Higher-order chromosome structure involves the packaging of chromatin beyond the nucleosome level. During both mitosis and meiosis, chromosomes restructure into highly condensed forms, which are essential for their correct segregation. Recent studies on human mitotic chromosomes at metaphase showed that they exhibit 2 levels of compaction: consecutive arrays of chromatin loops are anchored to axes, with each loop being about 80 kb in size, followed by axial compression [Nau-mova et al., 2013]. Mammalian chromosomes at meiosis share a similar loop size, suggesting that the higher-order structure of chromosomes is conserved between the 2 types of cell divisions [Kleckner et al., 2013]. Studies in
many groups of species, including plants, point to a critical importance of the higher-order structure of chromosomes for cellular processes. One of the intensely examined aspects on how the structure affects chromosomal function is its role in controlling chromosome interactions during meiosis.

In meiotic prophase, chromosomes undergo dramatic structural remodeling. Following replication during the pre-meiotic S phase, DNA remains dispersed throughout the nucleus. Meiosis begins with chromosome individualization and compaction which eventually results in highly condensed, rod-shaped metaphase chromosomes. However, organizing chromatin into compact chromosomes is not the only purpose of chromosome remodeling. During this process, chromosomes must also pair, synapse, and recombine with their homologous partners. The structure of chromosomes in early meiotic prophase is associated with the progression of these inter-chromosomal interactions, suggesting that chromosome morphology is an integral part of these processes [Yamada and Ohta, 2013]. In plants, chromatin reorganization during meiosis affects the progression of recombination and distribution of COs [Choi et al., 2013; Rosa et al., 2013; She et al., 2013]. The recombination pathway is also initiated during this stage, when the SPO11 protein introduces double-strand breaks (DSBs) into chromosomal DNA [Kee-ney, 2008]. DNA ends adjacent to these breaks are later bound by RAD51 and DMC1 that catalyze single-end invasion of the broken DNA ends into the homologous chromosome [San Filippo et al., 2008]. In most species, this process is thought to be a key feature in homology recognition.

As prophase continues into early zygotene, chromatin fibers expand, and their surface increases in complexity [Dawe et al., 1994]. Heterochromatic knobs elongate and telomeres cluster at the nuclear envelope into a cytological structure termed the bouquet [Tiang et al., 2012]. As homologs find each other, their axial elements, now called lateral elements, become connected by the installation of the central element of the synaptonemal complex (SC) [Fraune et al., 2012]. During late zygotene, recombination events become resolved in either crossovers (COs) or non-crossovers [Muyt et al., 2009]. The shortening of chromosomes continues through diplotene as the SC dissolves and the homologous chromosomes remain held together as bivalents through CO sites that form cytological linkages termed chiasmata.

Various levels of chromosome structure are important for meiotic processes in plants. Histone modifications and epigenetic reprogramming during meiosis affect the progression of recombination and distribution of COs [Choi et al., 2013; Rosa et al., 2013; She et al., 2013]. The installation of the SC affects recombination as well as pairing [Schommer et al., 2003; Kerzendorfer et al., 2006; Stronghill et al., 2010; Miao et al., 2013]. Most important, however, are the determinants of the higher-order chromosome structure, which are responsible for the compaction and reorganization of chromosomes. These factors

![Diagram of meiotic stages showing a single pair of homologous chromosomes. Following DNA replication in pre-meiotic interphase, cells enter meiosis starting in prophase I. Prophase I consists of 5 sub-stages: leptotene (L), zygotene (Z), pachytene (P), diplotene (Dip), and diakinesis (Dia). It is during leptotene, zygotene, and pachytene that homologs pair, synapse, and recombine.](image-url)
are the focus of our review. The main determinants for the higher-order of chromosome structure are cohesins and condensins. Cohesins have been well studied in multiple plant systems during both mitosis and meiosis. They are needed for chromatin organization and for the establishment of the meiotic chromosome structure which is a prerequisite for pairing and recombination as well as for providing cohesion of sister chromatids through meiosis I [Bai et al., 1999; Bhatt et al., 1999; Cai et al., 2003; Golubovskaya et al., 2006; Shao et al., 2011]. Condensins are responsible for compacting chromatin to ensure its proper segregation to daughter cells. Plant condensins are known to be critical during development [Lui and Meinke, 1998; Siddiqui et al., 2003, 2006; Tzafrir et al., 2004; Schubert et al., 2013], but little is known about how their establishment of chromosomal organization affects meiotic processes. In this review, we will combine the limited information about plant condensins with what is known about their roles in animals and fungi to make inferences about how they may function during plant meiosis. In addition to cohesins and condensins, there are other determinants of chromosome structure that have more specialized functions in meiotic processes. One of the best studied is the Ph1 locus which controls chromatin conformation and plays a role in proper chromosome pairing in polyploid wheat [Prieto et al., 2004, 2005; Knight et al., 2010; Greer et al., 2012].

