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Chromosome organization and dynamics in plants

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The past few years have brought renewed interest in understanding the dynamics of chromosomes in interphase cells as well as during cell division, particularly meiosis. This research has been fueled by new imaging methods, particularly three-dimensional, high-resolution, and live microscopy. Major contributors are also new genetic tools that allow elucidation of mechanisms controlling chromosome behavior. Recent studies in plants have explored chromatin arrangement in interphase nuclei, chromosome interactions and movement during meiotic prophase I, and mechanisms that ensure correct segregation of chromosomes during anaphase. These studies shed light on chromosome dynamics in a small-genome plant *Arabidopsis thaliana*, as well as in plants with large and complex genomes of polyploid origin, such as wheat and maize.

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Introduction

Behavior of chromosomes is a result of interplay between their two conflicting functions: firstly, providing access to the DNA-encoded genetic information, which is required for transcription and for exchange of genetic information during meiotic recombination, and secondly, protecting the structural integrity of the genome and its faithful segregation to daughter cells during cell division. These diverse roles of chromosomes are reflected in changes of their appearance during the cell cycle. Although it has been known for decades that chromosomes undergo profound alterations in their morphology and arrangement in the nucleus, it is only recently that the dynamic nature of these changes is being uncovered. The molecular mechanisms controlling chromosome behavior and the consequences that chromosome dynamic patterns have for gene expression and chromosome segregation are also subjects of intense investigations. These studies are conducted in a variety of taxa but plants, because of their large and conspicuous chromosomes, are excellent systems for studying chromosome dynamics.

Chromosome organization and dynamics in interphase cells

During interphase, chromosomes become largely decondensed but they still exhibit a high level of organization within the nucleus. In large-genome eukaryotes, such as mammals and plants, chromatin threads from individual chromosomes, instead of freely mixing, form distinct chromosome territories [1]. The existence of chromosome territories was proposed over 100 years ago [2] but only demonstrated conclusively with the advent of the fluorescence *in situ* hybridization (FISH) technology [3]. In *Arabidopsis thaliana*, interphase chromosomes exhibit rosette-like structures. In these structures, heterochromatic chromosome segments form condensed chromocenters while euchromatic segments remain as loops 0.2–2 Mb in length that emanate from the chromocenters (Figure 1a) [4••]. The heterochromatic centromeric regions are located within the chromocenters. The chromocenters are positioned near the nuclear periphery [4••] and their arrangement relative to each other is predominantly random [5–7] and can change following cell division [7,8]. No evidence has been found for associations between homologous chromosomes in Arabidopsis interphase nuclei. However, chromosomes that bear nuclear organizer regions (NORs) tend to be associated more often, probably by virtue of their attachment to the nucleolus [5,7]. Telomeres in Arabidopsis interphase cells show persistent clustering at the nucleolus [9], a unique arrangement that has not been observed in other plants.

In contrast to Arabidopsis, in plants with large genomes, such as wheat, chromosomes in interphase frequently exhibit Rabl orientation, in which clustered centromeres and telomeres are located on the opposite sides of the nucleus (Figure 1b) [10]. This arrangement is a remnant of the preceding anaphase. Centromere clustering in somatic cells has been investigated in hexaploid and tetraploid wheat, where it is regulated by the *Ph1* locus [11–13]. However, centromere clustering has also been reported in small-genome plant species that do not exhibit Rabl orientation. For example, centromere clustering has been found in somatic cells of rice [14]. However, while in wheat, centromeres of non-homologous chromosomes cluster, in rice the centromere associations involve homologous chromosomes.

