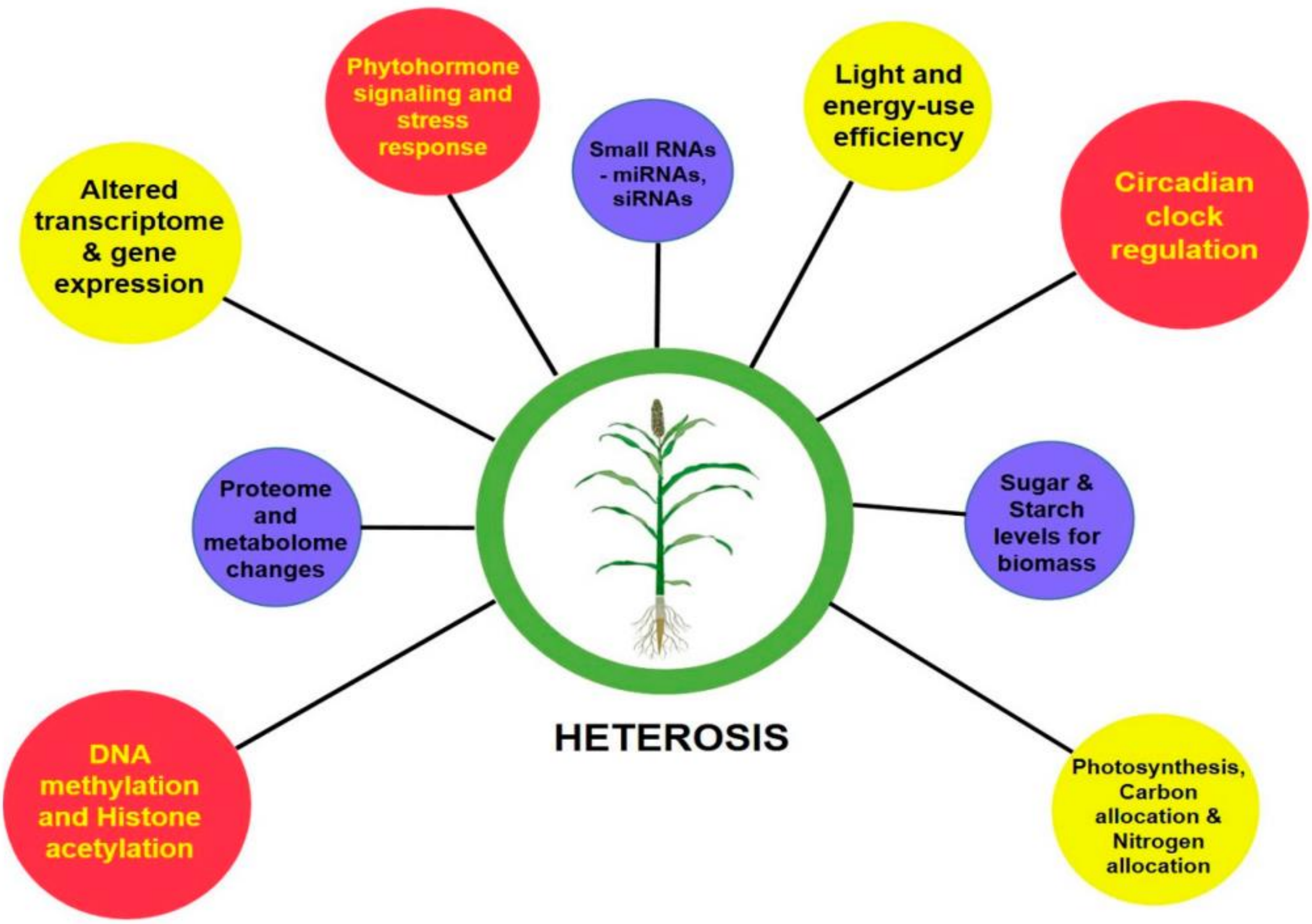

Fig 01. Exploitation uses Heterosis

Luxuriance

Luxuriance is the increased vigour and size of interspecific hybrids. The principal difference between heterosis and luxuriance lies in the reproductive ability of the hybrids. Heterosis is accompanied with an increased fertility, while luxuriance is expressed by interspecific hybrids that are generally sterile or poorly fertile. In addition, luxuriance may not result from either masking of deleterious genes or from balanced gene combinations brought together into the hybrid. Therefore, luxuriance does not have any adaptive significance.

Historical

Hybrid vigour in artificial tobacco (Nicotiana spp.) hybrids was first reported by **Koelreuter** in 1673. Subsequently, many workers reported hybrid vigour in a large number of plant species. These hybrids were produced from interspecific as well as intraspecific crosses. In 1876, **Darwin** concluded that hybrids from unrelated plant types were highly vigorous. Most of our present knowledge on heterosis comes from the work on maize. Maize is perhaps the most extensively studied crop species with respect to heterosis and inbreeding depression. **Beal** studied the performance of intervarietal hybrids between 1877 and 1882. He reported that some hybrids yielded as much as 40 per cent more than the parental varieties. From subsequent studies on intervarietal crosses in maize, it became clear that some of the hybrids showed heterosis, while others did not. Crosses between distinct types, i.e., genetically diverse varieties, exhibited greater heterosis than those involving closely related varieties.

