The Formation of Bivalents and the Control of Plant Meiotic Recombination

Yared Gutiérrez Pinzón, José Kenyi González Kise, Patricia Rueda and Arnaud Ronceret*

Laboratory of Cytogenomics of Meiosis, Instituto de Biotecnología, Departamento de Biología Molecular de Plantas, National Autonomous University of Mexico (UNAM), Cuernavaca, Mexico

During the first meiotic division, the segregation of homologous chromosomes depends on the physical association of the recombined homologous DNA molecules. The physical tension due to the sites of crossing-overs (COs) is essential for the meiotic spindle to segregate the connected homologous chromosomes to the opposite poles of the cell. This equilibrated partition of homologous chromosomes allows the first meiotic reductional division. Thus, the segregation of homologous chromosomes is dependent on their recombination. In this review, we will detail the recent advances in the knowledge of the mechanisms of recombination and bivalent formation in plants. In plants, the absence of meiotic checkpoints allows observation of subsequent meiotic events in absence of meiotic recombination or defective meiotic chromosomal axis formation such as univalent formation instead of bivalents. Recent discoveries, mainly made in Arabidopsis, rice, and maize, have highlighted the link between the machinery of double-strand break (DSB) formation and elements of the chromosomal axis. We will also discuss the implications of what we know about the mechanisms regulating the number and spacing of COs (obligate CO, CO homeostasis, and interference) in model and crop plants.

Keywords: Meiosis, recombination, synopsis, obligate crossing-over, interference, CO homeostasis, heterochiasmy

INTRODUCTION

Meiosis is one of the most dynamic processes for a plant genome (Ronceret and Pawlowski, 2010; Prusicki et al., 2019). To achieve a reductional division, the meiotic cell goes through one round of DNA replication followed by two cell divisions (Mercier et al., 2015). The meiotic divisions have evolved from the machinery toolkit used by the regular mitotic division with additional regulatory functions allowing the reductional division (Wilkins and Holliday, 2009). Several differences between meiosis and mitosis are discernible already at prophase I with the introduction of meiotic-specific processes such as meiotic recombination, pairing, and synopsis of homologs. During the whole meiotic prophase I, the nuclear chromosome content is duplicated and each homolog is constituted by two sister chromatids. Bivalents are defined as connected homologous chromosomes, forming a unit of four DNA molecules, essential for the equilibrated segregation of the chromosome pool. The formation of bivalents occurs during the prophase I of meiosis and involves the coordination between homologous recombination, pairing, and synopsis (Mercier et al., 2015). During meiotic metaphase I, a specific bipolar conformation of the meiotic spindle attachment to centromeres allows the segregation of these recombined bivalents.
In plants, male and female meiosis occur in different organs. Though most meiotic mechanisms are shared between sexes, some differences have long been observed between male and female meiotic recombination rates. After the two successive meiotic divisions, haploid spores, which contain only one set of each chromosome, are formed. These separated male or female spores undergo the gametophytic phase giving rise to distinct male and female gametes. Fertilization between gametes restores the diploid state crucial for the sexual life cycle and the genome maintenance of the species.

Understanding the formation of how new meiotic DNA molecules are formed is of special value for breeding since it is a fundamental basis for genetics, evolution, and genomic crop improvement (Melamed-Bessudo et al., 2016; Lambing et al., 2017; Blary and Jenczewski, 2019; Bolaños-Villegas and Argüello-Miranda, 2019; Taagen et al., 2020; Kuo et al., 2021).

This review will focus on the recent advances in the understanding of the genetic control of meiotic recombination and bivalent formation in diploid plant species, mainly Arabidopsis, rice, and maize. For the more complex bivalent and multivalent formation in polyploid plants [Refer the reviews of Cifuentes et al. (2010), Mason and Wendel (2020), and Sváčina et al. (2020)]. Several important discoveries have been made in these last few years concerning the mechanisms of crossing-over (CO) interference (impeding the formation of adjacent COs), non-crossing-over (NCO) pathways, obligate CO (to maintain at least one CO by bivalent), CO homeostasis [the buffering of CO numbers despite the reduction in double-strand breaks (DSBs) number], and heterochiasmy (difference in male and female CO frequencies). For an overview of the plant meiotic genes and mechanisms discovered before 2018, see the excellent reviews of Luo et al. (2014), Mercier et al. (2015), and Wang and Copenhagen (2018). An overview of the proteins regulating bivalent formation grouped by functional modules is listed in Figure 1.

**REGULATION OF THE MEIOTIC CELL FATE AND MEIOTIC TRANSCRIPTOME**

In plants, the germline fate acquisition where meiosis will occur involves the specific transcription factor SPOROCYTELESS also known as NOZZLE in Arabidopsis (Yang et al., 1999; Wei et al., 2015) and rice (Ren et al., 2018). In rice, the ARGONAUTE protein MEL1 plays an essential role in male and female meiotic cell fate (Nonomura et al., 2007; Komiya et al., 2014; Liu and Nonomura, 2016). The rice MEL2 is an RNA recognition motif protein binding the 3′-UTRs and involved in the translational regulation of key meiotic genes (Nonomura et al., 2011; Miyazaki et al., 2015). In Arabidopsis, no MEL orthologs have been described but AGO9 and AGO4 are involved in female gamete specification (Olmedo-Monfil et al., 2010), while small interfering RNA inhibits retrotranspositions in the male germ line (Long et al., 2021). Argonauts are the key players in distinct small RNAs (sRNAs) pathways involved in transcriptome regulation (Oliver et al., 2014). Transcriptional analysis of different steps of germline cells and meiocytes has revealed dramatic transcriptomic changes during prophase I in various plant species. In maize, single-cell RNA sequencing reveals a profound two steps reorganization of the transcriptome at the leptotene stage when meiotic recombination initiate (Nelms and Walbot, 2019). The sRNAs (micro-RNA and phased secondary small interfering RNA) are particular dynamics during prophase in rice, maize, sunflower, soybean, and cucumber (Dukowic-Schulze et al., 2016; Flórez-Zapata et al., 2016; Huang et al., 2020; Zhang et al., 2021) and, at least in Arabidopsis male meiocytes, play a critical role in meiotic recombination potentially via the AGO4 pathway (Oliver et al., 2016, 2017; Pradillo and Santos, 2018).

Though sex-specific transcriptomes have been obtained in various plant species (Dukowic-Schulze et al., 2020; Liu et al., 2020; Barakate et al., 2021), a systematic comparison between male and female meiotic transcriptomes has not yet been performed.

In maize, hypoxia arising naturally within growing anther tissue was reported to act as a positional cue to set male germ cell fate (Kellerher and Walbot, 2012). The cytology of plant female meiosis has been historically more challenging but is now prone to analysis due to new techniques of the whole immunolocalization of plant ovules (Escobar-Guzman et al., 2015; Gordillo et al., 2020). In Arabidopsis, the specification of only one germ cell line per ovule has been analyzed and involved complex positional cues and identify RBR1 as a central hub for female meiocyte differentiation (Zhao et al., 2017). RBR1 is also required for the recombine RAD51 localization to DNA lesions (Biedermann et al., 2017). SWITCH1/AM1IOIT is an essential gene allowing the entry in male and female meiosis. SW11 was recently identified as a functional Sororin-like antagonist (Yang et al., 2019) of the WINGS APART-LIKE (WAPL) that removes cohesin from chromosome via the prophase pathway before the action of seprase at anaphase onset (De et al., 2014). Accordingly, SW11/AM1 is a nuclear protein installed on the whole chromatin from premeiotic replication and is only maintained in centromere regions during pachytene in maize (Pawlowski et al., 2009). However, this remaining centromeric localization was not observed in rice (Che et al., 2011) suggesting plant-specific variations for this regulation.

**FORMATION OF THE MEIOTIC COHESIN COMPLEX**

DNA replication is followed by the appearance of meiotic-specific components of the cohesin complex (formed by SMC1, SMC3, SCC2, SCC3, and REC8) (Cai et al., 2003; Chelysheva et al., 2005; Wang et al., 2020). Cohesin turnover and localization on chromatins are mediated by WAPL (De et al., 2014), PDS5 (Pradillo et al., 2015), and CTF7 (Singh et al., 2013). REC8 is a meiotic-specific kleisin that replaces the mitotic SCC1 subunit in this complex. It was shown in tomato that the four subunits of the meiotic cohesin complex are discontinuously distributed along the chromosome length from leptotene through early diplotene (Qiao et al., 2011). In maize, SMC3 is essential for sister chromatid cohesion and facilitates centromere coupling (Zhang et al., 2020d), a peculiar configuration associating the centromeres before pairing commences along chromosome
arms (Ronceret et al., 2009). The current working models of chromatin organization suppose that the meiotic cohesin complex forms a ring attaching the two replicated sister chromatids and organizes the chromatin by forming the base of chromatin loops (Zickler and Kleckner, 2015; Kim and Choi, 2019; Grey and de Massy, 2021). Chromosome conformation capture (HiC) experiments have not yet been performed on plant meiotic genomes to analyze their chromosomal loop domain organization (Golicz et al., 2020). In Arabidopsis, ChIP-seq experiments have shown that REC8 is associated with repetitive centromeric and pericentromeric regions of high nucleosome occupancy, the opposite of where meiotic DSBs and crossovers are found at the chromosome and fine scales (Lambing et al., 2020b). REC8 containing cohesin complex is largely protected by the Shugoshin (SGO)-PP2A complex around centromeres during meiosis I (Zamariola et al., 2014; Yuan et al., 2018; Zhang et al., 2019) and by PAN during interkinesis (Cromer et al., 2019). These protections allow the coordinated separation of the homologous chromosomes during meiosis I and the release of the sister chromatin only during meiosis II via a separase-dependent proteolytic cleavage of the centromeric kleisin subunit REC8 (Cromer et al., 2019).

