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MEIOTIC CHROMOSOME ORGANIZATION AND SEGREGATION IN PLANTS

R. Kelly Dawe
Department of Botany and Department of Genetics, University of Georgia, Athens, Georgia 30602

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ABSTRACT

During meiosis, homologous chromosomes are brought together to be recombined and segregated into separate haploid gametes. This requires two cell divisions, an elaborate prophase with five substages, and specialized mechanisms that regulate the association of sister chromatids. This review focuses on plant chromosomes and chromosome-associated structures, such as recombination nodules and kinetochores, that ensure accurate meiotic chromosome segregation.

CONTENTS

OVERVIEW 371
CHROMOSOME PAIRING AND RECOMBINATION 373
Gross Chromosome Alignment 373
Homology Recognition and Recombination Nodules 376
Role of the Synaptonemal Complex 382
CHROMOSOME SEGREGATION 384
Chiasmata 384
The Meiotic Kinetochore 386
FUTURE PROSPECTS 390

OVERVIEW

Meiosis in most plants can be summarized as shown in Figure 1. After DNA replication in the premeiotic interphase, meiotic chromosomes are first

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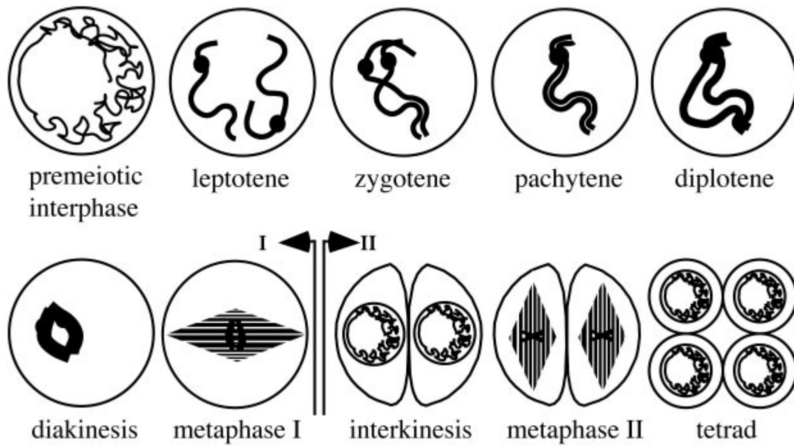

Figure 1 Meiosis in plants. The process of microsporogenesis beginning with the premeiotic interphase is illustrated in a plant that forms tetragonal tetrads (in other species the four daughters form a tetrahedron).

identifiable in leptotene as long threads with the sister chromatids tightly pressed together (e.g. 38, 68, 103). The two sister chromatids of each leptotene chromosome are bound to a common protein core known as an axial element, which appears to hold the meiotic chromatin in a looped configuration (at least in animals and fungi; 97). It is not known whether the axial element attachment regions correspond to the scaffold attachment regions of mitotic chromosomes (16). During zygotene, genetic recombination is probably initiated (see below), the chromosomes begin to coil (68, 103), and for a brief period the sister chromatids become visibly distinct (27). These specialized condensation patterns may be regulated in part by prophase I-specific chromatin proteins such as meiotin-1 (106). The homologous zygotene chromosomes begin to synapse along their length via a ribbon-like structure called the synaptonemal complex (SC). The axial elements become the lateral elements of the SC, which are joined together by transverse elements and a central element. Recent three-dimensional reconstructions indicate that the maize SC has the structure illustrated in Figure 2. For a review of plant SCs, consult Gillies (38), and for a more general discussion of SCs consult Heyting (48).

At pachytene, the chromosomes are fully synapsed and often dispersed in the nucleus so that they can be easily identified. Pachytene chromosomes are much longer than mitotic prophase chromosomes and have been used in several species to make rough cytological maps (e.g. 31, 100). In diplotene, the homologous chromosomes separate but remain associated by chiasmata

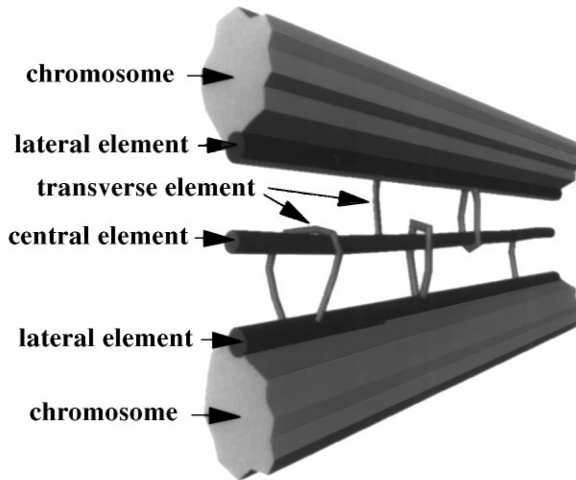

Figure 2 The synaptonemal complex in maize. The structure is an interpretation of data obtained using high voltage electron microscopy followed by computerized axial tomography (J Fung, J Sedat, D Agard, unpublished data).

(a result of crossovers). In diakinesis, the chromosomes contract lengthwise by a spiraling process (102, 124), and by prometaphase I (immediately before metaphase I) they are thickened and highly condensed. The spindle is formed in prometaphase-metaphase, and in anaphase I the chiasmata are released and sister chromatids segregate to the same pole (108).[1] During the interphase between meiosis I and II (called interkinesis) there is no DNA replication. The chromosomes again become visible at prophase II, and after a mitotic-like division in meiosis II, the sister chromatids disjoin to form four haploid daughter cells.

The focus in this review is on the major events that distinguish meiosis from mitosis: the pairing and recombination of chromosomes and the unique attributes of sister chromatids in meiosis that allow them to first segregate together in anaphase I and then away from each other in anaphase II.

