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REVIEW

Molecular Mechanisms of Homologous Chromosome Pairing and Segregation in Plants

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ABSTRACT

In most eukaryotic species, three basic steps of pairing, recombination and synapsis occur during prophase of meiosis I. Homologous chromosomal pairing and recombination are essential for accurate segregation of chromosomes. In contrast to the well-studied processes such as recombination and synapsis, many aspects of chromosome pairing are still obscure. Recent progress in several species indicates that the telomere bouquet formation can facilitate homologous chromosome pairing by bringing chromosome ends into close proximity, but the sole presence of telomere clustering is not sufficient for recognizing homologous pairs. On the other hand, accurate segregation of the genetic material from parent to offspring during meiosis is dependent on the segregation of homologs in the reductional meiotic division (MI) with sister kinetochores exhibiting mono-orientation from the same pole, and the segregation of sister chromatids during the equational meiotic division (MII) with kinetochores showing bi-orientation from the two poles. The underlying mechanism of orientation and segregation is still unclear. Here we focus on recent studies in plants and other species that provide insight into how chromosomes find their partners and mechanisms mediating chromosomal segregation.

KEYWORDS: Homologous chromosome pairing; Orientation and segregation; Meiosis

INTRODUCTION

Meiosis is a process by which diploid cells undergo a single round of DNA replication and two rounds of chromosome separation to yield haploid gametes. To accomplish reductional segregation, homologous chromosomes must recognize each other and identify its partner, and then align along their lengths. This process is called homologous pairing. Chromosome pairing is stabilized by installation of the synaptonemal complex between homologs, a process called synapsis. After homologous recognition, the meiotic recombination mediated by double-strand break (DSB) can lead to the formation of crossovers between homologs. The crossovers and sister chromatid cohesion provide physical linkage that enable homologs to attach and mono-orient on the first meiotic spindle, followed by homologous separation in meiosis I.

The hallmark of meiosis is homologous chromosome pairing, which is necessary for the correct recombination and segregation to yield viable gametes. The biggest unresolved problem is to understand the mechanism that allows homologous chromosomes to find their right partner. At the onset of meiosis, homologous chromosomes may be spatially separated from each other in the nucleus. Thus, they must be brought into close proximity from interaction of specific chromosome regions or sites. It is unknown whether these initial interactions are mediated by protein−protein interactions, DNA-based pathways, RNA-mediated interactions or other features.

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With regard to homologous segregation, sister chromatids are held together and move to one pole in anaphase I, which is called mono-orientation. The replicated sister chromatids are held together by cohesion. Genetic analysis in yeast and metazoans showed that the loss of cohesin function leads to chromosome misalignment, premature sister chromatid separation, and kinetochore, disfunction all of which can result in chromosome missegregation (Tanaka et al., 2000; Hoque and Ishikawa, 2002), indicating that cohesin is important for proper chromosome segregation.

In this review, we describe recent studies about homologous chromosome pairing in plants and other organisms, focusing on two related topics: the role of telomere bouquet formation and centromere interactions. We also discuss chromosome orientation and segregation with a focus on sister chromatid cohesion, monopolin complex and kinetochore−microtubule (KT−MT) attachment.

TELOMERE BOUQUET FORMATION AND CHROMOSOME PAIRING

In most species of plants, animals and fungi, telomeres attach to the inner nuclear envelop and cluster at a limited territory of the nuclear periphery during the early meiotic prophase I to form a structure called the telomere bouquet, which is found among most eukaryotes (Fig. 1) (Chikashige et al., 1994; Bass et al., 1997; Scherthan, 2001; Harper et al., 2004; Jain and Cooper, 2010). Telomere bouquet formation precedes homologous chromosome pairing. It has been proposed that the telomere bouquet may facilitate the subsequent meiotic prophase processes such as homologous pairing and synapsis (Chikashige et al., 1994; Niwa et al., 2000; Scherthan, 2007) by bringing chromosomes into close proximity. This may increase searching efficiency by collecting chromosome ends into a limited region and shorting the distance between homologs (Ding et al., 2004; Conrad et al., 2008; Kosaka et al., 2008; Wanat et al., 2008).