FORMATION OF THE AXIAL ELEMENT OF THE SYNAPTONEMAL COMPLEX

The synaptonemal complex (SC) is a proteinaceous ultrastructure formed of two axial elements (AEs) and a central element. Elements of the AEs are installed on chromatin during leptotene before synopsis occurs. In plants, several components of the AEs have been identified: the HORMA domain ASY1/PAIR2 (Armstrong et al., 2002; Nonomura et al., 2004a), the associated coiled-coiled proteins ASY3/DSY2/PAIR3 (Yuan et al., 2009; Ferdous et al., 2012; Lee et al., 2015; Osman et al., 2018) and ASY4 (Chambon et al., 2018). The cohesin REC8 is supposed to anchor chromatin to the AEs of the SC via PAIR3/ASY3 (Wang et al., 2011) though a direct interaction between REC8 and any AE protein is yet unknown. However, in Arabidopsis, ASY1 and REC8 Chip-seq strongly correlate suggesting that both proteins associate with similar regions of the genome at global and fine scales (Lambing et al., 2020b). In maize, DSY2 (homolog of ASY3 and PAIR3) forms an alternative pattern with ASY1 on AE and can interact with ZYP1 while ASY1 cannot (Lee et al., 2015). In addition, the AAA+ ATPase PACHYTENE CHECKPOINT 2 (PCH2)/CRC1 is essential for the ASY1 depletion before synopsis (Lambing et al., 2015). Its interacting partner P31 participates in ASY1 import in the nucleus and the removal of non-phosphorylated ASY1 from the chromosomal axis (Balboni et al., 2020). In rice, CRC1/PCH2 can directly interact with ZEP1/ZYP1 while P31 cannot (Ji et al., 2016). In addition, the role of some SC proteins in the initiation of meiotic recombination such as DSY2/ASY3 in maize (Lee et al., 2015), CRC1/PCH2 (Miao et al., 2013) and P31 in rice (Ji et al., 2016) pinpoints to the essential role of AE elements on the initiation of meiotic recombination.

FORMATION OF THE EARLY RECOMBINOSOME

During meiosis, two homologous DNA molecules can form new recombinated ones using the general mechanics of the error-proof DNA damage repair pathways (Mercier et al., 2015; Wang and Copenhaver, 2018; Zelkowski et al., 2019). The initiation of meiotic recombination starts with the introduction of DNA DSBs. The DSBs are formed by the SPO11 complex composed of the catalytical A subunits, SPO11-1 (Grelon et al., 2001; Edlinger and Schölglhofer, 2011; Da Ines et al., 2020) and SPO11-2 (Grelon et al., 2001; Edlinger and Schölglhofer, 2011; Da Ines et al., 2020) and...
Hartung et al., 2007b; Benyahya et al., 2020), associated with two B subunits, called MTOPVIB of the class II topoisomerase type VI (Fu et al., 2016; Vrielynck et al., 2016; Xue et al., 2016). The Arabidopsis spo11-I mutant has an interesting distinctive 23 and 24 nt sRNA profile than wild type in male meiocytes. These SPO11-1-dependent sRNAs are mapped to bind coding sequences and some CO feature motifs, while some sRNAs can target some meiotic genes such as RAD51 or ASK1 (Huang et al., 2019). Whether or not these sRNAs are produced at or near the site of DSBs and represent a signaling mode for repairing the DSB requires further work.

Though every CO is derived from a DSB event, not all DSBs are repaired as COs, and a vast majority of DSBs result in NCOs (Mercier et al., 2015). In maize, the CML228 inbred line that has naturally less DSBs (evaluated by the RAD51 number) has a correlated decreased CO number compare to B73 and other inbreds, indicating that the level of CO homeostasis is limited (Sidhu et al., 2015). In Arabidopsis, hypomorphic spo11-I mutants that reduce the DSB number also diminish the CO number but interestingly also alter the pattern of CO toward the telomeres (Xue et al., 2018). These data suggest that, at least in these two model plant species, CO homeostasis is not observed or limited.

In maize, using superresolution microscopy, it was observed that only a subset of SPO11-1 foci, the one closely associated with the AEs, correspond to the number of DSBs formed in leptotene (Ku et al., 2020). This suggests that the topoisomerase II-like nuclease function of the SPO11-1 complex occurs only when it is associated with the AE (Ku et al., 2020). Whether or not this particular configuration allows the nuclease activity of only one of the two attached sister chromatids is not known. The SPO11-1 "early recombinosome" complex also contains various accessory proteins that might participate in the tethering between the chromatin loop and the axis where DSBs are formed. SPO11-1 and MTOPVIB can interact with PRD1 (Vrielynck et al., 2016; Tang et al., 2017). In addition, rice and maize MTOPVIB, rice PRD1, and Arabidopsis PRD2/MP51 are required for the assembly of the meiotic bipolar spindle (Li et al., 2016; Xue et al., 2019; Jing et al., 2020; Shi et al., 2021). It was long recognized in maize that the meiotic spindle can associate around chromatin independently of the formation of the bivalent (Chan and Candé, 1998; Nannas et al., 2016) suggesting that the multipolar spindle observed in the meiotic recombination mutants might be a consequence of the formation of univalents instead of bivalents.

yeast DSB factor but has a divergent function in plants. It is involved in the nuclear localization of the RAD50 protein into the nucleus in maize and Arabidopsis (Ronceret et al., 2009). SKI8 is also not conserved between yeast and Arabidopsis (Jolivet et al., 2006). Interestingly, the PRD2/MP51 can form different splicing isoforms depending on the methylation status of its intron 9, dependent on the RNA-directed DNA methylation pathway (Walker et al., 2018).

GENOMIC MAPPING OF DSBs AND RECOMBINATION MOTIFS

Several studies using ChIP or SPO11 oligonucleotide sequencing have now revealed the genomic pattern of DSBs in maize and Arabidopsis. As previously well-known, genomes contain hotspots of COs, that are now correlated with genomic hotspots regions more prone to form DSBs (He et al., 2017; Choi et al., 2018; Tock and Henderson, 2018). In these two diploid species, DSBs are associated with specific active chromosome features such as transcriptional start sites that are depleted of nucleosomes. In Arabidopsis, several motifs associated with recombination have been defined. The A-rich motif is preferentially associated with promotors, while the CCN repeat and the CTT repeat motifs are preferentially associated with genes (Shilo et al., 2015). The motifs correlating with COs are not necessarily identical to motifs correlating with sites of DSB. This suggests that several genomic contexts required for the different steps of recombination progressively shape the choice of chromosomal exchange sites. The presence of a similar but not identical 20-bp-long GC-rich degenerate DNA sequence motif was correlated with DSB formation in maize and Arabidopsis (He et al., 2017; Choi et al., 2018). Interestingly, while DSBs are also formed in regions that will not form CO such as centromeric regions and repetitive DNA (especially RNA transposons), it was found that only DSBs formed in genic regions will form CO in maize (He et al., 2017). In Arabidopsis, mutants affecting the methylation of H3K9me2 and DNA CG and non-CG in the transposon-rich pericentromeric heterochromatin also increase the formation of DSB near centromeres (Underwood et al., 2018; Fernandes et al., 2019). In maize, the mop1 mutation (homolog of RDR2) that removes CHH methylation adjacent to hotspots also affects the recombination landscape, increasing it in the chromosome arm but decreasing it in pericentromeric regions (Zhao et al., 2021). These data indicate that though the molecular bases are distinct in species of different genome sizes, and with relative repetitive element contents, a strong effect of epigenetic and chromatin state controls the fate of the early meiotic recombinosome.

SIGNALING AND PROCESSING OF THE DSBs

The programmed DSBs are identified by the signaling pathway of DNA damages via the ATM and ATR kinases (Kim and Choi, 2019; Zhang et al., 2020a). In budding yeast, ATM/ATR can phosphorylate REC8 and other chromosome
axis proteins and, therefore, modulate CO homeostasis (Kim and Choi, 2019). It is not clear, however, if this is also the case in plants. The meiocyte nuclei use prepared recombination machinery to repair the numerous endogenous DSBs using a preferential homologous recombination pathway. The somatically preferred non-homologous end joining (NHEJ) is suppressed by the exonuclease (RAD9-RAD1-HUS1) 9-1-1 complex system (Che et al., 2014; Hu et al., 2016). This 9-1-1 complex itself is possibly recruited by the DNA damage sensor RAD17 (Hu et al., 2018). This inhibition is essential to avoid inaccurate interactions between non-homologous chromosomes during meiosis (Che et al., 2014). The DSBs are rapidly associated with the phosphorylation of histone H2AX and processed by endonuclease and exonucleases activities of the MRN complex composed of MRE11, RAD50, NBS1, and COM1 (Bleuyard et al., 2004; Puizina et al., 2004; Uanschou et al., 2007; Waterworth et al., 2007; Lohmiller et al., 2008; Šamanić et al., 2013; Wang Y. et al., 2018) creating 5’ overhang sequences. These sequences are recognized by specialized single DNA strand affine replication protein A (RPA) types such as RPA1a in Arabidopsis (Osman et al., 2009) or RPA1C and RPA2C in rice (Li et al., 2013). RPAs are generally involved in telomere-length maintenance (Aklilu et al., 2020) suggesting a functionalization of this single DNA strand capping for the processing of meiotic DSBs.

