

Review

## Does low yield heterosis limit commercial hybrids in wheat?

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Heterosis has contributed to productivity gains in several crops like maize, rice, sorghum, cotton etc. Wheat breeders have largely been unsuccessful to take advantage from this technology at commercial level. Lack of commercial level yield heterosis is regarded as a major reason for this failure as compared to other technical barriers like difficult pollination control and seed production. The allopolyploidy nature of wheat endows even wheat purelines with a fixed intergenomic heterosis which perhaps is the foremost reason for lack of classical yield heterosis in wheat. The coming together of three diverse but functionally similar genomes causes differential gene expression among several other outcomes and leads to a diploid behaving self-sustaining intergenomic hybrid. A long history of highly successful pureline breeding and shortage of nicking parents are other two reasons responsible for failure to realize commercial level heterosis in wheat. Molecular biology tools now make it possible to dissect the phenomenon of heterosis into detectable Mendelian factors to tailor nicking parents to develop commercially sustainable wheat hybrids. This review probes the reasons for the absence of commercial-scale heterosis in wheat.

**Key words:** Wheat, *Triticum*, hybrid, heterosis, yield.

### INTRODUCTION

Commercial exploitation of hybridity has been one of the greatest achievements of crop improvement research. Heterosis increases commercially utilizable yields in farmers' fields, leading to higher productivity and income levels. Farmers and breeders, especially for cross-pollinated crops like maize, have shifted emphasis from open-pollinated varieties to hybrids to gain from the technology. Shull (1952) defined heterosis as "the interpretation of increased vigour, size, fruitfulness, speed of development, resistance to disease and to insect pests, or to climatic rigors of any kind manifested by crossbred organisms as compared with corresponding inbreds, as the specific results of genetic unlikeness in the constitution of the uniting parental gametes." Heterosis has been studied extensively in maize because of (1) a large expression in terms of yield, (2) extensive exploitation in maize, and (3) ease of pollination control.

Wheat, on the other hand, employs cleistogamy in a relatively small flower, making pollination control extremely difficult. Single-plant and small-plot estimates have reported a wide range of yield heterosis in wheat (Singh et al., 2010), however, economically sustainable hybrid exploitation at farmer field level is still limited.

### WHAT EXPLAINS HETEROSIS?

Shull (1908, 1909) observed that when maize plants were selfed, their vigor and grain yield declined, but when two inbred lines were crossed, both vigor and grain yield increased and even exceeded the mean of the two parents. These reports established the concept of heterosis breeding, and efforts have been made since then to use the phenomenon to benefit all crop plants.

The International Maize and Wheat Improvement Centre (CIMMYT) convened an international congress in 1998 on heterosis breeding to take stock of the application of hybrid technology to different crops, including wheat. One essential characteristic of heterosis is that it happens only when hybridity brings together different alleles originating from different parents into one genotype. There have been several explanations for the phenomenon of heterosis:

**a) Dominance hypothesis:** Heterosis is the joint action of multiple loci, with favorable allele being either partially or completely dominant (Bruce, 1910; Keeble and Pellew, 1910; Jones, 1917; Collins, 1921).

**b) Overdominance hypothesis:** Heterosis occurs due to overdominant gene action at many loci (East, 1936; Hull, 1945; Crow, 1948).

**c) Epistasis hypothesis:** Heterosis arises because of epistatic interactions between non-allelic genes (Richey, 1942; Schnell and Cockerham, 1992).

**d) Quantitative genetic explanation:** Researchers have employed both first-degree and second-degree statistical estimates to explain heterosis (Hallauer and Miranda, 1981) and both provided a clear answer about the relative importance of various types of gene actions involved in expression of heterosis. Falconer and Mackay (1996) gave a quantitative genetic expression for heterosis in terms of gene effects. Heterosis for a cross between two populations was equal to  $hy^2$ , where “h” is the genotypic value of the heterozygote cross and “y” is the difference in gene frequencies of two parental populations. According to this concept, the first critical component determining extent of heterosis is the genotypic value of a heterozygote at any given locus, and it would be dependent on interallelic or within-locus interaction at a locus, namely, dominance or overdominance. Also, when  $hy^2$  is summed over all loci affecting the trait under consideration, non-allelic interactions would also be accounted for. Therefore, the quantitative expression draws its strength from all three above hypotheses.