Cohesins

An important player in determining chromosome morphology is the cohesin complex which forms a ring-like structure holding sister chromatids together during cell divisions. Meiotic sister chromatid cohesion (SCC) is needed for both the proper alignment of chromosomes at the metaphase plate and to create tension across the centromeres, which counteracts the pull of microtubules to allow for correct monopolar attachment to the spindle during anaphase I [Wassmann, 2013]. In addition, cohesins have been implicated in determining the meiotic chromosome structure that is required for proper chromosome pairing and recombination [Golubovskaya et al., 2006; Qiao et al., 2012]. In prophase I of meiosis, plant cohesins are present at the centromeres as well as over the length of the chromosome arms [Lam et al., 2005; Golubovskaya et al., 2006; Wang et al., 2009; Qiao et al., 2011; Shao et al., 2011]. Cohesins are loaded dynamically onto chromosomes, as the subunits of the complex show spatial and temporal differences in their localization through-out prophase I [Qiao et al., 2012]. SCC along chromosome arms during prophase is maintained by AtCTF7, a plant homolog of ScEco1 which acetylates cohesins, stabilizing the complex around chromatin [Bechouet et al., 2010; Bolanos-Villegas et al., 2013; Singh et al., 2013]. Prior to anaphase I, cohesins along the arms are released by separase in order to resolve chiasmata, allowing homologs to segregate [Wassmann, 2013]. However, SCC is maintained at the centromeres to ensure correct orientation of the centromeres to the kinetochores [Wantanabe, 2005].

Similarly to other species, plant centromeric cohesins are protected from separase cleavage by SHUGOSHINs (AtSGO1 and AtSGO2, ZmSGO1, OsSGO1) [Hamant et al., 2005; Wang et al., 2011; Cromer et al., 2013; Zamarriola et al., 2014]. Plant SHUGOSHINs are unique in that they function only during the meiotic divisions [Cromer et al., 2013]. AtSGO1 and AtSGO2 act redundantly during meiosis I to protect centromeric cohesins, thus preventing precocious separation of sister chromatids [Cromer et al., 2013; Zamarriola et al., 2014]. A novel protector of cohesins, AtPANS1, has recently been characterized in Arabidopsis. This protein directly interacts with the APC/C complex to maintain centromeric cohesin during interkinesis [Cromer et al., 2013].

The cohesin complex consists of 2 structural maintenance of chromosome (SMC) proteins, SMC1 and SMC3, and 2 additional non-SMC subunits, Scc3 and Scc1/Rec8 [Klein et al., 1999]. The 2 SMC proteins form a V-shaped heterodimer around sister chromatids that is closed by non-SMC subunits (fig. 2a) [Nasmyth and Haering, 2005]. During meiosis, the SMC proteins are found along chromosome arms and at centromeres, holding together sister chromatids along their entire length [Lam et al., 2005]. SMC1, SMC3, and SCC3 are found in both mitotic and meiotic cohesin complexes. Knockouts of SMC1, SMC3, and SCC3 in Arabidopsis are seedling-lethal [Lui et al., 2002; Chelysheva et al., 2005; Lam et al., 2005; Schubert et al., 2009], demonstrating that they are critical in plant development. Somatic cells defective in cohesin subunits show incorrect alignment of chromatid arms and centromeres [Schubert et al., 2009]. These defects lead to anaphase chromosome bridges and genome instability following mitotic cell divisions [Schubert et al., 2009]. Therefore, the cohesin complex is especially important in actively dividing tissues, such as meristems.

