

# Meiosis: vive la difference!

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The application of molecular and modern cell biological techniques is beginning to show that the classical picture of the meiotic process is an oversimplification. The comparison of different species and analysis of mutants have recently demonstrated that many of the features previously thought to be an integral part of meiosis can be altered in their timing or even entirely dispensed with. In plants, differences in the meiotic pathway have been observed, by using methods for 3-D optical imaging, between the polyploids maize and wheat. The fact that two such closely related species differ may be the result of different mechanisms for dealing with polyploidy or may be species differences, but shows that a detailed understanding of the process in the particular species of interest is necessary.

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### Abbreviations

**DSB** double-stranded break  
**SC** synaptonemal complex  
**SPB** spindle pole body

### Introduction

Meiosis — the process by which reductional cell division leads to haploid gametes — is central to the life cycle of all sexual eukaryotic organisms. Meiosis has been described by cytologists over many decades, but recently modern cell biological and genetic techniques have been applied to the analysis of the fundamental molecular mechanisms involved (reviews [1,2\*,3]). Detailed studies of meiosis have been limited to rather few species in the past, and the idea has developed that, as with mitosis, the fundamental mechanism is universally conserved across sexual higher eukaryotes, and thus that the few species studied are good models for all other species. As aspects of meiosis are dissected in detail in different organisms, however, it is becoming apparent that many of the features classically defined as being common to meiosis can either be dispensed with or substantially modified.

The recent progress in unravelling the cellular mechanisms of meiosis has depended to a large extent on the application of 3-D optical methods — either image deconvolution coupled with conventional fluorescence microscopy [4\*\*] or confocal fluorescence microscopy — to structurally well-preserved meiocytes and their precursors [5\*,6\*\*]. Often, fluorescent *in situ* hybridization has been used to mark specific chromosomes or chromosomal locations such as centromeres and telomeres.

The position of a cell in developing plant organs is the primary determinant of whether that cell becomes a meiocyte [7]. It has been apparent for some time that meiocytes are not irreversibly destined to enter meiotic prophase, as microsporocytes of *Lilium* and *Trillium* from pre-meiotic interphase revert to the mitotic cycle when cultured [8,9]. In plants, the functional definition of what is a meiotic process, rather than a somatic mitotic process, is not always clear. For example, tapetal cells within a developing wheat anther undergo homologue association, which is normally considered a meiotic process, but do not progress to meiotic prophase.

The manipulation of the process of meiosis in plants has major implications for commercial plant breeding. It is, therefore, important to gauge how relevant data from ‘model’ species are to any crop species being studied. In this review we summarize recent developments in the analysis of meiosis in plants, and highlight similarities and differences both within the plant kingdom and across the entire phylogenetic range.

### The classical picture

At the start of meiosis the chromosomes are replicated and the sister chromatids remain associated. In the first stage of meiotic prophase, leptotene, condensed threads of meiotic chromosomes first become visible [1,2\*,3]. The homologous chromosomes find and recognize each other and then associate. During zygotene, the homologues become intimately associated forming long thread-like synaptonemal complexes (SCs). By pachytene, SCs have been fully formed. Recombination is initiated during meiosis by forming double-stranded breaks (DSBs), followed by 5′ end cleavage to leave 3′ overhangs leading to strand invasion and formation of pairs of cross-strand exchanges (Holliday junctions). These structures may be resolved without cross-over (also called gene conversion), where the flanking chromosome arms are not exchanged and only sequences between the two Holliday junctions are affected, or can result in cross-over where an exchange of the flanking arms of the chromosomes occurs. Each crossover event produces a connection, called a chiasma, between the two homologues. The homologues, now connected by chiasmata, then further condense to a more standard mitotic appearance during diplotene and diakinesis, and attach to the spindle as they approach metaphase I. The connections at the chiasmata, but not those at centromeres between sister chromatids, are broken as the cell enters anaphase I. Finally, the centromeric connections between chromatids are broken during meiosis II. There are two checkpoints currently known in meiosis: the first ensures that recombination events are completed before progression to metaphase I; the second ensures that all chromosomes are attached to the spindle at metaphase I, which is similar to an equivalent mitotic checkpoint.

## Homologue association

The logical minimum requirement, without which meiosis cannot occur, is that the homologues associate and then segregate. Segregation can be envisaged as an elaboration of the mitotic segregation mechanism, with an added level of control firstly to segregate homologues in anaphase I, leaving the inter-chromatid attachments intact, and secondly to segregate chromatids, as in mitosis, in anaphase II. As yet, however, we have little in the way of a conceptual framework for understanding the mechanism of association of homologues. Such a mechanism must include homologue recognition, which has been suggested to include either direct DNA sequence homology searching [3], or recognition of a chromosome 'landscape', involving higher level chromatin structure, possibly mediated by specific unknown protein interactions [10]. It must also include mechanisms for movement — initially of parts of chromosomes, and ultimately entire chromosomes alongside each other. The current view of chromosomes in somatic interphase is that they occupy distinct, non-overlapping territories. In some species, homology searching occurs in interphase, and a strict territorial organization of the chromosomes cannot be maintained during homology searching, since, whatever the mechanism of the homology searching, parts of different chromosomes need to interact with each other. Furthermore, homologues could easily be separated by many micrometres prior to association — an enormous distance at the molecular scale [11•].

