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Progress of Segregation Distortion in Genetic Mapping of Plants

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Abstract: Segregation distortion is commonly encountered in actual genetic mapping populations which skews the frequency of genotypes from their Mendelian expectations. Segregation distortion is increasingly recognized as a potentially powerful evolutionary force and would affect the construction of genetic linkage map. In this study, the features influencing factors and causes of segregation distortion as well as the effects of segregation distortion on QTL mapping and the research progress of segregation distortion in plants were summarized which would provide useful reference for the further researches.

Key words: Segregation distortion, genetic mapping, Segregation Distortion Region (SDR), Quantitative Trait Locus (QTL), population, tomato, crop species, China

INTRODUCTION

Segregation distortion is a ubiquitous phenomenon in biosphere which deviates the frequency of genotypes from the expected Mendelian ratio within a segregating population and cannot be analyzed by traditional genetic methods (Lu *et al*., 2002; Li *et al*., 2010). It is thought to be a potent evolutionary force and paid more attention (Taylor and Ingvarsson, 2003; Charlesworth, 1988). In plants, segregation distortion was first reported in maize by Mangelsdorf and Jones (1926), using morphological markers and sub-sequently studied in many other crop species including rice (Mc Couch *et al*., 1988; Xu *et al*., 1997), sorghum (Pereira *et al*., 1994), tomato (Paterson *et al*., 1988), tobacco (Cameron and Moav, 1957), wheat (Faris *et al*., 2000; Peng *et al*., 2000; Kumar *et al*., 2007) and barley (Graner *et al*., 1991; Heun *et al*., 1991; Devaux *et al*., 1995). Segregation distortion is influenced by many factors, the proportion, degree, direction and genetic effects of which vary significantly with the species, crosses, mapping populations, marker types and so on (Kinoshita, 1993; Knox and Ellis, 2002; Yamagishi *et al*., 2010).

The development of high density molecular linkage maps provided a chance to survey the whole genome for loci showing distorted segregation (Harushima *et al*., 1996; Causse *et al*., 1994). Conversely, segregation distortion would affect the construction of genetic linkage map and the detection of QTL (Zhu *et al*., 2007). In this study, the phenomenon, features influencing factors and causes of segregation distortion as well as the effects of segregation distortion on QTL mapping and corresponding mapping strategies in plants were summarized.

THE PHENOMENON AND FEATURES OF SEGREGATION DISTORTION

Segregation distortion is commonly encountered in actual genetic mapping populations which skews the frequency of genotypes from the expected Mendelian ratio (Lu *et al*., 2002). Most distorted loci tend to be clustered which allow definition of Segregation Distortion Regions (SDRs) and have been reported in several crop species (Li *et al*., 2010; Xu, 2008; Tai *et al*., 2000).

The related genes of segregation distortion are throught to exist in SDRs. Whether the regions of segregation distortion are common in different mapping populations is unknown. Faris *et al*. (1998) analyzed the degree and direction of segregation distortion in an *Aegilops tauschii* F_2 population and found the most severely distorted regions were on chromosome 5D. Sub-sequently, other studies have shown that the homoeologous group 5 chromosomes of wheat and its relatives possess factors associated with segregation distortion (Faris *et al*., 2000; Peng *et al*., 2000;

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Kumar *et al*., 2007). Furthermore, a region of segregation distortion on barley chromosome 7 (5H) detected by Devaux *et al.* (1995) may represent a homoeologous distorter region in barley. Using the high-density composite map, Li *et al.* (2010) suggested that several SDRs had consistent map locations in two or more barley populations. However, Yamagishi *et al.* (2010) reported the regions of segregation distortion in the F_2 population were different from those in the DH population derived from the same cross.

INFLUENCING FACTORS AND CAUSES OF SEGREGATION DISTORTION

Genetic factors of segregation distortion: Segregation distortion of markers are considered to arise from Segregation Distortion Loci (SDL) (Xu, 2008). There is a variety of mechanisms that can cause segregation distortion and in most systems act in genetic factors including pollen tube competition, pollen lethal, preferential fertilization, sterility and chromosome translocation; the 1st three types were defined as gametic selection (Taylor and Ingvarsson, 2003; Zhu *et al*., 2007; Li *et al*., 2007; Hedrick and Muona, 1990; Lorieux *et al*., 1995a; Luo and Xu, 2003). These genetic elements causing segregation distortion may be potent evolutionary forces (Sandler and Novitski, 1957).

In maize, four of the identified SDRs were located in regions where known gametophytic factors occur (Yan *et al*., 2003). Liu *et al.* (2000) and Zhang *et al.* (1997) used the same soybean parents to construct F_2 and RIL populations, respectively and found that the main reason of segregation was gametic selection. Zhao *et al.* (2006) drew the same conclusion in rice.