Mitotic and meiotic cohesins are distinguished by α-kleisin that binds the complex. Orthologs of SCC1 are present in mitotic cohesins, while the binding of REC8...
orthologs specifies the meiotic cohesin complex. REC8 orthologs, AtSYN1/DIF1 in Arabidopsis, AFD1 in maize, and Rec8 in tomato and rice, are needed to maintain SCC prior to the first meiotic division [Bai et al., 1999; Bhatt et al., 1999; Kaszás and Cande 2000; Cai et al., 2003; Golubovskaya et al., 2006; Zhang et al., 2006; Qiao et al., 2011; Shao et al., 2011].

Meiotic Sister Chromatid Cohesion
The predominant role of the cohesin complex during meiosis is to hold sister chromatids together during the first division. Unlike mutations in other cohesin subunits, plant rec8 mutant phenotypes are specific to meiosis, resulting in severe fertility defects [Bai et al., 1999; Bhatt et al., 1999; Golubovskaya et al., 2006; Zhang et al., 2006; Shao et al., 2011]. In these mutants, sister chromatids separate precociously during prophase I [Kaszás and Cande, 2000; Cai et al., 2003; Shao et al., 2011]. Cohesin mutants are also defective in chromosome pairing. In maize afd1 mutants, univalents line up at the metaphase plate [Chan and Cande, 1998] and segregate equationally during meiosis I [Kaszás and Cande, 2000]. This phenotype is also seen in Arabidopsis ssc3 mutants where tangled bivalents and univalents separate equationally during the first meiotic division [Chelysheva et al., 2005]. The premature loss of SCC results in bipolar attachment of sister kinetochores to the spindle, as opposed to monopolar attachment. Consequently, a mitotic-like division occurs in which sisters instead of homologous chromosomes separate during anaphase I [Golubovskaya, 1989; Chelysheva et al., 2005].

Cohesins Are Major Determinants of Chromosome Structure
In early leptotene, sister chromatids begin the process of compaction by forming loops that are anchored to the axial elements. Cohesins are critical in establishing this meiotic chromosome morphology. Maize AFD1 has been shown to colocalize with ASY1, an axis-associated protein, starting in leptotene [Golubovskaya et al., 2006]. The colocalization persists until the SC is installed [Golubovskaya et al., 2006].

The distinctive chromosome structures of leptotene and zygotene are drastically altered in plant rec8 mutants [Bai et al., 1999; Kaszás and Cande, 2000; Zhang et al., 2006]. Instead of the characteristic chromatin fibers of these stages, the chromatin is intertwined and tangled, hampering individualization of chromosomes [Bai et al., 1999; Golubovskaya et al., 2006; Zhang et al., 2006]. In the strongest alleles of afd1 mutants, afd1–1 and afd1–2, the leptotene and zygotene fibers are completely absent, showing that SCC is critical for proper chromosome organization in maize [Golubovskaya et al., 2006] (fig. 3). Since the leptotene and zygotene fibers are altered or absent in rec8 mutants, the processes that rely on these chromatin structures, namely homologous pairing, synopsis, and recombination, are also affected.

In rice and maize cohesin mutants, the telomere bouquet, thought to facilitate chromosome pairing, is not formed [Golubovskaya et al., 2006; Shao et al., 2011]. In addition to pairing being absent, either because of the bouquet defect or because of direct disruption of homologous chromosome interactions, the defects in axial ele-
ment formation prevent central element installation, impeding synapsis [Bai et al., 1999; Bhatt et al., 1999; Golubovskaya et al., 2006; Zhang et al., 2006; Shao et al., 2011]. Synapsis defects contribute to the presence of univalents at metaphase I and result in chromosomes that are not able to align correctly at the metaphase plate [Bai et al., 1999; Bhatt et al., 1999; Shao et al., 2011].

