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CEREAL CHROMOSOME STRUCTURE, EVOLUTION, AND PAIRING

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■ **Abstract** The determination of the order of genes along cereal chromosomes indicates that the cereals can be described as a single genetic system. Such a framework provides an opportunity to combine data generated from the studies on different cereals, enables chromosome evolution to be traced, and sheds light on key structures involved in cereal chromosome pairing. Centromeric and telomeric regions have been highlighted as important in these processes.

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INTRODUCTION

More than 50% of angiosperms are polyploids that occur either by multiplication of a basic set of chromosomes (autopolyploidy) or as a result of combining two parental genomes (allopolyploidy). The introduction of alien variation into

polyploids during plant breeding clearly would benefit from an understanding of the genome relationships of polyploid crop species and their wild diploid relatives. As a result, the genomic relationships within the *Triticeae* (wheat and its wild relatives) have been extensively studied (110). By 1952, the work of Kihara and colleagues had established many of the genomic relationships of the diploid and polyploid *Triticum* and *Aegilops* species on the basis of chromosome pairing in hybrids (110). These studies have continued to the present and have accurately classified chromosome translocations (92, 115, 135, 136). Chromosome pairing is assessed by squashing meiocytes at metaphase I and classifying the specific chromosome configurations at this stage. The association of chromosomes implies some conservation of chromosomal structure (including genes) and suggests a high degree of conservation of gene order on the chromosomes of wheat and its wild relatives. Clearly, such studies could not be extended beyond species from which hybrids could be generated and in which chromosomes paired. Thus for much of the past 50 years, major cereals and their wild relatives (maize, wheat, rice, sorghum, and the millets) have been studied largely in isolation. Detection of variation between individuals at the DNA sequence level in the form of restriction fragment length polymorphisms (RFLPs) (97, 107) and the concept of an RFLP linkage map (158) enabled these comparisons to be extended and the actual structure of the *Triticeae* chromosomes to be assessed in more detail. The analysis of these comparisons revealed a framework by which all data generated on the cereals can be collated (127, 130, 132). The cereal genomes can be described by a series of conserved units based on the linkage of genes found within their genomes (130). The structure of the rice genome is pivotal to the analysis of other cereal genomes (131, 132).

GENOME ORGANIZATION

Genome Size

Although mammals possess different chromosomes, their genome sizes are similar. In contrast, cereals have different chromosome numbers and vary greatly in genome size (21). It was the size of barley, wheat, and rye genomes that initially restricted their molecular analysis. The genomes of barley (*Hordeum vulgare*) and hexaploid bread wheat (*Triticum aestivum*) are relatively large (5×10^9 bp and 1.7×10^{10} bp per haploid nucleus, respectively). Maize (*Zea mays*) is intermediate in size 2.4×10^9 bp, and sorghum (*Sorghum bicolor*) is 8×10^8 bp (21). In contrast, other cereals and wild grass genomes are relatively small; for example, those of rice (*Oryza sativa*) and slender false-brome (*Brachypodium sylvaticum*) are 4×10^8 bp and 5×10^8 bp in size, respectively (21). Clearly, major changes have occurred in genome size since their speciation from a common ancestor. Most of this additional DNA consists of repetitive sequences that evolve rapidly and hence diverge substantially with speciation (65, 66).

Base Composition

Nuclear DNA can be heavily methylated at cytosine residues. The base composition of genomic regions can therefore influence the distribution of methylation within them. Large mammalian genomes have a CpG content of 1%. This is lower than the 4% expected for a genome that is 40% G + C rich. Thus there is a marked underrepresentation of the CpG content in these genomes (26, 71, 148, 163). However, there are small regions, several hundred bases long, that have a CpG/GpC dinucleotide ratio of approximately one. Such regions (termed CpG islands) coincide with the promoters of genes (29). They are also marked by clusters of unmethylated CpG dinucleotides, which therefore contain recognition sequences for methylation-sensitive restriction enzymes. In mammalian genomes, methylation is largely confined to the sequence m5CpG. In mammalian DNA, 70% to 80% of CpG dinucleotides are methylated. More than 80% of CpG dinucleotides are also methylated in wheat. In plants, 5-methylcytosine is not confined to CpG dinucleotides but is also present in more than 80% of the trinucleotides CpXpGs (83). Therefore, in the nuclear DNA of wheat (and other higher plants), a higher proportion of the cytosine residues is methylated: 30% compared with 1% to 8% in vertebrates. A single study has assessed the dinucleotide composition of a cereal nuclear genome, namely *Triticum aestivum* (bread wheat) (163). The G + C content of its genome is 45%. In contrast to mammalian genomes, the genome of wheat exhibits only a slight reduction in CpG content (83, 148). Therefore, the observed/expected ratio of CpG content is 0.77 for bulk wheat genomic DNA compared with 0.2 for human genomic DNA, whereas the CpG/GpC ratio for wheat is 0.78 and for human DNA is 0.23. Because there is little suppression of the CpG dinucleotide in the wheat genome, both repetitive and single-copy sequences would be expected to exhibit similar CpG contents. However, sequence analysis of 60 Kb of the barley genome indicates that the promoter regions of the genes, as with mammalian genes, were marked by a CpG/GpC ratio of more than one (141).

