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RESEARCH ARTICLE

QTL mapping of general combining abilities of four traits in maize using a high-density genetic map



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Abstract

General combining abilities (GCAs) are very important in utilization of heterosis in maize breeding. However, its genetic basis is unclear. In the present study, a set of 118 doubled haploid (DH) lines were induced from F_1 generations produced from the cross between the inbred line Zheng 58 and the inbred line W499 belonging to the Reid subgroup. Using the MaizeSNP50 BeadChip, a high-density genetic map was constructed based on the DH population which included 1147 bin markers with an average interval length of 2.00 cM. Meanwhile, the DH population was crossed with three testers including W16-5, HD568, and W556, which belong to the Sipingtuo subgroup. The GCAs of the ear height (EH), the kernel moisture content (KMC), the kernel ratio (KR), and the yield per plant (YPP) were estimated using these hybrids in three environments. Combining the high-density genetic map and the GCAs, a total of 14 QTLs were detected for the GCAs of the four traits. Especially, one pleiotropic QTL was identified on chromosome 1 between the SNP SYN16067 and the SNP PZE-101169244 which was simultaneously associated with the GCAs of the EH, the KR, and the YPP. These QTLs pave the way for further dissecting the genetic architecture underlying GCAs of the traits, and they may be used to enhance GCAs of inbred lines under the fixed heterotic pattern Reid $\times$ Sipingtuo in China through a marker-assisted selection approach.

Keywords: maize, QTL mapping, general combining ability, high-density genetic map

1. Introduction

Maize is the largest crop in China in regarding to grain yield or sown area (<http://zzys.agri.gov.cn/nongqing.aspx>). Continuing improvement of maize grain yield and quality

can be significantly attributed to the employment of maize single-cross hybrids (Tollenaar 1989). A single-cross hybrid is produced from two parental inbred lines, and it often performs better than its parents in terms of important agronomic traits, such as yield, chemical quality, utilization of nutrition or fertilizer, drought, pest and disease tolerance (Saleh *et al.* 2002; Iqbal *et al.* 2010; Wei *et al.* 2016). The important basis for good performances of hybrids is heterosis (Tang *et al.* 2010).

Heterosis, or hybrid vigor, is the biological enhancement of a hybrid offspring compared to its parents. In most cases, heterosis is obvious in outcross species, such as maize, sugar beet, sorghum, and cotton (Flint-Garcia *et al.* 2009). Four formulas including relative heterosis, over-parent heterosis, competition heterosis and index of heterosis are employed to quantify heterosis of a hybrid (Prasad and Singh

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1986). Combining ability, which includes general combining ability (GCA) and special combining ability (SCA), is an important concept associated with utilization of heterosis (Griffing 1956; Betrán *et al.* 2003). GCA is defined as the average performance of an inbred line in its hybrid offspring, and SCA is defined as the performance of the hybrid produced from two certain inbred lines, which is relative higher or lower than the average performance of hybrid offspring produced from the involved inbred lines. Three methods have been used to determine combining abilities of lines including the top cross method, the diallel cross method, and the Line×Tester method. In maize breeding, the Line×Tester method was employed more frequently than the other two methods (Zambezi *et al.* 1986).

Heterosis often results from Mendelian or non-Mendelian inherited effects after mixing the genetic components of its parents, and two hypotheses have been proposed to explain heterosis, which are dominance and over dominance hypothesis (Lu *et al.* 2003; Guo *et al.* 2014; Shen *et al.* 2014; Wei *et al.* 2015). However, none of them is able to explain the heterosis in kinds of agronomic traits (Shen *et al.* 2014). This indicates that the mechanisms underlying heterosis are complex (Schon *et al.* 2010; Lariepe *et al.* 2012). In modern maize production, using of single-cross hybrids contributes significantly to the high yield and quality of maize. However, the basis of good performances in agronomic traits of single-cross hybrids, that is heterosis, is unclear. Therefore, it is meaningful for maize breeders to understand the genetic architecture underlying the heterosis or GCAs in important agronomic traits (Prasad and Singh 1986; Flint-Garcia *et al.* 2009; Thiemann *et al.* 2014; Jiang *et al.* 2015).

Quantitative trait locus (QTL) mapping is an important approach to investigate the genetic architecture underlying heterosis in traits of interest, which detects molecular markers statistically significantly associated with heterotic variances in segregating populations (Li *et al.* 2007; Lu *et al.* 2010). Recently, the power of QTL mapping has been improved by using high-density linkage maps and new statistic methods (Li *et al.* 2007; Liu *et al.* 2016b). For example, *qTBN5* for the maize tassel branch number was mapped within a small physical interval of ~800 kb based on a linkage map including 6 533 bin markers (Chen *et al.* 2014). Inclusive composite interval mapping (ICIM) is an improved method for QTL detection, which increased the QTL mapping power in extensive simulations and has been employed in many studies (Li *et al.* 2007; Liu *et al.* 2016a). QTL mapping has also been used to explore the genetic architecture underlying heterosis (Stuber *et al.* 1992; Lu *et al.* 2003; Guo *et al.* 2014; Wei *et al.* 2016). In 1992, QTL associated with the heterosis in maize grain yield were detected throughout the genome except on chromosome 6 using 76 molecular markers in a

cross between two inbred lines, B73 and Mo17 (Stuber *et al.* 1992). The genetic basis of GCAs has also been explored using QTL mapping (Qu *et al.* 2012; Huang *et al.* 2013; Qi *et al.* 2013). In rice, a total of 127 QTLs were identified for the GCAs of ten agronomic traits (Qu *et al.* 2012). In maize, a total of 56 loci for the GCAs of the five yield-related traits were commonly detected in at least two environments using a set of testcrosses with introgression lines (Qi *et al.* 2013), and in another study, a total of 25 significant loci for the GCAs of the seven yield-related traits were commonly identified under multiple environments (Huang *et al.* 2013). Although a few studies have investigated the genetic architecture of GCAs in maize, it was still unclear.

In Chinese maize breeding, there is an important heterotic pattern (SipingtouxReid) (Xie *et al.* 2007). And in this study, we used a doubled haploid (DH) population combining a high-density genetic map to reveal the genetic architecture underlying GCA of important agronomic traits in maize under the heterotic pattern SipingtouxReid.

2. Materials and methods

2.1. Materials and planting

The two inbred lines Zheng 58 and W499, which have high combining ability and belong to the Reid subgroup, were used to produce F_1 generations. A set of 118 DH lines were induced from the F_1 generations *via* a high oil inducer CAUHOI (Li *et al.* 2009). Three testers including W16-5, HD568, and W556, which all belong to the subgroup Sipingtoux, were used to estimate the GCAs of ear height (EH), kernel moisture content (KMC), kernel ratio (KR), yield per plant (YPP). W16-5 was developed from the inbred line D16 which was cultivated from the cross between the inbred line Huangzao 4 and the line P126. HD568 and W556 were developed from the inbred line Chang 7-2. In 2011, the 118 hybrids from the crosses between the tester W16-5 and the DH population were planted in Zhengzhou, Beijing, and Tieling, China, following a field design of randomized complete blocks with three replications. In 2012, the 236 hybrids from the crosses between the two testers (HD568 and W556) and the DH population were planted in the above three environments following the same field design. Each one-row plot contained 12 plants with a plant distance of 25 cm and a row distance of 50 cm, and the field management was the same as the local maize field.

2.2. Trait measurement and analysis

At R6 stage, the EH was quantified in centimeter (cm) using the middle five to eight representative plants in each plot,

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