Meiosis in crops: from genes to genomes

Yazhong Wang\textsuperscript{1,†}, Willem M. J. van Rengs\textsuperscript{1,†}, Mohd Waznul Adly Mohd Zaidan\textsuperscript{1,†} and Charles J. Underwood\textsuperscript{1,*}

\textsuperscript{†}These authors contributed equally

\textsuperscript{1} Department of Chromosome Biology, Max Planck Institute for Plant Breeding Research, Carl-von-Linné-Weg 10, 50829, Cologne, Germany

*Corresponding author: Charles J. Underwood (cunderwood@mpipz.mpg.de)

Email address': Y. W. (yawan@g@mpipz.mpg.de), W. M. J. v. R. (wrengs@mpipz.mpg.de), M. W. A. M. Z. (wzaidan@mpipz.mpg.de)
Highlight (34):

Meiosis generates genetic diversity in natural populations and during breeding. We highlight meiosis research in major crop species, including an in-depth resource of cloned crop meiotic mutants and an overview of genome-wide recombination maps.
Abstract (179):

Meiosis is a key feature of sexual reproduction. During meiosis homologous chromosomes replicate, recombine and randomly segregate, followed by the segregation of sister chromatids to produce haploid cells. The unique genotypes of recombinant gametes are an essential substrate for the selection of superior genotypes in natural populations and plant breeding. In this review we summarize knowledge on meiosis in diverse monocot and dicot crop species and provide a thorough resource of cloned meiotic mutants in six crop species (rice, maize, wheat, barley, tomato and brassicas). Generally, the functional roles of meiotic proteins are conserved between plant species, but we highlight notable differences in mutant phenotypes. The physical lengths of plant chromosomes vary greatly, for instance wheat chromosomes are roughly one order of magnitude longer than those of rice. We explore how chromosomal distributions of crossover recombination can vary between species. We conclude that research on meiosis in crops will continue to complement that in Arabidopsis, and alongside possible applications in plant breeding will facilitate a better understanding of how the different stages of meiosis are controlled in plant species.

Keywords (10): Meiosis, Recombination, Crossover, Crops, Plant breeding, Plant genomics, Maize, Rice, Wheat, Tomato
Tables and figures

Table 1) Cloned meiotic mutants characterized in crop species

Figure 1) Characteristics of different plant model systems for meiosis research

Figure 2) Chromosomal crossover distributions in Arabidopsis, rice, maize and wheat
Introduction

Meiosis is a specialized cell division that takes place during sexual reproduction and leads to the production of genetically unique, haploid spores. Meiosis consists of one round of chromosome replication followed by two rounds of segregation, thereby halving the chromosome number (Mercier et al., 2015; Gray and Cohen, 2016). In the first division, homologous chromosomes pair, recombine and segregate whilst in the second division sister chromatids separate. Meiotic recombination and random segregation of homologous chromosomes combine to generate genetic variation which is an important substrate for selection, be it natural during evolution or artificial during breeding. Notably, the first demonstration that physical recombination of chromosomes is the mechanism by which genetic linkage of traits can be broken was in maize (Creighton and McClintock, 1931), underscoring the historic role research on meiosis in crops has played in the meiosis field.

Meiosis can be broadly split into five key stages: meiotic entry, recombination initiation, chromosome synopsis, resolution of recombination intermediates, and the second meiotic division. Unlike animals, the specification of both male and female plant germlines occurs late in development during flowering. The transition from the sporophyte phase to the gametophyte state is initiated by meiotic entry. Upon meiotic entry the replication of chromosomes and establishment of sister chromatid cohesion is followed by the association of telomeres with the nuclear envelope during leptotene. Subsequently the initiation of meiotic recombination occurs via the formation of programmed meiotic DNA double strand breaks (DSBs) by a topoisomerase like complex containing conserved SPO11 proteins. Recombination between homologous chromosomes is tightly interlinked with the lengthwise alignment of homologous chromosomes (pairing) and the formation of the synaptonemal complex (synapsis). The synaptonemal complex (SC), a protein-rich structure, connects the paired homologous chromosomes during zygote and pachytene (the stages when recombination occurs). Meiotic DSBs are repaired by homologous recombination which can be resolved as either a crossover (CO), which is a full reciprocal exchange, or a non-crossover (NCO), which is either a gene conversion (from the homologous chromosome) or sister chromatid-based repair. In plant species studied to date approximately one in twenty meiotic DSBs sites are finally repaired as a CO, suggesting selection acts to restrict CO number (Choi et al., 2013; Mercier et al., 2015; Sidhu et al., 2015; Desjardins et al., 2020). Following genetic exchange and segregation of homologous chromosomes, the second division proceeds with the release of the cohesion of sister chromatids and the emergence of haploid spores.

Meiosis is crucial for the generation of elite crop genotypes. Artificial hybridization, F₁ hybrid propagation and the production of recombinant F₂ populations and/or doubled haploid populations remain key approaches in plant breeding. At the F₁ hybrid stage the number and position of meiotic CO events is important for the introduction of pre-breeding material into elite varieties. Increasing CO rates through the application of anti-CO mutants in crop F₁ hybrids can increase CO rates (Mieulet et al., 2018). However, such mutants only increase recombination in previously recombination-competent genomic regions and this is likely insufficient to satiate the needs of crop breeders (Blary and Jenczewski, 2019). Given that recombination suppressed regions remain suppressed in such mutants routes to redistribute highly-skewed chromosomal distributions of CO recombination remain of great interest.
In this review, we focus on monocot and dicot crop species where meiosis research is most established, and refer readers to recent reviews that have a greater focus on Arabidopsis meiosis research (Mercier et al., 2015; Wang and Copenhaver, 2018). We provide a thorough resource of all previously isolated meiotic mutants of maize (Zea mays), rice (Oryza sativa), wheat (Triticum aestivum), barley (Hordeum vulgare), tomato (Solanum lycopersicum) and brassicas (Brassica rapa, Brassica oleracea and Brassica napus). Rice and maize are by far the most studied crop species with 64 and 23 mutants cloned, respectively (Table 1). We use this resource to highlight insights into the five keys stages of meiosis introduced above.

Crop species have highly diverse physical genome and chromosome sizes, chromosome numbers, variable ploidy and a range of meiosis progression times (Figure 1). In general, physical differences in chromosome length do not alter the number of meiotic COs that occur, which tends to be between one and three COs per chromosome per meiosis (Mercier et al., 2015). Larger chromosomes tend to have larger regions that are suppressed for meiotic CO. We discuss how chromosomal distributions of CO are influenced by genetic and non-genetic factors, and explore genome-wide CO landscapes in those crops where such data is available. We integrate and compare the results in crops with Arabidopsis, which is by far the best characterized plant meiosis model. Together we make the case that pursuing meiosis research in diverse plant model systems will further our fundamental knowledge of meiosis and provide insights directly relevant for plant breeding.

Meiotic entry: the transition to sporogenesis

In plants, the transition from the sporophyte phase to the gametophyte phase requires two distinct processes: sporogenesis and gametogenesis. Sporogenesis occurs in both male and female reproductive organs when a subset of sub-epidermal cells differentiate to become cells destined to enter meiosis – the meiocytes. Meiocytes deviate from the mitotic cell cycle and enter the meiotic cell cycle.

Genetic and physiological factors have been identified that are required for the acquisition of meiocyte cell fate in plants. The differentiation of both male and female meiocytes requires SPOROCYTELESS in both Arabidopsis and rice (Yang et al., 1999; Ren et al., 2018). SPOROCYTELESS likely acts as a transcriptional repressor protein, and its mutation in rice leads to changes in gene expression of various genes involved in redox status and meiotic processes (Ren et al., 2018). Notably, mutants in glutaredoxin, a redox regulator, have been identified in rice and maize that have strong defects in male sporogenesis (Hong et al., 2012; Kelliher and Walbot, 2012). Related to this, increasing oxygen levels in developing maize anthers suppresses the formation of meiocytes, suggesting that a hypoxic microenvironment is important for stem cell maintenance and sporogenesis (Kelliher and Walbot, 2012).

Upon the acquisition of meiocyte cell fate, the mitotic cell cycle needs to transition to the meiotic cell cycle. This is thought to occur before the pre-meiotic S-phase when cohesion is established between the sister chromatids that are produced during DNA replication. Cohesion of chromosomes is necessary for progression through the meiotic stages, which is
driven by the activity of cyclin-CDK (cyclin dependent kinase) complexes (Marston and Amon, 2004; Harashima et al., 2013; Mercier et al., 2015). Cohesin mediates cohesion by trapping the sister chromatids inside tripartite ring structures made up of two SMC proteins (SMC1 and SMC3) and a third α-kleisin subunit (Mercier et al., 2015). Notably, sister chromatid cohesion is protected, specifically at centromeres, at the end of the first meiotic division when sister chromatids orient to a single pole. REC8, a highly conserved α-kleisin subunit forms part of the meiotic cohesin complex, differentiating it from mitotic cohesin complexes. In Arabidopsis, maize and rice, absence of REC8 leads to defects in sister chromatid cohesion and chromosome segregation, chromosome fragmentation at anaphase I, and sterility (Bai et al., 1999; Golubovskaya et al., 2006; Shao et al., 2011).

A family of a meiosis-specific nuclear proteins with a conserved SMC domain, play an important role in entering a normal meiosis in maize (ZmAM1), rice (OsAM1) and Arabidopsis (AtSWI1/AtDYAD). In four strong maize am1 alleles, including am1-489, meiocytes appear to enter a mitotic, rather than meiotic, division (Pawlowski et al., 2009). A weak allele, am1-pral, can enter meiosis although defects are observed at the leptotene-zygotene checkpoint (Pawlowski et al., 2009). The rice homologue, OsAM1, has a similar function in regulating proper chromosome structure and the leptotene-zygotene transition checkpoint during the early stage of prophase I (Che et al., 2011). In Arabidopsis the mutation of AtSWI1 leads to highly reduced fertility, although viable unreduced female gametes are produced at a low frequency (Mercier et al., 2003; Ravi et al., 2008). Recently AtSWI1 was shown to act as an antagonist to WAPL, a factor that removes cohesin during prophase, and therefore AtSWI1 likely acts to maintain the cohesion of sister chromatids (Yang et al., 2019). Overall, it appears that the role of AtSWI1, and related proteins, is to maintain a suitable chromosome structure for meiotic entry and progression.

Two meiosis arrested at leptotene mutants (mel1 and mel2) have been isolated in rice, that provide important insights into the transition to meiosis and the early stages of meiotic prophase I (Nonomura et al., 2007, 2011). In mel1 mutants, germ cells are formed normally (unlike sporocyteless mutants) but defects are found in pre-meiotic divisions of germ cells, chromosome condensation and meiotic progression, with arrested meiocytes having uncondensed chromosomes similar to leptotene or zygotene (Nonomura et al., 2007). MEL1 encodes an ARGONAUTE protein, suggesting a link to RNAi, that is specifically expressed during sporogenesis and mediates large-scale meiotic chromosome reprogramming during the premeiosis-to-meiosis transition (Nonomura et al., 2007; Liu and Nonomura, 2016). MEL2 encodes for an RNA-recognition-motif (RRM) protein that appears to control the translation of meiotic RNAs, and strikingly the pre-meiotic S-phase is asynchronous in mel2 mutants, indicating MEL2 likely functions in a separate pathway from MEL1 (Nonomura et al., 2011).

Single cell sequencing has recently provided new insights into the transcriptional changes before and during meiosis in maize (Nelms and Walbot, 2019). The transition from mitosis to meiosis was not accompanied by drastic global changes in transcription, but rather a smooth transition. For example, two cell cycle regulator genes (the D-type cyclin genes CycD2;1 and CycD2;3) that are constitutively expressed in mitotic stages are downregulated upon the transition to meiosis (Nelms and Walbot, 2019). A more drastic change in gene expression patterns was identified during leptotene when more than one quarter of all transcripts changed expression level by two-fold. Maize am1-489 and am1-pral mutants were also profiled and both mutants had remarkably similar transcriptional defects during
meiosis, despite strong differences in chromosome behavior between them (Pawlowski et al., 2009; Nelms and Walbot, 2019). In both am1 alleles the transcriptional changes associated with the onset of meiosis were delayed, yet the meiotic transcriptional profile was eventually established, suggesting that the transcriptional landscape can be uncoupled from chromosome morphologies during the entry into meiosis.

Studies into the initiation of meiosis have been carried out in Arabidopsis, maize and rice, yet our understanding of this process remains far from complete. Further understanding of this developmental transition could have useful applications. The artificial delay of the initiation of sporogenesis, or the transition from mitosis to meiosis, in crop plant species with hermaphrodite flowers (i.e. both male and female organs on the same flower) could be used in hybrid seed production. Currently, many hybrid seed production systems are based on cytoplasmic male sterility, which is genetically complex and not available in many important crops (Chen and Liu, 2014). Artificially delaying male meiosis compared to female meiosis, even by two or three days, would allow for avoidance of self-pollination, facilitate artificial hybridization (before pollen bearing anthers are produced) and hybrid seed production. In *Brassica napus*, different alleles of the early meiotic progression gene MS5 represent a relevant example of the potential application of meiotic mutants in genetic male sterility breeding systems (Xin et al., 2016). Overall, novel genetic, physiological or chemical approaches that delay (male) meiosis could represent a more flexible mode of hybrid breeding.