**SINGLE-END INVASIONS AND PAIRING**

These single ends can invade homologous sequences (process called single-end invasion or SEI) thanks to the recombinase activities of RAD51 and DMC1 (Couteau et al., 1999; Li et al., 2004). These recombinases have the properties to form a strong homology-based DNA triple helix called a displacement loop (D-loop) (Kurzbauer et al., 2012; Wang et al., 2016; Singh et al., 2017; Colas et al., 2019; Draeger et al., 2020). The RAD51 and DMC1 are part of the same recombinase protein family also containing RAD51C and XRCC3 that derive from the same ancestor but have undergone subfunctionalization (Bleuyard et al., 2004; Da Ines et al., 2013; Pradillo et al., 2014). RAD51C and XRCC3 facilitate the RAD51 chromosome localization (Su et al., 2017; Jing et al., 2019; Zhang et al., 2020c). RAD51 and DMC1 also associate with other proteins modulating their activities such as BRC2 (Siaud et al., 2004; Dray et al., 2006; Seeliger et al., 2012; Fu et al., 2020), FIG1 and FLIP (Zhang P. et al., 2017; Fernandes et al., 2018a; Kumar et al., 2019), or MND1, and HOP2 (Vignard et al., 2007; Uanschou et al., 2013; Aklilu et al., 2020). Rice MND1/MSF1 can interact with RPA2b and HOP2 (Lu et al., 2020), while OsHOP2 can directly interact with the SC central element ZEP1/ZYP1 suggesting a second mechanism for the link observed between early recombination and synopsis (Shi et al., 2019) at the SEI step. The excess number of SEI creating several interconnections between homologous chromosomes (also called interhomolog joint molecules) were proposed to be involved in the pairing process (Pawlowski et al., 2003). Pairing allows the recognition between accurate homologs before its stabilization by the polymerization and lateral extension of the SC during zygotene.

**ANTICROSSOVER PATHWAYS**

The number of DSB and SEI is far greater than the number of COs and the vast majority of DSBs [around 85% in Arabidopsis (Higgins et al., 2004) and 97.7% in durum wheat (Desjardins et al., 2020)] are resolved as NCOs. NCOs are formed when the SEI occurs on the sister chromatid but also when a D-loop formed on the homologous chromosome is resolved in a configuration that only involves the exchange of genetic material in a short sequence called conversion tracts (Mercier et al., 2015; Wang and Copenhaver, 2018). Three parallel anti-CO pathways have been discovered using suppressor genetic screens of *zmn* meiotic recombination mutants in Arabidopsis (Séguela-Arnaud et al., 2015).

The first NCO pathway involves the SGS1/BLM helicases homologs RECQ4A and RECQB (Hartung et al., 2007a; Higgins et al., 2011) and the topoisomerases TOP3a (Hartung et al., 2008) associated with BLAP75/RMI (Chelysheva et al., 2008), which unwinds D-loops leading to a sixfold CO number increase in Arabidopsis (Séguela-Arnaud et al., 2015). In rice, the MEICA protein that interacts with TOP3a also has an anticrossover activity (Hu et al., 2017).

The anti-CO pathway that involves the FANCM helicase possibly displaces the invading strand through the synthesis-dependent strand annealing (SDSA) process (Crismani et al., 2012). SDSA can form NCOs by annealing the SEI with the other end of the DSB, repairing the DSB using the original DNA molecules. FANCM has two binding cofactors MHF1 and MHF2 that also limit the number of COs formed via the type II non-interfering pathway (Dangel et al., 2014; Girard et al., 2014). Interestingly, the anti-CO effect due to FANCM is more pronounced in inbred than in hybrids backgrounds (Girard et al., 2015). The FANCM pathway also affects COs in a *Brassica rapa* pure line (Blary et al., 2018). In lettuce, the *fancm* mutant shows a univalent phenotype not observed in other species (Li et al., 2021) indicating possible divergence in the regulation of this pathway or different consequences between species of different genome sizes.

Another cumulative NCO pathway involves the FIDGETIN AAA-ATPase FIG1 (Girard et al., 2015; Zhang P. et al., 2017) and its partner FLIP (Fernandes et al., 2018a). FIG1 directly interacts with RAD51 and DMC1 and is proposed to limit SEI and CO number (Fernandes et al., 2018a). Using the mutants of these different pathways or combining them together or with elevated expression of the procrossover factors HEI10 (Serra et al., 2018) are particularly interesting for agronomy since it allows to unleash the number of CO by several folds in various plant species and potentially speed up new breeding strategies (Fernandes et al., 2018b; Mieulet et al., 2018). Interestingly, these CO increase do not cause problems in chromosome segregation. The relative role of these different pathways in male vs. female plant meiosis requires further analysis.
SYNAPSIS AND ROLE OF THE SC IN THE REGULATION OF RECOMBINATION

The central element ZYP1 of the SC starts polymerizing during zygotene to form a protein complex resembling a zipper structure connecting the two meiotic homologous chromosomes from telomere to telomere at pachytene. The two AEs are called lateral elements once they form this tripartite structure (Higgins et al., 2005; West et al., 2019; Darrier et al., 2020; Kurzbauer et al., 2021). Although two redundant ZYP1 proteins sharing 87% identity are present in Arabidopsis; their relative role is still unknown. The SC can regulate the number and spacing of CO. While barley zyp1 mutants show limited CO numbers (Barakate et al., 2014), the homolog rice zep1 mutants have the opposite effect (Wang et al., 2010). The SC components have diverged rapidly among eukaryotes but the general SC structure is conserved (West et al., 2019). These results might reflect divergent modes of regulation of the SC on CO between different species. ZYP1 was also recently reported as required for CO interference and the obligate CO (France et al., 2021). In Arabidopsis zyp1a/b null mutant, heterochiasmy is abolished (Capilla-Pérez et al., 2021). These recent data suggest that the SC coordinates the regulation of obligate CO, interference, and heterochiasmy. Arabidopsis asy1 mutants also abolish CO interference (Lambing et al., 2020a). ASY1 acts as an antagonist of telomere-led recombination in a gene dosage-sensitive manner (Lambing et al., 2020a). The ASY1 immunolocalization signal disappears concomitantly with the loading of the central element ZYP1 (Lee et al., 2015). This suggests that obligate CO, heterochiasmy, and interference mechanisms are not directly mediated by either ASY1 or ZYP1 but rather involve the regulation of the SC length. ASY1 can be phosphorylated by CDKA;1 counteracting the ASY1 disassembly activity of PCH2 and P31 (Yang et al., 2020), which suggests a dynamic control of SC length regulation. The phosphorylation of the ASY1 protein increases its binding affinity with the chromatin-anchoring ASY3/DSY2 protein (Yang et al., 2020). ATM is another meiotic protein kinase essential to limit DSB number; it regulates chromatin loop size and affects SC length and width (Kurzbauer et al., 2021). The relative role of ATM and CDKA;1 in the phosphorylation of SC components or other meiotic proteins is still unknown.

FORMATION OF THE LATE RECOMBINOSOME AND CROSSOVER PATHWAYS

The DNA repair of the damaged molecules involves the formation of double Holliday junctions (dHJs) that are resolved by resolvases leading to CO or NCO. Two pathways of CO formation have been described in plants.

The interfering pathway (CO type I) positions CO with non-random spacing between each CO event. In general, the CO type I accounts for the majority (80–95%) of all COs in plant species (Mercier et al., 2015). It involves the ZMM pathway, namely, MER3 (Chen et al., 2005; Mercier et al., 2005), ZIP4 (Chelysheva et al., 2007), the DNA mismatch repair mutS/mutL homologs MSH/MLH homologs MSH4, MSH5, MSH7, MLH1, and MLH3 (Higgins et al., 2004, 2008b; Chelysheva et al., 2010; Colas et al., 2016) and HEI10 (Chelysheva et al., 2012; Ziolkowski et al., 2017). In rice, a new member of the ZMM pathway was discovered through its interaction with HEI10, MSH4, and ZIP4 and named HEI1P1 (Li et al., 2018). SHOC1 and PTD, which were described in Arabidopsis as involved in the type I CO pathway (Macaisne et al., 2008, 2011), are conserved and play similar roles in rice (Ren et al., 2019). Interestingly, it was found that the obligate COs (that ensure the correct chromosome segregation during anaphase I) are maintained by MSH4 and MSH5 in durum wheat (Desjardins et al., 2020). In the allotetraploid Brassica napus, reducing the MSH4 copy number prevents non-homologous CO (Gonzalo et al., 2019). The analysis of hypomorph mutants of two essential B-class DNA polymerases (the delta POLD1 supposed to be involved in DNA lagging strand synthesis and the Epsilon POL2A thought to be involved in DNA leading strand synthesis) has shown that they are also involved in the formation of type I COs (Huang et al., 2015; Wang C. et al., 2018). It was first hypothesized that elongation activity of these polymerases is required for the process of meiotic recombination but the multifunctionality of these POL proteins, containing exonuclease proofreading domains (Ronceret et al., 2005), could complicate the interpretation of the activity required during meiotic recombination. In addition, DNA polymerases are involved in the deposition of the H3K4me3 transcriptionally active epigenetic marks linked to DSB formation and participate in DNA repair (Yin et al., 2009; Iglesias et al., 2015) suggesting other possibilities for the role of DNA POL in the formation of type I COs. However, since most of the pol mutants have embryo-lethality phenotypes (Ronceret et al., 2005; Wang et al., 2019) this is a difficult topic to study.

The second minor CO pathway (type II or non-interfering) can form closely spaced COs. In plants, it involves the dHJ resolvases (structure-specific endonuclease) MUS81 (Higgins et al., 2008a), GEN1 (Wang et al., 2017), and SEND1, which is also essential for telomere stability (Geuting et al., 2009; Olivier et al., 2015).

Though it was found to be involved in the mechanism of interference in yeast, the topoisomerase TOPII was not found to have an effect on CO interference in Arabidopsis but to facilitate interlocks resolution (remove interlacement of different bivalents at the time of synapsis) (Martínez-García et al., 2018) that are normally all resolved by pachytene (Wang et al., 2009). Interestingly, TOPII is associated with the chromosome axis and accumulates in entangled regions during the zygotene stage (Martínez-García et al., 2018). In Arabidopsis, a second non-interfering pathway of CO (called type III non-interfering CO in Figure 1), parallel to the MUS81 (type II) CO pathway, depends on FANCD2 and contributes to the formation of some non-interfering COs (Kurzbauer et al., 2018). The hotspots and coldspots of recombination are supposably due to the combined effects of chromatin features and the different anticrossover and crossover pathways. The relative mechanisms by which the CO rate is modulated at these sites still require further exploration.
EFFECTS OF GENOMIC REGIONS, CENTROMERE PAIRING, TELOMERE BOUQUET, AND REPEATED DNA RECOMBINATION

Various genomic regions are known to have variable recombination rates in various plant species. New whole genome sequencing techniques have now given us a clear vision of the recombination maps at a fine scale in several plant species (Hellsten et al., 2013; Luo et al., 2019; Rowan et al., 2019). It is known that the genomic recombination rate is influenced by epigenetic marks, the genetic background (Sidhu et al., 2015; Ziolkowski et al., 2017; Dreissig et al., 2019; Lawrence et al., 2019), and the level of heterozygosity (Ziolkowski et al., 2015). It also greatly depends on chromatin structural variation and the presence of fewer COs in the heterochromatic regions (NORs) acquired distinct chromatin characteristics that its chromatin localization is not homogenous on the genome.