Studies in Arabidopsis have shown that chromosome organization in interphase nuclei not only is genetically

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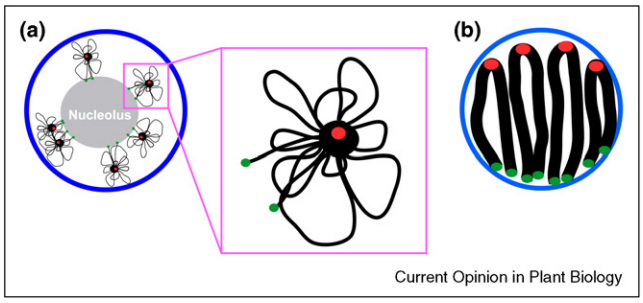
Figure 1



Chromosome arrangement in interphase nuclei. **(a)** The chromocenter-loop organization observed in Arabidopsis. Six chromosomes (black) with chromocenters (black dots) are depicted. Chromocenters are frequently located near the nuclear envelope (blue). Red = centromeres. Green = telomeres. One of the chromosomes (boxed in purple) is magnified in inset. **(b)** Rabl orientation observed in wheat and other plant species with large genomes. Centromeres (red) of all chromosomes (black) are located on the opposite side of the nucleus from telomeres (green). Blue = nuclear envelope.

controlled but also changes during plant development and as a response to environmental conditions. Chromocenters show extensive reduction in size in cells of Arabidopsis leaves before bolting, as some heterochromatic segments relocate away from chromocenters. However, the chromocenter size recovers after elongation of the floral stem [15]. These processes are controlled by the light signaling pathway. Furthermore, ecotypes acclimated to different latitudes exhibit varying, genetically programmed, levels of chromatin compaction, depending on the light intensity in their habitats [16••].

New imaging tools, such as fluorescently tagged centromeric proteins and genomic sites marked using bacterial operator/repressor systems, have enabled investigations of interphase chromosome dynamics in live cells [8,17,18,19•]. These studies demonstrated that Arabidopsis centromeres during interphase display a rather static behavior, exhibiting only diffusive movements with fairly low speeds when compared to the velocities of chromosome movements in anaphase or meiotic prophase [8]. Interstitial chromosome regions are also fairly static, although they are less restricted in their movements than centromeres [20].

Many tissues in plants become polyploid as a result of DNA endoreduplication, a phenomenon observed in species with relatively small genomes, such as Arabidopsis, as well as plants with large genomes. Endoreduplication-triggered polyploidy has been found to considerably affect chromosome dynamics [20,21]. Coalignment of sister chromatids decreases with the increase of ploidy levels in cells that undergo endoreduplication [21]. The freedom of movement of interstitial chromosome regions (i.e. the area within the nucleus to which movement is constrained) increases as well, although the movement speed decreases [20]. In contrast to endoreduplication, which increases the copy number of all chromosomes, increasing the number of copies of individual chromosomes, that is, trisomy, does not substantially alter the chromosome organization in interphase nuclei [22•].

Overall, studies revealed a large degree of variation in the patterns of chromosome arrangements and behavior in interphase cells in different plant species and among different tissues. It is quite likely that these diverse patterns reflect diverse roles of interphase chromosome dynamics. In yeast and mammals, detailed three-dimensional maps of chromosome arrangements in interphase nuclei have been constructed [1,23••] that allow functional analyses of interphase chromosome organization and dynamics. However, in plants such studies are still in their infancy and much more work is needed in this area.

Chromosome interactions in the prophase of meiosis I

During the prophase of meiosis, a specialized cell division leading to the production of gametes, homologous chromosomes find each other, pair, and recombine (see [24] for a review). In contrast to the somewhat static behavior of interphase chromosomes, chromosomes during meiotic prophase I are extremely dynamic [25••]. Meiotic prophase chromosome interactions have two distinct functions, firstly, facilitating genetic exchanges through the process of crossing-over and secondly, ensuring proper chromosome segregation in anaphase I. These interactions exhibit high levels of complexity [26].

During the past few years, several critical mechanisms involved in controlling pairing of homologous chromosomes have been identified. In plants, similarly to mammals and yeast, homologous chromosome pairing has been found to be tightly linked to the progression of meiotic recombination [27]. Meiotic recombination starts by programmed formation of double-stand breaks (DSBs) in chromosomal DNA at the onset of meiosis [28]. Arabidopsis and maize mutations that eliminate the formation of meiotic DSBs, or affect early stages of their processing and repair, have been shown to also cause severe chromosome pairing defects [29–33]. For example, Arabidopsis mutants lacking the SPO11-1 and SPO11-2 proteins, which are responsible for meiotic DSB formation, exhibit unpaired chromosomes (univalents) during pachytene, instead of chromosome pairs (bivalents) [29,30]. *phs1* mutants in maize and Arabidopsis, which exhibit defects in early stages of DSB repair, show frequent associations of non-homologous chromosomes that replace homologous pairing [34,35]. In *phs1* mutants, meiotic DSBs are formed but very few of them become resected to generate single-stranded DNA overhangs. The DNA overhangs are essential in the single-end invasion (SEI) process, in which a nucleoprotein filament