**Recombination initiation: meiotic DNA double strand break formation and strand invasion**

Meiotic recombination is initiated during the leptotene stage of meiotic prophase I by the programmed formation of meiotic DSBs, which is followed by DSB processing and repair by homologous recombination. Meiotic DSBs are produced in a huge excess compared with the final number of COs. In allotetraploid wheat 1400 DSBs (RAD51 foci) result in 29 class I COs (HEI10 foci) across 14 homologous chromosomes, in maize 500 DSBs (RAD51 foci) result in 16 COs (chiasma number) across 10 homologous chromosomes, and in Arabidopsis 200 DSBs (RAD51 foci) result in 10 class I COs (MLH1 foci) across five homologous chromosomes (Choi et al., 2013; Sidhu et al., 2015; Desjardins et al., 2020).

Meiotic recombination initiation requires key protein factors that are conserved between all eukaryotes, while co-factors to the core complex are variable between fungi, animals and plants. In all eukaryotes programmed meiotic DSBs are generated by the type II topoisomerase-like SPO11 family of proteins. In Arabidopsis, there are three SPO11 homologues. SPO11-1 and SPO11-2 form a heterodimer and are strictly required for meiotic DSB formation in Arabidopsis, while SPO11-3 plays no role in meiosis but spo11-3 mutants have somatic cell defects related to endo-reduplication (Grelon et al., 2001; Stacey et al., 2006). Arabidopsis spo11-1 mutants exhibit a classical phenotype of absence of homologous chromosome pairing and random segregation during the first meiotic division (Grelon et al., 2001). MTOPVIB is a part of the catalytic core complex that can be considered as the bridge to mediate the heterodimer formation between SPO11-1 and
SPO11-2, and \textit{mtopvib} mutants do not initiate recombination (Vrielynck \textit{et al.}, 2016). In rice, there are five SPO11 homologues. OsSPO11-1 and OsSPO11-2 are both absolutely required for fertility in rice, although Os\textit{spp}11-2 mutants still appear to form some DSBs unlike Os\textit{spp}11-1 mutants (Fayos \textit{et al.}, 2020). In wheat, at least one functional copy of \textit{TaSpo11-2} is required for meiotic recombination in diploid, tetraploid and hexaploid varieties (Benyahya \textit{et al.}, 2020). Interestingly, different polyploid wheat varieties contain loss of function mutations in the A genome copy of \textit{TaSpo11-2}, which are absent from the diploid A- relative, suggesting the mutation occurred after polyploidization (Benyahya \textit{et al.}, 2020).

In rice, \textit{OsSpp}11-4 mutants do not have obvious defects during meiosis but do have a 12% reduction in fertility (by panicles), while RNAi lines of Os\textit{spp}11-4 do display meiotic defects and have a more severe reduction in fertility (An \textit{et al.}, 2011; Fayos \textit{et al.}, 2020). Based on the mutant analysis it appears that OsSPO11-4 does not play a major role in rice meiosis but future analysis of high order mutants, including in OsSPO11-3 and OsSPO11-5, will be instructive.

The meiotic DSB catalytic core complex also requires a number of co-factors for DSB formation to occur properly. Co-factors that play a role in DSB formation in plants include PRD1, PRD2, AtPRD3/OsPAIR1 and DFO (Mercier \textit{et al.}, 2015). AtPRD1 acts as a key bridging factor by interacting directly with core complex members MTOPVIB, SPO11-1, SPO11-2, as well as the additional co factors DFO and PRD3 (De Muyt \textit{et al.}, 2007; Tang \textit{et al.}, 2017). OsPRD2 can interact with OsMTOPVIB directly and facilitates bipolar spindle construction, meiotic DSB formation and homologous pairing (Xue \textit{et al.}, 2019). OsPAIR1, is required for normal spindle formation and the proper establishment of homologous chromosome pairing during early meiosis (Nonomura \textit{et al.}, 2004).

In different species, meiotic DSB formation mutants can have different phenotypes. In budding yeast \textit{REC114} is essential for meiotic DSB formation, while the homologues in Arabidopsis and maize appear to play a role in pairing but not DSB formation (Pawlowski \textit{et al.}, 2004; Ronceret \textit{et al.}, 2009; Lam and Keeney, 2015). In rice the cyclin protein SOLO DANCERS (OsSDS) is essential for meiotic DSB formation, while the Arabidopsis homologue AtSDS is only necessary for meiotic DSB repair (De Muyt \textit{et al.}, 2009; Wu \textit{et al.}, 2015). In addition, two rice synaptonemal complex proteins CENTRAL REGION COMPONENT1 (OsCRC1) and Bivalent Formation 1 (OsBVF1/OsP31\textsubscript{comet}), are essential for DSB formation, however the Arabidopsis homologs AtPCH2 and AtP31\textsubscript{comet} are not required for DSB formation (Miao \textit{et al.}, 2013; Lambing \textit{et al.}, 2015; Ji \textit{et al.}, 2016; Zhou \textit{et al.}, 2017; Balboni \textit{et al.}, 2020).

In recent years next generation sequencing has been used to map the location of meiotic DSB sites along chromosomes (Underwood and Choi, 2019). A popular approach, first developed in budding yeast, has been to exploit the covalent linkage between SPO11 and a 30-50 nt oligonucleotide that corresponds to the DSB site by immunopurifying SPO11 and sequencing the associated oligonucleotide (Pan \textit{et al.}, 2011). This approach was successfully applied to Arabidopsis SPO11-1, where meiotic DSBs were found to be common at gene promoters, which are AT-rich and nucleosome depleted regions (Choi \textit{et al.}, 2018). Surprisingly, certain classes of Arabidopsis DNA transposons (\textit{Helitron}/\textit{Pogo}/\textit{Tc1}/\textit{Mariner}) are meiotic DSB hot spots while retrotransposons were depleted of meiotic DSBs (Choi \textit{et al.}, 2018). This is consistent with SPO11-1 acting as an ‘opportunistic’ enzyme in open chromatin. In contrast to meiotic DSB maps in Arabidopsis, mice and yeast, maize RAD51 ChIP-seq revealed that meiotic DSBs can form in all
chromosomal regions including retrotransposons (He et al., 2017; Underwood and Choi, 2019). In mice it has recently been shown by ChIP-seq that DMC1 binds to regions very close to the DSB site while RAD51 binds to adjacent regions, and as such this may have implications for the interpretation of the maize RAD51 ChIP-seq data (He et al., 2017; Hinch et al., 2020). In the future, genome-wide analyses on meiotic recombination initiation, ideally by orthogonal approaches (e.g. SPO11-oligo sequencing, DMC1 ChIP-seq, RAD51 ChIP-seq), in a wider array of plant species will provide insights into the roles of meiotic recombination in plant genome evolution. Related to this, it will be interesting to explore whether DSB interference, a phenomenon described in budding yeast which reduces the possibility of two DSB events occurring close to one another, is conserved in plant species (Garcia et al., 2015).

Following meiotic DSB formation, DSBs are processed and then repaired by homologous recombination. DSBs are first processed by the MRN complex (MRE11, RAD50 and NBS1) and COM1 to release SPO11 proteins, facilitating exonuclease end resection to produce the 3’ ssDNA overhangs (Ji et al., 2013; Luo et al., 2014; Mercier et al., 2015; Wang and Copenhaver, 2018; Wang et al., 2018). The highly conserved BRCA2 can recruit DMC1 and RAD51 (two RecA related recombinases) onto the ssDNA to facilitate homologous recombination (Wang and Copenhaver, 2018). DMC1 is specifically expressed in meiotic cells and is absolutely required for meiotic CO (Wang and Copenhaver, 2018). Many DSB repair mutants lead to meiotic chromosome fragmentation but Arabidopsis and rice plants lacking DMC1 have univalent meiotic chromosomes (Pradillo et al., 2012; Mercier et al., 2015; Wang et al., 2016; Wang and Copenhaver, 2018). DMC1 is essential for synapsis in both Arabidopsis and rice, but unlike Arabidopsis dmc1 mutants, homologous chromosome pairing can occur in rice plants lacking DMC1 (Wang et al., 2016). Additionally, in hexaploid wheat (Triticum aestivum) it appears that a specific DMC1 gene located on the D genome is required for the stabilization of chromosome pairing at low and high temperatures (Draeger et al., 2020).

Directing meiotic DSBs to genomic locations where they do not usually occur could be a useful technique in plant breeding. The presence of a meiotic DSB at a given genomic location is a pre-requisite for recombination but does not ensure a recombinant outcome, as meiotic DSBs can equally be repaired by sister chromatid-based repair. Directing meiotic DSB formation will likely require the recruitment of SPO11-1, SPO11-2 and MTOPVIB, and potentially other factors, to specific genomic locations. Meiotic DSBs are of a very specific molecular nature: a covalent linkage between the catalytic tyrosine residue of SPO11 proteins and the 5’ terminus of the broken DNA strand leaves a free 3’ hydroxyl group (Pan et al., 2011). Therefore, SPO11 induced breaks generate a unique molecular signature, that is distinct to endonuclease enzymes like Cas9, and this likely facilitates further processing by the MRN complex and COM1, as outlined above. Fusion proteins between dCAS9 (for targeting) and MTOPVIB have been recently tested in Arabidopsis, and although they do not lead to targeted meiotic DSBs they can complement mtopvib mutants (Yelina et al., 2021). In the future, alterations of such an approach, or simultaneous modulation of meiotic DSB interference, may allow for the direct targeting of meiotic DSB events in plant hybrids to expedite introgression breeding.
Chromosome synapsis: the formation of the synaptonemal complex (SC)

The formation of the SC, occurs in tandem with meiotic DSB formation and strand invasion. The SC is a proteinaceous connection between the homologous chromosomes and is made up of three main elements; axial/lateral elements (AE/LE), transverse filaments (TF), and the central element (CE) (Mercier et al., 2015; Wang and Copenhaver, 2018). The two axes act as a scaffold which is zipped together by the TFs and plays an important role in the maturation of meiotic recombination intermediates to facilitate CO events. During recombination initiation, the meiotic chromatin is arranged in loops that are anchored at the underlying axes. Meiotic DSBs are thought to occur on the loops and a subset of DSBs are then recruited to the axis for recombination with homologous chromosomes. This special relationship between DNA loop and chromosome axis is called the ‘Tethered loop-axis’ model and is based on findings in yeast and mice (Kleckner, 2006). However, the key proteins that mediate interactions between chromatin loops and AEs remain to be identified in plants. In plants, synapsis and SC formation requires meiotic DSB formation in rice, maize and Arabidopsis. SC formation is defective in rice sds and mre11 mutants, that have respective defects in DSB formation and processing (Ji et al., 2013; Wu et al., 2015). Likewise rice and maize mutants in the RAD51C gene, which is required for strand invasion, do not form a SC (Kou et al., 2012; Jing et al., 2019). The reliance of SC formation on DSBs in crops is found to be in line with reports in Arabidopsis (Mercier et al., 2015; Wang and Copenhaver, 2018).

Axial element proteins mark the two homologous chromosomes during the first stages of prophase I. Before synapsis, the chromatin is diffuse and sister chromatid cohesion is maintained by cohesion complexes that include REC8, which is itself an axes marker. After synapsis of homologous chromosomes, axial elements are described as lateral elements. ASY1, a HORMA domain protein, was initially described in Arabidopsis and Brassica oleracea as an AE (Armstrong et al., 2002). During early prophase I, ASY1 marks the diffuse chromatin and later, from leptotene to pachytene, it exclusively marks the axes of synapsed chromosomes, where it gradually disappears (Armstrong et al., 2002). Mutation of PAIR2 in rice, the AtASY1 orthologue, leads to 24 completely unpaired univalents at pachytene and diakinesis, suggesting a key role in homologous chromosome pairing and synapsis (Nonomura et al. 2004). Likewise, wheat RNAi lines that knockdown TaASY1 expression have reduced synapsis during prophase I (Boden et al., 2009). In rye ASY1 is exclusively located at axial/lateral elements in both A and B chromosomes where, unlike orthologous proteins in Arabidopsis and barley, it remains at the SC until its disintegration (Hesse et al., 2019). In autotetraploid potato, ASY1 staining has shown patches of higher and lower intensity compared to diploid potato indicating a difficulty in axis maintenance during prophase I, and also demonstrated possible switching of synapsis partners (Choudhary et al., 2020). Rice pair3 mutants revealed a new AE/LE factor that was later shown to be conserved in Arabidopsis, where the ortholog, AtASY3, interacts directly with ASY1 (Yuan et al., 2009; Ferdous et al., 2012). PAIR3, a coiled-coil domain protein is associated with both unsynapsed AEs and synapsed LEs, and is required for pairing, recombination and SC assembly (Wang et al., 2011b).
The transverse filament (TF) plays the role of bridging the homologous axes of the SC, and the central element (CE) is positioned along the centre of the SC. In rice, the ZEP1 protein has been identified as a central element protein (Wang et al., 2010). The ZEP1 gene was identified using a reverse genetics approach, based on the earlier study of ZYP1 genes in Arabidopsis, where two recently duplicated genes have made double mutant analysis difficult (Higgins et al., 2005). Interestingly, in the rice zep1 mutant SC assembly does not occur, yet the chromosomes can align along their entire lengths and an increased number of COs are observed despite reduced seed set (Wang et al., 2010). Increased CO formation has also recently been reported in Arabidopsis zyp1 null mutants (Capilla-Pérez et al., 2021; France et al., 2021). A second transverse filament protein identified in rice is CRC1 (CENTRAL REGION COMPONENT1) (Miao et al., 2013). In zep1 mutants CRC1 is not located on chromosomes, while in crc1 mutants ZEP1 is not found on meiotic chromosomes (Miao et al., 2013). Notably the meiotic roles of CRC1 and the Arabidopsis homologue PCH2 appear to be quite different. In rice CRC1 is required for DSB formation, loading of PAIR2/ASY1 and for SC formation, while in Arabidopsis PCH2 is not required for normal axis formation, although defects in ZYP1 polymerization are observed (Miao et al., 2013; Lambing et al., 2015). In B. rapa PCH2 is required for normal ASY1 loading and axis remodeling (Cuacos et al., 2021). B. rapa pch2 mutants (10 chiasmata per meiocyte) have significantly reduced COs compared to wild-type controls (17 chiasmata per meiocyte) (Cuacos et al., 2021). Cuacos et al. also demonstrate an important role for PCH2 in pericentromeric CO formation in both Arabidopsis and B. rapa (Cuacos et al., 2021). In the future, analysis of zep1/zyp1 and crc1/pch2 mutants in a wider number of plant species, as well as the cloning of classical synopsis mutants in maize and tomato mutants (Havekes et al., 1994; Pawlowski et al., 2003), will likely provide further answers on the role of the SC in meiosis.

