

Dissection of heterosis for yield and related traits using populations derived from introgression lines in rice

Chao Xiang^{a,1}, Hongjun Zhang^{a,1}, Hui Wang^b, Shaobo Wei^a, Binying Fu^a, Jiafa Xia^b, Zefu Li^b, Yongming Gao^{a,*}, Guoyou Ye^{c,*}

^aInstitute of Crop Sciences/National Key Facility for Crop Gene Resources and Genetic Improvement, Chinese Academy of Agricultural Sciences, Beijing 100081, China

^bRice Research Institute, Anhui Academy of Agricultural Sciences, Hefei 230031, China ^cGenetics and Biotechnology Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines

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ABSTRACT

Despite the great success achieved by the exploitation of heterosis in rice, the genetic basis of heterosis is still not well understood. We adopted an advanced-backcross breeding strategy to dissect the genetic basis of heterosis for yield and eight related traits. Four testcross (TC) populations with 228 testcross F_1 combinations were developed by crossing 57 introgression lines with four types of widely used male sterile lines using a North Carolina II mating design. Analysis of variance indicated that the effects of testcross F_1 combinations and their parents were significant or highly significant for most of the traits in both years, and all interaction effects with year were significant for most of the traits. Positive midparent heterosis (H_{MP}) was observed for most traits in the four TC populations in the two years. The relative H_{MP} levels for most traits varied from highly negative to highly positive. Sixty-two dominant-effect QTL were identified for H_{MP} of the nine traits in the four TC populations in the two years. Of these, 22 QTL were also identified for the performance of testcross F_1 . Most dominant-effect QTL could individually explain more than 10% of the phenotypic variation. Four QTL clusters were observed including the region surrounding the RM9-RM297 region on chromosome 1, the RM110-RM279-RM8-RM5699-RM452 region on chromosome 2, the RM5463 locus on chromosome 6 and the RM1146-RM147 region on chromosome 10. The identified QTL for heterosis provide valuable information for dissecting the genetic basis of heterosis.

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1. Introduction

Rice (Oryza sativa L.) is the staple food of more than half the world's population [1,2]. It is estimated that 40% more rice needs

to be produced to feed the increased population by 2025 [3]. To further improve yield potential through breeding remains a challenge. Exploitation of intra- or inter-subspecific heterosis has been demonstrated to be an effective method for significantly

* Corresponding authors. E-mail addresses: irriygao@126.com (Y. Gao), g.ye@irri.org (G. Ye). Peer review under responsibility of Crop Science Society of China and Institute of Crop Science, CAAS.

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¹ These authors contributed equally to this work.

varieties occupy 57% of the rice-growing area [6,7].

Despite the great success achieved by the exploitation of heterosis for improving rice yield [8,9], the genetic basis of the heterosis exhibited in hybrid rice is still not well characterized. Three classical genetic hypotheses (dominance, overdominance, and epistasis) have been proposed as the driving factors for heterosis [10]. The validity of each hypothesis seems to depend on genetic makeups of traits and hybrids in question, as indicated in many recent quantitative trait locus (QTL) mapping studies. For example, Xiao et al. [11] reported that dominance complementation was the major genetic basis of heterosis using the BC₁F₇ progeny of an intersubspecific cross between 9024 (indica) and LH422 (japonica). Most of the identified QTL for yield and a few yield-component traits had overdominant effects in the study of Yu et al. [12]. These authors [12] also found that epistasis played an important role in determining the heterosis observed in the cross Zhenshan 97 × Minghui 63. Similarly, the importance of epistasis was reported for heterosis of yield component traits by Li et al. [13] using the F_4 progeny of a cross between the japonica cultivar Lemont and the indica cultivar Teqing. Using a population of recombinant inbred lines (RILs) derived from the same cross (Lemont × Teqing), Li et al. [14] confirmed that epistasis and overdominance were the main factors in heterosis. Luo et al. [15] conducted a large QTL mapping study using two backcross and two testcross populations by crossing RILs derived from the cross Lemont × Teqing to the two parental lines plus two testers (Zhong 413 and IR64) and further confirmed that epistasis and overdominance were important for heterosis. Similarly, additive and overdominant effects resulting from epistatic loci may have been the primary genetic basis of heterosis in Luo et al. [16]. Hua et al. [17] found that overdominance at the single-locus level and all three forms of digenic interaction (additive ×additive, additive × dominance, and dominance × dominance) could adequately explain the genetic basis of yield heterosis observed in an elite indica hybrid, Shanyou 63 (Zhenshan 97 × Minghui 63) using an immortalized F₂ population produced by randomly permuted intermating of 240 RILs. The same immortalized F₂ population was recently genotyped by population sequencing to construct an ultra-dense bin map by Zhou et al. [8]. QTL mapping based on the bin map found that overdominance/pseudo-overdominance was the most important contributor to heterosis of yield, number of grains per panicle, and grain weight. Dominance × dominance interaction played an important role in the genetic basis of heterosis of tillers per plant and grain weight, as well as roles in vield and grain number, and single-locus dominance showed relatively small contributions for all of the traits [18]. These results suggested that the relative contributions of the genetic components varied with trait and that the cumulative effects of these components may adequately explain the genetic basis of heterosis.