At least two levels of association can be identified. First, homologous chromosomes can become located next to each other [3]; there is evidence that the initial interactions, in wheat and *Drosophila*, involve centromeric regions [12••]. This level of association has been observed prior to meiosis, but is also seen in other somatic cells. The second level is synapsis — a more intimate linkage of homologues, involving formation of the SC, which is specific to meiosis. The meiotic pathway of a species or mutant may involve either or both of these types of association.

It has been argued that homology searching involves double strand break formation and strand invasion. Non-homologous regions would interact only transiently, whereas interactions between homologous regions would be stabilised [3]. *S. cerevisiae* mutants deficient in DSB formation still undergo homologue association, however, albeit at a lower level than wild-type [13]. Moreover, *Drosophila* female mutants lacking DSB formation still align, associate and synapse [5•] their chromosomes. Thus association cannot absolutely require DSB formation. Rad51 is a protein involved in homologous pairing and DNA strand exchange in eukaryotes, and is homologous to the prokaryotic recA protein, which catalyses these reactions. Recent results from maize studies suggest that the recombination protein Rad51 may also be involved in homology searching (Franklin AE, McElver J, Sunjevaric I, Rothstein RJ, Bowen B, Cande WZ, personal communication).

In a number of species, including wheat ([12••]; Abranches R *et al.*, unpublished data), rye, *Drosophila* [14] and yeast [15•], the chromosomes are in a Rabl configuration prior to meiosis, that is, with the centromeres clustered at one pole and telomeres spread around the other pole. This is not absolutely required for meiosis, however, as other species, such as mouse and human, do not display a clear Rabl configuration [16]. The telomeres then cluster to form a structure often called the bouquet, which has been shown in maize to occur at the junction of leptotene and zygotene [4••,17]. Initial association of homologues in maize and human takes place at this stage, but the timing of both bouquet formation and chromosome association differs in other species.

In some species, the homologues can associate in somatic cell nuclei. For example, in *Drosophila* the homologues are associated in all somatic cells from the 14th division of embryogenesis; there is evidence that this association starts at the centromere and progresses down the chromosome arm [13]. In wheat, homologue association begins at a premeiotic stage in anther development, and homologues are associated in both meiocytes and the related somatic tapetal cells [12••,18]. The initial association seems to involve the centromeres, giving a V-shaped appearance to associating pairs of homologues and a haploid number of centromere sites. The meiocytes subsequently undergo telomere clustering/bouquet formation, but the tapetal cells do not. Thus, association itself cannot require telomere clustering/bouquet formation. In *Lilium*, centromeres also associate premeiotically, so that the haploid number of labelling sites is seen by immunocytochemical visualization of a meiotic histone [19••]. This occurs at a later premeiotic stage than in wheat, and as yet it is not known whether the rest of each chromosome associates at this stage, or just the centromeres.

In *S. cerevisiae* a significant level of pre-meiotic association is observed, but the level and significance of this association is still under debate [13,20]. In *S. pombe* the haploid parental sets have a centromere–telomere configuration with the centromeres located near the spindle pole body (SPB) [21•]. On induction of meiosis (conjugation/karyogamy), the telomeres and centromeres are attached to the same SPB. The centromeres detach from the SPB and the two sets of the telomeres associate in a single cluster. Thus in *S. pombe*, in contrast to wheat, it is the telomeres which lead chromosome movement.

It has been estimated that up to 50% of angiosperms are polyploid. This includes many important crop species such as hexaploid wheat. Each chromosome, however, only pairs with its ancestral homologue, and not with the closely related homoeologues. If homoeologues were to pair and undergo significant recombination, a polyploid genome could not be stably maintained. Previous studies have identified a locus (*Ph1*) as controlling the restriction of chromosome pairing to homologues in wheat. In contrast

Table 1

Summary of features of meiosis in different species and published mutants.

	Wheat	Maize	<i>Drosophila</i> female	<i>Drosophila</i> male	<i>S. cerevisiae</i>	<i>S. pombe</i>	Mammals
Pre-meiotic chromosome association	+	-	+	+	+	+	-
Pre-meiotic centromere grouping	+	?	+	+	+	+	-
Pre-meiotic telomere clustering	+	-	?	?	-	+	-
Meiotic telomere clustering	-	+	?	?	+	+	+
Synaptonemal complex	+	+	+	-	+ (-)	-	+
Double-stranded breaks	+	+	+	-	+ (-)	+	+
Chiasma formation	+	+	+	-	+ (-)	+	+
Recombination	+	+	+(-)	-	+ (-)	+	+

+, normally present; -, normally absent; (-), minus mutant reported; ?, unknown.