Chromosome conformation changes are highly dynamic during meiotic prophase, involving active mechanisms to gather telomeres at the nuclear envelope (called telomere bouquet), centromere coupling, and chromosome pairing and synapsis (Sepsi and Schwarzacher, 2020; Lenyk­ó-Thegeze et al., 2021).

In maize and rice, the SUN proteins are involved in telomere bouquet formation (Murphy et al., 2014), synapsis, and CO formation (Zhang et al., 2020b). SUN1 and SUN2 Arabidopsis mutants delay the progression of meiosis, affect synapsis, and reduce the chiasma number (Varas et al., 2015). The role of AtSUN1 and ATSUN2 on the bouquet has not yet been analyzed since the Arabidopsis telomere bouquet was only recently defined using techniques that maintain the 3D structure of the nucleus intact (Hurel et al., 2018). In rice, the bouquet is dependent on the PAIR3/ASY3 AE element (Wang et al., 2011) and on the F-Box ZYGO protein that also affects the initiation of homologous pairing (Zhang F. et al., 2017). In maize, SPO11-1 foci are transiently observed on the nuclear periphery and seem excluded from the nucleolus (Ku et al., 2020) suggesting a potential gathering of the DSBs machinery at the nuclear envelope and that its chromatin localization is not homogenous on the genome. Interestingly in Arabidopsis, the repetitive nucleolus organizing regions (NORs) acquired distinct chromatin characteristics during meiosis with strong ASY1 signals and the absence of the synaptic ZYP1 protein. The nucleolus employs an NHEJ mechanism requiring LIG4 (instead of the homologous recombination pathway dependent on RAD51) to repair the few DSBs produced in NORs and avoid unequal recombination in the repetitive recombinant DNA clusters (Sims et al., 2019). The presence of fewer COs in the heterochromatic repetitive knob region was observed cytogenetically in maize male meiocytes (Stack et al., 2017). However, by contrast to the nucleolus, knob meiotic recombination still uses the homologous recombination pathway as observed by the presence of MLH1 foci. This indicates that the diminution of meiotic recombination in distinctive heterochromatin regions probably uses several distinct mechanisms.

EFFECTS OF AGE AND SEX ON MEIOTIC RECOMBINATION

A moderate effect of the age of the shoot apical meristem on the number of CO was reported in Arabidopsis (Francis et al., 2007; Toyota et al., 2011; Li et al., 2017; Saini et al., 2020). Whether or not these age effects also occur in other plants is still unknown. Sex difference in CO frequency is called heterochiasmy. In Arabidopsis, the CO number is higher in male meiocytes than in female meiocytes (Drouaud et al., 2007; Girault et al., 2011; Saini et al., 2020). By sequencing Arabidopsis male and female backcrossed plants, 4.58 crossovers were found in male backcrossed compared to 3.08 in female backcrosses (Capilla-Pérez et al., 2021), noting that only half of the true CO number can be identified since gametes inherit a single chromatid and CO involves only two of the four chromatids of a bivalent. In Arabidopsis and maize, the difference is attributed to the length of the SC and the distribution of CO is also different in male and female meiocytes (Girault et al., 2011; Kianian et al., 2018; Lloyd and Jenczewski, 2019; Luo et al., 2019). It was recently demonstrated that heterochiasmy is enforced in Arabidopsis by the SC central element ZYP1 (Capilla-Pérez et al., 2021). This suggests that heterochiasmy and SC length differences in male and female meiocytes are regulated by a common molecular pathway.

EFFECT OF ENVIRONMENTAL CONDITIONS ON MEIOSIS

In plants, meiosis occurs in flowers whose development was initiated via various past and present environmental clues (Antoniou-Kourounioti et al., 2021). The temperature variation is also known to modify the meiotic and somatic recombination rate using fluorescent-tagged lines (Francis et al., 2007; Li et al., 2017; Saini et al., 2017) correlated with cytological MLH1 foci counting (Lloyd et al., 2018). In Arabidopsis, both high (28°C) and low (8°C) temperature conditions increase meiotic recombination compared to medium temperature (18°C). Interestingly, external temperatures are negatively correlated with the SC length that is itself correlated with the CO number. A correlation between SC length and CO number per chromosome was found (von Wettstein et al., 1984). Consequently, the longer SC length observed at low temperatures can explain the higher number of CO but not the increase of CO number observed at the higher temperatures. This increase in CO due to high temperature is not due to an increase in DSB formation as observed with γH2A.X and RAD51 foci. These extra COs are class I (ZMM) pathway as evidenced by increased MLH1 and HEI10 focus numbers in male meiocytes (Blary et al., 2018). Using mutants of different CO pathways in Arabidopsis, it was confirmed that the extra COs are derived from the interfering type I CO pathways and not to the type II (Modliszewski et al., 2018; De Storme and Geelen, 2020). The response of CO number to external temperature is not a universal stress response since saline stress does not affect it. Though the effect of temperature on COs was also observed and analyzed...
in barley, it seems that the mechanism of action is distinct. In contrast to Arabidopsis, the SC length in barley male meiocytes increases with higher temperature. The number of CO type I is not altered but their position shifted toward more internal non-telomeric regions as observed with cytologically mapped MLH3 foci (Phillips et al., 2015). The same effect of the position shifting from distal to more internal CO is also observed for some chromosome arms in wheat (Coulton et al., 2020). Though it seems an attractive and easy parameter that could modulate CO in crops, it appears that extremal temperatures have also other deleterious effects on the progression of meiosis such as defects of secondary division and wall formation reducing euploidy and seed set (De Storme et al., 2012; Draeger and Moore, 2017; De Storme and Geelen, 2020).

The presence of the histone H2A.Z was determined as the marker of the thermosensory response in Arabidopsis, with H2A.Z deposition decreasing with increasing temperatures (Kumar and Wigge, 2010). In addition, the CO sites overlap with the presence of H2A.Z nucleosome at gene promoters (Choi et al., 2013). Arabidopsis mutants of the H2A.Z placement show lower CO frequency. The correlation between H2A.Z and CO frequencies could explain the part of the effect of lower temperatures increasing CO frequency but not the effects of higher temperatures. Indeed, the higher CO frequency of Arabidopsis plants grown at 12°C compared to plants grown at 21°C disappears in mutants defective for H2A.Z deposition (Kumar and Wigge, 2010). The relation between the deposition of H2A.Z and the phosphorylation of γH2AX associated with the formation of DSB is currently unknown.

Another key factor of this regulation of the meiotic recombination by temperature is the cyclin-dependent kinase CDKG1. Arabidopsis cdkg1 mutants show temperature-sensitive meiotic defect at 23°C but not at 12°C with abnormally formed SC, lower CO frequency, and reduce the bivalent number (Zheng et al., 2014; Nibau et al., 2020b). There are temperatedependent isoforms of CDKG1 (Nibau et al., 2020a). These isoforms can interact with the spliceosome and can regulate the splicing of other spliceosome components and the Callose synthase5 forming the pollen wall (Huang et al., 2013; Cavallari et al., 2018). It is still not known that whether or not the CDKG1-dependent temperature-sensitive regulation affects the production of different splicing variants of meiotic genes or affects H2A.Z deposition.

Another meiotic cyclin CDKA;1 has an important role in the regulation of the recombination landscape (Wijnker et al., 2019). CDKA;1 is also involved earlier in the germline fate decision via the inactivation of RBR1 (Chen et al., 2011; Zhao et al., 2017) pointing out the coordinating role of a peculiar meiotic CDK as a key factor for the meiotic fate and the regulation of meiotic recombination. What are the relative roles of the meiotic CDKs, the associated meiotic cyclins (such as SDS and TAM), and CDK inhibitors (KRPs) in the coordinated control of meiotic recombination in different temperature conditions remain to be analyzed.

Other factors such as climate, agrochemicals, heavy metals, combustible gasses, pharmaceuticals, and pathogens are known to modify meiosis in plants (Modliszewski and Copenhaver, 2017; Fuchs et al., 2018; Dreissig et al., 2019) but their mechanistic modes of action still need to be explored.

**CONCLUSION**

The understanding of several fundamental meiotic processes has strongly advanced during the past few years thanks to many studies in model and non-model plant species. Figure 1 summarizes the different proteins and functional modules known to be involved in the formation of bivalents.

The new techniques of isolated cell high throughput sequencing will revolutionize the questions we can ask about the dynamic meiotic chromosome conformation through prophase I.

Though controversial for many years, the divergence of several basic molecular meiotic mechanisms is now clear between different plant species. Achiasmotic inverted meiosis has also been reported in few non-model plants (Cabral et al., 2014; Heckmann et al., 2014; Hofstatter et al., 2021) underlining the extreme diversity of the plant meiotic programs. It contradicts the predictive expected assumptions based on phylogenetic relationships between plant species. In this perspective, one of the future challenges will be to identify the actual biochemical functions of the meiotic proteins not only based on the putative function supposed by the homology of conserved protein families. These interspecific differences are probably the real essence of the meiotic process that has evolved to bring genomic diversity. Even in the same species, there are known sex and cell to cell variability (Wang et al., 2019). It underlines the importance of studying directly meiosis in crops to manipulate it properly. Increasing our meiotic manipulation tools for improving plant breeding strategies is essential to cope with the challenge of feeding 10 billion humans by 2050.