The correct chromosome structure during the early stages of prophase I is also essential for recombination in plants. Chromosome fragmentation seen in Arabidopsis syn1 and scc3 mutants is rescued by the spo11–1 mutation [Bai et al., 1999; Bhatt et al., 1999; Chelysheva et al., 2005], indicating that cohesin mutants are defective in DSB repair. Additionally, the localization of RAD51, a protein facilitating the first step of meiotic DSB repair and a marker of recombination, is abnormal in afd1 mutants [Golubovskaya et al., 2006]. In wild-type maize, approximately 500 RAD51 foci are seen on chromosomes during zygotene [Franklin et al., 1999]. However, in the afd1 mutant, the number of zygotene foci is greatly reduced, and those that are present appear as aggregates and patches [Pawlowski et al., 2003; Golubovskaya et al., 2006]. As recombination and homologous pairing are tightly associated in plants [Franklin et al., 1999, 2003; Pawlowski et al., 2003; Da Ines et al., 2012], the recombination defect in afd1 mutants must be linked with the pairing defect. Cohesins have differing effects on recombination between Arabidopsis and maize, as evident by normal RAD51 foci formation in Arabidopsis scc3 mutants [Chelysheva et al., 2005]. This difference could be related to the fact that the amount of DNA and the fraction of repetitive DNA in maize chromosomes are much higher than those in Arabidopsis which could result in meiotic chromosomes being differently organized in the 2 species.

SCC also appears to be needed for repairing DSBs in Arabidopsis somatic cells through homologous recombination. An additional SMC complex, SMCS/6, acts alongside cohesins to establish correct alignment of sister chromatids which helps to ensure that the correct template is used during homologous recombination [Watanabe et al., 2009].

**Fig. 3.** Effects of strong and weak afd1 alleles on the early prophase chromatin structure. In the strong afd1–1 allele, the leptotene fibers are completely absent, leading to severe defects later in meiosis. However, leptotene fibers are formed in the weak afd1–4 allele, yet chromatin structure is still affected in later stages. Modified from Golubovskaya et al. [2006]. Scale bar = 5 μm.
Sex-Specific Cohesins in Arabidopsis

The Arabidopsis genome contains 3 other genes that are closely related to SYN1 [Dong et al., 2001; Da Costa-Nunes et al., 2006; Jiang et al., 2007]: SYN2, SYN3, and SYN4 are expressed throughout the plant, with highest expression levels in the meristems, initially implicating their function in mitotic cohesin complexes [Dong et al., 2001; Da Costa-Nunes et al., 2006]. However, further studies point to SYN3 acting as a significant player during female meiosis [Yuan et al., 2012]. In SYN3 RNAi plants, male gametogenesis is only slightly affected, with a marginal reduction in pollen viability [Yuan et al., 2012]. Yet, these plants have significantly reduced fertility, resulting from the abortion of megaspore mother cells [Yuan et al., 2012]. This sex-specific difference in fertility is further apparent at the cytological level. While male meiocytes show moderate defects and produce wild-type looking microspores, female meiocytes display much more severe defects, including a lack of thin-thread fibers during leptotene/zygotene, presence of univalents and fragmented chromosomes at metaphase I, and chromosome bridges at anaphase I [Yuan et al., 2012]. These phenotypes parallel the meiotic aberrations in syn1 male meiocytes, indicating that SYN1 and SYN3 may have similar functions in the different sexes.

Condensins

Condensins are protein complexes that facilitate the compaction of chromosomes into discrete units prior to the cell divisions of mitosis and meiosis. However, their importance stretches beyond packaging DNA into chromosomes [Hirano, 2012]. Increasing evidence in animals and yeast points to the importance of the condensin-controlled chromosome structure for the processes of homologous pairing and recombination [Yu and Koshland, 2003; Hartl et al., 2008; Mets and Meyer, 2009; Hirano, 2012].