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consisting of single-stranded DNA coated with recombination proteins RAD51 and DMC1 finds and invades a homologous double-stranded DNA region [36,37]. SEI is hypothesized to facilitate DNA sequence-based recognition of chromosome homology [24]. However, the SEI-based interactions are rather short-distance and other mechanisms are likely to exist that bring chromosomes first to a close proximity [24]. Moreover, mechanisms that coordinate pairing interactions along longer chromosome stretches may be required to prevent ectopic pairing between repetitive DNA regions in complex genomes.

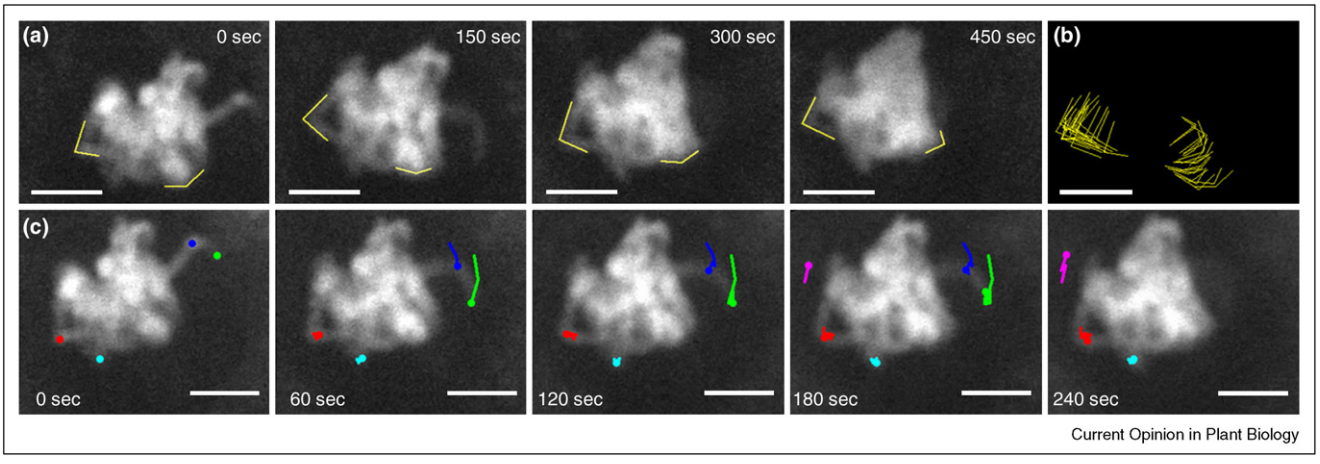
The onset of chromosome pairing is coincident with spatial reorganization of chromatin in the nucleus [38]. One of the most visible aspects of this reorganization is attachment of telomeres of all chromosomes to the nuclear envelope (NE) followed by their clustering to form a cytological structure known as the telomere bouquet. The bouquet formation has been observed in a large number of species, including several plants, such a maize, wheat, and rye [39]. In most species, telomeres cluster in early zygotene and the bouquet persists until early pachytene. Arabidopsis, in contrast, does not form a canonical telomere bouquet, although premeiotic telomere clustering at the nucleolus may play a role similar to that of the bouquet [9].

Research to conclusively determine the role that the bouquet plays in the progression of meiosis is still in progress. On the basis of studies of mutants defective in bouquet formation in maize, as well as yeast and mouse, it has been hypothesized that telomere clustering facilitates the subsequent chromosome pairing by prealigning them and bringing their ends together [39]. In plants, observations of subtelomeric initiation of chromosome pairing in Arabidopsis and wheat [40–42] provide evidence for this hypothesis.