**AUTHOR CONTRIBUTIONS**

YGP and AR prepared and wrote the manuscript. JKGK and PR contributed to the survey of bibliographic references. All authors read and approved the final manuscript.

**FUNDING**

Relevant research in the Ronceret lab was supported by a grant from the Mexican SEP-CONACYT Ciencia Básica CB-2017-2018-A1-S-8496 to AR.

**ACKNOWLEDGMENTS**

We would like to thank Mathilde Grelon (INRAE, Versailles, France) and Wojtek Pawłowski (Cornell University, United States) for the critical reading of the manuscript. We would also like to thank the constructive suggestions of the three reviewers. We would like to apologize for the colleagues that have not been cited due to limitations of manuscript length.
REFERENCES

Aklülo, B. B., Peurois, F., Saintomé, C., Culligan, K. M., Kobbe, D., Leasure, C., et al. (2020). Functional diversification of replication protein a paralogs and telomere length maintenance in Arabidopsis. Genetics 215, 899–1002. doi: 10.1534/genetics.120.303222

Antoniou-Kouroumiotis, R. L., Zhao, Y., Dean, C., and Howard, M. (2021). Feeling every bit of winter – distributed temperature sensitivity in vernalization. Front. Plant Sci. 12:628726. doi: 10.3389/fpls.2021.628726

Armstrong, S. J., Caryl, A. P., Jones, G. H., and Franklin, F. C. (2004). Meiotic defects in the Arabidopsis BLAP75/Rmi homologue plays crucial roles in meiotic double-strand break repair. PLoS Genet. 4:e1000309. doi: 10.1371/journal.pgen.1000309

Bleuyard, J. Y., Gallego, M. E., and White, C. I. (2014). Manipulation of crossover frequency and temperature on recombination in wheat. Triticum aestivum L.). Plant J. 104, 30–43. doi: 10.1111/tpj.14903

Capilla-Pérez, L., Durand, S., Halle, F., and Schubert, V. (2013). Nucleosomes and DNA methylation shape meiotic DSB frequency distribution for plant breeding. Theor. Appl. Genet. 126, 1297–1306. doi: 10.1007/s00122-013-2182-2

Da Ines, O., Degroote, F., Goubely, C., Amiard, S., Gallego, M. E., and White, C. I. (2014). An easy protocol for studying chromatin and recombination protein dynamics during Arabidopsis thaliana meiosis: immunodetection of cohensins and MLH1. Cytogenet. Genome Res. 129, 143–153. doi: 10.1159/000373409

Che, L., Wang, K., Tang, D., Liu, Q., Chen, X., Li, Y., et al. (2014). OsHUS1 Facilitates Accurate Meiotic Recombination in Rice. PLoS Genetics. 10:e1004405. doi: 10.1371/journal.pgen.1004405

Chelysheva, L., Diallo, S., Vezon, D., Gendrot, G., Vrielynck, N., Belcram, K., et al. (2005). AIREC8 and ASIC3 are essential to the monopolar orientation of the kinetochores during meiosis. J. Cell Sci. 118, 4621–4632. doi: 10.1242/jcs.02583

Che, L., Grandont, L., Vrielynck, N., le Guin, S., Mercier, R., and Grelon, M. (2010). An easy protocol for studying chromatin and recombination protein dynamics during Arabidopsis thaliana meiosis: immunodetection of cohensins, histones and MLH1. Cytogenet. Genome Res. 129, 143–153. doi: 10.1159/000373409

Chelysheva, L., Vezon, D., Belcram, K., Gendrot, G., and Grelon, M. (2008). The Arabidopsis BLAP75/Rmi homologue plays crucial roles in meiotic double-strand break repair. PLoS Genet. 4:e1000309. doi: 10.1371/journal.pgen.1000309

Chelysheva, L., Vezon, D., Chambon, A., Gendrot, G., Pereira, L., Lemhendi, A., et al. (2012). The Arabidopsis HEI10 is a new ZMM protein related to Zip3. PLoS Genet. 8:e1002799. doi: 10.1371/journal.pgen.1002799

Chelysheva, L. A., Gendrot, G., Vezon, D., Diouf, M. P. (1999). Random chromosome segregation without meiotic arrest in both Arabidopsis thaliana and Arabidopsis lyrata. Cytogenet. Genome Res. 89, 178, 233ñ246. doi: 10.1104/pp.17.01725

Choi, K., Zhao, X., Kelly, K. A., Venn, O., Higgins, J. D., Yelina, E. N., et al. (2013). Arabidopsis meiotic crossover hot spots overlap with H2A.Z nucleosomes at gene promoters. Nat. Genet. 45, 1327–1335.

Choi, K., Zhao, X., Tock, A. J., Lambing, C., Underwood, C. J., Hardcastle, T. J., et al. (2018). Nucleosomes and DNA methylation shape meiotic DSB frequency in Arabidopsis thaliana transposons and gene regulatory regions. Genome Res. 28, 532–546. doi: 10.1101/gr.225599.117

Cho, T., Zhang, W., Timofejeva, L., Gerardin, Y., and Ma, H. (2005). The Arabidopsis ROCK-N-ROLLERS gene encodes a homolog of the yeast ATP-dependent DNA helicase MER3 and is required for normal meiotic crossover formation. Plant J. 43, 321–334. doi: 10.1111/j.1365-315x.2005.0 2461.x

Choi, K., Zhao, X., Kelly, K. A., Venn, O., Higgins, J. D., Yelina, E. N., et al. (2013). Arabidopsis meiotic crossover hot spots overlap with H2A.Z nucleosomes at gene promoters. Nat. Genet. 45, 1327–1335.

Cijo, R. T., and Grbic, M. (2012). Disrupted Meiotic cDNA 1 in barley. J. Exp. Bot. 70, 2683–2698. doi: 10.1093/jxb/erz090

Coles, I., Barakate, A., Macaulay, M., Higgins, J. D., Phillips, D., Barakate, A., Posch, M., et al. (2016). A spontaneous mutation in MutL-Homolog 3 (HvMLH3) affects synopsis and crossover resolution in the barley desynaptic mutant der5. New Phytol. 212, 693–707. doi: 10.1111/nph.14061

Coulton, A., Burridge, A. J., and Edwards, K. I. (2020). Examining the effects of temperature on recombination in wheat. Front. Plant Sci. 11:230. doi: 10.3389/fpls.2020.00230

Couteau, F., Belzile, F., Horlow, C., Grandjean, O., Vezon, D., and Doutriaux, M. P. (1999). Random chromosome segregation without meiotic arrest in both male and female meiocytes of a dm1 mutant of Arabidopsis. Plant Cell 11, 1623–1634. doi: 10.1105/tpc.11.9.1623

Crismani, W., Girard, C., Froger, N., Pradillo, M., Santos, J. L., Chelysheva, L., et al. (2012). FANCM limits meiotic crossovers. Science 336, 1588–1590. doi: 10.1126/science.1220381

Cromer, L., Jolivet, S., Singh, D. K., Berthier, F., De Winne, N., De Jaeger, G., et al. (2019). Patronus is the elusive plant securin, preventing chromosome separation by antagonizing separase. Proc. Natl. Acad. Sci. U.S.A. 116, 16018–16027. doi: 10.1073/pnas.1902371116

Da Ines, O., Degroote, F., Goubely, C., Amiard, S., Gallego, M. E., and White, C. I. (2013). Meiotic recombination in Arabidopsis is catalysed by DMCl, with RAD51 playing a supporting role. PLoS Genet. 9:e1003787. doi: 10.1371/journal.pgen.1003787
Da Ines, O., Michard, R., Nayos, I., Bastianelli, G., Nicolas, A., Guiderdoni, E., et al. (2020). Bread wheat TaSP011-1 exhibits evolutionarily conserved function in meiotic recombination across distant plant species. Plant J. 103, 2052–2068. doi: 10.1111/tpj.14882

Dangel, N. J., Knoll, A., and Puchta, H. (2014). MHFI plays Fanconi anemia complementation group M protein (FANC-M)-dependent and FANC-M-independent roles in DNA repair and homologous recombination in plants. Plant J. 78, 822–833. doi: 10.1111/tpj.12507

Darrier, B., Arrieta, M., Mittmann, S. U., Sourdi, P., Ramsay, L., Waugh, R., et al. (2020). “Following the formation of synaptonemal complex formation in wheat and barley by high-resolution microscopy,” in Plant Meiosis: Methods and Protocols, eds M. Pradillo and S. Heckmann (New York, NY: Springer New York), 207–215. doi: 10.1007/978-1-4939-9818-0_15

De, K., Sterle, L., Krueger, L., Yang, X., and Makaroff, C. A. (2018b). Unleashing meiotic crossovers in hybrid plants. Proc. Natl. Acad. Sci. U.S.A. 115, 2431–2436.