Each condensin complex is made up of 5 subunits: 2 SMC proteins and 3 chromosome-associated proteins (CAPs) (fig. 2b). Both condensin I and II contain SMC2 and SMC4 which dimerize to form a V-shaped structure. This structure is closed on its other end by binding of the kleisin proteins CAP-H or CAP-H2 to form a ring that encircles chromatin [Nasmyth and Haering, 2005]. CAP-H is the kleisin subunit of condensin I, while CAP-H2 participates in the condensin II complex. The kleisins then serve as scaffolds for the binding of 2 HEAT repeat-containing proteins, CAP-G and CAP-D2 in condensin I and CAP-G2 and CAP-D3 in condensin II [Nasmyth and Haering, 2005; Hudson et al., 2009].

Homologs of condensin I and II are present in plants, including Arabidopsis, maize, and rice. The Arabidopsis genome contains genes encoding all putative condensin subunits, with 2 genes encoding SMC2 (AtCAP-E1 and AtCAP-E2) and 3 genes encoding SMC4 (including AtCAP-C and 2 other putative genes) [Siddiqui et al., 2003, 2006; Schubert, 2009]. Although there has been little research on the role of condensins in plant meiosis, several studies have shown their importance in plant development. Both SMC2-encoding genes as well as AtCAP-C are expressed throughout the plant, with the highest expression levels in floral organs and tissues with high mitotic indices [Lui et al., 2002; Siddiqui et al., 2003, 2006]. Mutations in these genes result in severe developmental defects, such as embryo lethality, developmental delays, defective seed development, abnormal gametogenesis as well as defective cell patterning and organization of the shoot apical meristem [Lui and Meinke, 1998; Siddiqui et al., 2003, 2006; Tzafir et al., 2004]. Knockout mutations in genes encoding the non-SMC condensin subunits in plants have only been studied for CAP-D2 and CAP-D3 and result in embryo lethality and dwarfism, respectively [Schubert et al., 2013]. This difference in phenotype indicates that condensin I and II play non-redundant roles during plant development. In the few studies addressing the role of the condensin complexes in plant meiosis, reduced pollen quantity and seed sets have been observed in Arabidopsis condensin mutants [Schubert et al., 2013], suggesting that plant condensins are also critical during meiosis.

Condensins and the Structure of Chromosomes

No studies have been conducted so far to address the role of condensins in establishing the structure of chromosomes specifically during meiosis in plants. However, studies on condensin functions in animals and fungi as well as reports on mitotic roles of condensins in plants allow inferences on the possible functions of these proteins in plant meiosis.

Studies in animals show that condensin I and II are loaded sequentially onto meiotic chromosomes. In mice, condensin II is loaded on the axes of chromosome arms during metaphase I, whereas condensin I appears at centromeres during this stage and then spreads to chromosome arms during anaphase I [Viera et al., 2007; Lee et al., 2011]. Condensin loading is closely linked to the loading of cohesins. Mouse condensins are interspersed with cohesins along chromosome arms at metaphase I, each oc-
cupying their own particular domains [Lee et al., 2011]. Furthermore, condensins affect the establishment of SCC and sister chromatid organization in Caenorhabditis elegans [Chan et al., 2004].

Studies on mitotic functions of plant condensins suggest that they may have similar roles to animal and fungal condensins. Arabidopsis condensin I and II complexes are loaded onto mitotic chromosomes separately, which is similar to the behavior of condensins in animal meiosis. The AtCAP-H protein is present in the cytoplasm from interphase until mitotic prophase when it becomes loaded onto the chromosomes [Fujimoto et al., 2005]. In contrast, AtCAP-H2 of condensin II is located in the nucleolus and nucleoplasm during interphase. By metaphase, both proteins are fully localized on the chromosomes where they remain until cytokinesis is completed [Fujimoto et al., 2005]. Studies on Arabidopsis CAP-D2 and CAP-D3 in interphase nuclei showed that these condensin subunits are needed for higher-order organization of the nucleus, such as compacting euchromatin, preventing associations between centromeric/pericentromeric repeats, and, in the case of CAP-D3, ensuring proper distribution of cohesins [Schubert et al., 2013].