Jiang *et al.* (2008) found that the segregation distortion might be caused by the joint gametic and zygotic effects. In wheat pollen killer systems, male gametes are produced that carry the non-driving allele but they are rendered inviable later in development (Loegering and Sears, 1963).

The presence of interspecific *Sterility* genes (S) could also result in strong segeregation distortion in rice (Gutierrez *et al*., 2010). Theory suggests that the meiotic drive elements such as gametophytic competition resulting in preferential fertilization or abortion of the male or female gametes or zygotes are the main influence factors of segregation distortion in plants (Taylor and Ingvarsson, 2003; Lyttle, 1991) and are highly important for the evolution of species (Hurst and Werren, 2001).

So far in maize, five *gametophytic* genes (ga) have been identified located on chromosomes and the locations of 11 male gametophytic genes have also been identified on various chromosomes in rice which would help to increase the understanding of genetic factors affecting segregation distortion (Li *et al*., 2010).

Segregation distortion and marker types: Segregation distortion can be detected in almost any kinds of markers including morphological markers, enzyme markers and molecular markers (Zamir and Tadmor, 1986; Abe and Tsuda, 1987; Konishi *et al*., 1990). Compared to other markers, molecular markers are immune to the influence of phenotype and more convenient for analysis of segregation distortion. Molecular marker analysis in multiple populations is therefore useful for finding common segregation distortion regions and for future identification of genes that cause segregation distortion in these regions (Lu *et al*., 2002).

The estimates of recombination frequency between codominant markers are thought to be less biased by segregation distortion than estimates of recombination between dominant markers (Lorieux *et al*., 1995b). Most of the Simple Sequence Repeats markers (SSR) are codominant, so the frequency of both alleles and genotypes can be analyzed to see whether there are gametic or zygotic selections. It is helpful for studying the genetic mechanism of segregation distortion. Li *et al.* (2007) reported a novel segregation distortion phenomenon resulted from interior genetic factors using 3 morphological markers, 20 SSR markers and 11 Sequence Related Amplified Polymorphism (SRAP) markers in cotton and some markers showed allele frequency and genotype frequency distortion which indicated that they were influenced by gametic and zygotic selections simultaneously.

Segregation distortion and mapping populations: Segregation distortion is closely related to the type of genetic populations. In plant, Backcrosses (BC), Doubled Haploids (DH), Recombination Inbred Lines (RIL) and F_2 populations are commonly used biparental genetic populations in QTL linkage mapping (Zhang *et al*., 2010). Comparisons have shown that segregation distortion is more prevalent in DH and RIL than in F_2 populations (Zhang *et al*., 2010).

Yamagishi *et al.* (2010) reported the proportion of skewed markers was higher in the rice DH population (19%) than in the F_2 population (7%) derived from the same cross because in addition to genetic factors another culture also affect the selective transmission of chromosomal regions resulting in higher percentages of skewed markers and also different skewed regions in DH populations compared to F_2 populations. Xu *et al.* (1997) and Barchi *et al.* (2010) drew the same conclusion in

eggplant and rice, respectively. In RIL population, high proportion of segregation distortion is possibly related to artificial sampling and natural selections of many generations. However, segregation distortion has been reported to occur the same frequently in rice BC populations as those in DH populations (Xu *et al*., 1997).

Genetic relationship of the parents influencing segregation distortion: Many researches indicated that the segregation distortion ratio in interspecific population was higher than that in intraspecific population. In tetraploid cotton, 135 (18%) and 10 (6.41%) markers showed distorted segregation in interspecific population and intraspecific population, respectively (Lin, 2005). Li *et al.* (2007) reported 40% of all markers showed significant segregation distortion in sorghum interspecific which was higher than distorted marker (27%) in intraspecific population.

In tomato, Xu *et al.* (1997) detected that 73% of 132 markers showed segregation distortion in interspecific BC population only 5.4% of all markers showed segregation distortion in intraspecific F_2 population. Indeed, marker polymorphism between the parents of an interspecific cross is typically higher than that between the parents of an intraspecific one but the cross progeny from different species tend to suffer from reduced fertility and show segregation distortion (Lefebvre *et al*., 2002).

However, there were some peculiare phenomenons in recent researches. In cotton intraspecific population, 24 (77.42%) out of the 31 molecular markers was found to show segregation distortion which was higher than that previously reported (Li *et al*., 2007). Recently in an eggplant, interspecific population only 6.5% of the 446 informative markers was detected to show segregation distortions (Barchi *et al*., 2010). This level is comparable to that observed by Nunome *et al.* (2001) in an intraspecific population.