France, M. G., Enderle, J., Röhrig, S., Puchta, H., Franklin, F. C. H., and Higgins, J. D. (2021). ZYP1 is required for obligate cross-over formation and cross-over interference in Arabidopsis. Proc. Natl. Acad. Sci. U.S.A. 118:e202171118. doi: 10.1073/pnas.201671118

Fuchs, L. K., Jenkins, G., and Phillips, D. W. (2018). Anthropogenic impacts on meiosis in plants. Front. Plant Sci. 9:1429. doi: 10.3389/fpls.2018.01429

Geuting, V., Kobbe, D., Hartung, F., Dürr, J., Focke, M., and Puchta, H. (2009). Two distinct MUS81-EME1 complexes from Arabidopsis process holliday junctions. Plant Physiol. 150, 1062–1071. doi: 10.1104/pp.109.136846

Girard, C., Chelysheva, L., Choinard, S., et al. (2015). AAA-ATPase FIDETIN-LIKE 1 and helicase FANC M antagonize meiotic crossovers by distinct mechanisms. PLoS Genet. 11:e1005369. doi: 10.1371/journal.pgen.1005369

Guiderdoni, E., and Schlögelhofer, P. (2011). Have a break: determinants of meiotic recombination in Arabidopsis. Front. Plant Sci. 10, 1539–1541. doi: 10.1016/j.molp.2017.09.006

Hartung, F., Suer, S., Knoll, A., Wurz-Wildersinn, R., and Puchta, H. (2008). Two Sp1 factors, AtBUB1 and AtBUB2, are essential for the prophase removal of cohesin during meiosis. Plant Physiol. 148, 4126–4137. doi: 10.1093/pcp/pec049

Hartung, F., Suer, S., Knoll, A., Wurz-Wildersinn, R., and Puchta, H. (2008). Two Sp1 factors, AtBUB1 and AtBUB2, are essential for the prophase removal of cohesin during meiosis. Plant Physiol. 148, 4126–4137. doi: 10.1093/pcp/pec049

Hartung, F., Suer, S., Knoll, A., Wurz-Wildersinn, R., and Puchta, H. (2008). Two Sp1 factors, AtBUB1 and AtBUB2, are essential for the prophase removal of cohesin during meiosis. Plant Physiol. 148, 4126–4137. doi: 10.1093/pcp/pec049

Hartung, F., Suer, S., Knoll, A., Wurz-Wildersinn, R., and Puchta, H. (2008). Two Sp1 factors, AtBUB1 and AtBUB2, are essential for the prophase removal of cohesin during meiosis. Plant Physiol. 148, 4126–4137. doi: 10.1093/pcp/pec049

Hartung, F., Suer, S., Knoll, A., Wurz-Wildersinn, R., and Puchta, H. (2008). Two Sp1 factors, AtBUB1 and AtBUB2, are essential for the prophase removal of cohesin during meiosis. Plant Physiol. 148, 4126–4137. doi: 10.1093/pcp/pec049
remodeling and maturation of crossovers. *PloS Genet.* 11:e1005372. doi: 10.1371/journal.pgen.1005372

Lambing, C., Tock, A. J., Topp, S. D., Choi, K., Kuo, P. C., Zhao, X., et al. (2020b). Interacting genomic landscapes of RE8-cohesin, chromatin, and meiotic recombination in *Arabidopsis*. *Plant Cell* 32, 1218–1239. doi: 10.1105/tpc.19-00866

Lawrence, E. J., Gao, H., Tock, A. J., Lambing, C., Blackwell, A. R., Feng, X., et al. (2019). Natural variation in TBP-ASSOCIATED FACTOR 4b controls meiotic crossover and germline transcription in *Arabidopsis*. *Curr. Biol.* 29, 2676–2686. doi: 10.1016/j.cub.2019.06.084

Lee, D. H., Kao, Y.-H., Ku, J.-C., Lin, C.-Y., Meeley, R., Jan, Y.-S., et al. (2015). The axial element protein DESYNAPTIC2 mediates meiotic double-strand break formation and synaptonemal complex assembly in maize. *Plant Cell* 27, 2516–2529. doi: 10.1105/tpc.15-00454

Lenykó-Thegze, A., Fábian, A., Mihók, E., Makai, D., and Cseh, A. (2021). *Perciconcentric chromatin reorganisation follows the initiation of recombination and coincides with early events of synopsis in cereals*. *Plant J.* doi: 10.1111/tpj.15391 [Epub ahead of print].

Li, F., De Storme, N., and Geelen, D. (2017). Dynamics of male meiotic recombination frequency during plant development using fluorescent tagged lines in *Arabidopsis thaliana*. *Sci. Rep.* 7:42353.

Li, W., Chen, C., Markmann-Mulisch, U., Timofejeva, L., Schmelzer, E., Ma, H., et al. (2020). Single gametophyte sequencing reveals homoeologous exchanges, segmental allopolyploidy, and polyploid genome evolution. *Front. Plant Sci.* 11:1014. doi: 10.3389/fpls.2020.01014

Macasaine, N., Vignard, J., and Mercier, R. (2011). SHOCl and PTD form an XPF-ERCC1-like complex that is required for formation of class I crossovers. *J. Cell Sci.* 124, 2687–2691. doi: 10.1242/jcs.088229

Martínez-Garcia, M., Schubert, V., Osman, K., Darbyshire, A., Sanchez-Moran, E., and Franklin, F. C. H. (2018). TOP2 and chromosome movement help remove interlocks between entangled chromosomes during meiosis. *J. Cell Biol.* 217, 4070–4079. doi: 10.1083/jcb.201803019

Mason, A. S., and Wendel, J. F. (2020). Homoeologous exchanges, segmental allopolyploidy, and polyploid genome evolution. *Front. Genet.* 11:1014. doi: 10.3389/fgene.2020.01014

Mielmer-Besucho, C., Shilo, S., and Levy, A. A. (2016). Meiotic recombination and genome evolution in plants. *Curr. Opin. Plant Biol.* 30, 82–87. doi: 10.1016/j.pbi.2016.02.003

Mercier, R., Jolivet, S., Vezon, D., Huppe, E., Chelysheva, L., Giovanni, M., et al. (2005). Two meiotic crossover classes cohabit in *Arabidopsis*: one is dependent on MER3, whereas the other one is not. *Curr. Biol.* 15, 692–701.

Mercier, R., Mezzard, C., Jenczewski, E., Macasaine, N., and Grelen, M. (2015). The molecular biology of meiosis in plants. *Annu. Rev. Plant Biol.* 66, 297–327. doi: 10.1146/annurev-arplant-050213-035923

Miao, C. B., Tang, D., Zhang, H. G., Wang, M., Li, Y. F., Tang, S. Z., et al. (2013). CENTRAL REGION COMPONENT1, a novel synaptonemal complex component, is essential for meiotic recombination initiation in rice. *Plant Cell* 25, 2998–3009. doi: 10.1105/tpc.113.113175

Mietuell, D., Aubert, G., Bres, C., Klein, A., Droc, G., Vieille, E., et al. (2018). Unleashing meiotic crossovers in crops. *Nat. Plants* 4, 1010–1016. doi: 10.1038/s41477-018-0311-x

Miyakazi, M., Sato, Y., Asano, T., Nagamura, Y., and Nonomura, K. I. (2015). Rice MEL2, the RNA recognition motif (RRM) protein, binds in vitro to meiosis-expressed genes containing U-rich RNA consensus sequences in the 3′-UTR. *Plant Mol. Biol.* 89, 293–307. doi: 10.1007/s11103-015-0369-z

Modliszewski, J. L., and Copenhagen, G. P. (2017). Meiotic recombination gets stressed out: CO frequency is plastic under pressure. *Curr. Opin. Plant Biol.* 36, 95–102. doi: 10.1016/j.pbi.2016.11.019

Modliszewski, J. L., Wang, H., Albright, A. R., Lewis, S. M., Bennett, A. R., Huang, J., et al. (2018). Elevated temperature increases meiotic crossover frequency via the interfering (Type 1) pathway in *Arabidopsis thaliana*. *PLoS Genet.* 14:e1007384. doi: 10.1371/journal.pgen.1007384

Murphy, S. P., Gumber, H. K., Mao, Y., and Bass, H. W. (2014). A dynamic meiotic SUN belt includes the zygotene-stage telomere bouquet and is disrupted in chromosome segregation mutants of maize (*Zea mays* L.). *Front. Plant Sci.* 5:314. doi: 10.3389/fpls.2014.00314

Nannas, N. J., Higgins, D. M., and Dawe, R. K. (2016). Anaphase asymmetry and dynamic repositioning of the division plane during meiotic meiosis. *J. Cell Sci.* 129, 4014–4024.

Nebel, R., and Walbot, V. (2019). Defining the developmental program leading to meiosis in maize. *Science* 364, 52–56. doi: 10.1126/science.aav6428

Nibau, C., Dadarou, D., Kargios, N., Mallioura, A., Fernandez-Fuentes, N., Cavallari, N., et al. (2020a). A functional kinase is necessary for cyclin-dependent kinase G3 (CDKGI) to maintain fidelity at high ambient temperature in *Arabidopsis*. *Front. Plant Sci.* 11:586870. doi: 10.3389/fpls.2020.586870

Nibau, C., Lloyd, A., Dadarou, D., Betekhtin, A., Tsilimigka, F., Phillips, D. W., et al. (2020b). CDKGI is required for meiotic and somatic recombination intermediate processing in *Arabidopsis*. *Plant Cell* 32, 1308–1322. doi: 10.1105/tpc.19-00942

Nonomura, K. I., Eiguchi, M., Nakano, M., Takashima, K., Komeda, N., Fukuchi, S., et al. (2020a). A novel RNA recognition-motif protein is required for premeiotic G1/S-phase transition in rice (*Oryza sativa* L.). *PloS Genet.* 7:e1001265. doi: 10.1371/journal.pgen.1001265

Nonomura, K. I., Morohoshi, A., Nakano, M., Eiguchi, M., Miyao, A., Hirochioka, H., et al. (2007). A germ cell specific gene of the ARGONAUTE family is essential for the progression of premeiotic mitosis and meiosis during sporogenesis in rice. *Plant Cell* 19, 2583–2594. doi: 10.1105/tpc.105319

Nonomura, K. I., Nakano, M., Eiguchi, M., Suzuki, T., and Kurata, N. (2004a). *PAIR2* is essential for homologous chromosome synopsis in rice meiosis I. *Cell Sci.* 119, 217–225. doi: 10.1242/jcs.02736

Nonomura, K. I., Nakano, M., Fukuda, T., Eiguchi, M., Miyao, A., Hirochioka, H., et al. (2004b). The novel gene HOMOLOGOUS PAIRING ABERRATION
IN RICE MEIOSIS, the cell cycle requires a coherent mechanism for meiosis to proceed normally. Plant Cell 16, 1008–1020. doi: 10.1105/tpc1020701

Oliver, C., Pradillo, M., Jover-Gil, S., Cuañado, N., Ponce, M. R., and Santos, J. L. (2017). Loss of function of Arabidopsis microRNA-machinery genes impairs fertility, and has effects on homologous recombination and meiotic chromatin dynamics. Sci. Rep. 7:9280.