Gene Distribution

Long-range mapping within a 4-Mb length of the wheat genome indicated five clusters of unmethylated CG-rich recognition sites for methylation-sensitive restriction enzymes defining active genes (36). The distribution of unmethylated sites between repetitive sequences and single-copy sequences is therefore not random (128). Also the distribution of unmethylated restriction sites along the chromosomes of the *Triticeae* is evidence of a reduced density in the proximal regions and a higher percentage in the distal regions (128). This implies that the gene distribution along a cereal chromosome is also not random, with a higher density of genes concentrated in the distal regions. Extensive physical mapping of genes with deletion stocks has been undertaken on wheat chromosomes by Gill and colleagues (62, 74). The data indicate that on all the wheat chromosomes, very few genes are located in the proximal third of the chromosome arm. They also reported that the genes located in the distal regions occur in clusters.

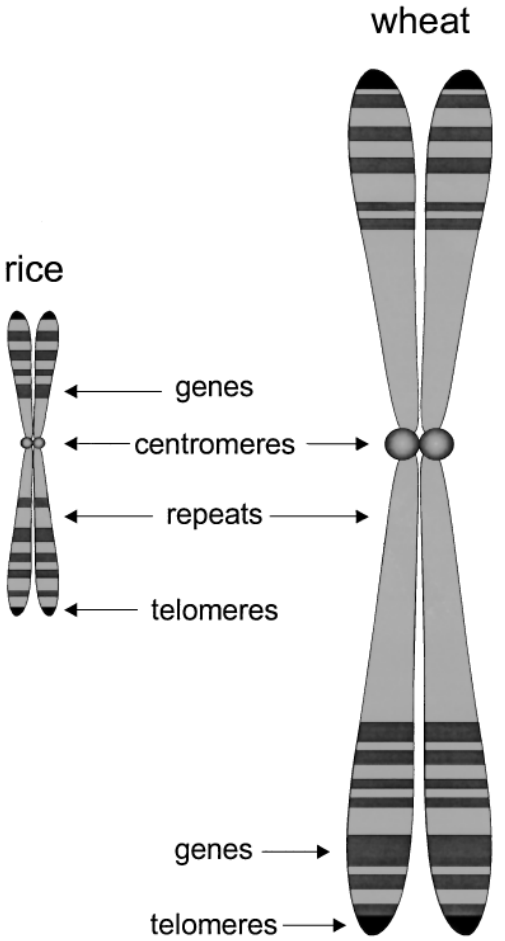

Figure 1 Schematic representation of metaphase chromosomes corresponding to rice chromosome 1 and a chromosome from wheat group 3. These chromosomes exhibit a similar gene content and extensive conservation in gene order. The rice chromosome has a more even distribution of clusters of gene-rich regions. The gene density in these gene-rich regions on the rice chromosome will be higher than in gene-rich regions in wheat. The proximal regions of wheat chromosomes are composed largely of repetitive blocks, with the distal regions composed of both clusters of gene-rich regions and repetitive blocks.

Although the sequence analysis of the 60-Kb region of the barley genome indicated a fivefold lower gene density than in *Arabidopsis*, the density was still six- to tenfold higher than expected from an equidistant gene distribution in the complex barley genome (141). This is consistent with the observations of Gill and colleagues. A schematic representation of the organization of a wheat chromosome compared to a rice chromosome is shown in Figure 1. If few genes are located in the proximal third of the chromosome arm, what is the nature of these regions? Analysis of repetitive sequence distribution indicated that they could be composed of blocks of amplified repetitive units that on restriction digestion reduce to discrete fragments of 200 Kb and upwards (24, 128). The rice genome, however, does not possess such large blocks of repetitive sequences. The proximal regions composed of large blocks of amplified repetitive sequences not only have reduced gene

densities but exhibit a reduced level of recombination. Therefore, no direct correlation exists between physical and genetic distances in species such as wheat and barley (111, 157).