CHROMOSOME PAIRING AND RECOMBINATION

Gross Chromosome Alignment

In an excellent review on the initiation of chromosome pairing, Loidl (72) identified three possible mechanisms for the early stages of chromosome alignment:

[1]A few plants, such as *Luzula echinata*, have nonlocalized kinetochores that extend all along the chromosomes (14). In *Luzula*, the sister kinetochores disjoin from each other in meiosis I in a process known as inverted meiosis (57, 108).

premeiotic associations, specific interactions at prophase (cross-talk over long distances), and random contacts. The first two, premeiotic associations and specific interactions at prophase, have received little support. In several studies premeiotic associations in plants (either the premeiotic mitosis or premeiotic interphase) were proposed, but these studies have been questioned on several grounds (72). The most serious argument against the role of premeiotic associations is that if they do exist premeiotically, they are not apparent in the stages that precede synapsis (2, 27, 51, 54, 68). Specific interactions at prophase have been discussed in the form of unsubstantiated "elastic connectors" (75) and with reference to an observed fibrillar material in cereal meiocytes (12). While the fibrillar material may have a function in chromosome pairing (discussed below), there is no evidence that it connects homologous chromosomes. Recent studies tend to support the third model in which random contacts initiate synapsis (9, 27).

THE BOUQUET STAGE It is generally thought that if homology is identified by a trial and error process, there must a mechanism(s) in the early prophase cell that increases the number or efficiency of random contacts. One such mechanism could be a widespread phenomenon known as the bouquet stage: the clustering of telomeres to a small region of the nuclear envelope during zygotene (29). The bouquet stage has been observed in every plant species where three-dimensional reconstructions have been performed (9, 38). Bouquet formation is an active process in plants (9, 27, 136). Using three-dimensional light microscopy in maize, it was shown that telomeres are randomly distributed in the premeiotic interphase and early leptotene and then transported to a small region of the nuclear envelope in prezygotene (9, 27). The clustering of telomeres preceded the alignment of nontelomeric loci (27), suggesting that the bouquet is one of the first steps in the pairing process.

Role of the bouquet in pairing Two views on the role of the bouquet have been presented (72). The first emphasizes the importance of telomeres in initiating synapsis, and the second emphasizes a general stirring process that brings chromosomes into close proximity. The central feature of the first proposal is that the complex three-dimensional problem of pairing could be reduced to two dimensions on the inner surface of the nuclear envelope. Homologs could be identified at the telomeres, the process of synapsis initiated, and synapsis completed by a zippering process (72, 108). Supporting this model is the observation that synapsis, as measured by SC formation (2, 38, 44) or cytogenetic analysis (17), is often initiated in telomeric regions. There are, however, several observations that conflict with the idea that synapsis must be initiated at telomeres (78). Ring chromosomes in maize, which lack telomeres, have been shown to pair normally with a homologous ring or rod chromosome (90, 114);

newly broken chromosomes deficient for telomeres pair normally in maize (91); and synapsis proceeds to completion in rye even though large heterochromatic regions at the ends of the chromosomes interfere with the end-to-end associations (40). While these data make it unlikely that telomeres are required for homology identification, it nevertheless remains possible that the efficiency of homology identification is improved by the close proximity of telomeres.

The alternative proposal is that the telomere cluster generates a general stirring process that brings otherwise distant chromosomes into close proximity and thereby increases the likelihood that homologous contacts will occur (27, 72). The extent to which telomere movement alone can affect the movement of chromosomes within the nucleus is not known, but early data from living plant meiocytes indicate that prophase I movements within the nucleus are quite fast (49). It was not possible to identify individual chromosomes in these early studies, but the nucleolus could be clearly resolved (attached to at least one chromosome). Nucleolar movement began in leptotene and became most rapid in zygotene and early pachytene, achieving rates as high as 3.9 $\mu m \cdot min^{-1}$ in *Acacia*, and 8.0 $\mu m \cdot min^{-1}$ in *Salvinia*. These rates are considerably higher than the rate of anaphase chromosome movement in plants (e.g. 145) and could conceivably be generated by forces within the nucleus. In several cereal species, a meiosis-specific intranuclear network of fibrillar material has been identified that might mediate such intranuclear movement (12). Chromosome movement may also be facilitated by the structure of the chromosomes and nucleus during the bouquet stage. Coincident with telomere migration in maize, the chromosomes undergo a global chromatin reorganization, involving a separation of chromatids, an elongation of heterochromatic knobs, and a 50% increase in chromosome and nuclear volume (27). Similar chromatin and nuclear changes have been documented in other plant species immediately before synapsis (11, 27, 68, 103, 108).

Mechanism of bouquet formation A better understanding of the role of the bouquet may be accomplished through further studies of how and when the bouquet is formed. One possibility for the mechanism of bouquet formation is that telomeres move by *trans*-nuclear envelope interactions with the microtubule cytoskeleton (29, 115). In plants, it has long been known that the microtubule-destabilizing drug colchicine interferes with chromosome pairing (72, 115), but the mode of action for colchicine is unknown. In rye and some wheat studies, pairing was only disrupted when colchicine was applied well before the bouquet stage, during the end of the preceding mitosis and early premeiotic interphase (72). In *Lilium* and *Allium*, however, colchicine reduced pairing when applied during bouquet formation (72, 131). A colchicine-binding protein was identified in the nuclear envelope of *Lilium*, suggesting that at least in

this species, colchicine affects chromosome/nuclear envelope interactions or a prerequisite step (131).

An important link between the telomeres and microtubule-based motility in plants has recently been demonstrated by Schmit et al (111, 112). Using a monoclonal antibody to calf centrosomes (6C6), they demonstrated cross-reactivity with kinetochores, the nuclear surface, and synaptonemal complex of several plant species. In early prophase I, the immunostaining was distributed over the entire nuclear surface; at zygotene, the ends of the chromosomes were also stained; and at pachytene, the nuclear surface lost its staining and the chromosomes became stained throughout their length. The facts that animal centrosomes interact with microtubules, and that the nuclear envelope functions as a microtubule-organizing center (MTOC) in plants, suggests that the 6C6 immunostaining identifies an epitope specific to plant MTOCs (69, 111). If so, the switch from nuclear envelope to chromosome-end staining in zygotene could provide the telomeres with the MTOC activity that enables them to interact with microtubules on the nuclear surface. A different antiserum (CREST EK, see below) reacts with both the kinetochores and synaptonemal complex in maize, providing a further link between an organelle that interacts with microtubules (the kinetochore) and the SC (Figure 3). In some species, distinctly staining structures have been observed at the telomeres (44, 51, 115, 125), which may have a role in mediating the interactions between telomeres and the cytoskeleton.