Oliver, C., Santos, J. L., and Pradillo, M. (2014). On the role of some ARGONAUTE proteins in meiosis and DNA repair in Arabidopsis thaliana. Front. Plant Sci. 5:177. doi: 10.3389/fpls.2014.00177

Oliver, C., Santos, J. L., and Pradillo, M. (2016). Accurate chromosome segregation at first meiotic division requires AGO4, a protein involved in RNA-dependent DNA methylation in Arabidopsis thaliana. Genetics 204, 543–553. doi: 10.1534/ genetics.115.189217

Oliver, M., Da Ines, O., Amiard, S., Serra, H., Goubely, C., White, C. I., et al. (2018). Massive crossover elevation via combination of HEI10 and OsPTD1 are essential for crossover formation during rice meiosis. Plant J. 98, 313–328.

Ronceret, A., Doutriaut, M.-P., Golubovskaya, I. N., and Pawlowski, W. P. (2009). PHS1 regulates meiotic recombination and homologous chromosome pairing by controlling the transport of RAD50 to the nucleus. Proc. Natl. Acad. Sci. U.S.A. 106, 20121–20126. doi: 10.1073/pnas.0906273106

Ronceret, A., Guillen, J. L., Lincker, F., Gadea-Vacas, J., Delorme, V., Bechtold, N., et al. (2005). Genetic analysis of two Arabidopsis DNA polymerase epsilon subunits during early embryogenesis. Plant J. 44, 223–236. doi: 10.1111/j.1365-313X.2005.02521.x

Ronceret, A., and Pawlowski, W. P. (2010). Chromosome dynamics in meiotic prophase I in plants. Cytogenet. Genome Res. 129, 173–183. doi: 10.1159/000313656

Rowan, B. A., Heavens, D., Feuerborn, T. R., Tock, A. J., Henderson, I. R., and Weigel, D. (2019). An ultra-high density Arabidopsis thaliana crossovers map that refines the influences of structural variation and epigenetic features. Genetics 213, 771–787. doi: 10.1534/g3.119.201046

Saini, R., Singh, A. K., Dhanapal, S., Saeed, T. H., Hyde, G. J., and Baskar, R. (2017). Brief temperature stress during reproductive stages alters meiotic recombination and somatic mutation rates in the progeny of Arabidopsis. BMC Plant Biol. 17:103. doi: 10.1186/s12870-017-1051-1

Saini, R., Singh, A. K., Hyde, G. J., and Baskar, R. (2020). Levels of heterochromatin during Arabidopsis development as reported by fluorescent tagged lines. G3 10, 2103–2110. doi: 10.1534/g3.120.101296

Šamanić, I., Simunić, J., Riha, K., and Puizina, J. (2013). Evidence for distinct functions of MRE11 in Arabidopsis meiosis. PLoS One 8:e78760. doi: 10.1371/journal.pone.0078760

Seeliger, K., Dukovic-Schulze, S., Wurz-Wildersinn, R., Pacher, M., and Puchta, H. (2012). BRCA2 is a mediator of RAD51- and DMC1-facilitated homologous recombination in Arabidopsis thaliana. New Phytol. 193, 364–375. doi: 10.1111/j.1469-8137.2013.03947.x

Séguela-Arnaud, M., Crismani, W., Larchevêque, C., Mazel, J., Froger, N., Choinard, S., et al. (2015). Multiple mechanisms limit meiotic crossovers: TOP5a and two BLM homologs antagonize crossovers in parallel to FANCM. Proc. Natl. Acad. Sci. U.S.A. 112, 4713–4718. doi: 10.1073/pnas.1421307112

Sepsi, A., and Schwarzacher, T. (2020). Chromosome–nuclear envelope tethering—a process that orchestrates homologous pairing during plant meiosis? J. Cell Sci. 133:jcs243667.

Serra, H., Lambing, C., Griffin, C. H., Topp, S. D., Nageswaran, D. C., Underwood, C. J., et al. (2018). Massive crossover elevation via combination of HEI10 and recQ4a recQ4b during Arabidopsis meiosis. Proc. Natl. Acad. Sci. U.S.A. 115, 2437–2442. doi: 10.1073/pnas.1713071115

Shi, W., Ji, J., Xue, Z., Zhang, F., Miao, Y., Yang, H., et al. (2021). PRD1, a homologous recombination initiation factor, is involved in spindle assembly in rice meiosis. New Phytol. 230, 585–600. doi: 10.1111/nph.17178

Shi, W., Tang, D., Shen, Y., Xue, Z., Zhang, F., Zhang, C., et al. (2019). OsHOP2 regulates the maturation of crossovers by promoting homologous pairing and synopsis in rice meiosis. New Phytol. 222, 805–819. doi: 10.1111/nph.15664

Shilo, S., Melamed-Benmdro, C., Dorone, Y., Barkai, N., and Levy, A. A. (2015). DNA crossover motifs associated with epigenetic modifications delineate open chromatin regions in Arabidopsis. Plant Cell 27, 2427–2436. doi: 10.1105/tpc.15.00391

Siaud, N., Dray, E., G., Gerard, E., Takvorian, N., and Doutriaut, M. P. (2004). BRCA2 is involved in meiosis in Arabidopsis thaliana as suggested by its interaction with Dmc1. EMBO J. 23, 1392–1401. doi: 10.1093/emboj/d7600146

Sidhu, K. G., Fang, C., Olson, M. A., Falque, M., Martin, O. C., and Pawlowski, W. F., and Cande, W. Z. (2004). Coordination of meiotic recombination, TOP3α, and two BLM homologs antagonize crossovers in parallel to FANCM. Proc. Natl. Acad. Sci. U.S.A. 110, 9825–9830. doi: 10.1073/pnas.0208808115

Singh, A. K., Andreuzza, S., Panoli, A. P., and Siddiqui, I. (2013). ATCT7 is required for establishment of sister chromatid cohesion and association of cohesin with chromatin during meiosis in Arabidopsis. BMC Plant Biol. 13:117. doi: 10.1186/1471-2229-13-117

Ren, Y., Chen, D., Li, W., Zhou, D., Luo, T., Yuan, G., et al. (2019). OsSHOC1 and OsPTD1 are essential for crossover formation during rice meiosis. Plant J. 98, 313–328.
Singh, G., Da Ines, O., Gallego, M. E., and White, C. I. (2017). Analysis of the impact of the absence of RAD51 strand exchange activity in Arabidopsis meiosis. *PLoS One* 12:e0183006. doi: 10.1371/journal.pone.0183006

Stacey, N. J., Kusumori, T., Azumi, Y., Roberts, G., Breuer, C., Wada, T., et al. (2006). Arabidopsis SPO1-1 functions with SPO1-1 in meiotic recombination. *Plant J.* 48, 206–216. doi: 10.1111/j.1365-313x.2006.02667.x

Stack, N., Shearer, L. A., Lohmiller, L., and Anderson, L. K. (2017). Meiotic crossing over in maize knob heterochromatin. *Genetics* 205, 1101–1112. doi: 10.1534/genetics.116.196089

Su, H., Cheng, Z., Huang, J., Lin, J., Copenhaver, G. P., Ma, H., et al. (2017). Arabidopsis RAD51, RAD51C and XRCC3 proteins form a complex and facilitate RAD51 localization on chromosomes for meiotic recombination. *PLoS Genet.* 13:e1006827. doi: 10.1371/journal.pgen.1006827

Sváčina, R., Sourdille, P., Kopecký, D., and Bartoň, J. (2020). Chromosome pairing impact of the absence of RAD51 strand exchange activity in recombination. *Trends Plant Sci.* 25, 455–465. doi: 10.1016/j.tplants.2019.12.017

Tang, Y., Yin, Z., Zeng, Y., Zhang, Q., Chen, L., He, Y., et al. (2017). MTOPVIB interacts with AtPRD1 and plays important roles in formation of meiotic DNA double-strand breaks in Arabidopsis. *Sci Rep.* 7:10007.

Termolino, P., Falque, M., Aiese Cigliano, R., Cremona, G., Paparo, R., Ederveen, A., et al. (2019). Recombination suppression in heterozygotes for a pericentric inversion induces the interchromosomal effect on crossovers in Arabidopsis. *Arabidopsis Plant J.* 100, 1163–1175. doi: 10.1111/tpj.14505

Tock, A. J., and Henderson, I. R. (2018). Hotspots for initiation of meiotic recombination. *Front. Genet.* 9:521. doi: 10.3389/fgen.2018.00521

Toyota, M., Matsuda, K., Kakutani, T., Terao Morita, M., and Tasaka, M. (2011). Arabidopsis SPO11-2 functions with SPO11-1 in meiotic recombination. *Plant Cell* 23, 5196–5206. doi: 10.1101/pc.227116.117

Uanschou, C., Siwiec, T., Pedrosa-Harand, A., Kerzendorfer, C., Sanchez-Moran, T., Yang, W., and Copenhaver, G. P. (2018). Meiotic recombination: mixing it up in plants. *Annu. Rev. Plant Biol.* 69, 577–609. doi: 10.1146/annurev-arplant-031518-124304

Varas, J., Graumann, K., Osman, K., Pradillo, M., Evans, D. E., Santos, J. L., et al. (2017). OsDMC1 is not required for homologous pairing in rice meiosis. *Plant Physiol.* 171, 230–241. doi: 10.1104/pp.17.00157

Wang, H., Xu, W., Sun, Y., Lian, Q., Wang, C., Yu, C., et al. (2020). The cohesin loader SCC2 contains a PHD finger that is required for meiosis in land plants. *PLoS Genet.* 16:e1008849. doi: 10.1371/journal.pgen.1008849

Wang, K., Wang, M., Tang, D., Shen, Y., Qin, B., Li, M., et al. (2011). PAIR3, an axis-associated protein, is essential for the recruitment of recombination elements onto meiotic chromosomes in rice. *Mol. Biol. Cell.* 22, 12–19. doi: 10.1091/mbc.e10-08-0667

Wang, M., Wang, K., Tang, D., Wei, C., Li, M., Shen, Y., et al. (2010). The central element protein ZEP1 of the synaptonemal complex regulates the number of crossovers during meiosis in rice. *Plant Cell* 22, 417–430. doi: 10.1105/tpc.109.070789

Wang, X., Guo, Z., Rui, S., Sun, F., Ruiz-Riera, A., Shang, Y., Liu, H., et al. (2019). Pincer: a novel meiosis gene. *Cell* 177, 326–338. doi: 10.1016/j.cell.2019.02.021

Waterworth, W. M., Altun, C., Armstrong, S. J., Roberts, N., Dean, P. J., Young, K., et al. (2007). NBS1 is involved in DNA repair and plays a synergistic role with ATM in mediating meiotic homologous recombination in plants. *Plant J.* 52, 41–52. doi: 10.1111/j.1365-313x.2007.02320.x

Wei, B., Zhang, J., Pang, C., Yu, H., Guo, D., Jiang, H., et al. (2015). The molecular mechanism of SPORECLEYES/NOZZLE in controlling Arabidopsis ovule development. *Cell Res.* 25, 121–134. doi: 10.1038/cr.2014.145

West, A. M. V., Rosenberg, S. C., Ut, S. N., Lehmer, M. K., Ye, Q., Hagemann, G., et al. (2019). A conserved filamentous assembly underlies the structure of the meiotic chromosome axis. *eLife* 8:e40372.