Dispersed Repetitive Sequences

The majority of the large genomes of cereals consist of dispersed repeats (65, 66). The most abundant elements are the retrotransposons (177). Retrotransposons can be divided into two classes, those flanked by long terminal repeats (LTRs) and those without LTRs, which terminate with poly (A) sequences. The non-LTR retrotransposons are also called LINES elements and possess an ORF that codes for proteins with homology to reverse transcriptase. The first such elements to be identified in plants were the *cin4* from maize (153). LINES elements can be found in great abundance, for example, *del2* identified in lily (108). Recent studies have suggested that they are ubiquitous in plant genomes (137). LTR retrotransposons have been classified according to Drosophila-type elements as either gypsy-like or copia-like, based on the order of the coding proteins between the LTRs. Gypsy elements, like retroviruses, possess LTR-gag-proteinase-rt-in-LTR and copia elements are characterized by a LTR-gag-proteinase-in-rt-LTR arrangement. Gypsy and copia elements are also ubiquitous in cereal genomes and can be found in great abundance (67, 162). BIS-1 constitutes in excess of 5% of the barley genome and probably a similar proportion of the genomes of wheat and rye (129). BARE1 is not only highly abundant in barley genome (160), it is also active (161). Retrotransposons constitute at least 50% of the maize genome (150). They are found in the spaces between genes (151, 159). Retrotransposons have increased the size of the maize genome two- to fivefold since the divergence of maize and sorghum from a common ancestor about 16 mya (150). Comparison of the *sh1–a1* regions in the genomes of maize and sorghum indicated that the retrotransposons were absent from the corresponding region in the sorghum genome (35). The gene density of the gene-rich regions in small genomes, such as rice, will be higher than in larger genomes, such as wheat (68). Virtually all of the retrotransposons had inserted in the past 6 million years and most in the past 3 million years in the maize genome (150). Sequencing of the *Arabidopsis* genome reveals little intergenic interspersion of retrotransposons; most are associated with the pericentromeric regions (121). The implication for the evolution of the cereal genome is that the common ancestral genome probably possessed few retrotransposons interspersed among their genes but that the retrotransposons were located in the pericentromeric regions. Genome expansion results from the accumulation of retrotransposons in such regions. Note, however, that not only can genomes expand, they can also contract, although it is unclear how this is achieved (23).

Other transposable elements, such as Ac in maize, possess inverted terminal repeats and transpose by excision and reintegration. They are present in only tens to hundreds of copies per genome and therefore do not make a major contribution to the total DNA content of the genome. They have, however, received special

attention due to their value in gene tagging (15). No active endogenous elements have yet been found from the *Triticeae* genomes. Another type of mobile inverted repeat element has been recently identified, MITE, that is associated with the genes of many cereals (30, 31).

Long Tandem Arrays

Long tandem arrays of essentially identical sequences are found in the subtelomeric (142, 171) and pericentromeric heterochromatin regions (91) and the array of ribosomal RNA genes within the nucleolus organizer regions (73). There is a close correlation between the site of C and N bands and the presence of long tandem arrays of short, repeating sequences in chromosomal DNA (66). In rye, the subtelomeric heterochromatin constitutes from 15% to 18% of the genome, 60% of which comprises four repetitive sequences (18). These can be organized in a head-to-head arrangement or in head-to-tail organization (170). Birchler and colleagues demonstrated that sequences in maize knob regions possess strong homology to a repeat family specific to the centric region of maize B chromosomes (4). Under certain conditions, these knobs can be activated to function as "neocentromeres" that form kinetochores during meiosis. The presence of several classes of tandem and nontandem repeats has been identified in the centromere regions. Two classes (CCS1 and pSau3A9) of conserved sequences are located at all cereal centromeric sites studied (maize, wheat, rice, oats, sorghum, barley, and rye) (8, 95). Recent studies indicate that both sequences are part of the same DNA element; CCS1 is the LTR region and pSau3A9 is the integrase region of a retrotransposon (5, 51, 124, 138, 144). The insertion of these retrotransposons into the satellite sequences present at the centromere regions creates a unique pattern and hence specificity to this region (5). Retrotransposons have also inserted into the satellite sequences present in the knob regions (6). Given the rapid evolution of tandem arrays, it is likely that retrotransposons inserting into such sequences are steadily being deleted. These families of retrotransposons must be continually active in order to provide further elements for reinsertion.

Telomeres are the termini of chromosomes and in most species are made up of a short tandem array of similar DNA repeat sequences (182). In plants, they are mostly composed of many tandemly repeated copies of basic oligonucleotides of the sequence (TTTAGGG)n characterized by the G-rich strand running in the 5′ to 3′ direction toward the end of the chromosome and the C-rich strand running toward the centromere (37, 154, 176). The conservation of the basic sequence has been used as a basis for cloning the repeat families adjacent to the telomeres in rice, barley, and wheat (11, 37, 99, 101, 147). The repetitive families identified from these studies have been used to develop RFLP markers with which to mark the ends of the linkage maps. Many of these repetitive families adjacent to the telomere termini are specific to these regions. Shorter tandem arrays also occur throughout the cereal genomes composed of reiterating units of tens of basepairs (minisatellites) or even shorter simpler repeats of several basepairs (microsatellites) (174). Markers

derived from these loci are highly polymorphic and prove useful for genetic mapping and fingerprinting varieties (120). Particular classes of microsatellite markers are associated with LTRs of retrotransposons (145).

Gene Order

The advent of RFLP markers in the early 1980s resulted in the development of RFLP linkage maps for many of the major cereals, including wheat (48, 69), rice (34, 104), barley (82, 103), sorghum (38), and maize (32, 33). By the mid-1990s, these genetic maps were relatively dense and were generated with markers that detected genic regions. Thus, they began to provide an indication of the gene order along particular chromosomes. The genetic map of hexaploid wheat that emerged was a comparative map of its three constituent ancestral genomes (A, B, and D genomes) (48, 69). Many markers map colinearily across these genomes and are separated by similar recombination distances. The comparative analysis revealed that the progenitor genomes had undergone some rearrangements, particularly chromosomes 4A, 5A, and 7B. In the diploid A genome progenitor, translocations involving 5AL and 4AL occurred. On polyploidization, a translocation involving 4AL and 7BS occurred, followed by an inversion of 4AL (106, 112). This was consistent with the predicted translocations proposed from analyzing chromosome pairing (136).