The genetic hypotheses to account for heterosis were first advanced during 1908. The dominance hypothesis was proposed **Davenport** in 1908 (it was later elaborated by **Keeble and Pellew** in 1910) , while the overdominance hypothesis was put forth by **East and Shull** in the same year, i.e., 1908. In 1912, **East and Hays** advocated heterosis breeding as an alternative plant breeding strategy. The concept of double cross hybrids was proposed by Jones in 1917, while that of top cross hybrids was advanced by Davis in 1927.

Heterosis in Cross - and Self-Pollinated Species

In general, cross-pollinated species show heterosis, particularly when inbred lines are used as parents. In many cross-pollinated species, heterosis has been commercially exploited, for example, in maize, bajra, jowar, cotton, sunflower, onion (A. cepa), alalfa, etc. Many crosses in self -pollinated species also show heterosis, but the magnitude of heterosis is generally smaller than that in the case of cross-pollinated species. But in some self -pollinated crops, heterosis is large enough to be used for the production of hybrid varieties. Hybrid varieties are commercially used in some vegetables, such as tomato, where a single fruit produces a large number of seeds, and in crops like rice. The chief drawback in the use of hybrid varieties in self-pollinated crops is the great difficulty encountered in the production of large quantities of hybrid seed.

Manifestations of Heterosis

Heterosis is the superiority of a hybrid over its parents. This superiority may be in yield, quality, disease and insect resistance, adaptability, general size or the size of specific parts, growth rate, enzyme activity, etc. These various manifestations of heterosis may be summarised as follows.

- **Increased yield.** Heterosis is generally expressed as an increase in the yield of hybrids. Commercially, this phenomenon is of the greatest importance since higher yields are the most important objective of plant breeding. The yield may be measured in terms of grain, fruit, seed, leaf, tubers or the whole plant.
- **Increased Reproductive Ability.** The hybrids exhibiting heterosis show an increase in fertility or reproductive ability. This is often expressed as higher yield of seeds or fruits or other propagules, e.g., tuber in potato (S. tuberosum), stem in sugarcane (S. officinarum), etc.
- **Increase in Size and General Vigour.** The hybrids are generally more vigorous, i.e., healthier and faster growing and larger in size than their parents. The increase in size is usually a result of an increase in the number and size of cells in various plant parts. Some examples of increased size are increases in fruit size in tomato, head size in cabbage, cob size in maize, head size in jowar, etc.
- **Better Quality.** In many cases, hybrids show improved quality. This may or may not be accompanied by higher yields. For example, many hybrids in onion show better keeping quality, but not yield, than open-pollinated varieties.
- **Earlier Flowering and Maturity.** In many cases, hybrids are earlier in flowering and maturity than the parents. This may sometimes be associated with a lower total plant weight. But earliness is highly desirable in many situations, particularly in vegetables. Many tomato hybrids are earlier than their parents.
- **Greater Resistance to Diseases and Pests.** Some hybrids are known to exhibit a greater resistance to insects or diseases than their parents.
- **Greater Adaptability.** Hybrids are generally more adapted to environmental changes than inbreds. In general, the variance of hybrids is significantly smaller than that of inbreds. This shows that hybrids are more adapted to environmental variations than are inbreds. In fact, it is one of the physiological explanations offered for heterosis.
- **Increase in the Number of A Plant Part.** In some cases, there is an increase in the number of nodes, leaves and other plant parts, but the total plant size may not be larger. Such hybrids are known in beans (P. vulgaris) and some other crops.

These are some of the characteristics for which heterosis is easily observed. Many other characters are also affected by heterosis, e.g. enzyme activities, cell division, vitamin content (vit. C content in tomato), other biochemical characteristics, etc., but they are not so readily observable.

CONCLUSION

In spite of the large experimental evidence accumulated, it is not possible to conclusively accept or reject one or the other hypothesis. There are definitely some genes that show heterozygote superiority. But the number of such genes appears to be rather small, and even these cases could be due to linkage in repulsion phase or epistasis or both. It is generally accepted that heterosis, to a large extent, is due to dominance gene action, but epistasis and over dominance are also involved (both in self- and cross-pollinated crops). The relative importance of these phenomena is, however, not clearly understood. Recent evidence accumulated with maize seems to suggest that over dominance may not be the primary cause of heterosis. Over dominance is easily imitated by epistasis and linkage, and that most reported cases of over dominance may not represent true overdominance.

Molecular markers linked to quantitative trait loci (QTLs) have been used to investigate the relative significance of dominance, overdominance and epistasis in heterosis. Some workers have reported important overdominance, others have observed preponderance of dominance and some others have found extensive epistasis in various crops.

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