

Proteomic patterns associated with heterosis[☆]



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ABSTRACT

Heterosis is characterized by higher seed yields, plant biomass or other traits in heterozygotes or hybrids compared with their genetically divergent parents, which are often homozygous. Despite extensive investigation of heterosis and its wide application in crops such as maize, rice, wheat and sorghum, its molecular basis is still enigmatic. In the past century, some pioneers have proposed multigene models referring to the complementation of allelic and gene expression variation, which is likely to be an important contributor to heterosis. In addition, there are potential interactions of epigenetic variation involved in heterosis via novel mechanisms. At the level of gene expression, many recent studies have revealed that the heterosis phenomenon can be deciphered not only at the transcriptional level but also at the proteomic level. This review presents an update on the information supporting the involvement of proteomic patterns in heterosis and a possible future direction of the field. This article is part of a Special Issue entitled: Plant Proteomics – a bridge between fundamental processes and crop production, edited by Dr. Hans-Peter Mock.

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1. Introduction

As the world population increases, improvement of crop production is urgently required to meet ever-growing demands. One practical strategy to solve this problem is the use of hybrid plants. Heterosis describes the situation in which an F₁ hybrid exhibits phenotypic performance that is superior to that of its parents (Fig. 1). An important feature of hybrid plants for guaranteeing crop management is phenotypic uniformity among F₁ individuals. Heterosis was initially recorded by various civilizations but has been systematically investigated for more than a century since the time of Charles Darwin (1876) [1], first in the absence of genetics and subsequently with genetic considerations [2–4]. The rediscovery of heterosis in maize a century ago revolutionized plant breeding and production [2,5]. However, the underlying mechanism of heterosis remains to be elucidated. In 1936, East et al. addressed it as a general rule that the degree of heterosis in hybrids is proportional to the genetic diversity between the parents [6]. At the genomic level, three hypotheses are routinely applied to explain the mechanism of heterosis. One is the so-called ‘dominance’ model, which attributes heterosis to the effect of beneficial dominant alleles over recessive alleles. The second is the so-called ‘overdominance’ model, in which heterozygous genotypes in

hybrids are advantageous compared with either parental homozygous state at a single locus [7]. With regard to practical agricultural applications, these two classical but unproven models lead to completely different strategies and prospects. The dominance model indicates that distinct sets of deleterious recessive alleles undergo genome-wide complementation in offspring. By contrast, the overdominance model proposes that intralocus allelic interactions at one or several heterozygous loci lead to hybrid vigor. Genes showing overdominance are the most attractive and noteworthy from both a fundamental and applied perspective because only a single heterozygous gene is needed to achieve crop heterosis under the theory of overdominance [8]. The third hypothesis is the so-called ‘epistasis’ model, which refers to the interactions between two or more favorable genes derived from different parents to generate a single improved phenotype. Although some evidence has been found for each mechanism, none of them appears to be a general mechanism, underscoring the complexity of heterosis at the gene regulatory level [9].

At the level of gene expression, it has been suggested that interactions between parental genomes lead to the alteration of transcripts and even protein abundance in F₁ hybrids [7]. Protein expression refers to the process in which proteins are synthesized, modified and regulated in living organisms. To obtain a more comprehensive understanding of the mechanism of heterosis, the idea that genome-wide changes in protein expression in hybrids contribute to heterosis has been presented and advanced in the past decade [10–13]. Consistent with the changes in gene expression observed at the transcriptional level in hybrids, additive and non-additive proteomic patterns have also been found in various tissues of different species (Table 1). Moreover, many post-