Although the results with 6C6 immunostaining provide a plausible explanation for the mechanism of telomere movement, it is not clear how the telomeres cluster in a defined region of the plant nuclear envelope. In animals and fungi, the telomere cluster interacts with the centrosomes or spindle pole bodies, which are nuclear envelope–associated microtubule-organizing organelles (29). This is especially pronounced in Mantids; during pachytene the telomere cluster is divided in two as the centrosomes separate in preparation for spindle formation (53). In contrast to the localized MTOCs in fungi and animals, plant MTOC activity is distributed over the entire surface of the nucleus (69, 112). In the absence of any polarity on the nuclear envelope it is difficult to envisage what could serve as the focus for the telomere cluster. Differential nuclear pore densities have been observed in the vicinity of the telomeres (38), but it is not clear whether the changes in pore density are a cause or an effect of the bouquet. Clear answers to questions about the mechanism of bouquet formation, as well as the function of the bouquet, will require either mutants or effective drug treatments that can be used to inhibit the process of telomere migration.

Homology Recognition and Recombination Nodules

Once chromosomes are brought into close contact, homology must be identified at the molecular level so that recombination can occur. Historically, it was

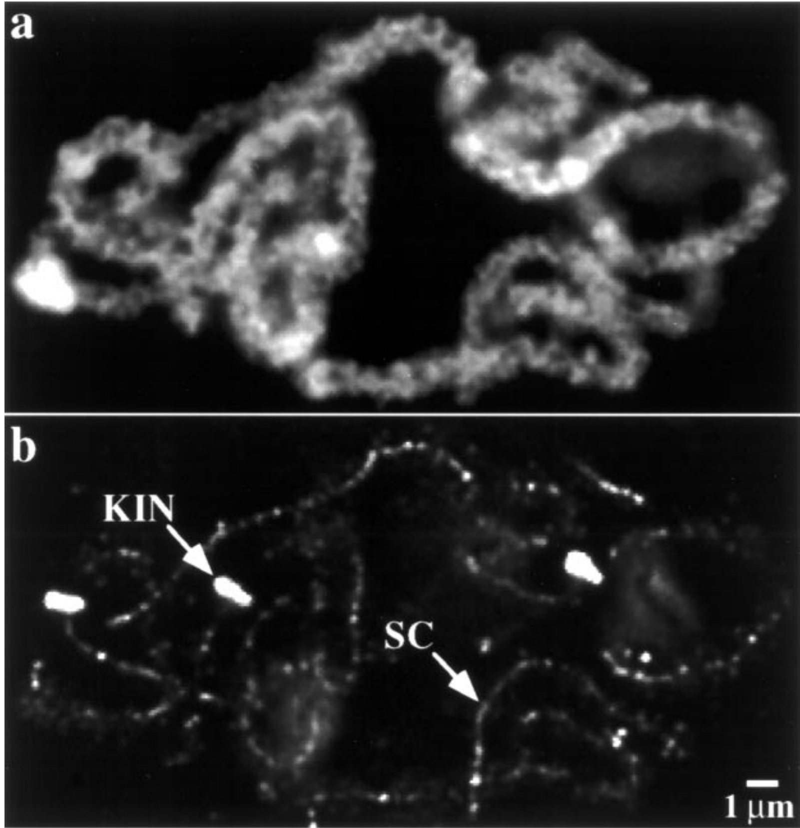

Figure 3 Labeling of maize kinetochores and synaptonemal complex by CREST EK serum. See text for description of the CREST serum. (*a*) DAPI (4,6-diamidine-2-phenylindole dihydrochloride)-stained chromosomes at pachytene. Only three chromosomes are shown. (*b*) Immunolocalization of CREST EK serum to the same chromosomes in A. Both kinetochores (KIN) and synaptonemal complex (SC) are labeled (RK Dawe & WZ Cande, unpublished data).

proposed that the chromosomes synapsed before recombination was initiated; however, it is now thought that the early events of recombination may precede synapsis (46). Three significant observations in yeast are most responsible for this reappraisal. First, a gene (*RAD50*) known to encode an enzyme that repairs double-strand breaks (which initiate recombination in yeast) is also required for SC formation. The simplest interpretation of this result is that recombination must be initiated before the SC can be installed. Second, recombination intermediates in yeast are first observed well in advance of SC formation. Finally, two yeast mutations that abolish SC formation (*zip1* and *mer1*) reduce but

do not abolish recombination (109). Early observations by Maguire indicate that a similar sequence of events occurs in plants (74, 82). Using a chromosomal inversion stock that included a ~19 map unit region, she demonstrated a nearly 1:1 correlation between the frequency of synapsis and the frequency of recombination in the inverted region. Because conventional wisdom would have predicted that only a fraction of the successful pairing events would lead to recombination (19/50 in this case), Maguire effectively argued that recombination is associated with the initiation of synapsis. As will been seen below, recent cytological studies further support the contention that the early events of recombination precede SC formation.

PRESYNAPTIC ALIGNMENT The first visual evidence of homology identification in many plants is a phenomenon known as presynaptic alignment (72). In species where it occurs regularly, presynaptic alignment is a discrete phase in the pairing process that results in a remarkably uniform and apparently accurate alignment of axial elements over distances that greatly exceed the width of the synaptonemal complex (up to 2.5 μm). Such long-distance alignment has been observed consistently in *Allium* species. In diploid and tetraploid *Allium*, presynaptic alignment can be detected in late leptotene, but it is most prevalent at zygotene between regions that have already completed synapsis (2, 127). The alignment is also pronounced in triploid *Allium*, where at any given position two zygotene chromosomes are completely synapsed while the third remains aligned at a distance (73). In late pachytene, the unsynapsed chromosome loses its long-distance alignment, indicating that the mechanism leading to presynaptic alignment is specific to zygotene-early pachytene. Similar evidence of presynaptic alignment was obtained in both tomato and maize (77, 125). Events akin to presynaptic alignment were also observed in maize homozygous for the *asynaptic* (*as1*) mutation (85). In *as1* plants, synapsis ceases in the early stages, leaving the centromeric regions with only fragments of synaptonemal complex (84). In some meiocytes, the interrupted pairing conditioned by *as1* revealed a long-distance interaction of apparently homologous axial elements (85). The authors speculate that the defect in *as1* confers weak or otherwise defective transverse elements that span the distance between homologs. An alternative interpretation is that the mutant plants cannot convert the long-distance interactions into close-range synapsis.