Although most organisms show telomere clustering during early prophase of meiosis, *Arabidopsis* is an exception. In *Arabidopsis*, telomeres exhibit homologous pairing with the nucleolus during early prophase, and then they moved to the nuclear envelop and formed a transient loose clustering, which may represent a transient bouquet. Thus, the homologous telomere pairing during early prophase in *Arabidopsis* may fulfill a similar role as the bouquet in other species (Roberts et al., 2009).

In maize, the *pam1* mutant (*plural abnormalities of meiosis 1*), which is deficient in the clustering but not the attachment of telomeres to the nuclear envelope, shows dramatic reduction in homologous pairing (Golubovskaya et al., 2002). However, some female meiocytes (<1%) in *pam1* mutant can complete normal meiosis, indicating that the telomere bouquet is not absolutely required for homologous chromosome pairing.

CENTROMERE INTERACTIONS AND CHROMOSOME PAIRING

The telomere bouquet formation and subsequent chromosome alignment facilitate homologous chromosome pairing, but telomere clustering are not responsible for the specificity of chromosome recognition, and recent study using computational modeling also indicates that telomere clustering alone can not complete large chromosome pairing (Penfold et al., 2012). Thus, there must be additional mechanisms to accomplish this process.

It has been initially reported that in polyploid wheat, premeiotic centromere association occurs in both meiocytes and surrounding somatic cells, and in effect that centromere pairing for meiosis is independent of the rest of chromosome. This process in wheat is dependent upon the *Ph1* locus (Martinez-Perez et al., 1999, 2001). Subsequently centromere coupling was described in a range of other species, including yeast, *Arabidopsis*, barley, *Brachypodium distachyon*, and *Drosophila* (Kemp et al., 2004; Tsubouchi and Roeder, 2005; Tsubouchi et al., 2008; Ronceret et al., 2009; Takeo et al., 2011; Da Ines et al., 2012; Phillips et al., 2012; Wen et al., 2012). The initial centromeric interactions mainly occur between non-homologous chromosomes. In budding yeast, centromere coupling or non-homologous centromere pairing is important for

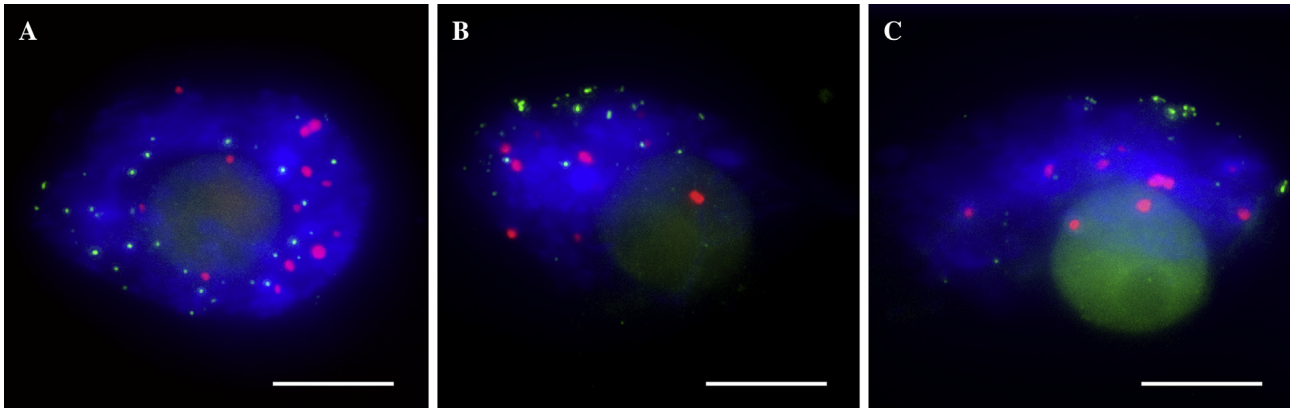

Fig. 1. Centromere and telomere dynamics during early prophase in maize.
A: Leptotene. **B:** Zygotene. **C:** Late zygotene. Maize has ten chromosome pairs; ten or fewer centromere signals indicate that all centromeres became associated. Antibody against centromeric histone CENH3 is red; telomere-specific FISH probe is green. Images are flat projections of three-dimensional images of whole nuclei. Chromosomes are counterstained with DAPI in blue. Bars = 10 μm.