

Heterosis in elite hybrid rice: speculation on the genetic and biochemical mechanisms

Stephen A Goff¹ and Qifa Zhang²

Because of the tremendous advances in functional genomics and the current availability of a large number of superior hybrids, rice is an excellent model crop system for heterosis research. Genetic dissection of yield and yield component traits of an elite rice hybrid using an ultra-high density linkage map identified overdominance as the principal genetic basis of heterosis in this hybrid. This is not an expected finding based on the reported effects of single genes. Here we propose a gene expression and protein quality control hypothesis as one possible explanation for the overdominance in hybrids bred for yield. Future studies will be directed toward the identification of the genetic and biochemical mechanisms underlying the biology of hybrid vigor.

Addresses

¹ iPlant Collaborative, BIO5 Institute, University of Arizona, Tucson, AZ 85721, USA

² National Key Laboratory of Crop Genetic Improvement, National Center of Plant Gene Research, Huazhong Agricultural University, Wuhan 430070, China

Corresponding author: Zhang, Qifa (qifazh@mail.hzau.edu.cn, qifazhgzau@gmail.com)

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Introduction

Heterosis, or hybrid vigor, refers to the superior performance of hybrids relative to their parents. Utilization of heterosis has tremendously increased the global productivity of many crops. Despite the obvious importance of heterosis, however, the understanding of the underpinning biological mechanism is still only fragmentary after a century of extensive research, analysis, observation, and debate. While there have been a range of studies on various aspects of heterosis, the key to understanding the biology of heterotic performance in crop hybrids lies within the framework of genetic and biochemical mechanisms, many of which remain to be fully characterized. Three classical genetic hypotheses, that is, dominance [1–4], overdominance [5–8], and epistasis [9,10] were proposed as explanations for the genetic basis

of heterosis. Although there have been a large number of genetic analyses in plants and various other species with results favoring one hypothesis or another, the full complement of genetic components pertaining to heterotic performance of crop hybrids has rarely been characterized in an experimental population for assessing the relative contributions of these genetic components to heterosis in a hybrid.

Zhou *et al.* [11**] suggested the following prerequisites for complete genetic characterization of heterosis relevant to crop production: first, the genetic materials are based on elite hybrids with demonstrated high heterotic performance and time-honored superiority in crop production; second, the targets are key traits of agronomic performance; third, the experimental population allows identification of all the genetic components concerned, including dominance, overdominance and epistasis; and fourth, a full set of markers that could detect the genetic effects of any region in the entire genome be used.

Rice provides a good model crop for heterosis studies

Rice is the staple food crop currently feeding over half of the world's population. Rice has also become an excellent model system in plant biology research for monocotyledon species because of its many advantages relative to other cereals [12]. The tremendous progress that has been achieved in rice functional genomics in the last decade, including construction and development of technological and resource platforms for high throughput functional analysis of the rice genome and cloning and molecular characterization of hundreds of genes, has greatly enhanced the understanding of a wide range of important biological processes [13]. Large scale resequencing has generated an unprecedented amount of comprehensive data for examining genetic and genomic diversity of both cultivated rice varieties and their wild relatives [14].

Tremendous efforts have been invested in the development and adoption of hybrid rice varieties in a number of countries, including China over the past half a century, and India, Bangladesh, Vietnam and other Asian countries in the past few decades. Breeding for rice hybrids has generated a large number of elite hybrid varieties including ones that have been widely used for many years. Such elite hybrids are usually highly heterotic showing greatly elevated yield potential. As much as or more than 100% mid-parent heterosis ($=F_1 - MP$, where MP is the mean of the parents) and over 40% high-parent heterosis

($=F_1 - HP$, where HP is the higher parent value) has been frequently observed in experimental plots [15–17]. It is estimated that hybrids can out-yield conventional cultivars by 30–40% in production fields [18]. Moreover, elite hybrids often display wider adaptability due to enhanced resistance to both biotic and abiotic stresses relative to inbreds, and therefore perform more stably across locations and over time. These hybrids offer excellent genetic materials for heterosis research. Together with the available rice genomic resources and the advances made in functional genomics, rice provides an ideal model and crop system for studying the molecular mechanisms of heterosis.