EARLY RECOMBINATION NODULES How homology can be identified over distances typical of presynaptic alignment (2.5 μm) is not known, but recent evidence suggests that it is a function carried out by recombination nodules. Recombination nodules (RNs) are small proteinaceous particles that associate with the SC (1, 2, 6, 38, 50, 125–128). In zygotene, the RNs are abundant and

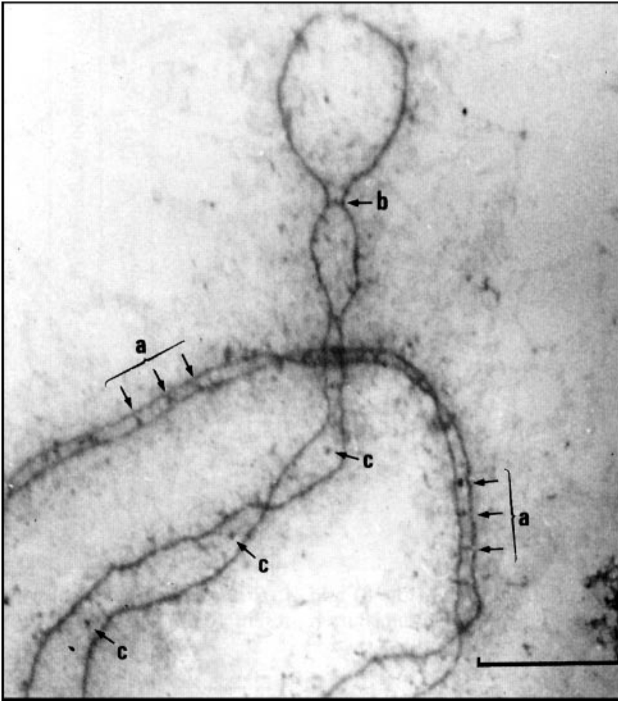

Figure 4 Recombination nodules at zygotene in *Allium cepa*. Early nodules (*a, b, c*) and axial elements (*long threads*) were stained with phosphotungstic acid. Bar is 2.5 μm. [From Albini & Jones (2) with permission from Springer-Verlag.]

referred to as early RNs (128). The idea that early RNs have a role in the homology search is supported by their location on unpaired chromosomes (2, 125) and by their occasional presence in regions of nonhomologous synapsis at zygotene (50, 128). Albini & Jones (2) observed that early RNs were associated with onion chromosomes at several different states of pairing (Figure 4). In some cases, two nodules were found at matching positions on presynaptically aligned (not synapsed) chromosomes. In other cases, single RNs were suspended between two aligned lateral elements (Figure 4*c*), and in still other cases an RN appeared to be centered in a region where two lateral elements had converged (Figure 4*b*). In regions of extended synapsis, RNs were observed at a density of greater than one every 2 μm (Figure 4*a*). Remarkably similar results were obtained in tomato and in the lower vascular plant *Psilotum nudum* (6, 128). In these species, RNs were not only observed suspended between converging lateral elements, but fibers were also frequently observed connecting the

two chromosomes and the RN. The data from *Allium*, tomato, and *Psilotum* collectively suggest that early RNs (and perhaps their associated fibers) have a contractile role by pulling chromosomes from presynaptically aligned distances (2–3 μm) to the proximity required to form the synaptonemal complex (0.3 μm) (128).

INITIATION OF SYNAPSIS An estimate of the number and location of successful homology identification events per chromosome can be obtained by direct observation of SC formation. With few exceptions, SC initiation sites are correlated with the presence of at least one early RN (128). Observations are consistent with the idea that telomeres frequently initiate pairing: SC is first formed in the subterminal regions of the chromosomes (2, 38, 39, 44, 125). Internal sites of pairing initiation are also very frequent (38). In maize, there are about 4 initiation sites per bivalent (36); in rye, there are 9 to 20 per bivalent (1); in lily, there are 5 to 36 per bivalent (51); in *Trandescantia*, up to an average of ~9 per bivalent (44); and in *Allium*, from 1 to 9 in per bivalent (2). The analysis of triploids and trisomics demonstrates that the observed initiation sites are converted into stable associations in pachytene. In triploid/trisomic plants, the individual chromosomes of a trivalent alternate between synapsis and asynapsis; the number of partner switches serves as a minimum estimate of the number of pairing initiation sites. An analysis of trisomic *Crepis capillaris* indicated an average of ~7 initiation sites per chromosome (139). Similarly, the number of partner switches in triploid *Allium* suggested that there were ~6.1 initiation sites per chromosome (73). The number of SC initiation sites invariably exceeds the number of chiasmata typical of the species, indicating that SC initiation sites, and their associated early RNs, do not necessarily correspond to sites of reciprocal recombination.

LATE RECOMBINATION NODULES During the transition between zygotene and pachytene, the majority of early RNs are either degraded or dissociate from the SC. In tomato, the number of RNs in pachytene is 15 times fewer than in zygotene (125): in *Allium*, an even greater discrepancy was reported (2). The RNs in pachytene are referred to as late RNs (128). With rare exceptions (e.g. 37), the number of late RNs very closely matches the number of chiasmata, suggesting that late RNs mediate reciprocal recombination or become associated with the sites where recombination occurs (1, 3, 117, 126). For instance, in *Lilium*, the average number of RNs was 55.1, and the average number of chiasmata was 54.8 (126). Most notable are the studies that have correlated changes in chiasmata frequency or localization with changes in late RN frequency. In one such study, Albini & Jones (3) compared the localization of late RNs in two *Allium* species that differ with respect to the localization of chiasmata. In

A. fistulosum, the chiasmata are localized almost exclusively in centromere-proximal regions, while in *A. cepa*, the chiasmata are found in more distal regions of the chromosome arms. When the localization of late RNs was determined in these species, a pattern remarkably similar to chiasma localization was observed (3). In another study, the frequency of late RNs was determined in tomato reciprocal translocation heterozygotes (47). The translocations were found to reduce the frequency of both chiasmata and late RNs, strongly supporting a one-to-one correspondence between late RNs and crossovers.