The availability of such genetic maps for the cereals permitted genome comparisons made over the past 70 years to be extended beyond species in which chromosome pairing studies could be undertaken. Chromosome pairing studies for mammals were inappropriate, so studies on their comparative genomics began later with the advent of somatic cell hybrids. The field of comparative mapping has spawned terms such as linkage or synteny, conserved linkage, conserved synteny, homology segment, colinearity, and microsynteny. Scientists studying plants or mammals have used these terms in different contexts. The basic observation is that groups of genes located together in the ancestral genome are still located together in the genomes of species that arise from speciation of this ancestor. Clearly, during evolution, rearrangements can occur that disrupt the order of genes along a chromosome but maintain their linkage, or disrupt the order so that the genes are no longer even linked. The important issue is how much disruption has occurred: Can linkage of genes still be observed between distantly related species and can this be exploited? If the gene order observed in the small genome of rice was sufficiently conserved with that in larger cereal genomes, the rice genome would provide a tool for gene isolation strategies in the other cereals. The rice genome would be, in effect, "the wheat genome without the repetitive sequences." Moreover, comparisons of genome organization across the different cereal genomes and the solution for these comparisons would mean that the cereals could be thought of as a single genetic system (22, 132).

The initial comparisons using RFLP maps involved wheat, barley, and rye (47, 49), and maize and sorghum (122, 143, 178). Although there had been some

major translocations in rye after its speciation from the progenitors of hexaploid wheat and barley, the gene order is essentially similar in these species. The comparison of related species, maize, and sorghum, which have speciated within the past 16 to 20 million years, also revealed a degree of conservation of gene order. Even comparisons of species that have been isolated by more than 60 million years (180), such as rice and wheat and rice and maize, indicated that genes have been maintained in a similar order despite gross differences in the genome size and chromosome number of these species (2, 3, 105). From these initial comparisons of gene order in the rice, maize, and wheat genomes, genes on the rice genetic map could be grouped into sets and the genetic maps of wheat and maize could be described by the same sets of genes (rice linkage segments) (131). Furthermore, this analysis could also be extended to include the sorghum, foxtail millet, and sugarcane genomes (127, 130). Thus, a series of sets of genes could be used to describe most of the major cereal genomes as shown in Figure 2 (see color plate). The collation of all the information generated from studies on the different cereals requires a common framework. A limited number of combinations of linkage segments were noted in the genomes of the various cereals studied. It was therefore possible to create a generalized genome structure using the rice linkage segments that, when cleaved in the case of each cereal at a different number of junctions between the linkage segments, produced structures that describe the gross chromosome structures found in the two sets of maize chromosomes, the wheat and barley chromosomes and the sorghum and millet chromosomes (70, 127, 130). The breakage and fusion of rice linkage segments to create the different cereal chromosomes are reminiscent of the chromosome evolution of the holocentric chromosomes, which are the closest relatives of the cereals (116, 139). The rushes and sedges possess holocentric/polycentric chromosomes with many sites along their chromosome length for microtubule attachment. Such chromosomes naturally fragment to create smaller viable chromosomes. In hybrids between parental lines carrying the original larger chromosomes and these small, fragmented chromosomes, the large and small chromosomes align during meiosis, which suggests that these species are very adept at rearranging their chromosomes.

A large number of more detailed comparative mapping studies have now been undertaken (50, 56–59, 84, 125, 134, 149, 166–168, 179, 183). In essence, these studies confirm the basic framework outlined previously (127, 130). The gene order of chromosome regions covering several megabases have also been compared and indicate a high level of conservation (25, 60, 68, 85, 100, 102). However, it is also apparent that genes can be "transposed" to other regions, that they have become duplicated or deleted, or that they have diverged significantly. The comparative analysis based on linkage segments provides a framework for gene order; however, there are imperfections in this framework. The more detailed analyses indicated that in maize, for example, there have been inversions of regions and some of the linkage segments can be subdivided further. Analysis of these translocations and other gross rearrangements will be helpful in further classifying the relationships between the cereals (98).