Recent studies in maize, as well as in several species outside of plants, show that chromosomes during zygotene and pachytene stages of prophase I exhibit very dramatic motility [25••,43•,44–46]. In maize, these movements include motions of individual chromosome segments, mostly chromosome ends, as well as oscillating rotations of the entire chromatin in the nucleus (Figure 2) [25••]. The motility patterns differ between zygotene and pachytene, particularly the movement of individual chromosome segments. In zygotene, the moving chromosome segments are fairly small and their motions are very rapid. In pachytene, much longer chromosome segments, sometimes entire chromosome arms, exhibit slow sweeping motions across large extents of the nucleus. Chromosome motility is associated with dynamic deformations of the NE. Analyses of movement patterns of both the chromatin and the NE suggest that the forces responsible for these movements originate in the cytoplasm and are transmitted through the NE and onto the telomeres attached to the NE [25••,47]. Studies in animals and fungi led to uncovering and characterization of SUN-domain proteins that bridge the NE and link the cytoplasmic cytoskeleton with chromosome ends [47]. Homologs of SUN-domain proteins have also been identified in Arabidopsis and shown to exhibit mobility within the NE, which would be required for facilitating chromosome movements [48•]. Specific roles of these proteins in facilitating chromosome movements, particularly in meiosis, are now being examined.

The exact function of meiotic prophase movements is still under investigation. However, most data so far suggest that the role of the zygotene movements is facilitating chromosome pairing interactions, while the slower pachytene movements may help resolving chromosome entanglements that remain after the conclusion of chromosome

Figure 2



Time-lapse imaging of chromosome motility in a live maize meiocyte in pachytene. **(a)** Rotational movements of the entire chromatin. Yellow lines mark chromatin mass edges. **(b)** Cumulative tracks from (a) after 570 s. **(c)** Trajectories of five anonymous chromosome marks (blue, cyan, green, magenta, and red). Bar = 5 μm.Modified from Sheehan and Pawlowski [25••].

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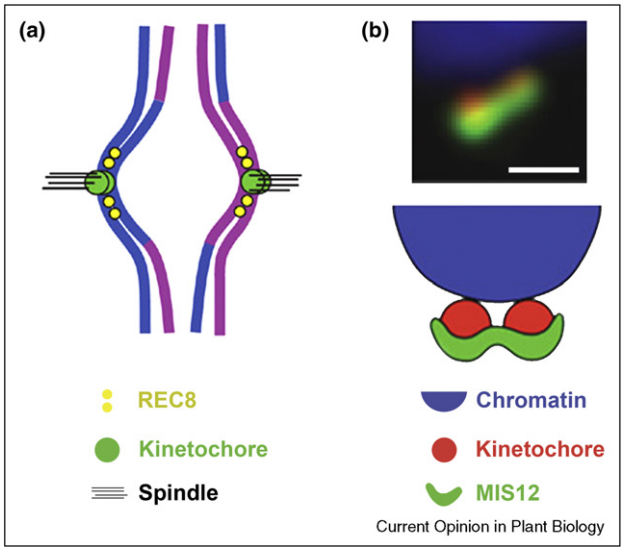
Figure 3



Chromosome segregation in anaphase I of meiosis. **(a)** An overview of the reductional division event. **(b)** Localization of the MIS12 protein (green) responsible for monopolar kinetochore attachment to the division spindle in meiosis I. Bar = 1 μm.Modified from Li and Dawe [51••].

pairing [25••,43•]. The observations of meiotic prophase chromosome motility also shed new light on the role of the telomere bouquet and suggest that the main role of the bouquet may be facilitating chromosome movements rather than prealigning chromosomes.