COMPOSITION OF RECOMBINATION NODULES The available data are consistent with a role of early RNs in the homology search and the initiation of synapsis (2, 128), whereas late RNs appear to be involved in completing and/or stabilizing crossover events (2, 125, 142). It has also been suggested by several authors that a subset of the early RNs (homologous contacts) are converted into late RNs (recombination events) (2, 18, 116, 128). A clear prediction from the cytological data is that RNs contain enzymes involved in recombination. Two of the genes that are thought to mediate recombination in yeast are *RAD51* and *DMC1* (109). Homologs for both *RAD51* and *DMC1* (called *LIM15*) were recently identified in *Lilium* by Teresawa et al (135). Immunolocalization of the Rad51 and Lim15 proteins revealed foci of staining on both zygotene and pachytene chromosomes. Whereas in zygotene the Rad51 and Lim15 co-localized to the same foci, in pachytene the number of Rad51-stained foci decreased, and Lim15 was no longer detected. The spot-like nature of the staining and the reduced number of foci in pachytene are consistent with antisera reaction with RNs and further suggested that Lim15 has a function that is specific to early RNs (135). Confirmation that the Rad51 and Lim15 proteins are a component of early RNs was recently provided by Anderson and coworkers (5) using electron microscopic immunogold localization and an antibody that identifies both proteins. The localization data of Anderson and coworkers not only indicate that RNs contain enzymes that mediate meiotic recombination but provide strong support for the idea that the early events of recombination precede synapsis.

The next important step will be to identify mutations in plant genes with the functions of yeast *RAD51* and *DMC1/LIM15*. A *DMC1* homolog has been identified in *Arabidopsis*, but the mutant phenotype is unknown (65). In maize, the genes for at least two homologs of *RAD51* and two homologs of *LIM15/DMC1* have been cloned, and mutations have been generated at each locus using a reverse genetics procedure (B Bowen and S Tabata, personal communication; and see 92 for reverse genetics in maize). None of the single *rad51* mutations alone have definite meiotic phenotypes; it is likely that the individual *Rad51*-like genes have overlapping functions and that double mutant analysis will be

required for functional analysis. Mutations that affect RN function may also exist among the large collection of plant mutants that cause premature desynapsis in late pachytene-diplotene (43, 66).

Role of the Synaptonemal Complex

Although the SC normally forms only between homologous chromosomes at pachytene, intimate pairing and SC formation can occur between nonhomologous chromosomes. Nonhomologous associations were first observed by McClintock (89) in monosomics, trisomics, and a variety chromosomal rearrangements in maize. Nonhomologous pairing, mediated by apparently normal SC, has now been documented in a number of plants (e.g. 37, 44, 50, 51, 73, 118, 138). In addition, mutations in both maize and onion that cause failures in homologous pairing are associated with indiscriminate synapsis and fold-back pairing (55, 86). Late RNs are not observed on nonhomologously synapsed chromosomes (SM Stack, personal communication), and nonhomologous associations generally do not lead to recombination. The one exception is in haploids, where very limited recombination (rarely more than one event per cell) has been detected in specific, presumably homologous, regions (99, 142). Because nonhomologous pairing can occur during zygotene as well as pachytene (44, 50, 51, 118), homology is probably not a prerequisite for SC formation at any stage of meiosis (118).

It would be appropriate to suggest that there is no causal relationship between the SC and genetic recombination in plants if not for the *asynaptic* mutation of wheat (var. Aziziah). No recombination is observed in the wheat *asynaptic* mutation (87). Lateral elements are present, but a mature synaptonemal complex is not formed (67). If the mutation was simply recombination-defective, nonhomologous pairing and SC formation would be expected (as observed in other synaptic mutants; 55, 86). The data suggest that *asynaptic* is defective for a component of the SC, and that either the protein encoded by *asynaptic* or the mature SC is required to complete recombination. The effect of the SC on recombination may be indirect. For instance, the SC may be required as a scaffold to house and/or stabilize recombination nodules during the final stages of recombination.

INTERFERENCE An important role for the SC may be in the regulation of recombination frequency. A consistent feature of meiosis is that the distribution of mature recombination events leading to chiasmata are not evenly distributed. In *Hyacinthus amethystinus*, for example, there is a 20-fold variation in chromosome length, but the frequency of chiasmata on the smallest chromosomes is only slightly less than half the frequency on the largest chromosomes (23). The uneven distribution of recombination can be explained by genetic interference,

which refers to the observation that a single recombination event inhibits additional recombination in nearby regions (60). How the existence of a crossover is detected and then communicated to nearby regions of a chromosome is not known, but recent authors have argued that it is a function of the SC (33, 60). The observation that several fungi lack both SC and genetic interference has been used to support this argument (33). Perhaps the strongest evidence that the SC mediates interference was provided by an analysis of the yeast *Zip1* gene, which encodes a structural component of the SC. In loss-of-function *zip1* mutants, recombination levels are slightly reduced, but interference is abolished (132, 134).

The idea that the SC mediates interference is consistent with the available data from plants. In an elegant study, Parker (105) determined chiasmata frequency in two regions that flanked a centromere in *Hypochoeris radicata*. When one chromosome of the bivalent was broken at the centromere such that the region available for synapsis was separated into two parts, interference between the two regions was significantly reduced. Single gene mutations are also available in both tomato and maize that provide a direct connection between the SC and interference. The as_1, as_4, and as_b mutations of tomato show incomplete synapsis at pachytene and reduced number of chiasmata per cell. By measuring the effect on recombination and interference over a 36-map unit interval, it was shown that each mutation caused a significant reduction in interference (96). The as_b mutation had the most severe effect, reducing interference by 80%. A limited ultrastructural analysis indicated that apparently normal SC as well as unpaired axial elements were present in the tomato *asynaptic* mutants. Similarly, the *as1* mutation of maize shows a variable degree of desynapsis (93) and a reduction of interference. Dempsey (28) measured recombination over two intervals on chromosomes 2 and 9 in *as1* plants, finding that recombination increased overall and that interference dropped by ~30% in both regions. The maize *as1* mutation is not a null allele but a hypomorph (8), which may explain the incomplete synaptonemal complex formation (84, 85) and limited effect on interference.