The pairing and synopsis of homologous chromosomes is a unique feature of meiosis. In the plant species studied to date meiotic DSBs play an important role in SC formation. Yet, in budding yeast and Drosophila the SC can be formed in a DSB-independent manner (Bhuiyan and Schmekel, 2004; Joyce and McKim, 2009; Tanneti et al., 2011). It remains to be seen whether DSB-independent SC formation can occur naturally in plants or even if this could be achieved in an engineered fashion. For instance, the pairing of homologous chromosomes in the absence of CO formation could be used to generate non-recombinant reverse breeding populations as it could facilitate balanced segregation of homologous chromosomes which occurs rarely in non-recombinant mutants like spo11-1 (Grelon et al., 2001; Wijnker et al., 2012). On the other hand, forcing the synopsis of, and CO between, homoeologous chromosomes from divergent species could be useful for introducing wild germplasm in crop breeding programmes.
Resolution of recombination intermediates: to crossover or not to crossover?

Meiotic DSBs are repaired by homologous recombination with the homologous chromosome or the sister chromatid. Recombination intermediates with homologous chromosomes can be resolved, and genetically detected, either as CO or non-CO (also known as gene conversion) recombinant products. In Arabidopsis, maize and wheat only 5% of repair events are through meiotic CO (Choi et al., 2013; He et al., 2017; Desjardins et al., 2020). At least one meiotic CO, the so called ‘obligate’ CO, is required per homologous chromosome pair per meiosis to ensure that correct chromosome segregation occurs in meiosis I (Martini et al., 2006). Meiotic COs generate a new combination of alleles which increases genetic diversity in gametes (Youds and Boulton, 2011).

There are two types of meiotic CO pathways - the class I and class II CO pathways. In Arabidopsis and rice, the majority of CO events occur via the class I pathway, which accounts for 80-90% of total CO events (Higgins et al., 2004; Mercier et al., 2015). Class I COs depend on the activity of ZMM proteins (named after the budding yeast proteins Zip1-4, Mer3, Msh4, and Msh5), which are proposed to protect joint molecule recombination intermediates. For instance, purified human MSH4/5 heterodimers, otherwise known as the MutSγ complex, bind and stabilize double Holliday junctions (Lynn et al., 2007). Class I COs are subjected to CO interference, which means that CO events are spread apart more than would occur at random, yet the mechanism of CO interference is still not fully understood (Lynn et al., 2007).

Many class I CO mutants have been studied in Arabidopsis and various crops (Higgins et al., 2004; Mercier et al., 2015). Rice mer3 mutants are completely sterile with an obvious reduction in bivalent formation (12 bivalent in wild type, 5 bivalent in mer3) and chiasma frequency (20.8 in wild type, 5.8 in mer3) (Wang et al., 2009). Rice msh5 mutants are similarly sterile but exhibit less chiasma (2.10) per meiocyte than mer3 mutants (Luo et al., 2013). Less chiasma per meiocyte were also reported in rice msh4 (1.71) and msh4/msh5 (1.76) double mutants than other ZMM mutants suggesting the MutSγ complex may play an earlier role to stabilize progenitor Holliday junctions in rice (Zhang et al., 2014). In allotetraploid Brassica napus, the reduction of functional copies of MSH4 genes prevents non-homologous COs suggesting that stabilization of allopolyploid meiosis can be facilitated by the loss of functional copies of MutSγ genes (Gonzalo et al., 2019). In allotetraploid wheat (Triticum turgidum), the MutSγ complex maintains ~85% of all COs and is required for the obligate chiasma. Intriguingly, much like in Brassica napus, in allopolyploid wheat the loss of function of MutSγ genes (MSH5B in allotetraploid wheat; MSH5B and MSH4D in allohexaploid wheat) has been described, suggesting a possible adaptive role in the control of CO (Desjardins et al., 2020).

MLH1 and HEI10 are two important proteins for the formation of class I COs and mark chiasmata on late pachytene chromosomes. MutL-homolog (MLH) proteins play a crucial role in the DNA mismatch repair (MMR) pathway, and in eukaryotes the MLH1-MLH3 complex has been co-opted for the resolution of double Holliday junctions as meiotic COs. In tomato, MLH1 foci mark 70% of late recombination nodules and their distribution suggests
they mark strongly interfering COs (Lhuissier et al., 2007). Spontaneous exonic deletion in the barley MLH3 gene led to a 50% reduction in chiasmata, consistent with the 39% reduction in chiasmata in the Arabidopsis mlh3 mutant (Colas et al., 2016). Barley mlh3 mutants are also defective in synopsis, which was not previously observed in the Arabidopsis mlh3 mutant (Colas et al., 2016). In rice, Osmlh3 (14.9 chiasmata per cell) and Osmlh1 (15.2 chiasmata per cell) mutants have relatively modest reductions in chiasmata frequency (19.5 chiasmata in wild type) (Mao et al., 2021). This reduction is far less than rice ZMM mutants (Zhang et al., 2014), suggesting other proteins may be able to act as class I CO resolvases in rice (Mao et al., 2021). Unlike MLH1 foci which first appears at late pachytene stage to mark class I CO foci, HEI10 is first found on meiotic chromosomes at synapsed regions before later specifically co-localizing with MLH1 on class I CO foci. Rice hei10 mutants form 6.5 chiasmata per cell, and those chiasmata appear to lack CO-interference, while early recombination events and SC formation is normal (Wang et al., 2012). In rice the HE10 Interaction Protein 1 (HEIP1) was found via a yeast two-hybrid screen for HEI10 interaction partners. heip1 mutants are sterile and HEIP1 interacts directly with ZIP4 and MSH5, and is proposed as a novel ZMM protein (Li et al., 2018).

The class II COs account for around 10-20% of total COs and do not exhibit interference (Berchowitz et al., 2007). Class II COs do not rely on the MutSy complex but require the action of MUS81 which has been implicated in the resolution of class II COs in Arabidopsis, but mutants have yet to be studied in any crop species (Santos et al., 2003; Berchowitz et al., 2007; Olivier et al., 2016). In tetraploid wheat, an antibody raised against TaMUS81 demonstrated that 4 MUS81 foci were formed per cell in mutSγ loss of function mutants, consistent with about 12% of CO coming from class II (Desjardins et al., 2020).

There is emerging evidence that meiotic CO genes can influence pairing and meiotic CO between homoeologous chromosomes in polyploid plant species. Mutants of the wheat ZMM gene TaZIP4-B2, located within the Pairing homoeologous 1 (Ph1) locus, leads to increased homoeologous CO in crosses with related wild species, suggesting ZIP4 gene dosage may influence the choice between homologous and homoeologous CO (Rey et al., 2017). Meanwhile, the wheat DNA mismatch repair protein MSH7-3D was identified as a key inhibitor of homoeologous recombination and its loss is likely responsible for the classical Pairing homoeologous 2 (Ph2) mutant phenotype (Serra et al., 2021). In allopolyploid Brassica napus the Pairing Regulator in B. napus (PrBn) locus on Chromosome 9 (C genome) was identified as a controlling factor of homoeologous chromosome pairing in haploid Brassica napus (Jenczewski et al., 2003; Liu et al., 2006). Remarkably, using a different population and approach, Higgins et al. identified a QTL in a syntenic region of Chromosome 9 (A genome) that controls homeologous recombination in Brassica napus allotetraploids (Higgins et al., 2021). The identification of the causal gene at this locus will illuminate the molecular mechanisms of the stabilization of allopolyploid meiosis in Brassica napus.

The majority of meiotic DSBs are not repaired by CO repair pathways but by non-CO repair (Gray and Cohen, 2016; Xue et al., 2018). In Arabidopsis, the protein products of FANCM (Crismani et al., 2012), RECQ4 (Schröpfer et al., 2013; Séguéla-Arnaud et al., 2015) and TOP3α (Séguéla-Arnaud et al., 2015), have all been implicated in distinct non-CO repair pathways. Mutants in the afore mentioned genes were retrieved from ZMM mutant suppressor screens, and their mutation led to an increase in CO via the class II pathway, resulting in increased fertility. Simultaneous mutation of multiple anti-CO pathways (e.g.
fancm recq4 double mutants and figl1 recq4 double mutants) can further increase CO rate in inbred, and hybrid, Arabidopsis compared with the single pathway mutants (Fernandes et al., 2018). Mutants in anti-CO genes have been reported in some crop species. Cultivated tomato recq4 mutants are fertile and have a 2.7 fold increase in CO recombination (Mieulet et al., 2018). Similarly, in recq4 mutant interspecific tomato hybrids between S. lycopersicum and S. pimpinellifolium CO increases were observed by ring bivalents and SNP marker genotyping of F₂ progeny at respective rates of 1.54 and 1.8 folds (de Maagd et al., 2020). Further to this, rice and pea mutants (Pisum sativum) for FANCM and RECQ4 genes have increased CO rates (Mieulet et al., 2018). B. rapa and B. napus fancm mutants also have increased CO rates at 3.0 and 1.3 folds respectively (Blary et al. 2018). Mutants in FIGL1, which caused a 1.8 fold increase in meiotic CO rate in Arabidopsis hybrids, are sterile in rice, pea and tomato, demonstrating the potential for altered fertility of anti-CO mutants in different plant species (Girard et al., 2015; Mieulet et al., 2018).

Genomic analysis of crossover distribution

In plants, as in other eukaryotes, meiotic COs are not uniformly distributed in the genome. CO hot spots recombine at a rate higher than the genome average, while cold spots do not recombine (Mézard et al., 2015; Mercier et al., 2015; Choi and Henderson, 2015). COs mostly occur within gene-rich areas, close to gene promoter and terminator regions, where AT-rich DNA motifs are enriched and nucleosome occupancy is low (Wijnker et al., 2013; Choi et al., 2013; Marand et al., 2017, 2019; Kianian et al., 2018; Rommel Fuentes et al., 2020). Recombination cold spots are observed in heterochromatin rich centromeres and telomeres in most plant species (Si et al., 2015; Marand et al., 2017; Kianian et al., 2018; Gardiner et al., 2019; Rowan et al., 2019; Rommel Fuentes et al., 2020).

We selected four meiosis model species (Arabidopsis, rice, maize and wheat) with varying genome sizes (Figure 1) and compared CO landscapes of representative chromosomes (Figure 2) (Choulet et al., 2014; Choi et al., 2016; Furuta et al., 2017; Kianian et al., 2018). Representative chromosomes were chosen from Arabidopsis, rice and maize based on the physical size and the distribution of CO events on the chromosomes fairly reflecting all chromosomes within that species (Si et al., 2015; Kianian et al., 2018; Underwood et al., 2018). Wheat chromosome 3B was included due to the public availability of CO data (Choulet et al., 2014). In order to illustrate the distribution of CO events we plotted CO rate (in cM/Mbp) per physical position on the chromosome and normalized for physical chromosome length leading to a visual chromosomal landscape of meiotic COs.

Arabidopsis subtelomeres and pericentromeric regions are areas with higher recombination than the genome average (Underwood et al., 2018; Rowan et al., 2019). On Arabidopsis chromosome 3, the CO rate is relatively evenly distributed along the chromosome arms (Fig 2A). The centromeric region (13.5-14 Mbp) completely lacks COs, while the highest cM/Mbp values are found adjacent to the centromere (at ~11 Mbp) (Fig 2A). In Arabidopsis, a positive correlation between meiotic DSB levels and meiotic CO levels is found at the broad scale (Choi et al., 2018). COs do not form in inverted and
translocated regions, while mutants that lose non-CG DNA methylation have increased COs in centromeric regions (Zapata et al., 2016; Underwood et al., 2018).