The second crucial component is the difference in gene frequency, meaning how diverse two parental populations are or how diverse the parents are. Therefore, two “Ds” viz., -diversity, reflected in differences in gene frequency, and desirability, measured as “h” summed over all loci contributing to the trait under study will decide whether the trait will manifest heterosis or not. A similar analogy was put forward by Fu and Dooner (2002) on the basis of DNA sequencing data in maize. They suggested that different maize lines often lack different functional genes. When a nicking pair of lines is crossed, the lines complemented each other's weaknesses, bringing in the two “Ds,” and heterosis results.

#### **e) Physiological and molecular diagnosis:**

Developments in molecular biology enabled molecular dissection of heterosis. Quantitative trait locus (QTL) analyses have begun to further our understanding of heterosis by breaking it down into Mendelian factors and studying their modes of inheritance (Yuan et al., 2012; Hua et al., 2003; Li et al., 2001). However, the relative importance of different genetic phenomena explaining heterosis varies from system to system and trait to trait. One important outcome of several such studies is that heterosis can be defined by a limited number of Mendelian factors. Though an association between QTLs and heterosis has been shown, cloning and further utilization are yet to be accomplished (Lippman and Zamir, 2007). Lack of genetic colinearity at gene level has also been proposed as a reason for heterosis. Gene deletions causing lack of colinearity are also said to be functionally compensated by duplicate copies elsewhere in the genome (Fu and Dooner, 2002). However, a hemizygous complementation of these gene deletions by the other genome leads to heterosis in a hybrid.

Altered gene expression in a hybrid, as a result of two genomes coming together, has been proposed as another molecular regulatory mechanism causing heterosis. Song et al. (2009) proposed differential protein expression as a cause of heterosis in wheat. A total of 49 of approximately 900 protein spots expressed differentially in seedling leaves in a hybrid between common wheat and spelt wheat. Of the 49 differentially expressed proteins, 30 were involved in metabolism, signal transduction, energy, cell growth and division, disease defense mechanism and secondary metabolism. Song et al. (2009) postulated that these protein differences were involved in diverse physiological pathways that might be responsible for observed heterosis. Wang et al. (2006), observed differential expression in roots for 27.52% of 990 fragments among hybrids and their parents at the jointing stage and concluded that this differential expression was important for heterosis in root system traits. However, Bottley et al. (2006) observed differential transcriptional silencing of up to 27% of genes in leaves and about 26% of those in roots, in which one (and rarely two) members of a set of three homoeoalleles were not present in the cDNA (complementary DNA) of either roots or leaves. They failed to detect a trend in their study of 236 single-copy genes, each of which mapped to one locus of the three homoeologous chromosomes, but the phenomenon of differential transcriptional silencing definitely hints at some method of genome/ allele compensation. On the other hand, Feldman et al. (2012) discovered that non random intergenomic silencing occurred only for about 10% of the genes and that for most other genes, the extra copies were making a favorable effect through positive intergenomic interactions. Gu et al. (2004) compared a sequence of a 307 kb physical contig covering the high molecular weight (HMW) glutenin locus

from the A genome of durum wheat (*Triticum turgidum* [T. durum] AABB) with the orthologous regions from the B genome of the same wheat and the D genome of the diploid wheat *Aegilops tauschii*. Based on sequence comparison, they concluded that hexaploid wheat might have more than one tetraploid ancestor, further supporting allelic diversity contributing to intergenomic heterosis.