Cytoplasm factor: In some studies, segregation distortion was directly or indirectly associated with the effect of cytoplasm which was 1st recorded as a putative factor altering chromosome transmission by Grun (1976) in experiments on *Vicia faba*. Goloenko *et al.* (2002) investigated the effect of cytoplasmic factors on the transmission of nuclear marker genes with the use of barley sub-stitution lines with various cytoplasms and a common nucleus and found that segregation distortion depended not only on the cross direction but also on the cytoplasm-type of the sub-stitution lines.

This confirms the effect of cytoplasm on the transmission of female and male gametes. In addition to the above influencing factors another culture (for DH population), physiological and environmental factors can also lead to segregation distortion (Xu *et al*., 1997).

EFFECT OF SEGREGATION DISTORTION ON QTL MAPPING

Quantitative Trait Locus (QTL) mapping has been extensively utilized in modern genetic studies of complex traits by the linkage association of markers and phenotypic values in plants (Paterson *et al*., 1991; Barton and Keightley, 2002; Doerge, 2002). It has been applied in locating genes and consequently, isolating genes by positional cloning and in breeding programs by marker-assisted selection. The segregation distortion influence on recombination frequencies and then impede mapping precision and the linkage analysis of QTLs (Wu *et al*., 2010) and the degree of impact will depend on the the linkage distance between the distorted marker and QTL as well as the mapping population size. Furthermore if segregation distortion is caused by an SDL, all markers in the vicinity of the SDL will be affected (Wang *et al*., 2005).

Common practice in QTL mapping with segregation distortion markers is to use Mendelian marker loci to construct a linkage map and then to insert distorted markers in the existing map one by one. This approach increases the marker coverage of the genome (Wang *et al*., 2005). If markers in these regions are deleted from the map in QTL analysis, more QTL will be missed (Wang *et al*., 2005). Cervera *et al.* (2001) and Doucleff *et al.* (2004) suggested that markers that deviated from the expected segregation ratio at the 5% level but not at the 1% level should be included in mapping procedures to reduce the frequency of false positives.

Some researchers reported that the inclusion of even highly distorted markers was beneficial (Kuang *et al*., 1999; Fishman *et al*., 2001). Zhang *et al.* (2010) suggested in general, segregation distortion will not produce more false QTL, nor will it have significant impact on the estimation of QTL position and effect. So in practice if the distortion is not extremely serious, the effect from distortion can be ignored in large-size mapping populations. Xu (2008) also showed that the presence of SDL was not necessarily detrimental to QTL mapping because SDL could decrease as well as increase the statistical power of QTL mapping.

Recently, some programs such as MapManager, Mapdisto and PROC QTL provide options for calculating genetic distances of markers with segregation distortion and several algorithms were developed to adjust recombination frequency for deviated markers (Zhu *et al*.,

2007; Xu, 2008; Lorieux *et al*., 2000). A multipoint method of Maximum Likelihood (ML) was developed by Wang *et al.* (2005) which could estimate the positions and effects of the Segregation Distortion Loci (SDLs). Xu and Hu (2009) newly developed a method of QTL mapping that can make use of distorted markers and an EM (Expectation-Maximization) algorithm is used to estimate QTL and SDL parameters simultaneously. Nevertheless, the assumptions of these models are theoretically simplified, more comprehensive and delicate models need to be developed to address the problems of genetic mapping with segregation distortion.

CONCLUSION

Segregation distortion as a common phenomenon is often reported in the plant genetic researches. It affects the evolution of sex and recombination frequencies, gametic selection, reproductive barriers and consequently, the evolution of species. At present, some segregation distortion loci have been detected and located. However, the research work about segregation distortion is still at the primary stage. Such as few segregation distortion loci were detected and DNA level report is thin.

The informations provided by segretation distortion too lack to conduct future researches. Furthermore, the programs estimating the positions and effects of the segregation distortion loci are theoretically simplified. More comprehensive and delicate models need to be developed to address the problems of genetic mapping with segregation distortion. In order to increase the understanding of segregation distortion in-depth study of all above the aspects is necessary.

It is helpful to understand the phenomenon on pollen lethal, preferential fertilization, sterility and chromosome translocation, localize related genes of segregation distortion and detect more SDLs, construct precise genetic mapping and correctly detect the position and effect of QTLs. These are important for plant genetic research and improvement. The development of high density molecular linkage maps provided a chance to survey the whole genome for loci showing distorted segregation, allow biologists and breeders to understand the molecular mechanism of segregation distortion and evolution of species and accelerate the breeding process.

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