The rice genome is relatively compact compared with other monocot crop species and this results in a CO distribution that is more similar to Arabidopsis than maize and wheat (Fig 1 and Fig 2B) (Si et al., 2015). On rice chromosome 1 (Fig 2B), the highest cM/Mbp values are found in the distal regions (0-3 Mbp and 40-43 Mbp) and adjacent to the centromere (~20-25 Mbp) (Fig 2B). Like in Arabidopsis, historical recombination events in rice are associated with gene promoters and terminators (Choi et al., 2013; Marand et al., 2019). More than 80% of the historical recombination events occurred in 5.3% and 4.2% of the whole genome sequence in indica and japonica rice subspecies, respectively, demonstrating the existence of CO hot spots (Marand et al., 2019). However, relatively few hot spots are conserved between the two subspecies despite sharing a common ancestor 400,000 years ago. In both subspecies, specific DNA transposon classes (PIF, Harbinger, Stowaway) and also simple sequence repeats were over-represented within CO hot spots, while retrotransposon classes are depleted (Marand et al., 2019).

In contrast to Arabidopsis and rice, plant species with higher repeat contents tend to have large interstitial and centromeric regions that are devoid of CO, and the majority of CO events occur in distal euchromatic regions (Choulet et al., 2014; Demirici et al., 2017; Marand et al., 2017; Kianian et al., 2018; Dreissig et al., 2019; Rommel Fuentes et al., 2020). A clearly polarized chromosomal distribution of CO is observed for maize (Fig 2C) and wheat (Fig 2D). In both species, cM/Mbp values are elevated in the distal subtelomeric regions, compared to much lower values in the interstitial and centromeric regions. On maize chromosome 7, COs mainly occur in the subtelomeric euchromatin (Fig 2C), correlating to higher gene densities (Schnable et al., 2009; Kianian et al., 2018). In maize COs are restricted to less than 10% of the physical genomic length and therefore vast interstitial and centromeric regions are devoid of CO in all maize chromosomes (Fig 2C) (Kianian et al., 2018; Luo et al., 2019). Mirroring Arabidopsis and rice, maize COs are generally excluded from retrotransposons, despite reported meiotic DSBs in these elements (He et al., 2017; Kianian et al., 2018). Gene conversion events have been observed in maize centromeres, where it is predicted to be widespread and may contribute to centromere evolution (He et al., 2010). On wheat chromosome 3B, the CO rate is variable within the interstitial regions, showing locally elevated rates, although the average CO rate in these regions is substantially lower compared to the subtelomeric regions (Fig 2D). In wheat a correlation has been found between two simple DNA motifs (A-stretch and CCG) and two DNA transposon related motifs (from TIR-Mariner and CACTA elements) and CO rate at the whole genome level (Darrier et al., 2017). Similar to maize and wheat, polarized CO landscapes are observed in other crop species, such as tomato (Demirici et al., 2017; Rommel Fuentes et al., 2020), potato (Marand et al., 2017) and barley (Higgins et al., 2012; Dreissig et al., 2019).

Multiple factors have been demonstrated to affect the distribution of CO events, which can be simply separated into genetic and non-genetic factors. Genetic polymorphism between homologous chromosomes is largely seen as inhibitory to CO, since sequence divergence inhibits homologous recombination, as exemplified by introducing polymorphism at yeast CO hot spots (Borts and Haber, 1987). Classical examples include large genetic inversions which prevent pairing, synapsis and ultimately CO (Anderson et al., 2010; Zapata et al., 2016). Other structural variants (including translocations, insertions and deletions) are
also likely inhibitory to CO formation, while copy number variants and transpositions could lead to non-allelic homologous recombination (Zapata et al., 2016; Underwood and Choi, 2019). A relevant example is the comparison of the CO landscapes of melon and cucumber, two cucumis species that diverged ten million years ago. In cucumber meiotic CO frequency is relatively constant along the chromosomes, whereas melon, which experienced an expansion of LTR class I TEs after divergence, has a distalized CO landscape where the expanded pericentromeric regions are suppressed for meiotic CO (Morata et al., 2018). Similar differences in CO positioning have been found between between onion (distalized CO positioning) and welsh onion (more proximal CO positioning), although the basis of this is not understood (Albini and Jones, 1987). In general, large CO cold spots are observed in species with larger chromosome sizes (Fig 2), and consistent with this centromere size has a linear relationship with genome size (Zhang and Dawe, 2012).

The relationship between genetic polymorphism and meiotic CO appears to be more complex than increasing genetic polymorphism leading to increased meiotic CO suppression. For instance, in Arabidopsis intermediate SNP densities associate positively with CO rate before a threshold is reached and a negative association is found, suggesting a non-linear relationship (Blackwell et al., 2020). Genetic factors can also control CO distribution in trans, for instance in Brassica where A genome CO rate is redistributed to pericentromeric regions in AAC triploids compared with AA controls (Pelé et al., 2017). This phenomenon is most apparent when certain A and C genomes are combined suggesting a potential QTL could underlie this redistribution effect.

Alongside genetic control of CO distribution, DNA methylation, histone modification, nucleosome occupancy and DNA accessibility, DNA replication timing, dosage of meiotic proteins, sex and 3D chromosomal confirmation have all been implicated in the control of CO distribution (Giraut et al., 2011; Higgins et al., 2012; Choi et al., 2013, 2018; Ziolkowski et al., 2017; Underwood et al., 2018; Lambing et al., 2020; Golicz et al., 2020). The interactions of genetic and non-genetic control of CO distribution will likely be further unraveled in the coming years.

**Maintenance of sister chromatid cohesion and the second meiotic division: the emergence of haploid gametes**

After COs have been resolved, homologous chromosomes segregate to opposite poles during anaphase I. In meiosis I cohesion is maintained at centromeres due to maintenance of cohesin complexes and facilitates the two sister chromatids of one homologue orienting towards the same pole. During anaphase II, the kinetochores of sister chromatids are oriented towards opposite poles and the previously protected centromeric cohesin is released. Release of the centromeric cohesion allows for proper segregation of sister chromatids and eventually the formation of haploid gametes at the end of Meiosis II (Mercier et al., 2015).

In yeast, metazoa and plants Shugoshin, literally ‘guardian spirit’ in Japanese, is required for the protection of centromeric cohesin complexes from cleavage by separase (Watanabe, 2005). The maize shugoshin mutant, Zmsgo1, precociously separates sister
chromatids centromeres during telophase I, leading to infidelity of chromosome segregation during meiosis II and complete sterility (Hamant et al., 2005). ZmSGO1 centromeric localization is dependent on REC8, whereas OsSGO1 localization is independent from REC8 but does require is dependent on OsAM1 (Hamant et al., 2005; Wang et al., 2011a). In rice, Ossgo1 mutants also fail to maintain cohesion at centromeres during meiosis I and the centromeric localization of OsSGO1 depends on the main spindle checkpoint kinase Bub1-related kinase 1 (BRK1) (Wang et al., 2011a, 2013).

Like mitosis, progression through the meiotic stages is driven by the activity of cyclins-CDKs, which phosphorylate universal cell cycle proteins and meiosis specific factors (Marston and Amon, 2004; Harashima et al., 2013; Mercier et al., 2015). CDKA1 has peak activities at both metaphase I and metaphase II, suggesting it is required for progression through these important meiotic stages (Dissmeyer et al., 2007; Bulankova et al., 2010). However, continuation to anaphase and exit from the division phase requires a decrease in CDK activity which is achieved by the anaphase-promoting complex/cyclosome (APC/C) targeting cyclins for degradation (Marston and Amon, 2004; Pesin and Orr-Weaver, 2010; Harashima et al., 2013; Mercier et al., 2015). Thus, a fine-tuned cyclin-CDK activity is required for the transition from meiosis I to meiosis II. However, molecular players involved in this regulation, which mostly modify the cyclin-CDK-APC/C module, appear to be poorly conserved across eukaryotes (Mercier et al., 2015).

Arabidopsis mutants in genes that play a role in the cyclin-CDK-APC/C module have been shown to skip the second meiotic division and give rise to unreduced gametes (Mercier et al., 2015). OMISSION OF SECOND DIVISION1, OSD1, encoding an APC/C inhibitor, is required for meiosis II entry in both Arabidopsis and rice (D’Erfurth et al., 2009; Cromer et al., 2012; Mieulet et al., 2016). Both Arabidopsis and rice osd1 mutants undergo only the first meiotic division leading to the production of unreduced male (100% penetrance in Arabidopsis and rice) and female gametes (85% penetrance in Arabidopsis and 91% penetrance in rice) (D’Erfurth et al., 2009; Mieulet et al., 2016). Both Arabidopsis and rice osd1 mutants undergo only the first meiotic division leading to the production of unreduced male (100% penetrance in Arabidopsis and rice) and female gametes (85% penetrance in Arabidopsis and 91% penetrance in rice) (D’Erfurth et al., 2009; Mieulet et al., 2016). TAM, TARDY ASYNCHRONOUS MEIOSIS, is a type A cyclin (CYCA1;2), essential for the entry to meiosis II in Arabidopsis (d’Erfurth et al., 2010). Arabidopsis tam null mutants undergo the first meiotic division leading to the production of unreduced gametes in both male (~90% penetrance) and female (~30% penetrance) lineages (Bulankova et al., 2010; d’Erfurth et al., 2010). Specific mutations in Arabidopsis TDM1 (THREE DIVISION MUTANT1) that are close to a conserved CDK phosphorylation site terminate at the end of meiosis I and produce diploid gametes, whereas tdm1 loss of function mutants fail to exit meiosis and enter a third aberrant division (Cifuentes et al., 2016).

Hybrid vigour contributes to the high yield of commercial seeds and could be fixed through seeds by synthetic apomixis (Birchler et al., 2006; Khanday et al., 2019). The combination of mutants that skip the second meiotic division, with those that do not initiate meiotic recombination (e.g. spo11-1) or establish sister chromatid cohesion (e.g. rec8) leads to the ‘Mitosis instead of Meiosis’ (MiMe) phenotype (D’Erfurth et al., 2009; Mieulet et al., 2016). MiMe was first demonstrated in Arabidopsis where self-fertile spo11 rec8 osd1 triple mutants produce non-recombined, unreduced eggs that can be fertilized by non-recombined, unreduced sperm, to generate fully hybrid tetraploid offspring (D’Erfurth et al., 2009). MiMe can be an important element in the realization of synthetic apomixis in crop species (D’Erfurth et al., 2009). Mirroring the work in Arabidopsis, rice osd1 pair1 rec8 triple mutants, produce non-recombined diploid male and female gametes and give rise to tetraploid...
offspring (Mieulet et al., 2016). Notably the osd1 pair1 rec8 triple mutant shows varied fertility (from full fertility to highly reduced fertility) in different rice genetic backgrounds, suggesting possible modification by genetic or environmental factors (Mieulet et al., 2016; Wang et al., 2019). The combination of MiMe with engineering embryo development in the absence of paternal genetic contribution, the second element of synthetic apomixis, has been recently reported in rice via parthenogenesis (egg cell specific expression of OsBBM1) and haploid induction (mutation of OsMTL) (Khanday et al., 2019; Wang et al., 2019). Apart from osd1 mutants in rice, mutants that modify the meiotic cell cycle are largely underexplored outside of Arabidopsis, therefore reverse genetic approaches will likely help resolve of known genes in various crop species. Forward genetic screens for genes involved in unreduced gamete formation in crops, alongside the isolation of known genetic factors in brassica and potato (Jongedijk et al., 1991; Mason et al., 2011), may identify novel meiotic (cell-cycle) regulators.

Conclusion

The core function of meiosis is to recombine chromosomes and reduce the chromosome number by half, and it is therefore essential to the process of sexual reproduction because it derives haploid cells from diploid cells (Mercier et al., 2015). Meiotic recombination and reduction division are key aspects of vertical models of genetic transfer as well as the evolution of sex (Bell, 1993). Unsurprisingly the core protein factors involved in meiotic DSB formation, synaptonemal complex formation and meiotic CO are known to be conserved between fungal, animal and plants species. Despite the conservation of the meiotic process through eukaryotic life, there are notable variations, including the evolution of the meiotic DSB hot spot specifying factor PRDM9 in vertebrates, and the complete loss of class I CO pathways in fission yeast cells (Mercier et al., 2015; Grey et al., 2018). Modifications of the meiotic process also occur in plant species. For instance, natural alleles of the Arabidopsis HEI10 gene control meiotic CO rate in trans (Ziolkowski et al., 2017) while in wheat a novel RECO7 gene was shown to be important for meiotic gene conversion despite it having been lost in many plant species including Arabidopsis (Gardiner et al., 2019). Starkly, Arabidopsis mutants in rmi1 cannot progress in meiosis due to chromosome fragmentation and formation of chromatin bridges, (Chelysheva et al., 2008; Hartung et al., 2008), while tomato rmi1 mutants have no meiotic defects (Whitbread et al., 2021). For most plant biologists Arabidopsis will always be the ground truth, or gold standard, yet embracing a wide panel of model species is clearly valuable because each species has followed a distinct evolutionary trajectory leading to unique epistatic contexts.

In the coming years various topics and approaches are likely to play a role in the better understanding of plant meiosis. The interaction between meiosis and the environment appears to be an emerging topic, especially in a time of global climatic variation. Plants are sessile organisms that cannot determine their environment and meiosis is an important, and potentially vulnerable, aspect of plant reproduction. Already in Arabidopsis and barley, temperature has been demonstrated to alter meiotic CO rates (Higgins et al., 2012; Phillips et al., 2015; Lloyd et al., 2018). Diploid gamete formation has also been demonstrated to be partially controlled by temperature (de Storme et al., 2012). The interaction of meiotic
processes with temperature and other abiotic and biotic stresses, will be important to establish whether meiotic CO recombination can be adaptive under stress conditions. Emerging technologies including live cell imaging of meiosis, long read sequencing and single cell genomics will improve the resolution by which meiosis can be observed visually and genetically (Prusicki et al., 2019; Sun et al., 2019).