How the synaptonemal complex could promote interference is a matter of debate (33, 45, 64). Because the number of SC initiation sites greatly exceeds the number of chiasmata, interference presumably occurs after the SC has assembled. Genetic evidence in yeast suggests that the role of the SC might be to "transmit stress" along the chromosome (64, 132). Presumably, the stress occurs in the form of DNA coiling but could involve the interaction of the DNA with the lateral element of the SC (64). According to this model, crossover events are promoted by stress, and noncrossover-events are the default pathway (132). When a crossover occurs, stress is relieved in surrounding regions and all flanking homologous contacts are resolved into noncrossover events. An alternative model suggests that RNs generate interference, and that the SC

simply serves as scaffold for RN movement along the chromosome (45). While either model would accommodate the observations in plants, they both remain highly speculative.

CHROMOSOME SEGREGATION

A unique feature of meiosis I in most plants is that the homologous chromosomes, each containing two sister chromatids, segregate away from each other. As shown in Figure 5, two conditions must be met for this to happen: At least one chiasma must be present (the result of pairing and recombination), and the sister kinetochores must orient together to the same spindle pole. When a chiasma is not present, the resulting univalents are free to segregate randomly and may arrive at the same pole (Figure 5*b*). When the sister kinetochores fail to orient together, the chromatids may disjoin (Figure 5*c*). Disjoined sister chromatids are not only subject to random segregation in meiosis I but are incapable of regular disjunction in meiosis II. The orientation of sister chromatids typical of meiosis I is referred to as a *co*-orientation, and the behavior of sister chromatids typical meiosis II is referred to as *auto*-orientation (108).

Chiasmata

CHIASMA MAINTENANCE Chiasmata are the result of recombination between at least two nonsister chromatids in a bivalent (Figure 5; 81, 108). A variety

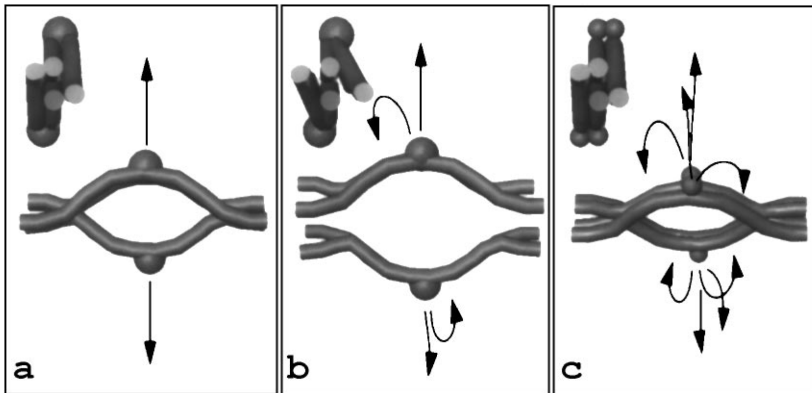

Figure 5 Metaphase I chromosome structure. In each panel, a side view (*upper left*) and frontal view are shown. (*a*) In normal cells, the chiasmata hold the chromosomes together, and the two sister kinetochores are observed as a single unit. (*b*) If chiasmata do not form (as in the maize *dy* mutant), the homologous chromosomes can segregate in either direction and may arrive at the same pole. (*c*) If the sister kinetochores are separated (as in the tomato *pc* mutant), they can interact with different spindle poles and randomly segregate.

of data indicate that chiasmata are stable structures (59, 60, 71) that do not "terminalize" as once thought (24). Maguire (80, 81) has recently emphasized that recombination is insufficient to hold the chiasmata in place; additional factors, located either at the chiasmata or between sister chromatids, are required to maintain chiasmata. In several fungi, remnants of the SC have been detected at crossover sites, indicating that the SC may be partly responsible for holding chiasmata in place (140). Remnants of SC at diplotene have also been detected in plants, but the fragments that remain generally do not coincide with the location of chiasmata (36, 52, 125, 126). It is possible that as yet unidentified proteins (or protein complexes) bind specifically to chiasmata and hold them in place.

An alternative view is that the association of sister chromatids distal to the crossover provides the glue that holds chiasmata in place (57, 81, 95). Evidence that sister chromatid cohesiveness is responsible for chiasma maintenance in plants was provided by Maguire (76) working with the desynaptic (*dy*) mutation of maize. The *dy* mutation is representative of a large group of mutations typified by univalent formation at diakinesis (66). Most desynaptic mutations are thought to be defects in recombination. In *dy* plants, however, it was possible to determine that at least some of the univalents had undergone recombination of cytological markers, suggesting a defect in chiasma maintenance. The *dy* mutation also conferred a general tendency of the univalents to prematurely dissociate, suggesting that the plants were defective for sister chromatid cohesiveness (76). More recent studies demonstrating that *dy* plants have defective SC have led to the suggestion that the substance binding sister chromatids is derived from the SC (83, 86). This idea is supported by the recent observation that a component of the animal SC (Cor1) is present along chromosome arms at metaphase 1 (30). Whether components of the SC remain associated with plant chromosomes during metaphase I is unclear (34, 124).

CHIASMATA IN CELL CYCLE CONTROL AND SPINDLE FORMATION In insect spermatocytes, chiasmata formation is required for the cell to proceed from metaphase I to anaphase I (101). The formation of a chiasma provides a connection between the homologs that restrains poleward movement and causes tension at the kinetochores. In the absence of a chiasma, the resulting univalent kinetochores do not sense tension and produce a signal that causes the cell to delay anaphase. Among the factors that are thought to sense tension at the kinetochores in *Drosophila melanogaster* is a protein called ZW10 (4, 143). An Arabidopsis homolog of the *zw10* gene has recently been identified, suggesting that the tension-sensing mechanisms similar to those described in animals could operate in plants (129).