Chromosome segregation in mitosis and meiosis

Chromosome segregation is a very dynamic series of events, in which chromosomes congress to the equatorial plane of the cell, attach to division spindle microtubules, and become pulled to the two opposed cell poles. These processes take place during the metaphase — anaphase stages of mitosis as well as meiosis. Chromosome segregation is diametrically different in mitosis than in meiosis [49]. In mitosis, chromosomes exhibit bipolar spindle attachment (i.e. each chromatid attaches to microtubules coming from a different pole), cohesion between sister chromatids is released along the entire chromosome length, and sister chromatids travel to opposing poles. In the reductional division of meiosis, chromosomes show monopolar spindle attachment (i.e. both chromatids attach to microtubules coming from the same pole), sister-chromatid cohesion (SCC) is preserved in the centromeric region of the chromosome, and both sister chromatids travel to the same pole. Mechanisms by which kinetochores of sister chromatids limit their interactions to a single pole in meiosis but interact with both poles in mitosis are intensely investigated. Studies in Arabidopsis have shown that meiosis-specific SCC mediated by the REC8 and SCC3 proteins is required for the monopolar attachment in meiosis I [50]. Recent data from maize suggest a specific mechanism by which the monopolar attachment is achieved, showing that sister kinetochores in meiosis are fused by a kinetochore protein MIS12, which causes both kinetochores to present a shared face to microtubule-binding proteins (Figure 3) [51••].

Central for chromosome movements and their segregation in anaphase of meiosis and mitosis is also the assembly of the microtubule spindle. The molecular mechanisms involved in spindle formation are being explored in many taxa, including plants. Kinesins, a group of microtubule-based motor proteins, play key roles in spindle assembly and dynamics. Higher plants contain a large number of kinesins; over 60 have been identified in Arabidopsis [52]. However, roles in mitotic and meiotic chromosome segregation have been described for only a few of them so far [53,54]. More data in this area should be forthcoming in the next few years.

Conclusions

The past decade brought a renewal of interest in understanding chromosome dynamics, particularly during interphase and early meiosis. The work on chromosome dynamics has been made possible by the availability of new tools, particularly cellular markers and new imaging methods [26]. The force driving this research is an increasing appreciation of functional links between chromosome dynamics in interphase cells and gene expression, as well as links between chromosome dynamics during nuclear division and patterns of chromosome segregation (and gene inheritance). In the future, two areas of chromosome dynamic studies are likely to gain prominence. The first is identifying and characterizing plant mutations that affect chromosome dynamics, which will bring better understanding of the genetic regulation of chromosome behavior and enable the study of mechanisms controlling chromosome dynamics at the molecular level. The second area is modeling chromosome dynamics, which will help elucidating the mechanistic bases of chromosome motility. Research in both these areas will also serve a larger goal of explaining how biochemical and physical processes become integrated in biological systems.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Cremer T, Cremer M, Dietzel S, Muller S, Solovei I, Fakan S: **Chromosome territories — a functional nuclear landscape**. *Curr Opin Cell Biol* 2006, **18**:307-316.

2. Rabl C: **Über Zellheilung**. *Morphol Jahrb* 1885, **10**:214-330.

3. Cremer T, Cremer C: **Chromosome territories, nuclear architecture and gene regulation in mammalian cells**. *Nat Rev Genet* 2001, **2**:292-301.

4. •• Fransz P, De Jong JH, Lysak M, Castiglione MR, Schubert I: **Interphase chromosomes in Arabidopsis are organized as well defined chromocenters from which euchromatin loops emanate**. *Proc Natl Acad Sci U S A* 2002, **99**:14584-14589.
A landmark paper that proposed the chromocenter-loop model for interphase chromosome organization in Arabidopsis.

5. Pecinka A, Schubert V, Meister A, Kreth G, Klatte M, Lysak MA, Fuchs J, Schubert I: **Chromosome territory arrangement and homologous pairing in nuclei of *Arabidopsis thaliana* are predominantly random except for NOR-bearing chromosomes**. *Chromosoma* 2004, **113**:258-269.

6. de Nooijer S, Wellink J, Mulder B, Bisseling T: **Non-specific interactions are sufficient to explain the position of heterochromatic chromocenters and nucleoli in interphase nuclei**. *Nucleic Acids Res* 2009, **37**:3558-3568.

7. Berr A, Schubert I: **Interphase chromosome arrangement in *Arabidopsis thaliana* is similar in differentiated and meristematic tissues and shows a transient mirror symmetry after nuclear division**. *Genetics* 2007, **176**:853-863.