Condensins and Chromosome Interactions

Since chromosome structure is important for facilitating chromosome interactions, not surprisingly, condensins have been observed to play a role in these processes. Condensins are important in chromosome pairing in Drosophila males through resolving linkages between chromosomes. In condensin mutants in Drosophila males, paired homologs are not fully individualized before being separated, which results in chromatin bridges between homologous and non-homologous chromosomes during anaphase I [Hartl et al., 2008]. As Drosophila males do not undergo recombination, these linkages cannot be due to unresolved recombination events and are thought to be results of the pairing process. Formation of anaphase bridges in Drosophila condensin II mutants is suppressed when they are combined with mutations in teflon, a gene required for the maintenance of chromosome pairing [Arya et al., 2006; Hartl et al., 2008]. Therefore, it is hypothesized that the Teflon protein introduces entanglements between chromosomes to facilitate homolog pairing, and condensin II is required to resolve these linkages prior to homolog separation.

Although it is not known if plant condensins play a role in chromosome pairing, their role in resolving linkages between sister chromatids is conserved in Arabidopsis. This is evident by chromosome bridges forming during mitosis in Arabidopsis cap-e1, cap-e2, and cap-c mutants [Siddiqui et al., 2003, 2006]. Interestingly, mitotic bridges are not observed in mutants with disrupted cap-d2 or cap-d3 [Schubert et al., 2013]. It is possible that these subunits play a role in resolving chromosome linkages in meiosis rather than mitosis, as the mutants exhibit significant reduction in pollen quantity [Schubert et al., 2013].

The Effect of Condensins on Meiotic Recombination

Condensins also have a major effect on meiotic recombination. Studies in C. elegans indicate that condensin I and II play a role in meiotic DSB formation. Mets and Meyer [2009] showed that condensins influence both the number and distribution of DSBs and serve as a means of controlling CO formation. These effects are most likely mediated by the influence that condensins exert on chromosome axis formation [Tsai et al., 2008]. In C. elegans, condensin I and II act independently to affect the DSB number and distribution, with each complex affecting DSB formation by controlling chromosome axis length and structure in its domain of control along the chromosome [Mets and Meyer, 2009]. These studies point to an active mechanism which guarantees that at least 1 DSB, and therefore 1 CO (the obligate CO), is formed on each bivalent [Mets and Meyer, 2009].

It remains uncertain whether the phenomenon of the condensin-controlled chromosome structure influencing recombination patterns is conserved in other species. Yu and Koshland [2003] found that the Saccharomyces cerevisiae condensin does not affect DSB formation. As yeast and C. elegans are the only 2 species in which a connection between condensins and DSBs has been investigated, it is unclear whether this role is specific to C. elegans or if it evolved after the divergence of yeast and higher eukaryotes. Since C. elegans exhibits a very tight control of the number of COs, condensins may have evolved specifically to help uphold the strict obligate CO requirement in this species. Alternatively, this level of CO control may have evolved with larger and more complex genomes.

Currently, there are no studies investigating how condensins influence recombination in plants. However, Arabidopsis condensin II has been implicated in playing a role in somatic genome maintenance after genotoxic stress [Sakamoto et al., 2011]. Mutations in AtCAP-G2 and AtCAP-H2 increase the frequency of DSBs following exposure to a DNA break-inducing agent [Sakamoto et al., 2011]. During interphase, when condensin II is found in the nucleus, the complex is able to reduce DNA damage by either physically protecting the genome or playing
a direct role in DSB repair [Fujimoto et al., 2005; Sakamoto et al., 2011]. It is yet to be seen if condensins play a similar role in the formation and repair of meiotic DSBs in plants.

At the final steps of recombination, condensins play a role in resolving meiotic COs. Prior to anaphase I, chiasmata between chromosomes must be resolved to allow the homologs to separate to opposite poles. In S. cerevisiae, condensin is needed for the separation of chromosomes by resolving these linkages [Yu and Koshland, 2003]. Without condensin, the homologs are held together as they are pulled to separate poles, resulting in chromosome bridges and fragmentation [Yu and Koshland, 2003]. In Arabidopsis smc2 and smc4 mutants, chromosome bridges have been observed during meiotic anaphase I and II. Therefore, it is likely that plant condensins share the role in resolving chiasmata prior to homolog separation with fungal condensins.