Meiosis research in crop species is intrinsically linked with crop improvement and breeding, as meiotic recombination is a key substrate of breeding. The application of approaches that can increase CO rate and change CO distribution can be useful in crop breeding for increasing genetic gain per breeding cycle. The approaches discovered so far have been tested in a limited number of plant species and genetic contexts. Future research will no doubt unravel whether anti-CO and epigenetic mutants, that respectively modify the absolute number and distribution of COs, can have similar or different effects in genetic backgrounds with varying levels of genetic polymorphism. This will help identify if there are particular levels, or types, of genetic polymorphism where modulation of CO level and/or position can lead to negative effects including chromosomal rearrangements or reduced fertility. On the other hand, harnessing the MiMe system and the application of synthetic apomixis in more crop species could represent a route to fixing hybrid vigour in commercial seed production.

Above and beyond the useful applications of meiosis in plant breeding, using crops as model systems has become much more accessible to basic scientists due to the developments in genome editing and genomics. Using crop species strengthens our understanding of meiosis and should not be obligatorily categorized as applied research. Indeed, we expect that the use of in rapid cycling crop varieties that are amenable to generate mutants by CRISPR/Cas9 may be useful for not only reverse genetic studies but as a means for generating mutants for suppressor and/or enhancer screens. As outlined, we propose that meiosis research in Arabidopsis and other plant model systems will continue to complement one another and lead to the discovery of novel genes, processes and mechanisms that are involved in meiosis.
Acknowledgments

We thank Ian R. Henderson (Arabidopsis); Kazuyuki Doi and Stefan Reuscher (rice); Penny M. A. Kianian, Shahryar F. Kianian and Wojciech P. Pawlowski (maize); Frederic Choulet (wheat) for the respective data used to generate the chromosomal distributions of meiotic recombination. We thank Qichao Lian for help with bioinformatic scripts. This work was supported by the Max Planck Society and a PhD fellowship awarded to M. W. A. M. Z. from the Malaysian Agricultural Research and Development Institute (MARDI).

Figure Legends

Fig. 1) Characteristics of different plant model systems for meiosis research

The genome size, chromosome number, ploidy and meiotic time of nine different plant species are presented. The species are Arabidopsis (Arabidopsis thaliana), barley (Hordeum vulgare), rye (Secale cereale), maize (Zea mays), tomato (Solanum lycopersicum), potato (Solanum tuberosum), rice (Oryza sativa), brassicas (Brassica oleracea, Brassica rapa and Brassica napus) and bread wheat (Triticum aestivum). Mbp = Mega base pairs, Gbp = Giga base pairs, h = hours. The duration of meiosis in different species came from the papers (Bennett, 1977; Armstrong et al., 2003; Ma et al., 2008; Sanchez-Moran and Armstrong, 2014). Created with BioRender.com.

Fig. 2) Chromosomal crossover distributions in Arabidopsis, rice, maize and wheat

A) cM/Mbp on Arabidopsis chromosome 3 (Arabidopsis thaliana Col-0 × Ler F2 population with 192 individuals from published sequencing data (Choi et al., 2016) followed by calling of CO locations using TIGER (Rowan et al., 2015), 0.1333 Mbp sliding window). B) cM/Mbp on rice chromosome 1 (Oryza sativa ssp. japonica cv. Nipponbare × O. longistaminata F2 population with 241 individuals selected from published genotyping data (Furuta et al., 2017), 0.25 Mbp sliding window). C) cM/Mbp on maize chromosome 7 (Zea mays ssp mays cv. B73 × (B73 × Mo17) Male BC1 population with 135 individuals from published sequencing data (Kianian et al., 2018), 1 Mbp sliding window). D) cM/Mbp on wheat chromosome 3B (SSD population derived from a Triticum aestivum L. Chinese Spring × Renan cross with 305 individuals from published genotyping data (Choulet et al., 2014), 4 Mbp sliding window). The grey shading beneath each chromosome represent the centromeres, which we genetically defined as the contiguous windows lacking COs that flank published centromere co-ordinates from each species (Cheng et al., 2002; Wolfgruber et al., 2009; Choulet et al., 2014; Underwood et al., 2018) The red dashed lines represent the
mean cM/Mbp value for each chromosome. Plots were produced using ggplot2 within R version 4.0.3.

Author contributions

C.J.U conceived the review topic and structure. Y. W., W. M. J. v. R. and M. W. A. M. Z. and C. J. U. wrote the review. Y. W. prepared Figure 1 and Table 1. W. M. J. v. R. prepared Figure 2. C. J. U. provided feedback and edited the review. All authors approved the final version.
References

Albini SM, Jones GH. 1987. Synaptonemal complex spreading in Allium cepa and A. fistulosum - I. The initiation and sequence of pairing. Chromosoma 95, 324–338.

An XJ, Deng ZY, Wang T. 2011. OsSpo11-4, a Rice Homologue of the Archaeal TopVIA Protein, Mediates Double-Strand DNA Cleavage and Interacts with OsTopVIB (Z Li, Ed.). PLoS ONE 6, e20327.

Anderson LK, Covey PA, Larsen LR, Bedinger P, Stack SM. 2010. Structural Differences in Chromosomes Distinguish Species in the Tomato Clade. Cytogenet. and Genome Research 129, 24–34.

Armstrong SJ, Caryl AP, Jones GH, Franklin FCH. 2002. Asy1, a protein required for meiotic chromosome synapsis, localizes to axis-associated chromatin in Arabidopsis and Brassica. Journal of Cell Science 115, 3645–3655.

Armstrong SJ, Franklin FCH, Jones GH. 2003. A meiotic time-course for Arabidopsis thaliana. Sexual Plant Reproduction 16, 141–149.

Bai X, Peirson BN, Dong F, Xue C, Makaroff CA. 1999. Isolation and characterization of SYN1, a RAD21-like gene essential for meiosis in Arabidopsis. Plant Cell 11, 417–430.

Balboni M, Yang C, Komaki S, Brun J, Schnittger A. 2020. COMET Functions as a PCH2 Cofactor in Regulating the HORMA Domain Protein ASY1. Current Biology.

Bell G. 1993. The sexual nature of the eukaryote genome. The Journal of heredity 84, 351–9.

Bennett MD. 1977. The time and duration of meiosis. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 277, 201–226.

Benyahya F, Nadaud I, Da Ines O, Rimbert H, White C, Sourdille P. 2020. SPO11.2 is essential for programmed double- strand break formation during meiosis in bread wheat (Triticum aestivum L.). The Plant Journal 104, 30–43.

Berchowitz LE, Francis KE, Bey AL, Copenhaver GP. 2007. The Role of AtMUS81 in Interference-Insensitive Crossovers in A. thaliana. PLOS Genetics 3, e132.

Bhuian H, Schmekel K. 2004. Meiotic chromosome synapsis in yeast can occur without spo11-induced DNA double-strand breaks. Genetics 168, 775–783.

Birchler JA, Yao H, Chudalayandi S. 2006. Unraveling the genetic basis of hybrid vigor. Proceedings of the National Academy of Sciences of the United States of America 103, 12957–12958.

Blackwell AR, Dluzewska J, Szymanska- Lejman M, et al. 2020. MSH2 shapes the meiotic crossover landscape in relation to interhomolog polymorphism in Arabidopsis. The EMBO Journal 39, e104858.

Blary A, Jenczewski E. 2019. Manipulation of crossover frequency and distribution for plant
breeding. Theoretical and Applied Genetics 132, 575–592.

**Boden SA, Langridge P, Spangenberg G, Able JA.** 2009. TaASY1 promotes homologous chromosome interactions and is affected by deletion of Ph1. Plant Journal 57, 487–497.

**Borts RH, Haber JE.** 1987. Meiotic recombination in yeast: alteration by multiple heterozygosities. Science (New York, N.Y.) 237, 1459–65.

**Bulankova P, Riehs-Kearnan N, Nowack MK, Schnittger A, Riha K.** 2010. Meiotic progression in Arabidopsis is governed by complex regulatory interactions between SMG7, TDM1, and the meiosis I-specific cyclin TAM. Plant Cell 22, 3791–3803.

**Capilla-Pérez L, Durand S, Hurel A, Lian Q, Chambon A, Taochy C, Solier V, Grelon M, Mercier R.** 2021. The synaptonemal complex imposes crossover interference and heterochiasmy in Arabidopsis. Proceedings of the National Academy of Sciences of the United States of America 118.

**Che L, Tang D, Wang K, Wang M, Zhu K, Yu H, Gu M, Cheng Z.** 2011. OsAM1 is required for leptotene-zygotene transition in rice. Cell Research 21, 654–665.

**Chelyscheva L, Vezon D, Belcram K, Gendrot G, Grelon M.** 2008. The Arabidopsis BLAP75/Rmi1 homologue plays crucial roles in meiotic double-strand break repair. PLoS Genetics 4.

**Chen L, Liu YG.** 2014. Male sterility and fertility restoration in crops. Annual Review of Plant Biology 65, 579–606.

**Cheng Z, Dong F, Langdon T, Ouyang S, Buell CR, Gu M, Blattner FR, Jiang J.** 2002. Functional rice centromeres are marked by a satellite repeat and a centromere-specific retrotransposon. Plant Cell 14, 1691–1704.

**Choi K, Henderson IR.** 2015. Meiotic recombination hotspots - a comparative view. The Plant Journal 83, 52–61.

**Choi K, Reinhard C, Serra H, et al.** 2016. Recombination Rate Heterogeneity within Arabidopsis Disease Resistance Genes. PLoS Genetics 12, 1–30.

**Choi K, Zhao X, Kelly KA, et al.** 2013. Arabidopsis meiotic crossover hot spots overlap with H2A.Z nucleosomes at gene promoters. Nature genetics 45, 1327–36.

**Choi K, Zhao X, Tock AJ, et al.** 2018. Nucleosomes and DNA methylation shape meiotic DSB frequency in Arabidopsis thaliana transposons and gene regulatory regions. Genome Research 28, 532–546.

**Choudhary A, Wright L, Ponce O, Chen J, Prashar A, Sanchez-Moran E, Luo Z, Compton L.** 2020. Varietal variation and chromosome behaviour during meiosis in Solanum tuberosum. Heredity.

**Choulet F, Alberti A, Theil S, et al.** 2014. Structural and functional partitioning of bread wheat chromosome 3B. Science 345, 1–8.

**Cifuentes M, Jolivet S, Cromer L, et al.** 2016. TDM1 Regulation Determines the Number of
Colas I, Macaulay M, Higgins JD, et al. 2016. A spontaneous mutation in MutL-Homolog 3 (HvMLH3) affects synopsis and crossover resolution in the barley desynaptic mutant des10. New Phytologist.

Cleary HB, McClintock B. 1931. A Correlation of Cytological and Genetical Crossing-Over in Zea Mays. Proceedings of the National Academy of Sciences of the United States of America 17, 492–7.

Crismani W, Girard C, Froger N, Pradillo M, Santos JL, Chelysheva L, Copenhaver GP, Horlow C, Mercier R. 2012. FANCM limits meiotic crossovers. Science 336, 1588–1590.

Cromer L, Heyman J, Touati S, et al. 2012. OSD1 promotes meiotic progression via APC/C inhibition and forms a regulatory network with TDM and CYCA1;2/TAM. PLoS Genetics 8.

Cuacos M, Lambing C, Pachon-Penalba M, Osman K, Armstrong SJ, Henderson IR, Sanchez-Moran E, Franklin FCH, Heckmann S. 2021. Meiotic chromosome axis remodelling is critical for meiotic recombination in Brassica rapa (A Dobritsa, Ed.). Journal of Experimental Botany 72, 3012–3027.

d’Erfurth I, Cromer L, Jolivet S, Girard C, Horlow C, Sun Y, To JPC, Berchowitz LE, Copenhaver GP, Mercier R. 2010. The CYCLIN-A CYCA1;2/TAM is required for the meiosis I to meiosis II transition and cooperates with OSD1 for the prophase to first meiotic division transition. PLoS Genetics 6, 1–12.

D’Erfurth I, Jolivet S, Froger N, Catrice O, Novatchkova M, Mercier R. 2009. Turning meiosis into mitosis. PLoS Biology 7.

Darrier B, Rimbert H, Balfourier F, Pingault L, Josselin AA, Servin B, Navarro J, Choulet F, Paux E, Sourdille P. 2017. High-resolution mapping of crossover events in the hexaploid wheat genome suggests a universal recombination mechanism. Genetics 206, 1373–1388.

Demirci S, van Dijk ADJ, Sanchez Perez G, Attilos SA, de Ridder D, Peters SA. 2017. Distribution, position and genomic characteristics of crossovers in tomato recombinant inbred lines derived from an interspecific cross between Solanum lycopersicum and Solanum pimpinellifolium. Plant Journal 89, 554–564.

Desjardins SD, Ogle DE, Ayoub MA, Heckmann S, Henderson IR, Edwards KJ, Higgins JD. 2020. MutS homologue 4 and MutS homologue 5 maintain the obligate crossover in wheat despite stepwise gene loss following polyploidization.