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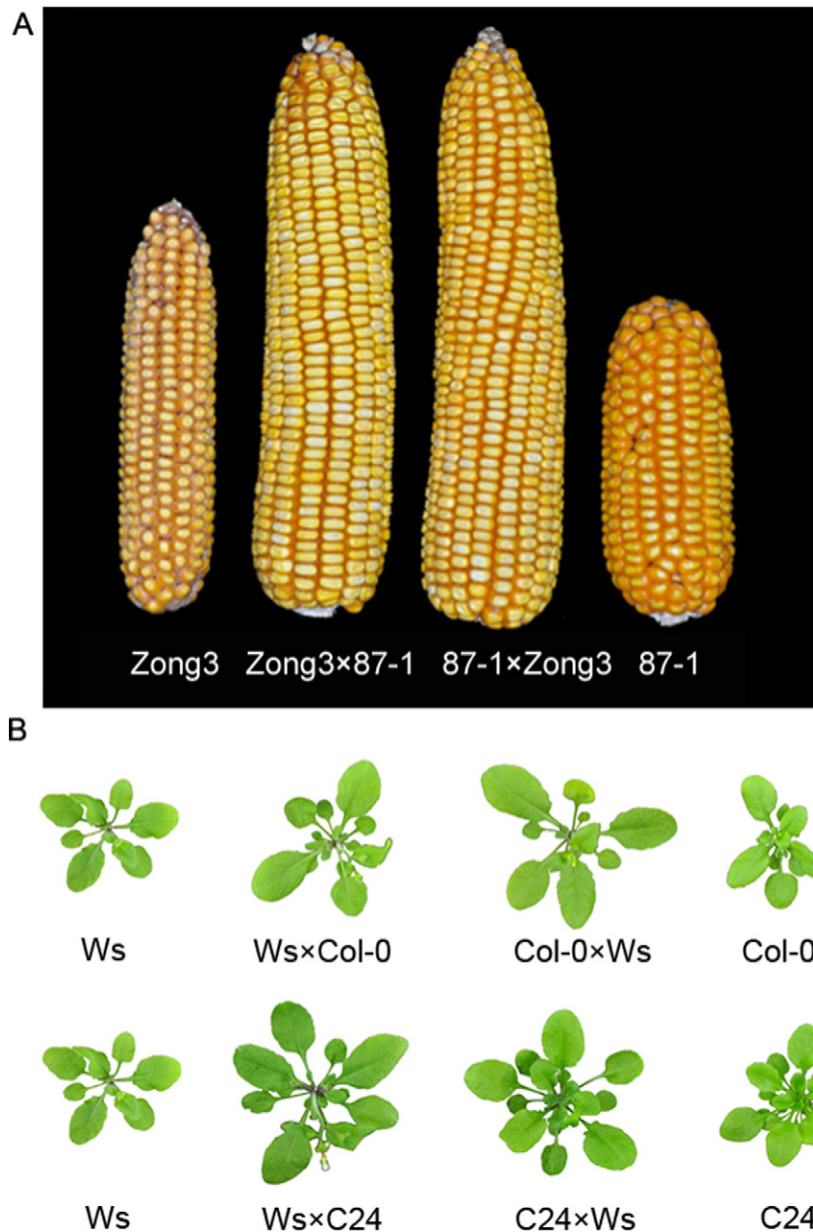


Fig. 1. Heterotic phenotypes in maize and *Arabidopsis*. (A) A typical example of heterosis. Yield vigor was similar in the reciprocal F₁ hybrids (Zong3 × 87–1 and 87–1 × Zong3) but higher than in the inbred parents (Zong3 and 87–1). (B) The plants shown here are the parents and their reciprocal F₁ hybrid progeny. The biomass vigor of the hybrids is significantly higher than that of the parents. Photos courtesy of Zhipeng Sui and Tianya Wang, Sun Laboratory.

translational modifications (PTMs) are crucial for the regulation of protein functions, which may be important for determining heterosis. However, some cases of heterosis can be explained by heterozygote advantage of different protein isoforms encoded by the same locus. This review will mainly focus on exploring the mechanistic basis of heterosis from the perspective of proteins and proteomics.

2. The application of isozyme allelic diversity in heterosis

The original application of proteomic tools to investigate heterosis can be traced back to the use of isozymes. Isozymes were first described by Markert et al., who defined them as different variants of the same enzyme with identical functions that are present in the same individual [14]. With the advent of electrophoresis and the consequent convenience of data collection related to isozyme variability, a number of attempts have been made to use the variability of genes encoding isozymes as a criterion for genetic relatedness between plants [15]. As

early as the 1970s, several investigators estimated the correlations between isozyme allelic diversity and the grain yield of single-cross maize hybrids [16–19]. For instance, a significant, but relatively small correlation was detected when Tsafaris et al. (1995) analyzed 16 inbreds for 47 isozymic loci [10]. The diversity index (DI) was used to denote the number of isozymes that were dissimilar in two inbred lines. Hybrids produced from inbred combinations with a higher DI out-yielded those with a low DI. However, investigators found that although the isozyme DI was significantly associated with a higher yield in single-cross hybrids, there was limited predictive value of these markers, primarily to lines with similar pedigrees [16]. In another study, Smith et al. (1991) used more than 100 maize hybrids derived from 37 elite inbred lines, in which associations were evaluated based on 30 isozymic loci, but these authors reported an r^2 value of only 0.36 when the F₁ yield was plotted against isozyme allelic diversity [20]. From the above studies, it became clear that isozyme diversity provides limited value in the prediction of hybrid performance. In addition, when

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