## HYBRID WHEAT

Heterosis was first reported in wheat by Freeman (1919) for plant height. Since then, there have been several reports on heterosis in wheat since then. The whole subject of hybrid wheat was reviewed by Pickett and Galwey in 1997 and more recently by Singh et al. (2010). A few successful hybrids have been reported by the private sector, for example in Europe and India (Saaten, 2013; Mahyco, 2013); however, even the hybrids currently available in market offer the best economic advantage only under less than optimum growing conditions. This has been observed in several other studies (Sharma and Tandon, 1995; Solomon et al., 2007).

The question remains why wheat breeders are unable to bring together best of the two “Ds” to develop profitable commercial hybrids. Wheat is the third most important cereal crop in the world, and perhaps the number one cereal consumed directly as food by humans. A number of reasons have been suggested for the lack of a commercial hybrid, including the absence of economical, sustainable hybrid seed production and the absence of a high enough level of heterosis to compensate for the costs involved in seed production and thus become a profitable option for farmers and seed companies. This paper focuses on the reasons for the absence of commercial-scale heterosis.

### What limits yield heterosis in wheat?

Pickett and Galwey (1997) concluded that the most serious technological barrier to the development of a successful commercial wheat hybrid is the absence of adequate heterosis. They argued that if the benefits of hybrid varieties were sufficiently attractive, other difficulties could be overcome by researchers, as is evident from several promising recent reports on male sterility and seed production systems (Song et al., 2013; Titan and Meglic, 2011). Three key factors limit yield heterosis in wheat: multiple genomes, the long history of wheat breeding, and the lack of nicking parents.

#### **Multiple genomes**

Polyploids are organisms that contain two or more sets of

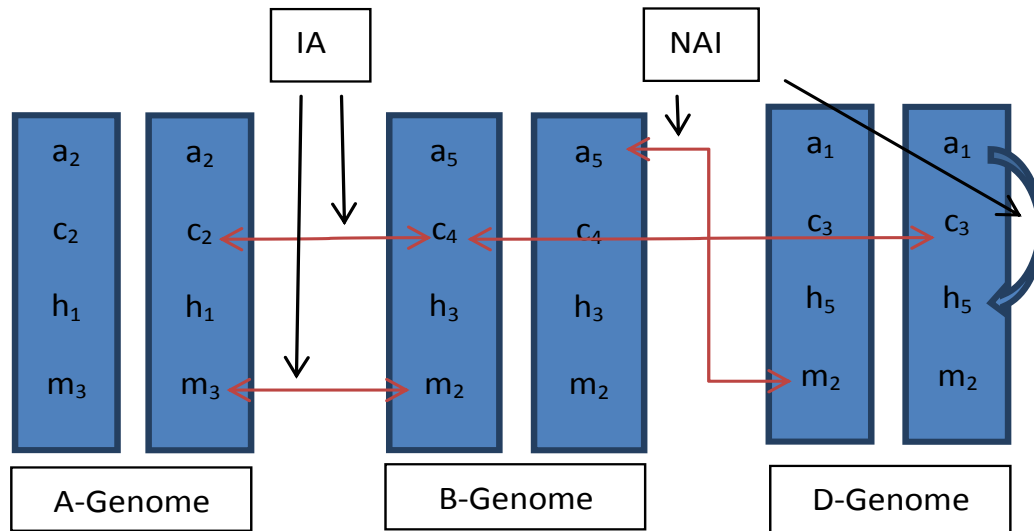
basic chromosomes. Allopolyploids contain doubled interspecific genomes, meaning that hybrid vigor and heterozygosity are permanently fixed like in wheat, *Brassica napus*, and *Geum urbanum* (Vandepitte et al., 2011). Polyploids often not only exceed the diploid progenitors' phenotypes but also exhibit phenotypes not existing in diploid progenitors. Some of these traits either contribute to heterosis or confer adaptation to new ecological niches. The advent of molecular tools (Aversano et al., 2012) offers opportunities to explore the molecular effects of polyploidization. These allopolyploids allow heterosis-causing interactions between homoeologous genes on different genomes, much like between different alleles of one gene, causing heterosis in heterozygote diploid genotypes (Figure 1). In allopolyploids, such interactions occur even in genotypes (Figure 1a), and thus they are supposed to have fixed heterosis.