8. Fang Y, Spector DL: **Centromere positioning and dynamics in living Arabidopsis plants**. *Mol Biol Cell* 2005, **16**:5710-5718.

9. Armstrong SJ, Franklin FC, Jones GH: **Nucleolus-associated telomere clustering and pairing precede meiotic chromosome synapsis in *Arabidopsis thaliana***. *J Cell Sci* 2001, **114**:4207-4217.

10. Cowan CR, Carlton PM, Cande WZ: **The polar arrangement of telomeres in interphase and meiosis. Rabl organization and the bouquet**. *Plant Physiol* 2001, **125**:532-538.

11. Martinez-Perez E, Shaw P, Reader S, Aragon-Alcaide L, Miller T, Moore G: **Homologous chromosome pairing in wheat**. *J Cell Sci* 1999, **112(Pt 11)**:1761-1769.

12. Martinez-Perez E, Shaw P, Moore G: **The *Ph1* locus is needed to ensure specific somatic and meiotic centromere association**. *Nature* 2001, **411**:204-207.

13. Martinez-Perez E, Shaw PJ, Moore G: **Polyploidy induces centromere association**. *J Cell Biol* 2000, **148**:233-238.

14. Prieto P, Santos AP, Moore G, Shaw P: **Chromosomes associate premeiotically and in xylem vessel cells via their telomeres and centromeres in diploid rice (*Oryza sativa*)**. *Chromosoma* 2004, **112**:300-307.

15. Tessadori F, Schulkes RK, van Driel R, Fransz P: **Light-regulated large-scale reorganization of chromatin during the floral transition in Arabidopsis**. *Plant J* 2007, **50**:848-857.

16. •• Tessadori F, van Zanten M, Pavlova P, Clifton R, Pontvianne F, Snoek LB, Millenaar FF, Schulkes RK, van Driel R, Voesenek LA *et al.*: **Phytochrome B and histone deacetylase 6 control light-induced chromatin compaction in *Arabidopsis thaliana***. *PLoS Genet* 2009, **5**:e1000638.
This study showed that chromatin organization in interphase nuclei in Arabidopsis is controlled by genes involved in light signal transduction.

17. Matzke AJ, Huettel B, van der Winden J, Matzke M: **Use of two-color fluorescence-tagged transgenes to study interphase chromosomes in living plants**. *Plant Physiol* 2005, **139**:1586-1596.

18. Matzke AJ, Huettel B, van der Winden J, Matzke M: **Fluorescent transgenes to study interphase chromosomes in living plants**. *Methods Mol Biol* 2008, **463**:241-265.

19. • Matzke AJ, Watanabe K, van der Winden J, Naumann U, Matzke M: **High frequency, cell type-specific visualization of fluorescent-tagged genomic sites in interphase and mitotic cells of living Arabidopsis plants**. *Plant Methods* 2010, **6**:2.
The authors developed a robust method that allows monitoring dynamics of specific chromosome regions throughout the cell cycle using the bacterial *lacO* operator/repressor system.

20. Kato N, Lam E: **Chromatin of endoreduplicated pavement cells has greater range of movement than that of diploid guard cells in *Arabidopsis thaliana***. *J Cell Sci* 2003, **116**:2195-2201.

21. Schubert V, Klatte M, Pecinka A, Meister A, Jasencakova Z, Schubert I: **Sister chromatids are often incompletely aligned in meristematic and endopolyploid interphase nuclei of *Arabidopsis thaliana***. *Genetics* 2006, **172**:467-475.

22. • Huettel B, Kreil DP, Matzke M, Matzke AJ: **Effects of aneuploidy on genome structure, expression, and interphase organization in *Arabidopsis thaliana***. *PLoS Genet* 2008, **4**:e1000226.
Live cell imaging of transgene-encoded fluorescent tags on Arabidopsis chromosome 5 was used in this paper to examine 3D interphase chromosome arrangement in trisomic and triploid plants.