Wijnen, E., Harashima, H., Müller, K., Parra-Núñez, P., de Snoo, C. B., van de Belt, J., et al. (2019). The Cdkl1/Cdka2 homolog CDKA1 controls the recombination landscape in Arabidopsis. *Proc. Natl. Acad. Sci. U.S.A.* 116, 12534–12539. doi: 10.1073/pnas.1820531116

Wilkins, A. S., and Holliday, R. (2009). The evolution of meiosis from mitosis. *Genetics* 181, 3–12. doi: 10.1534/genetics.108.099762

Xue, Z., Liu, C., Shi, W., Miao, Y., Shen, Y., Tang, D., et al. (2019). OsMTOPVIB promotes meiotic DNA double-strand break formation in rice. *Mol. Plant* 9, 1535–1538. doi: 10.1016/j.molp.2016.07.005

Xue, Z., Liu, C., Shi, W., Miao, Y., Shen, Y., and Tang, D., et al. (2019). OsMTOPVIB is required for meiotic bipolar spindle assembly. *Proc. Natl. Acad. Sci. U.S.A.* 116, 19567–19572. doi: 10.1073/pnas.1821315116

Yang, C., Hamamura, Y., Sofroni, K., Bower, F., Stolze, S. C., Nakagami, H., et al. (2019). SWITCH1/DYAD is a WINGS APART-LIKE antagonist that maintains sister chromatid cohesion in meiosis. *Nat. Commun.* 10:1755.

Yang, C., Sofroni, K., Wijnen, E., Hamamura, Y., Carstens, L., Harashima, H., et al. (2020). The Arabidopsis Cdk1/Cdka2 homolog CDKA1 controls the recombination axis assembly during plant meiosis. *EMBO J.* 39:e101625.

Yang, W. C., Ye, D., Xu, J., and Sundaresan, V. (1999). The OsGEN1 gene. *Plant Physiol.* 123, 1316–1329. doi: 10.1104/pp.123.7.1316

Yin, H., Zhang, X., Li, J., Wang, Y., He, J., Yang, T., et al. (2009). Epigenetic regulation, somatic homologous recombination, and abscisic acid signaling are required for initiation of sporogenesis and encodes a novel nuclear protein. *Genes Dev.* 13, 2108–2117. doi: 10.1101/gad.13.16.2108

Yin, H., Zhang, X., Liu, J., Wang, Y., He, J., Yang, T., et al. (2009). Epigenetic regulation, somatic homologous recombination, and abscisic acid signaling are required for initiation of sporogenesis and encodes a novel nuclear protein. *Genes Dev.* 13, 2108–2117. doi: 10.1101/gad.13.16.2108

Yu, G., Ahoatapah, B. H., Komaki, S., Schnitter, A., Lillo, C., De Storme, N., et al. (2018). PROTEIN PHOSHTATE 2A B′ and β maintain centromeric sister chromatid cohesion during meiosis in Arabidopsis. *Plant Physiol.* 178, 317–328. doi: 10.1104/pp.18.00281
Yuan, W. Y., Li, X. W., Chang, Y. X., Wen, R. Y., Chen, G. X., Zhang, Q. F., et al. (2009). Mutation of the rice gene PAJR3 results in lack of bivalent formation in meiosis. *Plant J.* 59, 303–315. doi: 10.1111/j.1365-313X.2009.03870.x

Zamarello, L., De Storme, N., Vannier, K., Vandepoele, K., Armstrong, S. I., Franklin, E. C. H., et al. (2014). SHUGOSHINs and PATRONUS protect meiotic centromere cohesion in *Arabidopsis thaliana*. *Plant J.* 77, 782–794. doi: 10.1111/tjp.12432

Zelkowski, M., Olson, M. A., Wang, M., and Pawlowski, W. (2019). Diversity and determinants of meiotic recombination landscapes. *Trends Genet.* 35, 359–370. doi: 10.1016/j.tig.2019.02.002

Zhang, C., Song, Y., Cheng, Z. H., Wang, Y. X., Zhu, J., Ma, H., et al. (2012). The *Arabidopsis thaliana* DSB formation (AtDFO) gene is required for meiotic double-strand break formation. *Plant J.* 72, 271–281. doi: 10.1111/j.1365-313x.2012.05075.x

Zhang, C., Zhang, F., Cheng, X., Liu, K., Tang, J., Li, Y., et al. (2020a). OsATM safeguards accurate repair of meiotic double-strand breaks in rice. *Plant Physiol.* 183, 1047–1057. doi: 10.1104/pp.20.00053

Zhang, F., Ma, L., Zhang, C., Du, G., Shen, Y., Tang, D., et al. (2020b). The SUN domain proteins OsSUN1 and OsSUN2 play critical but partially redundant roles in meiosis. *Plant Physiol.* 183, 1517–1530. doi: 10.1104/pp.20.00140

Zhang, F., Shen, Y., Miao, C., Cao, Y., Shi, W., Du, G., et al. (2020c). OsRAD51D promotes homologous pairing and recombination by preventing nonhomologous interactions in rice meiosis. *New Physiol.* 227, 824–839. doi: 10.1111/nph.16595

Zhang, F., Tang, D., Shen, Y., Xue, Z., Shi, W., Ren, L., et al. (2017). The F-box protein ZYG01 mediates bouquet formation to promote homologous pairing, synopsis, and recombination in rice meiosis. *Plant Cell* 29, 2597–2609. doi: 10.1105/tpc.17.00287

Zhang, J., Feng, C., Su, H., Liu, Y., Liu, Y., and Han, F. (2020d). The cohesin complex subunit ZmSMC3 participates in meiotic centromere pairing in maize. *Plant Cell* 32, 1323–1336. doi: 10.1105/tpc.19.00834

Zhang, M., Ma, X., Wang, C., Li, Q., Meyers, B. C., Springer, N. M., et al. (2021). CHH DNA methylation increases at 24-PHAS loci depend on 24-nt phased small interfering RNAs in maize meiotic anthers. *New Physiol.* 229, 2984–2997. doi: 10.1111/nph.17060

Zhang, P., Zhang, Y., Sun, L., Sinumporn, S., Yang, Z., Sun, B., et al. (2017). The Rice AAA-ATPase OsFIGNL1 Is essential for male meiosis. *Front Plant Sci.* 8:1639. doi: 10.3389/fpls.2017.01639

Zhang, Y.-L., Zhang, H., Gao, Y.-J., Yan, L.-L., Yu, X.-Y., Yang, Y.-H., et al. (2019). Protein Phosphatase 2A B’α and B’β protect centromeric cohesion during meiosis I. *Plant Physiol.* 179, 1556–1568. doi: 10.1104/pp.18.01320

Zhao, M., Ku, J.-C., Liu, B., Yang, D., Yin, L., Ferrell, T. J., et al. (2021). The mop1 mutation affects the recombination landscape in maize. *Proc. Natl. Acad. Sci. U.S.A.* 118:e2009475118. doi: 10.1073/pnas.2009475118

Zhao, X. A., Bramsiepe, J., Van Durme, M., Komaki, S., Prusicki, M. A., Maruyama, D., et al. (2017). RETINOBLASTOMA RELATED1 mediates germine entry in *Arabidopsis*. *Science* 356:eaaf6532. doi: 10.1126/science.aaf6532

Zheng, T., Nibau, C., Phillips, D. W., Jenkins, G., Armstrong, S. J., and Doonan, J. H. (2014). CDKG1 protein kinase is essential for synopsis and male meiosis at high ambient temperature in *Arabidopsis thaliana*. *Proc. Natl. Acad Sci. U.S.A.* 111, 2182–2187. doi: 10.1073/pnas.1318460111

Zickler, D., and Kleckner, N. (2015). Recombination, pairing, and synopsis of homologs during meiosis. *Cold Spring Harb. Perspect. Biol.* 7:a016626. doi: 10.1101/cshperspect.a016626

Ziolkowski, P. A., Berchowitz, L. E., Lambing, C., Yelina, N. E., Zhao, X., Kelly, K. A., et al. (2015). Juxtaposition of heterozygous and homozygous regions causes reciprocal crossover remodelling via interference during *Arabidopsis* meiosis. *Elife* 4:e03708.

Ziolkowski, P. A., Underwood, C. J., Lambing, C., Martinez-Garcia, M., Lawrence, E. J., Ziolkowska, L., et al. (2017). Natural variation and dosage of the HEI10 meiotic E3 ligase control *Arabidopsis* crossover recombination. *Genes Dev.* 31, 306–317. doi: 10.1101/gad.295501.116

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2021 Gutiérrez Pinzón, González Kise, Rueda and Ronceret. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.