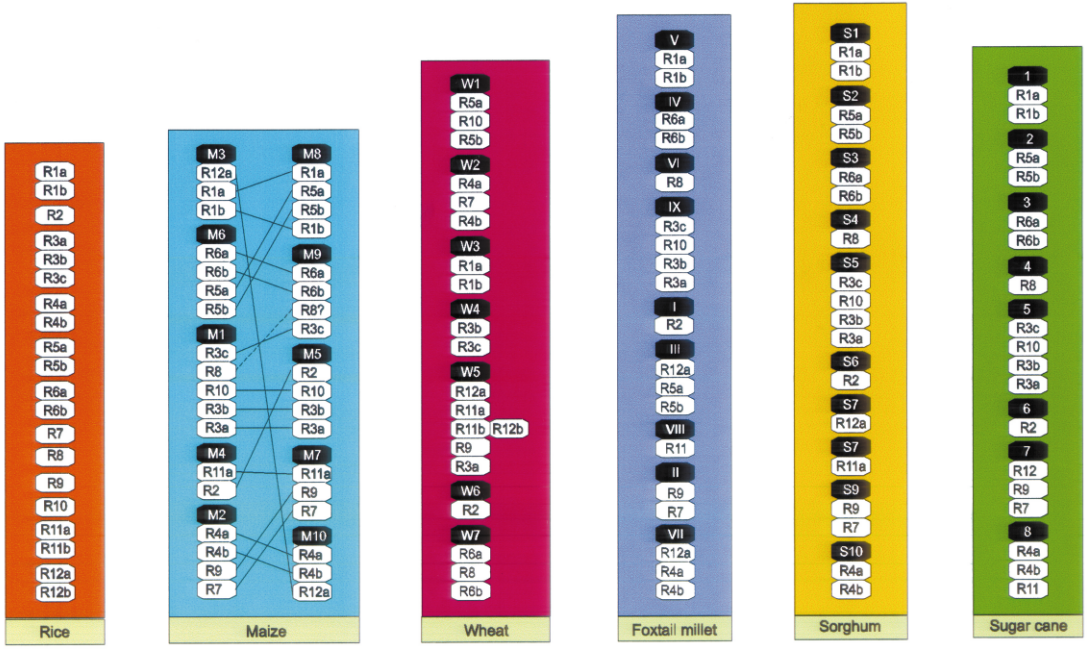

Figure 2 Comparisons of the cereal genome evolution based on rice linkage segments. (R1–R2) rice chromosomes dissected into linkage blocks (R1a, R1b, etc); 10 (M1–M10) maize; 7 (W1–W7) wheat, based on the linkage map of the D genome; 9 (I–IX) foxtail millet; 10 (S1–S10) sorghum; and 8 (1–8) basic sugarcane chromosomes represented as linkage segments on the basis of the conservation of gene order. Connecting lines indicate duplicate segments within the maize chromosomes. The designation of the sorghum and sugarcane linkage groups has varied between laboratories and publications.

The Maize Genome

Maize and sorghum are members of the Andropogoneae tribe consisting of over 900 species. Of more than 500 species analyzed from this tribe, 90% of the species possess a chromosome number that is a multiple of five. A basic number of nine occurs sporadically throughout the tribe. Consistent with this, the ten chromosomes of maize could be divided into two sets of five chromosomes, based on the linkage segment analysis (86, 131) (Figure 2, see color plate). The two sets of five chromosomes possess a different arrangement of the linkage segments. The maize chromosomes are divided into a set of the largest and a set of the smallest chromosomes. Moreover, the chromosome arms of one set are all larger than the corresponding homoeologous arms in the other set (Figure 3, see color plate). The two ancestral genomes of maize diverged some 20 mya, and one of the genomes is more closely related to sorghum, which diverged some 16 mya (72). The allotetraploidization took place some 11 million years ago (72). If the structure of the ancestral progenitor genomes of maize were similar to other small genomes (*Arabidopsis* and rice) studied to date, most of the repetitive sequences would be localized in the pericentromeric regions with the genic regions containing few repetitive elements. Bennetzen and colleagues have indicated that most of the major expansion of maize genome has taken place in the past 3 million years and has been intergenic (150). Since tetraploidization, it is unlikely that there has been preferential expansion of one of the sets of chromosomes. Thus, one set of chromosomes must have already possessed larger chromosomes than the other set.

The segmental relationship of the two chromosome sets of maize in which homoeology relationships are confined to chromosome arms generates a "circular organizational relationship" based around the centromeres (Figure 3). Such an arrangement is distinctive but not unique to plants. It bears a striking similarity to the chromosome relationships of translocation heterozygotes observed in diploid *Oenothera* and *Rhoeo* species (44). Their homologous chromosomes can be ordered into two sets, one structured as A○B, C○D, E○F (○ being the centromere) and the other set as F○A, B○C, D○E. At meiosis the homologous chromosomes will pair as a ring or a chain. Some *Oenothera* species possess two sets of, for example, A○B, C○D, E○F chromosomes and will pair as homologous chromosome pairs (bivalents). F1 progeny of two such ring-pairing species can occur and can undergo spontaneous amphidiploidy (45). Some 60 years ago, prior to any knowledge of its genome structure, cytogenetists considered the possibility of maize being a translocation heterozygote (28). Thus maize could be the amphidiploid of a F1 hybrid between two related ring-pairing (translocation heterozygotes) species. Our knowledge of the structure of the maize genome does not rule out this possibility. This event would have diploidized the two differently structured haploid genomes that were originally capable of recombining. McClintock and others reported nonhomologous chromosome pairing in maize (75, 76, 119). From our knowledge of the structure of the two sets of five chromosomes, this nonhomologous pairing can be reinterpreted as pairing between homoeologous segments derived from the two