23. •• Duan Z, Andronescu M, Schutz K, McIlwain S, Kim YJ, Lee C, Shendure J, Fields S, Blau CA, Noble WS: **A three-dimensional model of the yeast genome**. *Nature* 2010, **465**:363-367.
The authors used chromosome confirmation capture technique that allows identification of interacting chromosome segments to generate a high-resolution three-dimensional map of the nucleus in budding yeast. This map will be a powerful tool for identifying links between nuclear organization and function.

24. Bozza CG, Pawlowski WP: **The cytogenetics of homologous chromosome pairing in meiosis in plants**. *Cytogenet Genome Res* 2008, **120**:313-319.

25. •• Sheehan MJ, Pawlowski WP: **Live imaging of rapid chromosome movements in meiotic prophase I in maize**. *Proc Natl Acad Sci U S A* 2009, **106**:20989-20994.
Using a novel live imaging system, the authors described the patterns of chromosome motility in early meiotic prophase in maize. This is the first account of meiotic prophase chromosome movements in plants.

26. Ronceret R, Pawlowski WP: **Chromosome dynamics in meiotic prophase in plants**. *Cytogenet Genome Res* 2010, **129**:173-183.

27. Pawlowski WP, Cande WZ: **Coordinating the events of the meiotic prophase**. *Trends Cell Biol* 2005, **15**:674-681.

28. Keeney S, Giroux CN, Kleckner N: **Meiosis-specific DNA double-strand breaks are catalyzed by Spo11, a member of a widely conserved protein family**. *Cell* 1997, **88**:375-384.

29. Grelon M, Vezon D, Gendrot G, Pelletier G: **AtSPO11-1 is necessary for efficient meiotic recombination in plants**. *EMBO J* 2001, **20**:589-600.

30. Stacey NJ, Kuromori T, Azumi Y, Roberts G, Breuer C, Wada T, Maxwell A, Roberts K, Sugimoto-Shirasu K: **Arabidopsis SPO11-2 functions with SPO11-1 in meiotic recombination**. *Plant J* 2006, **48**:206-216.

31. Puizina J, Siroky J, Mokros P, Schweizer D, Riha K: **Mre11 deficiency in Arabidopsis is associated with chromosomal instability in somatic cells and Spo11-dependent genome fragmentation during meiosis**. *Plant Cell* 2004, **16**:1968-1978.

32. De Muyt A, Pereira L, Vezon D, Chelysheva L, Gendrot G, Chambon A, Laine-Choinard S, Pelletier G, Mercier R, Nogue F *et al.*: **A high throughput genetic screen identifies new early meiotic recombination functions in *Arabidopsis thaliana***. *PLoS Genet* 2009, **5**:e1000654.

33. Kerzendorfer C, Vignard J, Pedrosa-Harand A, Siwiec T, Akimcheva S, Jolivet S, Sablowski R, Armstrong S, Schweizer D, Mercier R *et al.*: **The *Arabidopsis thaliana* MND1 homologue plays a key role in meiotic homologous pairing, synapsis and recombination**. *J Cell Sci* 2006, **119**:2486-2496.

34. Pawlowski WP, Golubovskaya IN, Timofejeva L, Meeley RB, Sheridan WF, Cande WZ: **Coordination of meiotic recombination, pairing, and synapsis by PHS1**. *Science* 2004, **303**:89-92.

35. Ronceret A, Doutriaux MP, Golubovskaya IN, Pawlowski WP: **PHS1 controls homologous chromosome pairing in plants by directing transport of RAD50 into the nucleus**. *Proc Natl Acad Sci U S A* 2009, **106**:20121-20126.

36. Neale MJ, Keeney S: **Clarifying the mechanics of DNA strand exchange in meiotic recombination**. *Nature* 2006, **442**:153-158.

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37. San Filippo J, Sung P, Klein H: **Mechanism of eukaryotic homologous recombination**. *Annu Rev Biochem* 2008, **77**:229-257.

38. Dawe RK, Sedat JW, Agard DA, Cande WZ: **Meiotic chromosome pairing in maize is associated with a novel chromatin organization**. *Cell* 1994, **76**:901-912.