Regulation of Homologous Chromosome Pairing by Chromatin Structure Controlled by the Ph1 Locus in Wheat

A very strong link between chromosome structure and function has been demonstrated and extensively studied in hexaploid wheat which contains 3 fairly closely related (homoeologous) chromosome sets as a result of an allopolyploidization event that took place ca. 10,000 years ago [Matsuoka, 2011]. For stability of the hexaploid genome, it is critical that during meiosis chromosome pairing and recombination are limited to within-chromosome set (homologous) interactions and that pairing and recombination of chromosomes from different sets is prevented. To keep its 3 genomes distinct during meiosis, polyploid wheat has evolved a special mechanism that is controlled by the Ph1 locus [Riley and Chapman, 1958].

Ph1 has been mapped to a region on chromosome 5B containing a cluster of cdk-like genes [Sears, 1976; Roberts et al., 1999; Griffiths et al., 2006; Sidhu et al., 2008; Yousafzai et al., 2010a]. Additional clusters of cdk genes are found in syntenic regions in the other 2 genomes of polyploid wheat, and Ph1 activity suppresses the transcription of these cdk genes on the homoeologous chromosomes [Griffiths et al., 2006; Al-Kaff et al., 2008; Yousafzai et al., 2010b]. The role of cdk suppression in ensuring proper chromosome pairing has been confirmed by treatment with the CDK activator okadaic acid (OA). In wheat-rye hybrids containing haploid chromosome sets from wheat and rye, chromosomes do not pair in the presence of Ph1, since there are no homologs present. However, in the ph1 mutant, or when treated with OA, some wheat and rye chromosomes undergo homoeologous pairing [Knight et al., 2010]. It is hypothesized that the increased cdk activity in the ph1 mutant leads to homoeologous pairing through altering chromosome structure [Mikhailova et al., 1998; Maestra et al., 2002; Greer et al., 2012]. CDK activity is also important in Arabidopsis meiosis. At high temperatures (23 °C), AtCDKG1 is needed for the formation of proper chromosome structure and pairing [Zheng et al., 2014], indicating that CDK activity plays a conserved role in the pairing of plant chromosomes.

Chromosomes Are in an Altered Conformation during Pairing in ph1 Mutants

It has been proposed that Ph1 controls chromosome pairing in wheat by affecting the remodeling of heterochromatic regions of the chromosomes [Prieto et al., 2004, 2005; Colas et al., 2008; Knight et al., 2010; Greer et al., 2012]. In polyploid wheat, chromatin is remodeled and elongated in early meiosis to facilitate the pairing process [Mikhailova et al., 1998; Maestra et al., 2002; Prieto et al., 2004]. In the wheat-rye hybrids, euchromatic regions elongate and decondense, regardless of Ph1, to allow a more open conformation during pairing [Maestra et al., 2002; Prieto et al., 2005]. However, subtelomeric heterochromatin in rye chromosomes of the hybrid behaves differently in the presence and absence of Ph1 (fig. 4a–f). When Ph1 is present, these regions stay tightly compacted throughout prophase I [Prieto et al., 2004]. However, in ph1 mutants, the heterochromatin regions also elongate [Prieto et al., 2004]. The Ph1-controlled remodeling of heterochromatin is affected by the degree of sequence similarity between the homoeologous chromosomes undergoing pairing (fig. 4g–i) [Colas et al., 2008]. In wheat-rye translocation lines containing a pair of identical rye chromosome arm segments, rye heterochromatin elongates, allowing pairing and recombination to take place [Colas et al., 2008]. However, when the rye regions are diverged in sequence and are of different sizes, heterochromatin does not expand and pairing as well as recombination are significantly reduced [Colas et al., 2008]. Possibly, the compaction of heterochromatic domains by Ph1 excludes these highly repetitive regions from influencing chromosome pairing [Prieto et al., 2005].