Polyploids are in fact very successful as about 70% (Masterson, 1994) of flowering plants are polyploids, and about 75% of those are allopolyploids (Grant, 1981; Brochmann et al., 2004). Allopolyploids are formed spontaneously either by crossing unreduced gametes of the participating species or by chromosomal doubling of the interspecific hybrid. Some allopolyploids, such as Brassicas (UN, 1935), evolve through multiple origins involving reciprocal crosses, whereas others, like wheat (Salamini et al., 2002), are formed by a single or a few hybridization events. It is interesting to note, however, that some allopolyploids, like cotton, are still able to have highly successful commercial hybrids over and above their allopolyploid character, while we are still struggling to achieve full scale commercial hybrids in wheat. Having understood the role of desirable diversity in realizing commercial heterosis, it is critical to assess whether there is sufficient desirable allelic diversity in wheat or its inadequacy itself has become a limiting factor.

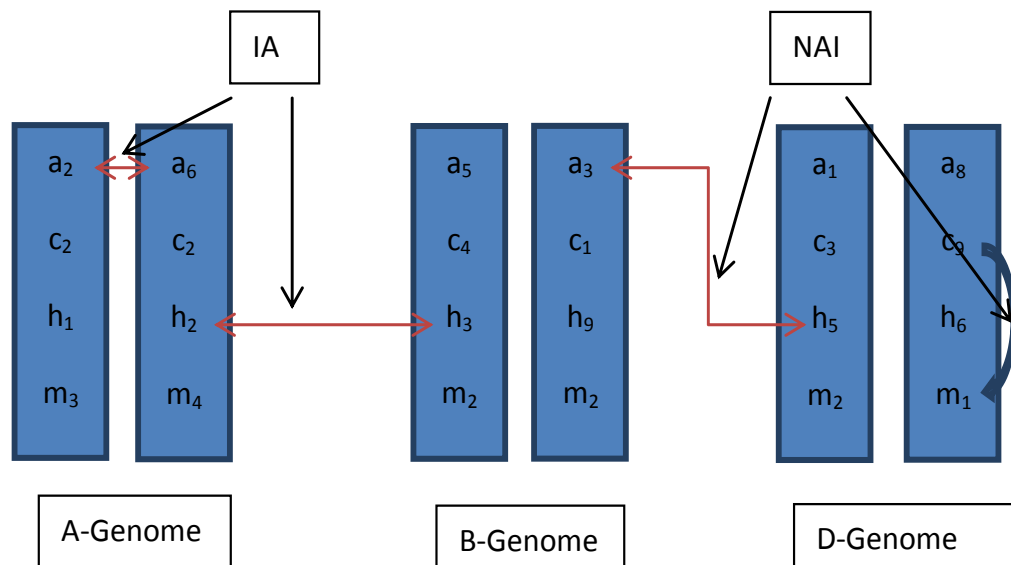
Wheat, being an amphiploid, has three genomes and is therefore considered to be a natural hybrid. This multiple-genome ancestry perhaps increases wheat's ecological amplitude and evolutionary success (Meimberg et al., 2009) and gives it a very wide agro-climatic adaptability.

The allopolyploidization in wheat causes genome restructuring, including sequence elimination from the parental genomes, which appears to be dictated by parental genomes, ploidy level, and sequence type (repetitive, low-copy, or coding) and affects preferentially the larger parental genome (Bento et al., 2011). This elimination phenomenon was found to be non-random and reproducible and augmented the differentiation of homoeologous chromosomes, providing the physical basis for a diploid-like meiotic behaviour (Ozkan et al., 2002).