to the wild-type, in which homologues associate in pre-meiotic interphase, in wheat *Ph1* deletion mutants there is little pre-meiotic association [12\*\*]. Instead the homologues associate during meiotic prophase, but there is a degree of homoeologous association. Recent work suggests that the *Ph1* locus is involved in maintaining chromatin organization, and that deletion of the *Ph1* locus disrupts early homologue association [18] and leads to non-homologues associating. This misassociation is then largely resolved during the subsequent meiotic prophase (E Martinez-Perez, PJ Shaw, G Moore, unpublished data). It is also surprising and noteworthy that meiotic prophase is significantly shorter in polyploid plant species than in the related diploid species [22]. We hypothesize that early homologue association is necessary to maintain stable polyploidy. Thus, the lengthy homology searching has been accomplished in polyploid wheat before entry into meiotic prophase. In diploid species or mutants lacking this mechanism, homology searching has to take place during meiotic prophase, thus lengthening this stage.

### Meiotic prophase

In the classical picture, synapsis begins at zygotene and is complete at pachytene. The currently available evidence is consistent with synapsis requiring telomere clustering [2\*]; however, there is debate about the role of the SC in the meiotic process. In *S. cerevisiae*, *Zip2* mutants exhibit no SC formation but still undergo recombination [23\*]. The number of chiasmata observed in many species is one or two per chromosome arm. The occurrence of too many cross-overs can result in chromosome instability and breakage, and may cause steric problems during segregation. It has been argued that the SC is responsible for limiting the number of cross-overs/chiasmata formed — a phenomenon termed interference. *S. pombe* does not have SCs but has linear elements whose disruption cause problems in chromosome pairing and which may be partly equivalent to SCs [24]. The absence of conventional SCs in this species may explain the lack of cross-over interference, with some bivalents having as many as 11 exchange events. Similarly, *Aspergillus nidulans* also seems to lack SCs as well as cross-over interference and has a high level of exchanges [2\*]. Thus SC formation is not an absolute requirement for meiosis, but may modulate recombination.

Analysis of specific loci indicates that most recombination occurs within genic regions in maize [25\*\*]. The distribution of recombination on plant chromosomes is not random; there is a high level of exchanges in the distal regions of chromosomes which correlates with a higher gene density [26]. Again one must be cautious in generalising; in *C. elegans* exchange events occur mostly in gene-poor regions [27].

Male *Drosophila* chromosome pairing and segregation occur without either SC formation or recombination [28,29]. Furthermore, it appears that the ribosomal DNA is involved in pairing and segregation of the X and Y chromosomes [30]. In female *Drosophila* where recombination and SCs do occur, the fourth chromosome pair is achiasmatic but still segregates; association of these chromosomes seems to depend on centromeric heterochromatin [10]. In *S. cerevisiae* non-homologous chromosomes, introduced by crossing double monosomic lines, are also capable of association and segregation, probably interacting via centromeric or telomeric sequences [31]. Accurate segregation, therefore, is not dependent on extensive homology between partners.

### Conclusions

Although the classical features of meiosis are usually present, there are exceptions that show that many of these features can be dispensed with, and the relative timing of the various processes is variable. There is a clear mechanistic link between DSBs, recombination and chiasmata formation, but SC formation is not obligatory, and none of these is absolutely required for meiosis.

There is substantial information about the enzymes involved in recombination in *E. coli* and *S. cerevisiae*, and many of the genes are highly conserved. Several enzymes involved in recombination have been isolated in plant species, generally as homologues to yeast or mammalian proteins [32,33\*\*]. We may expect that in the near future a great deal of mechanistic information will emerge about meiosis from mutant studies in yeast. It remains to be demonstrated, however, how far information from other kingdoms can be directly applied to plants, and what level of conservation there is of the mechanisms and pathways.

It may be that overall conservation will be high, and all the important genes in plants can be found by analogy with these model species. It may also be that similar enzymes and other proteins are used in different ways in different organisms. There are already many meiotic mutants available in plant species, particularly in *Arabidopsis*, and detailed analysis of these in the coming years will complement cross-kingdom homology studies [34–36].

Much of the recent progress in the detailed analysis of meiosis in plants, as in other kingdoms, has come from applying detailed 3-D optical microscopy methods to well-preserved cells and tissues. It is clear that traditional cytological methods, involving squashing and spreading, cause considerable disruption and have masked important features or even produced incorrect interpretations [6••]. We may expect more detailed and precise descriptions of the cellular events of meiosis from continued application of these techniques. Meiosis, however, is a highly dynamic process, and no technique using fixed, dead material will reveal all its subtleties. It will be necessary to apply imaging techniques that can reveal dynamic events in living organisms. The use of green fluorescent protein fusions is having a major impact on all aspects of cell biology, and we expect these methods to be applied in the near future to the study of meiosis.

The differences already found between quite closely related plant species suggest that currently no one species will provide a good model for the rest. For plants, the ability to manipulate meiosis and recombination would have great commercial importance, but this goal will require a detailed understanding of the mechanisms in each crop species of interest.

## Note added in proof

The work referred to in the text as (Abranches *et al.*, unpublished data) has now been accepted for publication [37••].

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