In addition to controlling chromatin remodeling, Ph1 also affects the timing of chromosome pairing [Prieto et al., 2005; Knight et al., 2010]. Chromosome pairing in
wheat, similar to many other plant species, is thought to begin at the telomeres at the stage of bouquet formation [Prieto et al., 2004]. In the absence of Ph1, chromatin begins to associate and pair while the bouquet is still being formed and chromatin is still being elongated [Prieto et al., 2004]. Consequently, the chromatin is in a more open state, which may allow repetitive regions of homoeologous chromosomes to associate. The hypothesis that a lack of Ph1 results in incorrect pairing due to a more open chromosome conformation is further supported by an observation of increased histone H1 phosphorylation in ph1 mutants [Greer et al., 2012]. H1 phosphorylation is associated with an open chromatin state [Hale et al., 2006]. In polyploid wheat, histone H1 is a target of Cdk2 phosphorylation, and the phosphorylation levels of H1 in the presence of Ph1 can be increased using OA treatment to levels similar to those observed in the ph1 mutant [Greer et al., 2012]. Interestingly, this more open chromatin state in ph1 may also allow greater access for condensins to bind, possibly providing a link between cdk activity and altered chromatin organization.

Without Ph1, chromosomes are still able to synapse, albeit incorrectly, indicating that Ph1 affects some part of the homolog recognition process [Gillies, 1987]. It is speculated that the altered chromosome state seen in ph1 mutants affects the choice of template used to repair DSBs, which then allows homoeologous chromosome pairing [Greer et al., 2012]. When Ph1 is absent, homoeologous chromosomes could be used as repair-templates, whereas in the presence of Ph1, sister chromatids would be used. It is possible that homoeologous chromosomes synapse even in the presence of Ph1, yet DSBs are repaired using the sister chromatid as a template, and therefore the homoeologs do not remain connected through chiasmata once the SC disassembles. Arabidopsis CDKG1 may play a similar role in regulating the choice of repair template. The number of CO intermediates is reduced in cdkg1 mutants, yet DSBs are still re-

Fig. 4. Chromatin remodeling affects pairing efficiency in wheat. Chromosomal interactions were assessed using telomere-specific (red) and rye subtelomeric (green) FISH probes. In wheat-rye hybrids, Ph1 prevents the rye subtelomeric heterochromatin from elongating (a–c), which precludes pairing between chromosomes bearing the heterochromatic segments. However, when Ph1 is absent, rye heterochromatin elongates (d–f) and pairing occurs. Ph1 affects remodeling of heterochromatin blocks based on their similarity (g–l). When the heterochromatin segments are identical (g–i), heterochromatin elongates and the segments pair. However, elongation of the heterochromatin regions does not occur if they are different (j–l). Modified from Colas et al. [2008]. Scale bar = 5 μm.
paired, as no chromosome fragmentation is observed [Zheng et al., 2014]. Likely, incomplete synopsis in the mutant results in DSBs being repaired using the sister chromatid.

Regulation of chromosome structure may also be involved in meiotic adaptation to whole genome duplication in other polyploid species. Analysis of A. arenosa tetraploids found that numerous genes involved in chromosome structure and synopsis have been targeted by selection following polyploidization [Hollister et al., 2012; Yant et al., 2013]. One of these genes is SMC3 [Hollister et al., 2012; Yant et al., 2013]. Consequently, A. arenosa may represent another polyploid taxon that uses chromosome structure as a means of controlling chromosome interactions.

**Outlook**

The large sizes of plant genomes make the packaging of chromatin into chromosomes a major undertaking. This process not only reduces the chromatin volume but also facilitates complicated chromosome functions. Studies in plants show increased transcriptome complexity during meiotic prophase when chromosomes are already fairly condensed [Chen et al., 2010; Yang et al., 2011], suggesting that chromosome condensation may specifically act to facilitate gene expression. Chromosomes in meiotic prophase also exhibit dynamic and complex motility [Sheehan and Pawlowski, 2009]. These interactions are undoubtedly affected by chromosome structure, which makes it even more imperative to better understand how meiotic processes depend on chromosome structure. Chromosome interactions during pairing and recombination, as we documented in this review, also require special chromatin conformation. Recent advances, such as structured illumination microscopy [Wang, 2013] and the method of chromosome conformation capture [Naumova et al., 2013], will allow a more thorough understanding of how plant chromosomes are structured. However, more studies and more sophisticated experimental approaches will be needed to connect chromosome structures to their functions at the mechanistic level.

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