Introgression lines (ILs) are developed using one parent (recurrent parent, RP) as the genetic background and others as introgression parents (donors) by sequential backcrossing and selfing, and there are no differences between RP and each ILs except the introgressed loci. Consequently, a library (population) of ILs offers an accurate means of investigating the genetic effects of introgression in a relatively uniform and elite background [19,20]. Thus, ILs are well suited to defining the core genomic segments influencing target traits and further genetic improvement. Recently, several studies have used ILs to identify favorable genes/QTL for heterosis [20-22]. Luo et al. [20] tested a set of 265 ILs derived from the indica cultivar Guichao 2 and Dongxiang common wild rice (O. rufipogon Griff.) and found that 71.5% of heterotic loci (HL) showed significantly positive effects, indicating that favorable HL capable of improving agronomic traits were available in O. rufipogon. Xin et al. [21] identified HL using a set of 70 ILs carrying introgressed segments of a japonica cultivar Asominori in the background of an indica cultivar IR24 and corresponding testcross F1 populations. A total of 41 HL were detected on the basis of midparent heterosis values using single-point analysis. Of the HL, 24 had positive effects and could be used in improving yield potential.

Recently, we developed a large number of ILs using Shuhui 527 (SH527), an elite *indica* hybrid rice restorer line, as a recurrent parent and three high-yielding *indica* cultivars ZDZ057, Fuhui 838 and Teqing as donor parents. These ILs have been used in genetic analysis of various traits [22]. In the present study, we analyzed the genetic effects and main features of HL associated with yield and yield-related traits. We developed four testcross populations by crossing a set of high yielding ILs and tested, in two years, four male sterile lines representing the four most commonly used types of male sterile lines in Chinese hybrid rice breeding programs.

2. Materials and methods

2.1. Plant materials

Shuhui 527 (SH527) is an elite *indica* restorer line of hybrid rice in China. High-yielding $BC_2F_{3:4}$ ILs were developed using SH527 as recurrent parent and ZDZ057 and Teqing as donor parent [22]. Four types of male sterile lines (MSL) including Xieqingzao A (XA), II-32 A (IIA), Gang 46 A (GA), and Jin 23 A (JA) were selected and crossed as females with the selected ILs and the three parental lines (Shuhui 527, ZDZ057, and Teqing) to generate hybrids based on the North Carolina II mating design. Only 57 ILs were successfully crossed with all MSL. According to the MSL, these testcross F_1 (TCF₁) hybrids were divided into four testcross populations: TCP₁ (IIA/ILs), TCP₂ (XA/ILs), TCP₃ (GA/ILs), and TCP₄ (JA/ILs). In addition, Xieyou 527 (XA × SH527), IIyou 527 (IIA × SH527), Gangyou 527 (GA × SH527), and Jinyou 527 (JA × SH527) were included as check combinations (CC).

2.2. Phenotypic evaluation

The experiment was conducted in the growing seasons of 2008 and 2009 (May–September) at the experimental station of Anhui Academy of Agricultural Sciences, Hefei, China. The 62 parental lines (four maintainer lines, 57 ILs, and SH527), four TC populations, and four CC were planted in a randomized complete block design with two replicates. Thirty-day-old seedlings were transplanted into four-row plots (10 plants per row) with a spacing of 26.4 cm within rows and 16.5 cm between rows.

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