An additional role for chiasmata in plants is to ensure proper meiotic spindle assembly. In synaptic mutations where recombination or chiasma maintenance

are disrupted (resulting in univalents), a general failure in bipolar spindle formation is observed (66). The effects of univalents in meiosis I can range from small extra minispindles to tripolar, quadripolar, and multiple spindles in the same cell (e.g. 10). Similar observations have been made in triploid and haploid plants (88, 137), indicating that spindle aberrations are a secondary effect caused by the presence of unpaired chromosomes. The simplest explanation for these findings is that unpaired chromosomes disrupt the spindle because they have only a single functional kinetochore (25). The idea that chromosomes can affect spindle structure is well supported by data from both plant mitotic cells and animal meiotic cells (107, 122).

The Meiotic Kinetochore

The kinetochore is known to regulate chromosome movement in plant meiosis (145), and its structure predicts its behavior: When the two sister kinetochores compose a single structure in meiosis I they usually segregate together (15, 70, 144); when the kinetochores are visibly separated from each other they usually disjoin (14, 70, 123). More direct data on the importance of the kinetochore in meiosis I segregation are available from yeast. In strains of yeast that undergo a phenomenon known as single-division meiosis, some chromosomes preferentially undergo a meiosis I–type disjunction (co-orient), and some undergo a meiosis II–type segregation (auto-orient). By moving centromeric DNA sequences from one chromosome to another it was shown that the segregation behavior of a chromosome was encoded by the centromere itself (119). Limited data suggest that this is also true in plants. An analysis of maize trisomic strains indicates that each chromosome has its own propensity to co-orient or auto-orient in meiosis I, and a minichromosome with a reduced centromeric region has been identified that auto-orients nearly 100% of the time (79).

COMPOSITION OF THE MEIOTIC KINETOCHORE Plant meiotic kinetochores are most often described as amorphous and ball-shaped with a granular substructure (e.g. 15, 35, 144). Little is known of the composition of kinetochores in plants, but significant progress has been made in understanding the structure of animal kinetochores (32). The most valuable tool in animal kinetochore research was discovered in patients with the CREST variant of systemic sclerosis. Sera from the majority of CREST patients recognizes antigens in the centromeric region of mammalian mitotic and meiotic chromosomes (32). Several proteins recognized by CREST sera have been characterized and studied extensively (32). One CREST serum (EK) identifies an 80-kDa protein that is required to complete meiosis in mice (120). The 80-kDa protein identified by CREST EK is presumably CENP-B, a centromere-binding protein. The same CREST serum was

shown to identify mitotic kinetochores in *Haemanthus* (98) and *Tradescantia* (104) and identifies the meiotic kinetochores in pachytene-diplotene chromosomes of maize (Figure 3). These data suggest that CENP-B-like proteins may be present in plant meiotic kinetochores; however, the function of CENP-B is not well understood even in animals (32).

In addition to protein, DNA is found in animal kinetochores (21). The observation that some plant kinetochores contain aceto-orcein-stained chromomeres that stretch towards the poles in anaphase (Figure 6) suggests that there may be DNA in plant kinetochores as well. With the availability of several plant centromere sequences (7, 56, 61), it should be possible to test for the presence of DNA in plant kinetochores.

MEIOSIS I KINETOCHORE CO-ORIENTATION An important first step toward understanding the mechanism of co-orientation in meiosis I was taken by Stern & Hotta (130). They discovered that in *Lilium*, meiocytes from the leptotene stage or later could be removed and cultured in an artificial medium where they completed a normal meiotic division. In contrast, when meiocytes in S

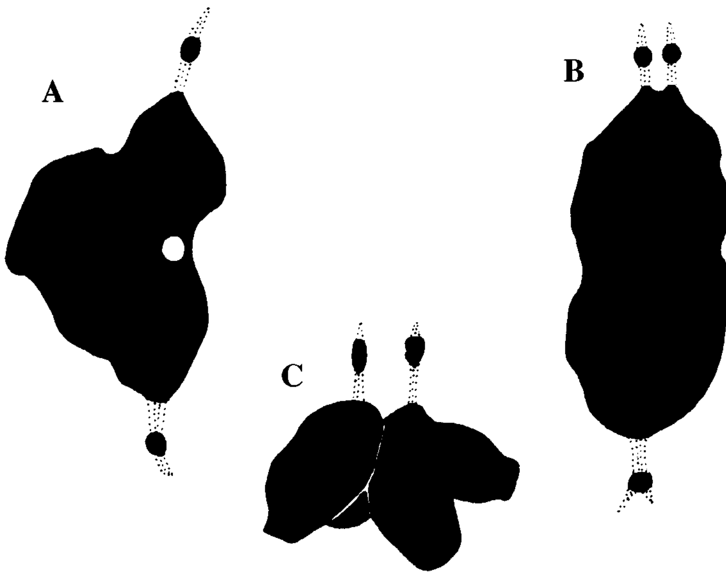

Figure 6 Kinetochore maturation in *Tradescantia*. Chromosomes were stained with aceto-orcein. (*a*) Early metaphase in *T. virginiana*. (*b*) Late metaphase in *T. virginiana*. (*c*) Anaphase in *T. bracteata*. Note the centromeres appear to be pulled poleward and each contains a conspicuous chromomere (*darkly-stained region of the chromosome*). [From Lima-de-Faria (70) with permission from *Hereditas*.]

phase were removed, mitosis occurred instead of meiosis. Interestingly, meiocytes removed immediately after S phase underwent a normal mitotic prophase followed by failed anaphase, apparently because the centromeres could not divide (130). The simplest interpretation of the data is that the orientation of the kinetochores is one of the first events to be determined as a cell initiates meiosis.

The contention that kinetochore co-orientation occurs very early in meiosis is supported by studies of the maize *absence of first division* (*afd1*) mutation (42). In *afd1* meiocytes, all the chromosomes auto-orient in meiosis I, and the sister chromatids segregate away from each other. Meiosis II is ineffective (only single chromatids are present) but appears to occur on schedule, indicating that *afd1* does not convert the meiotic program to a mitotic one. Analysis of the early prophase stages indicates that the chromosomes do not condense into the long thin threads typical of leptotene but appear thick and short as if they preceded directly to diakinesis without the intervening pairing stages (42). Electron micrographs of *afd1* meiocytes indicate that SC formation ceases quickly after it is initiated and produces only ~12% of the SC found in wild-type plants (41). Much of the SC that is installed in *afd1* plants appears defective, lacking either the lateral or the central elements (41). After their analysis of *afd1*, Golubovskaya & Mashnenkov (42) argued that if the cell passes through leptotene, the kinetochores become committed to co-orientation. The *afd1* phenotype is similar to a *Drosophila* mutation called *orientation disrupter* (*ord*) (94). In *ord* mutants, recombination is reduced to 10–13% of the wild-type levels, and sister kinetochore separation regularly occurs during prometaphase, metaphase, and anaphase of meiosis I. The recombination defect in *ord* may be associated with a defect in the SC, but the appropriate studies have not yet been carried out. The *ORD* gene encodes a novel protein with characteristics that suggest it is regulated by proteolysis (13).