Dissmeyer N, Nowack MK, Pusch S, Stals H, Inzé D, Grini PE, Schnittger A. 2007. T-loop phosphorylation of Arabidopsis CDKA;1 is required for its function and can be partially substituted by an aspartate residue. Plant Cell 19, 972–985.

Draeger T, C. Martin A, Alabullah AK, Pendle A, Rey MD, Shaw P, Moore G. 2020. Dmc1 is a candidate for temperature tolerance during wheat meiosis. Theoretical and Applied Genetics.
Dreissig S, Mascher M, Heckmann S, Purugganan M. 2019. Variation in Recombination Rate Is Shaped by Domestication and Environmental Conditions in Barley. Molecular Biology and Evolution 36, 2029–2039.

Fayos I, Meunier AC, Vernet A, Sanz SN, Portefaix M, Lartaud M, Bastianelli G, Périn C, Nicolas A, Guiderdoni E. 2020. Assessment of the roles of OsSPO11-2 and OsSPO11-4 in rice meiosis using CRISPR/Cas9 mutagenesis. Journal of Experimental Botany.

Ferdous M, Higgins JD, Osman K, et al. 2012. Inter-homolog crossing-over and synapsis in Arabidopsis meiosis are dependent on the chromosome axis protein AtASY3. PLoS genetics 8, e1002507.

Fernandes JB, Séguéla-Arnaud M, Larchevêque C, Lloyd AH, Mercier R. 2018. Unleashing meiotic crossovers in hybrid plants. Proceedings of the National Academy of Sciences 115, 2431–2436.

France MG, Enderle J, Röhrig S, Puchta H, Franklin FCH, Higgins JD. 2021. ZYP1 is required for obligate cross-over formation and cross-over interference in Arabidopsis. Proceedings of the National Academy of Sciences 118, e2021671118.

Furuta T, Ashikari M, Jena KK, Doi K, Reuscher S. 2017. Adapting genotyping-by-sequencing for rice F2 populations. G3: Genes, Genomes, Genetics 7, 881–893.

Garcia V, Gray S, Allison RM, Cooper TJ, Neale MJ. 2015. Tel1ATM-mediated interference suppresses clustered meiotic double-strand-break formation. Nature 520, 114–118.

Gardiner LJ, Wingen LU, Bailey P, et al. 2019. Analysis of the recombination landscape of hexaploid bread wheat reveals genes controlling recombination and gene conversion frequency. Genome Biology 20, 1–16.

Girard C, Chelysheva L, Choix S, Froger N, Macaisne N, Lehmemdi A, Mazel J, Crismani W, Mercier R. 2015. AAA-ATPase FIDGETIN-LIKE 1 and Helicase FANCM Antagonize Meiotic Crossovers by Distinct Mechanisms. PLoS genetics 11, e1005369.

Giraut L, Falque M, Drouaud J, Pereira L, Martin OC, Mézard C. 2011. Genome-Wide Crossover Distribution in Arabidopsis thaliana Meiosis Reveals Sex-Specific Patterns along Chromosomes (M Lichten, Ed.). PLoS Genetics 7, e1002354.

Golicz AA, Bhalla PL, Edwards D, Singh MB. 2020. Rice 3D chromatin structure correlates with sequence variation and meiotic recombination rate. Communications Biology 3, 1–9.

Golubovskaya IN, Hamant O, Timofejeva L, Wang CJR, Braun D, Meeley R, Cande WZ. 2006. Alleles of afd1 dissect REC8 functions during meiotic prophase I. Journal of Cell Science 119, 3306–3315.

Gonzalo A, Lucas M-O, Charpentier C, Sandmann G, Lloyd A, Jenczewski E. 2019. Reducing MSH4 copy number prevents meiotic crossovers between non-homologous chromosomes in Brassica napus. Nat Commun 10, 2354.

Gray S, Cohen PE. 2016. Control of Meiotic Crossovers: From Double-Strand Break
Grelon M, Vezon D, Gendrot G, Pelletier G. 2001. AtSPO11-1 is necessary for efficient meiotic recombination in plants. EMBO Journal 20, 589–600.

Grey C, Baudat F, de Massy B. 2018. PRDM9, a driver of the genetic map (PE Cohen, Ed.). PLOS Genetics 14, e1007479.

Hamant O, Golubovskaya I, Meeley R, Fiume E, Timofejeva L, Schleiffer A, Nasmyth K, Cande WZ. 2005. A REC8-dependent plant shugoshin is required for maintenance of centromeric cohesion during meiosis and has no mitotic functions. Current Biology 15, 948–954.

Harashima H, Dissmeyer N, Schnittger A. 2013. Cell cycle control across the eukaryotic kingdom. Trends in Cell Biology 23, 345–356.

Hartung F, Suer S, Knoll A, Wurz-Wildersinn R, Puchta H. 2008. Topoisomerase 3α and RMI1 suppress somatic crossovers and are essential for resolution of meiotic recombination intermediates in Arabidopsis thaliana. PLoS Genetics 4.

Havekes FWJ, de Jong VH, Heyting C, Ramanna MS. 1994. Synapsis and chiasma formation in four meiotic mutants of tomato (Lycopersicon esculentum). Chromosome Research 2, 315–325.

He Y, Wang M, Dukowic-Schulze S, et al. 2017. Genomic features shaping the landscape of meiotic double-strand-break hotspots in maize. Proceedings of the National Academy of Sciences of the United States of America 114, 12231–12236.

Hesse S, Zelkowski M, Mikhailova EI, Keijzer CJ, Houben A, Schubert V. 2019. Ultrastructure and Dynamics of Synaptonemal Complex Components During Meiotic Pairing and Synapsis of Standard (A) and Accessory (B) Rye Chromosomes. 10.

Higgins JD, Armstrong SJ, Franklin FCH, Jones GH. 2004. The Arabidopsis MutS homolog AtMSH4 functions at an early step in recombination: evidence for two classes of recombination in Arabidopsis. Genes & development 18, 2557–70.

Higgins EE, Howell EC, Armstrong SJ, Parkin IAP. 2021. A major quantitative trait locus on chromosome A9, BnaPh1, controls homoeologous recombination in Brassica napus. New Phytologist 229, 3281–3293.

Higgins JD, Perry RM, Barakate A, Ramsay L, Waugh R, Halpin C, Armstrong SJ, Franklin FCH. 2012. Spatiotemporal asymmetry of the meiotic program underlies the predominantly distal distribution of meiotic crossovers in barley. Plant Cell 24, 4096–4109.

Higgins JD, Sanchez-Moran E, Armstrong SJ, Jones GH, Franklin FCH. 2005. The Arabidopsis synaptonemal complex protein ZYP1 is required for chromosome synopsis and normal fidelity of crossing over. Genes and Development 19, 2488–2500.

Hinch AG, Becker PW, Li T, et al. 2020. The Configuration of RPA, RAD51, and DMC1 Binding in Meiosis Reveals the Nature of Critical Recombination Intermediates. Molecular Cell 79, 689-701.e10.
Hong L, Tang D, Zhu K, Wang K, Li M, Cheng Z. 2012. Somatic and reproductive cell
development in rice anther is regulated by a putative glutaredoxin. Plant Cell 24, 577–588.

Jenczewski E, Eber F, Grimaud A, Huet S, Lucas MO, Monod H, Chèvre AM. 2003.
PrBn, a major gene controlling homeologous pairing in oilseed rape (Brassica napus)
haploids. Genetics 164, 645–653.

Ji J, Tang D, Shen Y, Xue Z, Wang H, Shi W, Zhang C, Du G, Li Y, Cheng Z. 2016.
P31comet, a member of the synaptonemal complex, participates in meiotic DSB formation in
rice. Proceedings of the National Academy of Sciences of the United States of America 113,
10577–10582.

Ji J, Tang D, Wang M, Li Y, Zhang L, Wang K, Li M, Cheng Z. 2013. MRE11 is required
for homologous synapsis and DSB processing in rice meiosis. Chromosoma 122, 363–376.

Jing J, Zhang T, Wang Y, Cui Z, He Y. 2019. ZmRAD51C is Essential for Double-Strand
Break Repair and Homologous Recombination in Maize Meiosis. International journal of
molecular sciences 20, 5513.

Jongedijk E, Ramanna MS, Sawor Z, Hermsen JGT. 1991. Formation of first division
restitution (FDR) 2n-megasporophylls through pseudohomotypic division in ds-1 (desynapsis)
mutants of diploid potato: routine production of tetraploid progeny from 2xFDR × 2xFDR
crosses. Theoretical and Applied Genetics 82, 645–656.

Joyce EF, McKim KS. 2009. Drosophila PCH2 Is Required for a Pachytene Checkpoint
That Monitors Double-Strand-Break-Independent Events Leading to Meiotic Crossover
Formation. 181, 39–51.

Kelliher T, Walbot V. 2012. Hypoxia triggers meiotic fate acquisition in maize. Science 337,
345–348.

Khanday I, Skinner D, Yang B, Mercier R, Sundaresan V. 2019. A male-expressed rice
embryogenic trigger redirected for asexual propagation through seeds. Nature 565, 91–95.

Kianian PMA, Wang M, Simons K, et al. 2018. High-resolution crossover mapping reveals
similarities and differences of male and female recombination in maize. Nature
Communications 9.

Kleckner N. 2006. Chiasma formation: Chromatin/axis interplay and the role(s) of the
synaptonemal complex. Chromosoma 115, 175–194.

Kou Y, Chang Y, Li X, Xiao J, Wang S. 2012. The rice RAD51C gene is required for the
meiosis of both female and male gametocytes and the DNA repair of somatic cells. Journal
of Experimental Botany.

Lambing C, Kuo PC, Tock AJ, Topp SD, Henderson IR. 2020. ASY1 acts as a dosage-
dependent antagonist of telomere-led recombination and mediates crossover interference in
Arabidopsis. Proceedings of the National Academy of Sciences of the United States of
America 117, 13647–13658.
Lambing C, Osman K, Nuntasootorn K, et al. 2015. Arabidopsis PCH2 Mediates Meiotic Chromosome Remodeling and Maturation of Crossovers. PLoS Genetics 11, e1005372.

Lhuissier FGP, Offenberg HH, Wittich PE, Vischer NOE, Heyting C. 2007. The mismatch repair protein MLH1 marks a subset of strongly interfering crossovers in tomato. The Plant cell 19, 862–876.

Li Y, Qin B, Shen Y, Zhang F, Liu C, You H, Du G, Tang D, Cheng Z. 2018. HEIP1 regulates crossover formation during meiosis in rice. Proceedings of the National Academy of Sciences of the United States of America.

Liu Z, Adamczyk K, Manzanares-Dauleux M, Eber F, Lucas M-O, Delourme R, Chèvre AM, Jenczewski E. 2006. Mapping PrBn and Other Quantitative Trait Loci Responsible for the Control of Homeologous Chromosome Pairing in Oilseed Rape (Brassica napus L.) Haploids. Genetics 174, 1583–1596.

Liu H, Nonomura KI. 2016. A wide reprogramming of histone H3 modifications during male meiosis I in rice is dependent on the Argonaute protein MEL1. Journal of Cell Science 129, 3553–3561.

Lloyd A, Morgan C, Franklin FCH, Bomblies K. 2018. Plasticity of meiotic recombination rates in response to temperature in arabidopsis. Genetics 208, 1409–1420.

Luo Q, Li Y, Shen Y, Cheng Z. 2014. Ten Years of Gene Discovery for Meiotic Event Control in Rice. Journal of Genetics and Genomics 41, 125–137.

Luo C, Li X, Zhang Q, Yan J. 2019. Single gametophyte sequencing reveals that crossover events differ between sexes in maize. Nature Communications 10.

Luo Q, Tang D, Wang M, Luo W, Zhang L, Qin B, Shen Y, Wang K, Li Y, Cheng Z. 2013. The Role of OsMSH5 in Crossover Formation during Rice Meiosis. Molecular Plant 6, 729–742.

Lynn A, Soucek R, Börner GV. 2007. ZMM proteins during meiosis: crossover artists at work. Chromosome research : an international journal on the molecular, supramolecular and evolutionary aspects of chromosome biology 15, 591–605.

Ma J, Skibbe DS, Fernandes J, Walbot V. 2008. Male reproductive development: Gene expression profiling of maize anther and pollen ontogeny. Genome Biology 9, R181.

de Maagd RA, Loonen A, Chouaref J, Pelé A, Meijer-Dekens F, Fransz P, Bai Y. 2020. CRISPR/Cas inactivation of RECQ4 increases homeologous crossovers in an interspecific tomato hybrid. Plant Biotechnology Journal 18, 805–813.

Mao B, Zheng W, Huang Z, et al. 2021. Rice MutLy, the MLH1–MLH3 heterodimer, participates in the formation of type I crossovers and regulation of embryo sac fertility. Plant Biotechnology Journal.

Marand AP, Jansky SH, Zhao H, et al. 2017. Meiotic crossovers are associated with open chromatin and enriched with Stowaway transposons in potato. Genome Biology 18, 1–16.

Marand AP, Zhao H, Zhang W, Zeng Z, Fang C, Jianga J. 2019. Historical meiotic
crossover hotspots fueled patterns of evolutionary divergence in rice. Plant Cell 31, 645–662.

Marston AL, Amon A. 2004. Meiosis: Cell-cycle controls shuffle and deal. Nature Reviews Molecular Cell Biology 5, 983–997.