This process also prevented intergenomic recombination, ensuring full fertility and permanent heterosis between alleles of different genomes (homoeoalleles). However, polyploidization causes some degree of intergenomic homoeologous gene silencing and differential gene expression and perhaps contributes



**Figure 1a.** Fixed interallelic (IA) and non-allelic (NAI) interactions among three wheat genomes in a wheat pureline leading to fixed intergenomic heterosis.



**Figure 1b.** Heterozygosity conferred interallelic (IA) and non-allelic (NAI) interactions among three wheat genomes in a conventional  $F_1$  wheat hybrid.

to intergenomic heterosis (Mochida et al., 2003). It possesses fixed heterosis resulting from homoeologous alleles on its three homoeologous chromosomes, which in fact is even better than classical heterosis, as the latter has only two genes at each locus (Figure 1a). When two such hexaploid wheat lines are crossed, the fixed intergenomic heterosis is considered to be one of the reasons for low classical heterosis.

The presence of three homoeologous alleles (homoeoalleles) in any pure line already imparts enough

hybridity to benefit from the phenomenon of heterosis, and a classical cross, which brings in six homoeoalleles at each locus, perhaps fails to bring in enough desirable hybridity across all loci to endow the resultant hybrid with a significantly higher commercial-level heterosis over and above the fixed intergenomic one in best commercial cultivars (Figure 1b). Developments in molecular biology are now allowing investigations into fixed heterosis employing specially constructed amphiploid populations using their diploid progenitors (Abel et al., 2005;

Bansal et al., 2012).

### **Long history of breeding**

It can be argued that centuries of wheat breeding have already accumulated three diverse desirable alleles at most loci and that a gradual improvement in this direction is under way in all conventional breeding programs around the world. A collection of 9,000 gene-associated single nucleotide polymorphisms were used to study a worldwide sample of 2,994 hexaploid wheat landraces and modern cultivars to detect regions of wheat genome subject to selection during improvement (Colin et al., 2013). The study revealed that ancestral variation has been used extensively, selection likely acting on multiple functionally equivalent alleles. Can we really conclude that this long-term selection accumulated different but functionally similar alleles over decades, further enhancing intergenomic heterosis within wheat?

While maize has a heterozygous balance, wheat has a homozygous balance, meaning there are no deleterious alleles in pure lines. However, this does not rule out the dominance model as an explanation of heterosis at some loci in wheat. The dominance model (Bruce, 1910; Jones, 1917) postulates that inbred parents contain deleterious or inferior alleles at several loci, inhibiting overall good performance, and that these are dominated by superior dominant alleles from the other parent in a hybrid, resulting in a superior performance. Wheat can be a little different in that there might not be deleterious alleles in a pure line (because there is no inbreeding depression), but there could be inferior alleles (decreasers in case of quantitative traits) in one parent and superior alleles (increasers in case of quantitative traits) in the other parent, which, when brought together, result in a superior performing hybrid.

For example, for a thoroughly investigated locus like HMW glutenin subunits (HMW-GS), Ribeiro et al. (2011) reported a total of 56 patterns in a set of 134 hexaploid wheat accessions in Portugal. For the three loci Glu-A1, Glu-A2, and Glu-A3 of HMW-GS, they discovered 4, 10, and 6 alleles, respectively. This type of not-yet-investigated allelic variability for other economically important traits in different genomes has been utilized by breeders over centuries and has been accumulated in pure lines conferring a high level of intergenomic heterosis to present-day wheat cultivars. This also implies that it is theoretically possible to accumulate all possible desirable alleles to get pure lines as high-yielding as a hybrid. This theoretical possibility might have been turned into a reality by centuries of wheat improvement work throughout the world, and even if this has been partially achieved, it would explain lack of frequent commercial-level heterosis in wheat (Figure 1). This was somewhat supported by Cui et al. (2002) when they found only 11.14% heterosis in 20 intervarietal

hybrids compared to 111.39% in interspecific hybrids involving spelt wheat, highlighting the importance of interspecific gene transfer to broaden the common wheat gene pool for further yield improvement, including heterosis exploitation. A potential useful introgression from *T. tauschii* has been suggested (Mohammadi et al., 1999), and this possibility was demonstrated by Snape and Parker (1985) when they successfully combined yield-determining alleles dispersed between two parents in one inbred line.