Studies of synaptic mutants further support the idea that sister kinetochore co-orientation is an early meiotic event. As a rule, the phenotypes of synaptic mutations are first observed late in meiotic propase and are classed together by their failure to form bivalents. Surveys of published synaptic mutants, identified in over 90 plant species, indicate that there is no correlation between synaptic defects and the segregation behavior of the univalents at anaphase I (66). For example, no univalents divide equationally (in half) in *Vicia faba* (121), whereas in *Oenothera* (19), all univalents divide equationally. In *Brassica campestris* (133) there is a positive correlation between the degree of asynapsis and the frequency of equational division, while in rice there is no such correlation (63). The data are broadly consistent with the interpretation that meiosis I kinetochore orientation is determined at or around leptotene. The fact that univalents sometimes do divide in meiosis I is best interpreted as the result of kinetochore maturation during late metaphase/anaphase, as discussed in the next section.

Although largely circumstantial, the available data suggest that the orientation of kinetochores in meiosis I is determined at or around leptotene, either directly or indirectly by *Afd1* or similar genes. Because *afd1* plants are deficient for axial elements, it is possible that these elements promote co-orientation simply by holding the sister chromatids together during kinetochore formation. Other factors promoting or stabilizing the close apposition of kinetochores could be the inherent "stickiness" of the prophase I kinetochores (e.g. 38, 125) and the tendency for the microtubules that are attached to the kinetochores to bundle together (e.g. 22).

KINETOCHORE MATURATION AND MEIOSIS II Whereas the onset of anaphase I is marked by the dissolution of chiasmata, the onset of anaphase II is marked by the separation of sister kinetochores. Therefore, in the period between anaphase I and anaphase II, the kinetochores must lose their co-orientation and adopt an auto-orientation. An important clue to the timing of kinetochore separation can be inferred from the behavior of univalents in synaptic mutants. The great majority of synaptic mutants have phenotypes that for one reason or another produce both univalents and bivalents at meiosis I (43, 66). It has been reported in all cases that the univalents divide after the bivalents. In most species, the univalent division occurs very late, if at all, during anaphase. A notable exception occurs in *asynaptic Oenothera*, where the univalents divide after bivalents but still early enough to be segregated properly to telophase nuclei. In such plants, Catcheside (19) noted that when the univalents divide, they divide at roughly the same time regardless of whether they are located in the polar region or plate region of the meiosis I spindle (19). The overall synchrony of equational segregation at late anaphase indicates that sister kinetochores are not physically torn apart by their interactions with the spindle but rather that they are separated in a regulated manner.

The idea that sister kinetochores begin their separation during late metaphase and anaphase is supported by light microscopic observations of the kinetochores themselves (70, 113). As shown in Figure 6, Lima-de-Faria (70) demonstrated that the sister kinetochores of *Tradescantia* appear as a single unit in early metaphase, whereas in late metaphase and anaphase the kinetochores become visibly distinct. Essentially, the same results were obtained by silver-staining of *Allium cepa* and *Rhoeo discolor* kinetochores (123). Similarly in maize, it was demonstrated using a cloned cereal centromere repeat (56) that the late metaphase I kinetochore consists of two units (145; EN Hiatt & RK Dawe, unpublished observations). Two distinct sister kinetochores at metaphase I were also demonstrated in wheat univalents at the electron microscope level (141). The univalents first adopted positions close to a pole, presumably reflecting the close apposition of the two kinetochores. Later in metaphase, even though the sister kinetochores remain closely apposed, the wheat univalents moved

to the spindle midzone. Only after anaphase I was in progress (as judged by the segregation of bivalents) did the sister chromatids separate, allowing the chromatids to segregate equationally (140).

At least one mutation has been identified that alters the timing of sister kinetochore separation. The tomato *precocious centromere division* (*pc*) mutation causes the kinetochores to separate prematurely during anaphase I and interkinesis such that at prophase II only single chromatids are observed (20). During anaphase I, it appeared that a few univalents became auto-oriented and divided. A similar phenotype was described in *Alopecurus myosuroides*, although the genetic basis of this defect is not known (58). The kinetochore separation phenotypes in these plants is almost identical to the phenotype of the *Drosophila mei-S332* mutation. *Mei-S332* has been cloned, and the encoded protein localizes to kinetochores in meiosis I but disappears at the onset of anaphase II (62). The localization pattern of the MEI-S332 protein suggests that it is not only responsible for maintaining the association of sister chromatids during meiosis I but may also regulate the disjunction of chromosomes in meiosis II.

FUTURE PROSPECTS

In recent years, significant progress has been made in understanding chromosome pairing and recombination nodules (RNs) in plants (e.g. 5, 9, 112, 128). In other areas the most important research progress has been made in yeast and *Drosophila* (e.g. 62, 109), and it is only possible to speculate on the similarities to plants. Future studies will likely make use of randomly sequenced cDNAs (ESTs) and genome-sequencing projects to identify plant homologs to important proteins from other species. With the availability of plant homologs to fungal and animal genes it will be possible to use immunolocalization and newly established reverse genetic strategies (92) to determine whether there are functional similarities across organismal boundaries. This approach has already been employed in recombination nodules studies, where it has been established that plants have homologs to yeast *RAD51* and *DMC1* (5, 135). In addition, it will be important to pursue forward genetic approaches in combination with high-resolution cytological analysis (e.g. 26) to identify genes that have roles unique to plant meiosis. Genetics and cytology can be combined in maize, tomato, and even Arabidopsis, which despite its small genome size can be analyzed cytologically at all stages of meiosis (110).

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