Martini E, Diaz RL, Hunter N, Keeney S. 2006. Crossover homeostasis in yeast meiosis. Cell 126, 285–95.

Mason AS, Nelson MN, Yan G, Cowling WA. 2011. Production of viable male unreduced gametes in Brassica interspecific hybrids is genotype specific and stimulated by cold temperatures. BMC Plant Biology 11, 103.

Mercier R, Armstrong SJ, Horlow C, Jackson NP, Makaroff CA, Vezon D, Pelletier G, Jones GH, Franklin FCH. 2003. The meiotic protein SWI1 is required for axial element formation and recombination initiation in Arabidopsis. Development 130, 3309–3318.

Mercier R, Mézard C, Jencczewski E, Macaisne N, Grelon M. 2015. The Molecular Biology of Meiosis in Plants. Annual Review of Plant Biology 66, 297–327.

Mézard C, Tagliaro Jahns M, Grelon M. 2015. Where to cross? New insights into the location of meiotic crossovers. Trends in Genetics 31, 393–401.

Miao C, Tang D, Zhang H, Wang M, Li Y, Tang S, Yu H, Gu M, Cheng Z. 2013. Central region component1, a novel synaptonemal complex component, is essential for meiotic recombination initiation in RiceC. Plant Cell 25.

Mieulet D, Aubert G, Bres C, et al. 2018. Unleashing meiotic crossovers in crops. Nature Plants 4, 1010–1016.

Mieulet D, Jolivet S, Rivard M, et al. 2016. Turning rice meiosis into mitosis. Cell Research 26, 1242–1254.

Morata J, Tormo M, Alexiou KG, Vives C, Ramos-Onsins SE, Garcia-Mas J, Casacuberta JM. 2018. The Evolutionary Consequences of Transposon-Related Pericentromer Expansion in Melon (R Cordaux, Ed.). Genome Biology and Evolution 10, 1584–1595.

De Muyt A, Pereira L, Vezon D, et al. 2009. A High Throughput Genetic Screen Identifies New Early Meiotic Recombination Functions in Arabidopsis thaliana (GP Copenhaver, Ed.). PLoS Genetics 5, e1000654.

De Muyt A, Vezon D, Gendrot G, Gallois JL, Stevens R, Grelon M. 2007. AtPRD1 is required for meiotic double strand break formation in Arabidopsis thaliana. EMBO Journal 26, 4126–4137.

Nelms B, Walbot V. 2019. Defining the developmental program leading to meiosis in maize. Science 364, 52–56.

Nonomura KI, Eiguchi M, Nakano M, Takashima K, Komeda N, Fukuchi S, Miyazaki S, Miyao A, Hirochika H, Kurata N. 2011. A novel RNA-recognition-motif protein is required for premeiotic G1/s-phase transition in rice (Oryza sativa L.). PLoS Genetics 7.
Nonomura KI, Morohoshi A, Nakano M, Eiguchi M, Miyao A, Hirochika H, Kurata N. 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.

Nonomura KI, Nakano M, Fukuda T, Eiguchi M, Miyao A, Hirochika H, Kurata N. 2004. The novel gene Homologous Pairing Aberration In Rice Meiosis1 of rice encodes a putative coiled-coil protein required for homologous chromosome pairing in meiosis. Plant Cell 16, 1008–1020.

Olivier M, Da Ines O, Amiard S, Serra H, Goubely C, White CI, Gallego ME. 2016. The structure-specific endonucleases MUS81 and SEND1 are essential for telomere stability in arabidopsis. Plant Cell.

Pan J, Sasaki M, Kniewel R, et al. 2011. A hierarchical combination of factors shapes the genome-wide topography of yeast meiotic recombination initiation. Cell 144, 719–31.

Pawlowski WP, Golubovskaya IN, Timofejeva L, Meeley RB, Sheridan WF, Cande WZ. 2004. Coordination of Meiotic Recombination, Pairing, and Synapsis by PHS1. Science 303, 89–92.

Pawlowski WP, Golubovskaya IN, Zacheus Cande W. 2003. Altered nuclear distribution of recombination protein RAD51 in maize mutants suggests the involvement of RAD51 in meiotic homology recognition. Plant Cell 15, 1807–1816.

Pawlowski WP, Wang CJR, Golubovskaya IN, Szymaniak JM, Shi L, Hamant O, Zhu T, Harper L, Sheridan WF, Cande WZ. 2009. Maize AMEIOTIC1 is essential for multiple early meiotic processes and likely required for the initiation of meiosis. Proceedings of the National Academy of Sciences of the United States of America.

Pelé A, Falque M, Trotoux G, et al. 2017. Amplifying recombination genome-wide and reshaping crossover landscapes in Brassicas. (K Bomblies, Ed.). PLoS genetics 13, e1006794.

Pesin and Orr-Weaver. 2010. Regulation of APC/C Activators in Mitosis and Meiosis Jillian. 48, 1–6.

Phillips D, Jenkins G, Macaulay M, Nibau C, Wnetrzak J, Fallding D, Colas I, Oakey H, Waugh R, Ramsay L. 2015. The effect of temperature on the male and female recombination landscape of barley. New Phytologist 208, 421–429.

Pradillo M, López E, Linacero R, Romero C, Cuñado N, Sánchez-Morán E, Santos JL. 2012. Together yes, but not coupled: new insights into the roles of RAD51 and DMC1 in plant meiotic recombination. The Plant Journal 69, 921–933.

Prusicki MA, Keizer EM, Van Rosmalen RP, Komaki S, Seifert F, Müller K, Wijnker E, Fleck C, Schnittger A. 2019. Live cell imaging of meiosis in arabidopsis thaliana. eLife 8.

Ravi M, Marimuthu MPA, Siddiqi I. 2008. Gamete formation without meiosis in Arabidopsis. Nature 451, 1121–1124.

Ren L, Tang D, Zhao T, et al. 2018. OsSPL regulates meiotic fate acquisition in rice. New Phytologist 218, 789–803.
Rey MD, Martín AC, Higgins J, Swarbreck D, Uauy C, Shaw P, Moore G. 2017. Exploiting the ZIP4 homologue within the wheat Ph1 locus has identified two lines exhibiting homoeologous crossover in wheat-wild relative hybrids. Molecular Breeding.

Rommel Fuentes R, Hesselink T, Nieuwenhuis R, et al. 2020. Meiotic recombination profiling of interspecific hybrid F1 tomato pollen by linked read sequencing. Plant Journal 102, 480–492.

Roncere A, Doutriaux MP, Golubovskaya IN, Pawlowski WP. 2009. PHS1 regulates meiotic recombination and homologous chromosome pairing by controlling the transport of RAD50 to the nucleus. Proceedings of the National Academy of Sciences of the United States of America 106, 20121–20126.

Rowan BA, Heavens D, Feuerborn TR, Tock AJ, Henderson IR, Weigel D. 2019. An Ultra High-Density Arabidopsis thaliana Crossover. Genetics 213, 771–787.

Rowan BA, Patel V, Weigel D, Schneeberger K. 2015. Rapid and inexpensive whole-genome genotyping-by-sequencing for crossover localization and fine-scale genetic mapping. G3: Genes, Genomes, Genetics 5, 385–398.

Sanchez-Moran E, Armstrong SJ. 2014. Meiotic chromosome synapsis and recombination in Arabidopsis thaliana: New ways of integrating cytological and molecular approaches. Chromosome Research 22, 179–190.

Santos T de los, Hunter N, Lee C, Larkin B, Loidl J, Hollingsworth NM. 2003. The Mus81/Mms4 Endonuclease Acts Independently of Double-Holliday Junction Resolution to Promote a Distinct Subset of Crossovers During Meiosis in Budding Yeast. Genetics 164, 81 LP – 94.

Schnable PS, Pasternak S, Liang C, et al. 2009. The B73 Maize Genome: Complexity, Diversity, and Dynamics. Science 326, 1112–1115.

Schröpfer S, Kobbe D, Hartung F, Knoll A, Puchta H. 2013. Defining the roles of the N-terminal region and the helicase activity of RECQ4A in DNA repair and homologous recombination in Arabidopsis. Nucleic acids research 42, 1684–1697.

Séguéla-Arnaud M, Crismani W, Larchevêque C, et al. 2015. Multiple mechanisms limit meiotic crossovers: TOP3α and two BLM homologs antagonize crossovers in parallel to FANCM. 112, 4713–4718.

Serra H, Svačina R, Baumann U, Whitford R, Sutton T, Bartoš J, Sourdille P. 2021. Ph2 encodes the mismatch repair protein MSH7-3D that inhibits wheat homoeologous recombination. Nature Communications 12, 803.

Shao T, Tang D, Wang K, Wang M, Che L, Qin B, Yu H, Li M, Gu M, Cheng Z. 2011. Osrec8 is essential for chromatid cohesion and metaphase i monopolar orientation in rice meiosis. Plant Physiology 156, 1386–1396.

Shi J, Wolf SE, Burke JM, Presting GG, Ross-Ibarra J, Dawe RK. 2010. Widespread Gene Conversion in Centromere Cores (HS Malik, Ed.). PLoS Biology 8, e1000327.

Si W, Yuan Y, Huang J, Zhang X, Zhang Y, Zhang Y, Tian D, Wang C, Yang Y, Yang S.
2015. Widely distributed hot and cold spots in meiotic recombination as shown by the sequencing of rice F2 plants. New Phytologist 206, 1491–1502.

Sidhu GK, Fang C, Olson MA, Falque M, Martin OC, Pawlowski WP. 2015. Recombination patterns in maize reveal limits to crossover homeostasis. Proceedings of the National Academy of Sciences of the United States of America 112, 15982–15987.

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

de Storme N, Copenhagen GP, Geelen D. 2012. Production of diploid male gametes in Arabidopsis by cold-induced Destabilization of postmeiotic radial microtubule arrays. Plant Physiology 160, 1808–1826.

Sun H, Rowan BA, Flood PJ, Brandt R, Fuss J, Hancock AM, Michelmore RW, Huettel B, Schneeberger K. 2019. Linked-read sequencing of gametes allows efficient genome-wide analysis of meiotic recombination. Nature Communications 10, 1–9.

Tang Y, Yin Z, Zeng Y, Zhang Q, Chen L, He Y, Lu P, Ye D, Zhang X. 2017. MTOPVIB interacts with AtPRD1 and plays important roles in formation of meiotic DNA double-strand breaks in Arabidopsis. Scientific Reports 7.

Tanneti NS, Landy K, Joyce EF, McKim KS. 2011. A pathway for synapsis initiation during zygotene in Drosophila oocytes. Curr Biol 21, 1852–1857.

Underwood CJ, Choi K. 2019. Heterogeneous transposable elements as silencers, enhancers and targets of meiotic recombination. Chromosoma 128, 279–296.

Underwood CJ, Choi K, Lambing C, et al. 2018. Epigenetic activation of meiotic recombination near Arabidopsis thaliana centromeres via loss of H3K9me2 and non-CG DNA methylation. Genome research 28, 519–531.

Vrielynck N, Chambon A, Vezon D, Pereira L, Chelysheva L, De Muyt A, Mégard C, Mayer C, Grelon M. 2016. A DNA topoisomerase VI-like complex initiates meiotic recombination. Science 351, 939–943.

Wang Y, Copenhagen GP. 2018. Meiotic Recombination: Mixing It Up in Plants. Annual Review of Plant Biology 69, 577–609.

Wang H, Hu Q, Tang D, Liu X, Du G, Shen Y, Li Y, Cheng Z. 2016. OsDMC1 is not required for homologous pairing in rice meiosis. Plant Physiology 171, 230–241.

Wang Y, Jiang L, Zhang T, Jing J, He Y. 2018. ZmCom1 is required for both mitotic and meiotic recombination in maize. Frontiers in Plant Science.

Wang C, Liu Q, Shen Y, et al. 2019. Clonal seeds from hybrid rice by simultaneous genome engineering of meiosis and fertilization genes. Nature Biotechnology 37, 283–286.

Wang M, Tang D, Luo Q, Jin Y, Shen Y, Wang K, Cheng Z. 2013. BRK1, a Bub1-related kinase, is essential for generating proper tension between homologous kinetochores at metaphase i of rice meiosis. Plant Cell 24, 4961–4973.
Wang K, Tang D, Wang M, et al. 2009. MER3 is required for normal meiotic crossover formation, but not for presynaptic alignment in rice. Journal of Cell Science.

Wang M, Tang D, Wang K, Shen Y, Qin B, Miao C, Li M, Cheng Z. 2011a. OsSGO1 maintains synaptonemal complex stabilization in addition to protecting centromeric cohesion during rice meiosis. Plant Journal 67, 583–594.

Wang K, Wang M, Tang D, Shen Y, Miao C, Hu Q, Lu T, Cheng Z. 2012. The Role of Rice HEI10 in the Formation of Meiotic Crossovers. PLOS Genetics 8, e1002809.

Wang K, Wang M, Tang D, Shen Y, Qin B, Li M, Cheng Z. 2011b. PAIR3, an axis-associated protein, is essential for the recruitment of recombination elements onto meiotic chromosomes in rice. Mol Biol Cell 22, 12–19.

Wang M, Wang K, Tang D, Wei C, Li M, Shen Y, Chi Z, Gu M, Cheng Z. 2010. The central element protein ZEP1 of the synaptonemal complex regulates the number of crossovers during meiosis in rice. Plant Cell 22, 417–430.