### **Lack of nicking parents**

It is understood that yield is a complex trait-the sum of several qualitative and quantitative traits-and yield heterosis cannot be fully explained by the oversimplified hypotheses that have been put forward by several researchers. One certain requirement for any commercial heterosis is the presence of genetic differences in the two parental lines (East, 1936); however, diverse parents will not always yield heterosis (Solomon et al., 2007). Choosing the right parental combination is central to achieving heterosis. Overdominance (Shull, 1908; East, 1936; Crow, 1948) and pseudo-overdominance (Semel et al., 2006) models can definitely explain heterosis happening at several loci, even in a crop with homozygous balance like wheat. Overdominance postulates interallelic interaction as the cause of heterosis at some loci, whereas pseudo-overdominance results from complementation of two or more linked dominant and recessive alleles in repulsion, in which the dominant and recessive alleles are located on opposite homologues of the two genes acting as overdominance.

Since heterosis is a genome-wide expression, and one model explaining heterosis for one locus does not preclude other models explaining heterosis for other loci, different models might explain different locus-specific heterosis expressions. These different genetic models, therefore, only explain different temporal and/or spatial changes in gene regulatory network caused by hybridity (Omholt et al., 2000). However, it needs to be realized that the unique intergenomic hybridity of bread wheat also fixes all forms of non additive heterosis available in the three constituent genomes (Figure 1a). A simple estimate of diversity does not necessarily mean that parents will be heterotic. The allelic constitutions of the three constituent genomes of both the parents need to nick well to give a commercial heterosis over and above the heterosis already fixed in the two parents (Figure 1b). Most studies estimating diversity using molecular markers (El-Zanaty et al., 2013; Chen et al., 2010; Solomon et al., 2007; Zhan et al., 2006; Dreisigacker et al., 2005; Zhang et al., 2003; Corbellini et al., 2002; Xu et al., 2002) concluded that this simple diversity estimate was unable to predict the heterotic potential of the identified parents.

## CONCLUSION

Heterosis is a powerful tool benefitting several important crops with yield advantages ranging from 15 to 50%. Wheat breeders have naturally been interested in exploiting this option. A molecular deciphering of the phenomenon of heterosis will definitely help explain the lack of commercial-level heterosis in wheat. Any phenotype, especially those involved in commercial heterosis, involves multiple quantitative traits expressed sequentially or simultaneously during development. A molecular dissection will relate genome-wide tempo-spatial gene expression data with the relevant phenotypes.

Zachary et al. (2006) proposed a “phenomics” platform to measure multiple traits in the context of high-resolution QTL mapping as a tool to dissect heterosis into its fundamental components. QTL mapping in both rice (Hua et al., 2002, 2003; Li et al., 2001; Luo et al., 2001; Xiao et al., 1995; Yu et al., 1997) and maize (Stuber et al., 1992) have broken down heterosis into Mendelian factors displaying inheritance as hypothesized in classical models of dominance, overdominance, and epistasis. The central idea remains to identify the responsible markers/QTLs/phenomena and then select the right type of parental combinations to maximize heterosis. QTL mapping/cloning approach can be effective in identification of heterosis-causing Mendelian factors and heterotic parental combinations in a multigenomic amphiploid like wheat. What is therefore needed is substantial basic research to determine causes of yield heterosis in wheat and then identify right type of parental combinations.

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