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Research

High-resolution molecular karyotyping uncovers pairing between ancestrally related *Brassica* chromosomes

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Summary

- How do chromosomal regions with differing degrees of homology and homeology interact at meiosis? We provide a novel analytical method based on simple genetics principles which can help to answer this important question. This method interrogates high-throughput molecular marker data in order to infer chromosome behavior at meiosis in interspecific hybrids.
- We validated this method using high-resolution molecular marker karyotyping in two experimental *Brassica* populations derived from interspecific crosses among *B. juncea*, *B. napus* and *B. carinata*, using a single nucleotide polymorphism chip.
- This method of analysis successfully identified meiotic interactions between chromosomes sharing different degrees of similarity: full-length homologs; full-length homeologs; large sections of primary homeologs; and small sections of secondary homeologs.
- This analytical method can be applied to any allopolyploid species or fertile interspecific hybrid in order to detect meiotic associations. This genetic information can then be used to identify which genomic regions share functional homeology (i.e., retain enough similarity to allow pairing and segregation at meiosis). When applied to interspecific hybrids for which reference genome sequences are available, the question of how differing degrees of homology and homeology affect meiotic interactions may finally be resolved.

Introduction

Successful transfer of genetic information from one generation to the next is essential for all organisms. The mechanism for this transfer in most sexually reproducing eukaryotic species is meiosis. Chromosome behavior during meiosis must be strictly controlled: in order to ensure correct segregation of chromosomes into daughter cells, each chromosome must pair with its homologous partner. However, homolog recognition is one of the least well understood meiotic processes (Tiang *et al.*, 2012). In most species, the broader process of meiosis is the same: each homologous chromosome must find its partner, associate with it and undergo the reciprocal 'crossing-over' process of genetic exchange, creating one or more physical ties (chiasma) between the chromosomes to ensure correct first division disjunction (Wilson *et al.*, 2005). During homologous chromosome pairing, homologs are roughly aligned before close-range 'homology checking' and elimination of associations based on repetitive DNA sequences is then thought to occur (Bozza & Pawlowski, 2008). Although homologous chromosome pairing relies on DNA sequence homology (Bozza & Pawlowski, 2008), the exact relationship between DNA sequence similarity and homolog recognition is unknown (Tiang *et al.*, 2012): how similar do genomic sequences have to be to initiate chromosome pairing at meiosis? In particular, how are homologs recognized, and how are meiotic interactions regulated between genomic regions with different degrees of sequence homology?

This question can be addressed in allopolyploid species that are formed when two related diploid species hybridize. Polyploidy is common in many, if not most, plant and animal species lineages (Otto & Whitton, 2000; Leggatt & Iwama, 2003; Van de Peer *et al.*, 2009; Jiao *et al.*, 2011). Some angiosperm families such as the Brassicaceae have undergone multiple polyploidy events such that the present-day species contain homeologous (i.e., ancestrally related) chromosomal regions with a spectrum of sequence similarities (Fig. 1). High-resolution molecular karyotyping is now becoming feasible in nonmodel species with the increasing availability of high-density genotyping arrays and genotyping-by-sequencing (Elshire *et al.*, 2011; Poland *et al.*, 2012; Cavanagh *et al.*, 2013; Edwards *et al.*, 2013). Therefore, the stage is set for significant advances in our understanding of just how similar DNA sequences have to be for homolog recognition to occur, and of how hybrids and polyploids regulate meiosis when several genomic regions with different degrees of sequence homology exist. However, the analytical tools for interrogating large molecular genotyping datasets to answer these questions remain underdeveloped.