Current understanding of the genetic basis of heterosis from an elite rice hybrid

Shanyou 63, a cross between the two *indica* lines Zhen-shan 97 and Minghui 63, is an elite hybrid that has been widely adopted in rice production in China and other Asian countries over the past three decades. The area planted with Shanyou 63 reached 6.7 million hectares in its peak production period in the late 1980s and early 1990s. This level of production accounted for over 25% of the total rice area in China during that period. Using this hybrid cross as a model, Zhang and co-workers have conducted a series of studies in an attempt to characterize the genetic basis of heterosis [15,19,20^{*},21^{**},22^{**}] displayed by Shanyou 63. In particular, they generated an experimental population by intercrossing recombinant inbred lines (RILs) derived from a cross between the two parents, which they referred to as an ‘immortalized F_2 ’. Such a population possesses a number of distinct advantages for heterosis research. The genetic composition of this population is similar to an F_2 , allowing estimation of all the genetic components, including dominance and overdominance at a single locus level, and epistasis involving two or more loci.

Recently Xie *et al.* [23^{*}] genotyped the RILs by population sequencing with a parent-independent method they developed for constructing ultra-high density linkage maps composed of high quality SNPs, based on 0.055-fold genome sequence depth per line. This enabled inference of the genotype of each cross in the immortalized F_2 population based on the parental RILs, providing data for the construction of an ultrahigh-density genetic map, which divided the genome into 1619 bins. They performed genome-wide analyses of single-locus genetic effects and digenic interactions for yield, number of tillers per plant, number of grains per panicle and grain weight to assess the relative contributions of genetic components that they considered pertinent to heterosis in the hybrid. This analysis included single-locus dominance and overdominance, and digenic dominance, which measures the advantage of the double heterozygote over the mean of the two parental genotypes, resulting from epistatic interactions that showed significant dominance by dominance

interactions (Figure 1a,b). The results showed that both the overall levels of heterosis and the relative contributions of the genetic components to heterosis varied with traits. Yield showed the highest level of heterosis followed by number of grains per panicle and grain weight, while the amount of heterosis of tiller number per plant was low and inconsistent between years. Overdominance was the most important contributor to heterosis of yield, number of grains per panicle and grain weight. Digenic dominance was important for heterosis of tillers per plant, grain weight and also had a role in yield and in grain number per panicle. Single-locus dominance had a relatively small contribution in all analyzed traits. Although the results appear to be consistent with the general expectation that cumulative effects of these components may well explain the genetic basis of yield heterosis in the hybrid, the prevalence of overdominance was unexpected, and seemed to differ substantially from the perspective of previous results obtained using low-density markers [20^{*},21^{**},22^{**}].

The cause of overdominance in hybrids is still a controversial issue in the literature. In tomato, it was reported that the flowering gene *SINGLE FLOWER TRUSS* showed overdominance for fruit number, in that the heterozygote for this gene displays higher performance than both parental lines in a near isogenic background [24]. However, there is no reported evidence of overdominance in any of the single genes cloned from rice to date, or any other published data from the comparison of rice NILs, suggesting that it is difficult to explain the overdominance observation based on specific individual genes. Thus Zhou *et al.* [11^{**}] proposed pseudo-overdominance, resulting from genes with opposite additive effects linked in repulsion [25,26], each of which shows partial dominance but not overdominance, as a possible explanation (Figure 1c). However, testing of such a hypothesis via high-resolution genetic recombination of the experimental materials would be difficult. An alternative hypothesis and/or approach may be needed to resolve these conflicting observations. In the following section, we propose a biochemical hypothesis to explain the observed dominance and overdominance contributing to hybrid performance.

Biochemical observations and interpretations

Hybrid shellfish display increased growth and vigor over inbreds when compared in crowded or otherwise stressed conditions. Such hybrids display more efficient protein deposition per unit oxygen consumption than inbreds, and therefore grow faster and more efficiently. Gene expression analysis together with metabolic labeling studies in a number of different species suggests that hybrids have a lower basal level of protein metabolism and more efficient growth relative to their inbred parents [27–31,32^{*},33]. Likewise, inbreeding is known to cause increased protein turnover and slower overall growth

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