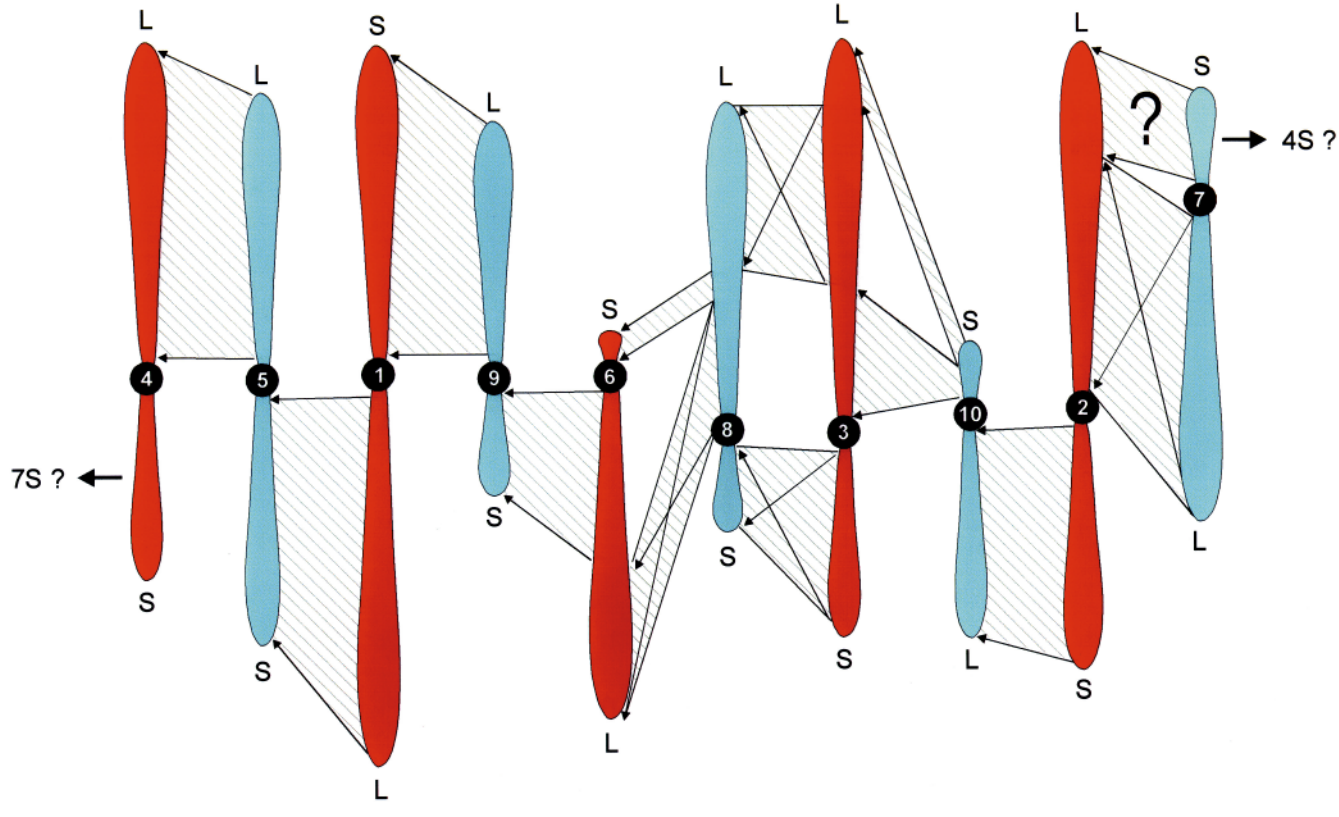

Figure 3 The homoeologous relationships of the two parental sets of maize (interphase) chromosomes forming a "translocation heterozygote." Chromosomes 4, 1, 6, 3, 2 are derived from one parental set and the rest from the other.

ancestral genomes. It is also consistent with the observations that there has been shuffling of genes between the homoeologous segments (72). Gaut & Doebley also observed from the sequence divergence of pairs of genes mapping on homoeologous segments that the genes fell into two classes, which is consistent with the hypothesis that they were derived originally from two diverged genomes (72). Translocation heterozygotes have been observed to have an unusual behavior of their centromeric heterochromatin regions during prophase. During early meiotic prophase in most species, the telomeric heterochromatin aggregates together into a bouquet that results in the intimate alignment (synapsis) of chromosomes. In translocation heterozygotes, the centromere heterochromatin also fuses as a single site or chromocenter during meiotic prophase (39). The aggregation of centromeres of paired bivalents and some knobs (neocentromeres) has also been observed in maize at meiotic prophase (75).

There has been some discussion as to whether there is homoeology between maize chromosome 3, maize chromosome 10, and rice chromosome 12, as some groups have failed to cross-map any markers between these regions in particular segregating populations (179). However, researchers using different segregating populations have identified markers mapping to both the centromere regions of maize 3 and maize 10 (57). This group of markers (including *UMC18*) mapping on both chromosomes is also located on rice chromosome 12. It is not the relationship of maize 3 and maize 10 that is unclear, but whether there is a duplicate region for maize 4S, which has homoeology with rice chromosome 11. This maize chromosome arm carries a large number of resistance genes and storage proteins. Disease-resistance genes are subject to rapid evolution. As a class of genes they tend not to reflect conservation in gene order (109). Many of these genes probably have diverged significantly from those of other species and probably from the duplicate region in maize. However, there are eight RFLP loci from maize 4S duplicated on 7S, which may indicate an ancient relationship (86) (Figure 3).