39. Harper L, Golubovskaya I, Cande WZ: **A bouquet of chromosomes**. *J Cell Sci* 2004, **117**:4025-4032.

40. Carvalho A, Delgado M, Barao A, Frescatada M, Ribeiro E, Pikaard CS, Viegas W, Neves N: **Chromosome and DNA methylation dynamics during meiosis in the autotetraploid *Arabidopsis arenosa***. *Sex Plant Reprod* 2010, **23**:29-37.

41. Corredor E, Lukaszewski A, Pachon P, Allen DC, Naranjo T: **Terminal regions of wheat chromosomes select their pairing partners in meiosis**. *Genetics* 2007, **177**:699-706.

42. Corredor E, Naranjo T: **Effect of colchicine and telocentric chromosome conformation on centromere and telomere dynamics at meiotic prophase I in wheat-rye additions**. *Chromosome Res* 2007, **15**:231-245.

43. • Koszul R, Kleckner N: **Dynamic chromosome movements during meiosis: a way to eliminate unwanted connections?** *Trends Cell Biol* 2009, **19**:716-724.
An excellent review on the patterns, mechanisms, and potential roles of meiotic prophase chromosome movements in a variety of species.

44. Conrad MN, Lee CY, Chao G, Shinohara M, Kosaka H, Shinohara A, Conchello JA, Dresser ME: **Rapid telomere movement in meiotic prophase is promoted by *NDJ1, MPS3*, and *CSM4* and is modulated by recombination**. *Cell* 2008, **133**:1175-1187.

45. Chikashige Y, Haraguchi T, Hiraoka Y: **Another way to move chromosomes**. *Chromosoma* 2007, **116**:497-505.

46. Koszul R, Kim KP, Prentiss M, Kleckner N, Kameoka S: **Meiotic chromosomes move by linkage to dynamic actin cables with transduction of force through the nuclear envelope**. *Cell* 2008, **133**:1188-1201.

47. Hiraoka Y, Dernburg AF: **The SUN rises on meiotic chromosome dynamics**. *Dev Cell* 2009, **17**:598-605.

48. • Graumann K, Runions J, Evans DE: **Characterization of SUN-domain proteins at the higher plant nuclear envelope**. *Plant J* 2010, **61**:134-144.
The first account of existence of SUN-domain proteins higher plants. SUN-domain-containing proteins are known to tether telomeres to the nuclear envelope and provide the bridge between the telomeres and the cytoplasmic cytoskeleton, which facilitates chromosome movements.

49. Ghosh SK, Hajra S, Paek A, Jayaram M: **Mechanisms for chromosome and plasmid segregation**. *Annu Rev Biochem* 2006, **75**:211-241.

50. Chelysheva L, Diallo S, Vezon D, Gendrot G, Vrielynck N, Belcram K, Rocques N, Marquez-Lema A, Bhatt AM, Horlow C *et al.*: **AtREC8 and AtSCC3 are essential to the monopolar orientation of the kinetochores during meiosis**. *J Cell Sci* 2005, **118**:4621-4632.

51. •• Li X, Dawe RK: **Fused sister kinetochores initiate the reductional division in meiosis I**. *Nat Cell Biol* 2009, **11**:1103-1108.
The authors described the mechanism that ensures monopolar attachment of chromosomes in the reductional division of meiosis in plants.

52. Lee YR, Liu B: **Cytoskeletal motors in Arabidopsis. Sixty-one kinesins and seventeen myosins**. *Plant Physiol* 2004, **136**:3877-3883.

53. Ambrose JC, Cyr R: **The kinesin ATK5 functions in early spindle assembly in Arabidopsis**. *Plant Cell* 2007, **19**:226-236.

54. Chen C, Marcus A, Li W, Hu Y, Calzada JP, Grossniklaus U, Cyr RJ, Ma H: **The Arabidopsis ATK1 gene is required for spindle morphogenesis in male meiosis**. *Development* 2002, **129**:2401-2409.

Please cite this article in press as: Pawlowski WP. Chromosome organization and dynamics in plants, Curr Opin Plant Biol (2010), doi:10.1016/j.pbi.2010.09.015