Watanabe Y. 2005. Shugoshin: Guardian spirit at the centromere. Current Opinion in Cell Biology 17, 590–595.

Whitbread AL, Dorn A, Röhrig S, Puchta H. 2021. Different functional roles of RTR complex factors in DNA repair and meiosis in Arabidopsis and tomato. The Plant Journal, tpj.15211.

Wijnker E, van Dun K, de Snoo CB, Lelivelt CLC, Keurentjes JJB, Naharudin NS, Ravi M, Chan SWL, de Jong H, Dirks R. 2012. Reverse breeding in Arabidopsis thaliana generates homozygous parental lines from a heterozygous plant. Nature genetics 44, 467–70.

Wijnker E, James GV, Ding J, et al. 2013. The genomic landscape of meiotic crossovers and gene conversions in Arabidopsis thaliana. eLife 2013, 1–22.

Wolfgruber TK, Sharma A, Schneider KL, et al. 2009. Maize Centromere Structure and Evolution: Sequence Analysis of Centromeres 2 and 5 Reveals Dynamic Loci Shaped Primarily by Retrotransposons (HS Malik, Ed.). PLoS Genetics 5, e1000743.

Wu Z, Ji J, Tang D, Wang H, Shen Y, Shi W, Li Y, Tan X, Cheng Z, Luo Q. 2015. OsSDS is essential for DSB formation in rice meiosis. Frontiers in Plant Science 6.

Xin Q, Shen Y, Li X, et al. 2016. MS5 mediates early meiotic progression and its natural variants may have applications for hybrid production in Brassica napus. Plant Cell 28, 1263–1278.

Xue Z, Liu C, Shi W, et al. 2019. OsMTOPVIB is required for meiotic bipolar spindle assembly. Proceedings of the National Academy of Sciences of the United States of America 116, 15967–15972.

Xue M, Wang J, Jiang L, Wang M, Wolfe S, Pawlowski WP, Wang Y, He Y. 2018. The Number of Meiotic Double-Strand Breaks Influences Crossover Distribution in Arabidopsis. 30, 2628–2638.
Yang C, Hamamura Y, Sofroni K, Böwer F, Stolze SC, Nakagami H, Schnittger A. 2019. SWITCH 1/DYAD is a WINGS APART-LIKE antagonist that maintains sister chromatid cohesion in meiosis. Nature Communications 10, 1–15.

Yang WC, Ye D, Xu J, Sundaresan V. 1999. The SPOROCYTELESS gene of Arabidopsis is required for initiation of sporogenesis and encodes a novel nuclear protein. Genes and Development 13, 2108–2117.

Yelina NE, Gonzalez-Jorge S, Hirsz D, Yang Z, Henderson IR. 2021. CRISPR targeting of MEIOTIC-TOPOISOMERASE VIB-dCas9 to a recombination hotspot is insufficient to increase crossover frequency in Arabidopsis. bioRxiv, 2021.02.01.429210.

Youds JL, Boulton SJ. 2011. The choice in meiosis - Defining the factors that influence crossover or non-crossover formation. Journal of Cell Science.

Yuan W, Li X, Chang Y, Wen R, Chen G, Zhang Q, Wu C. 2009. Mutation of the rice gene PAIR3 results in lack of bivalent formation in meiosis. Plant Journal 59, 303–315.

Zapata L, Ding J, Willing E-M, et al. 2016. Chromosome-level assembly of Arabidopsis thaliana Ler reveals the extent of translocation and inversion polymorphisms. Proceedings of the National Academy of Sciences of the United States of America 113, E4052-60.

Zhang H, Dawe RK. 2012. Total centromere size and genome size are strongly correlated in ten grass species. Chromosome Research 20, 403–412.

Zhang L, Tang D, Luo Q, Chen X, Wang H, Li Y, Cheng Z. 2014. Crossover Formation During Rice Meiosis Relies on Interaction of OsMSH4 and OsMSH5. 198, 1447–1456.

Zhou L, Han J, Chen Y, Wang Y, Liu YG. 2017. Bivalent formation 1, a plant-conserved gene, encodes an OmpH/coiled-coil motif-containing protein required for meiotic recombination in rice. Journal of Experimental Botany 68, 2163–2174.

Ziolkowski PA, Underwood CJ, Lambing C, et al. 2017. Natural variation and dosage of the HEI10 meiotic E3 ligase control Arabidopsis crossover recombination. Genes & Development 31, 306–317.
| Meiotic pathway         | Gene name    | Nic | Maize | Tomato | Wheat | Brassica | Barley | Arabidopsis | Arabidopsis Gene ID |
|-------------------------|--------------|-----|-------|--------|-------|----------|--------|--------------|---------------------|
| Meiosis initiation      | AM1/SWI1/DYAD| ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT5G51330    |                     |
|                         | SPL          | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT4G27330    |                     |
|                         | MIL1         | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT5G14070    |                     |
|                         | MEL1         | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT4G37590    |                     |
|                         | MEL2         | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT5G67440    |                     |
|                         | AGOS/AGO104  | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT5G21150    |                     |
|                         | DTM1         | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT1G34640    |                     |
| Sister chromatid cohesion | SYN1/REC8/AFD1 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | AT5G06490 |                     |
|                         | SMC2         | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT5G62410    |                     |
|                         | SMC3         | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT2G27170    |                     |
|                         | SMC4         | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT5G48660    |                     |
|                         | SCC4         | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT5G51340    |                     |
|                         | SMC6         | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT5G07660    | AT5G61460           |
| Centromeric cohesion    | SGO1, SGO2   | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT3G10440    | AT5G04320           |
| DSB formation           | SPO11-1      | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT3G13170    |                     |
|                         | SPO11-2      | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT1G63990    |                     |
|                         | PRD1         | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT4G14180    |                     |
|                         | PRD3/PAIR1   | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT1G01690    |                     |
|                         | MTOPVIB      | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT1G60460    |                     |
|                         | P31COMET/BVF1| ✓   |       | ✓      | ✓     | ✓        | ✓      | AT1G01690    |                     |
|                         | RDR6         | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT3G49500    |                     |
|                         | SDS          | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT1G14750    |                     |
|                         | SPO11-4*     | ✓   |       | ✓      | ✓     | ✓        | ✓      | No ortholog  |                     |
|                         | PHST*        | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT1G10710    |                     |
|                         | RH24/LEPT01/AR R12* | ✓ |       | ✓      | ✓     | ✓        | ✓      | AT2G25180    |                     |
| DSB processing          | MRE11        | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT5G54260    |                     |
|                         | COM1         | ✓   | ✓     | ✓      | ✓     | ✓        | ✓      | AT3G52115    |                     |
|                         | RPA/RPA1a    | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT2G06510    |                     |
| DSB repair              | ZYGO1        | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT5G36000    | AT5G61730           |
|                         | MOF          | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT1G69630    |                     |
|                         | ATM          | ✓   |       | ✓      | ✓     | ✓        | ✓      | AT3G48190    |                     |
| Gene     | | | | Gene ID |
|----------|--------|--------|--------|----------|
| RAD1     | √      |        |        | AT4G17760 |
| BRCA2    | √      |        |        | AT4G00020 |
|          |        |        |        | AT5G01630 |
| RAD17    | √      |        |        | AT5G66130 |
| RAD51A   | √      |        |        | AT5G20850 |
| RAD51B   | √      |        |        | AT2G28560 |
| RAD51C   | √      |        |        | AT2G45280 |
| RAD51D   | √      |        |        | AT1G07745 |
| XRCC3    | √      |        |        | AT5G57450 |
| DMC1     | √      |        |        | AT3G22880 |
| FIGL1/FIGNL1 | √ | √ |        | AT3G27120 |
| GEN1     | √      |        |        | AT1G01880 |
|          |        |        |        | AT3G48900 |
| HCP2/AMP2| √      |        |        | AT1G13330 |
| MS5      | √      |        |        | AT4G09000 |
| ASY1/PAIR1 | √ |        |        | AT1G67370 |
| ASY3/DSY2/PAIR3 | √ | √ |        | AT1G13330 |
| ZYP1/ZEPI | √ |        |        | AT1G22260 |
| PCH2/CRC1 | √ |        |        | AT1G04650 |
| MEICA1/FLIP | √ |        |        | AT1G04650 |
| SUN1     | √      |        |        | AT5G04990 |
| SUN2     | √      |        |        | AT3G10730 |
| PSS1     | √      |        |        | AT3G63480 |
| AGG1     | √      |        |        | AT2G30480 |
| HUS1     | √      |        |        | AT1G52530 |
| MLH3     | √      |        |        | AT4G35520 |
| MLH1     | √      |        |        | AT4G09140 |
| MSH2     | √      |        |        | AT3G18524 |
| MSH4     | √      | √      |        | AT4G17380 |
| MSH5     | √      |        |        | AT3G20475 |
| MSH7     | √      | √      |        | AT3G24495 |
| HEI10/ZIP3 | √ |        |        | AT1G53490 |
| SHOC1/ZIP2 | √ |        |        | AT5G52290 |
| PTD1     | √      |        |        | AT1G12790 |
| MER3/RMC1/RCK | √ |        |        | AT3G27730 |

**Synaptonemal complex**

**Crossover formation**

**Class I crossover**
| Non-crossover repair | | | | | |
|----------------------|---|---|---|---|---|
| SPO22/ZIP4/PH1       | √ | √ | √ | √ | AT5G48390 |
| RPA1C                | √ | | | √ | AT5G45400 |
| RPA2C                | √ | | | | AT3G02920 |
| HEIP1                | √ | | | | AT2G30480 |
| MSH6                 | √ | | | √ | AT4G02070 |
| TOP3a                | | √ | √ | | AT5G63920 |
| RM1                  | | √ | | √ | AT5G63540 |
| FANCM                | √ | √ | √ | | AT1G35530 |
| RECQ4                | √ | √ | | √ | AT1G10990
|                     |   |   |   | AT1G66930 |
| Cell cycle regulator | | | | | |
| CSD1                 | √ | | | √ | AT3G57860 |
| DLC1                 | | √ | | | AT2G25180 |
| RSS1                 | √ | | | | AT3G14910 |
| Chromosome           | | | | | |
| segmentation         | | | | | |
| CENH3                | √ | | | √ | AT1G01370 |
| MLK52/SINE1          | √ | | | | AT1G54385 |
| DV1/ATK1             | √ | | | √ | AT4G21270 |
| MIS12                | √ | | | | AT5G35520 |
| BRK1                 | √ | | | | AT2G20635 |
| Meiotic cytokinesis  | | | | | |
| DCM1                 | | | | √ | AT1G21580 |

**Table 1. Cloned meiotic mutants characterized in crop species**

This table consists of all the cloned meiotic mutants (and in some instances RNAi knockdown lines) as of February 28 2021 in six crop plants (rice, maize, tomato, wheat, brassica and barley). Each cell is hyperlinked to the PubMed (https://pubmed.ncbi.nlm.nih.gov/) or Europe PMC (https://europepmc.org/) page of the original publication. Where a mutant has been characterized in Arabidopsis the original study is also hyperlinked and the Arabidopsis gene is hyperlinked to TAIR (https://www.arabidopsis.org/). It should be noted this is not an exhaustive collection of all Arabidopsis meiotic mutants. Those genes marked with an asterisk (*) have defects in DSB formation but their roles are not completely clear.
Fig. 1. Characteristics of different plant model systems for meiosis research

The genome size, chromosome number, ploidy and meiotic time of nine different plant species are presented. The species are Arabidopsis (Arabidopsis thaliana), barley (Hordeum vulgare), rye (Secale cereale), maize (Zea mays), tomato (Solanum lycopersicum), potato (Solanum tuberosum), rice (Oryza sativa), brassicas (Brassica oleracea, Brassica rapa and Brassica napus) and bread wheat (Triticum aestivum). Mbp = Mega base pairs, Gbp = Giga base pairs, h = hours. The duration of meiosis in different species came from the papers (Bennett, 1977; Armstrong et al., 2003; Ma et al., 2008; Sanchez-Moran and Armstrong, 2014). Created with BioRender.com.
A) cM/Mbp on Arabidopsis chromosome 3 (Arabidopsis thaliana Col-0 × Ler F2, population with 192 individuals from published sequencing data (Choi et al., 2016) followed by calling of CO locations using TIGER (Rowan et al., 2015), 0.1333 Mbp sliding window). B) cM/Mbp on rice chromosome 1 (Oryza sativa ssp. japonica cv. Nipponbare × O. longistaminata F2, population with 241 individuals selected from published genotyping data (Furuta et al., 2017), 0.25 Mbp sliding window). C) cM/Mbp on maize chromosome 7 (Zea mays ssp. mays cv. B73 × (B73 × Mo17) Male BC1, population with 135 individuals from published sequencing data (Kianian et al., 2018), 1 Mbp sliding window). D) cM/Mbp on wheat chromosome 3B (SSD population derived from a Triticum aestivum L. Chinese Spring × Renan cross with 305 individuals from published genotyping data (Choulet et al., 2014), 4 Mbp sliding window). The grey shading beneath each chromosome represent the centromeres, which we genetically defined as the contiguous windows lacking COs that flank published centromere co-ordinates from each species (Cheng et al., 2002; Wolfgruber et al., 2009; Choulet et al., 2014; Underwood et al., 2018) The red dashed lines represent the mean cM/Mbp value for each chromosome. Plots were produced using ggplot2 within R version 4.0.3.