Centromeres, Telomeres, and Chromosome Evolution

Comparison of the location of the junctions of the linkage segments in the different cereal genomes, in particular rice (156), indicates that the borders fall in centromere and telomere regions (133). The region in one species is a centromere site and in another species a telomere site. Moreover, telomeric heterochromatin in maize, rye, wheat, and Bromus can, under certain conditions, function as neocentromeres (reviewed in 133). Centromere/telomere sites have been the major focus of rearrangements, probably indicating why the markers flanking these regions exhibit a loss of gene order. The structure of the maize genome indicates the importance of centromeres and telomeric regions in the evolution of its genomes (Figure 3). Because the centromeric sites have been subject to breakage and fusion events, the comparative relationship of specific centromere and telomere sites across species remains unclear. Among the cereals, the locations of centromere and telomere sites have been conserved at the gross level. Thus the potential location of these

structures is not random but rather is limited to a number of sites. In mammals, in contrast, the locations of centromere sites have not been found to be conserved across species (126).

The rice genome has been a useful tool for determining the structural relationships of the cereal genomes. One explanation is that its structure is similar to that of the ancestral progenitor genome. An alternative explanation is that it is the diploid with the highest basic number of chromosomes that has been analyzed. The rice genome reveals more potential (centromere and telomere) sites involved in breakage and fusion events of chromosomes than other species. However, still unclear is how and why certain sites in the cereal genomes are activated as centromere sites in some species and not in other closely related genomes and how this activity is modified. This issue is important in the debate about whether sorghum with its 10 chromosomes is an ancient tetraploid (38). In situ hybridization shows that five of the sorghum centromeres are distinct from the other five sites. It has been argued that this observation supports the ancient tetraploid concept (81). However, comparative mapping with rice indicates that the gene order in the sorghum genome is similar to that of rice (57). There is no clear duplication of the sorghum genome with respect to the rice genome. Sorghum chromosomes are metacentric but share homoeology with whole or parts of chromosome arms of maize (57). Thus, active centromeric sites do not map comparatively between sorghum and the two maize chromosome sets. The lack of knowledge on how sites are activated or suppressed during chromosome evolution makes it difficult to interpret the different sorghum centromere structures.

CHROMOSOME PAIRING

Chromosome pairing is the process by which homologous chromosomes (termed homologues) start in a premeiotic somatic nucleus randomly organized with respect to each other but end up during the pachytene stage of meiotic prophase in close association. Homologue pairing is important for the correct segregation of the chromosomes to gametes. The process of bringing homologues together involves their reciprocal recognition, coalignment, and synapsis. The term chromosome pairing has often been applied to one or more of these individual stages. An S phase occurs between premeiotic interphase and meiotic prophase in which the chromosomes are replicated, generating two sister chromatids. To that effect the intimate association of the homologues, which are composed of sister chromatids, is facilitated by a protein structure, the synaptonemal complex (177a). A protein structure, the lateral element, is formed by the two sister chromatids of each homologue. The lateral elements of each homologue are then aligned and associated by a third protein structure forming between them.

Chromosome-pairing studies provided early indications as to the genome relationships between polyploid species and diploid relatives. In essence, these were the first comparative genomic studies. Conversely, have the recent comparative

genomic studies contributed to our understanding of the chromosome-pairing process? As described, these studies reveal that two chromosome structures have been important in cereal evolution, the telomeres and the centromeres. Both chromosome structures in plants such as wheat, rye and barley are located on the nuclear membrane. In interphase cells the centromeres are at one pole of the nucleus and the two chromosome arms extend to the other pole where the telomeres are dispersed over the membrane (1, 9, 10). This chromosome organization has been described as a "Rabl" configuration (144a).

In Diploids

Early studies indicated an important role for telomeres/subtelomeric regions during the pairing process. Subtelomeric heterochromatin knobs are clearly visible in interphase nuclei in rye (27, 164). Light microscopy revealed that early during meiotic prophase, the telomere regions of diploid species form a single cluster or bouquet. Meiocytes visualized in premeiotic interphase exhibited no association of telomeric regions. This is consistent with the observations made on *Lilium longiflorum*. This species' chromosomes undergo a preleptotene contraction and become visible. There was no clear association of chromosomes at this stage, which suggests that there is no premeiotic alignment in this diploid species (172, 173). The intimate alignment of rye chromosomes during meiotic prophase was assessed by spreading and squashing meiocytes at the zygotene stage to reveal their synaptonemal complex structures (77). The initiation of synapsis occurred after the bouquet had formed. The telomere regions are among the first sites to undergo synapsis. However, many other sites along the chromosome are also involved in synapsis of the bivalents (pair of homologues). The intimate alignment process could not be explained simply by zipping up of these initiation sites from the telomeres (77). The sizes of heterochromatin knobs in rye can vary greatly. Synapsis between such homologous chromosomes differing in heterochromatin knob size is largely unaffected in rye (80). One lateral element was slightly longer than the other, which resulted in an unpaired telomeric end. However, there was only slight reduction in the level of recombination. Importantly, the length of the lateral elements did not correlate directly with the difference in size of the chromosomes. This is more marked in hybrids between two Lolium (diploid) species, which differ by 50% in their chromosome size (94). These different-sized chromosomes (homoeologues) intimately associate, which results in the alignment of lateral elements of similar size. The synapsed structures resemble perfectly paired bivalents. There is no indication of a substantial correction to the lateral element length during the process of synapsis. Thus the chromosomes, which are substantially different in size, produce only lateral elements of a length similar to the chromosome with which it will become associated. The implication is that the pair of chromosomes that are going to be synapsed as a bivalent are already associated at more than one site prior to synapsis. If the searching process for chromosomes took place after lateral elements had been formed, synapsed chromosomes with different lengths

of lateral elements would be observed. Two chromosome structures, telomeres and centromeres, both located on the nuclear membrane, could be involved in the initial chromosome searching process. The clustering of the telomeres to form a bouquet brings the telomeres together. Data presented by Martinez-Perez at the recent 9th Botanical Congress indicates that in diploid *Triticum* and *Aegilops* species the centromeres also associate in pairs at this stage (118). Other sites along the chromosome arms would also have to be involved. It is unclear how these sites search and recognize each other without an elaborate system of motors and pulleys moving the chromosome sites around the nucleus. An attractive hypothesis proposed by Cook is that these sites are genes that are being associated at transcriptional sites (40). Homologous genes would be transcribed by being looped out to the same transcription factory, thereby enabling association to occur. Thus, chromosomes of different sizes but possessing similar gene orders would associate through their telomeres and centromeres on the nuclear membrane and the genic regions in the transcriptional factories.

In Autotetraploids

Synaptonemal complex spreading studies have also been undertaken on autotetraploids of *Triticum monococcum* (the A genome donor of hexaploid wheat) and autotetraploids of rye (*Secale cereale*) (79, 152). These plants contain seven basic chromosomes with four homologous chromosomes for each chromosome group (i.e. 28 chromosomes in all). The spreading data indicated that the chromosomes could synapse as seven cross-like structures. Thus, although the telomere regions had the potential to associate with three other homologous regions, they only formed pair-wise associations. This was the case for all the regions along the chromosome arm except for one site halfway along the chromosome. Most sites on the *Triticeae* chromosomes can only synapse in pairs, and these associations are with the same chromosome. Only a single site on the chromosome engages in multiple interactions. Martinez-Perez also observed that centromeres associate premeiotically in autotetraploids of the *Triticeae* species, reducing to approximately seven sites during meiotic prophase (118). The implication is that the centromeres of four homologous chromosomes associate, forming cross-like structures of synapsed chromosomes.

In Allopolyploids

Synaptonemal complex spreading studies on allotetraploids and allohexaploids (species possessing two or three sets of related but not identical genomes) including allotetraploid *Aegilops* species sharing D genomes (42), *Aegilops* species sharing U genomes (41), allotetraploid oats, and allohexaploid oats (96) all show that the vast majority of chromosomes are synapsed as bivalents. Multivalent structures are occasionally observed at low frequency. A study on hexaploid wheat also reported predominantly bivalent formation (165). The regions adjacent to the telomeres were among the first to synapse. However, other sites were also

involved in initiating synapsis, producing bivalent structures resembling beads on a necklace. Thus, although chromosomes have the potential to associate with three other chromosomes (two homoeologues and an homologue), they associate with their homologue to form a bivalent structure. In this case, centromere regions are associated as pairs at meiotic prophase in hexaploid wheat (118). Thus the homoeologous and homologous centromere regions are distinguished in the allotetraploid and allohexaploid situations and resolve as pairs.

Bennett and colleagues showed that the length of meiotic prophase is shorter in polyploids compared to their diploid progenitors, which is the opposite from what would be expected (20). The more genomes or chromosomes are present, the shorter the meiotic prophase, and hence the time required to sort them. The implication is that the chromosome-sorting process in autotetraploids and allotetraploids has been extended outside meiotic prophase. In that regard, it is now apparent that centromeres associated in pairs in floral tissues of all the *Triticeae* allopolyploids studied including hexaploid wheat (118). Thus centromere association is occurring prior to telomere association in these species (9, 10, 117). However, the diploid progenitors do not associate their centromeres until meiotic prophase (118). Thus, polyploidization results in the early association of centromeres. This is consistent with the early studies by researchers who, when treating hexaploid wheat anthers with colchicine prior to their meiocytes being in meiotic prophase, observed an effect on chromosome pairing at metaphase I (17, 52–54, 169). The observation that centromeres are associated in pairs during floral development in hexaploid wheat and wild polyploid relatives but not in their diploid progenitors suggests that the chromosome-sorting process was initially taking place at the centromeres in polyploids. Pairs of homologous chromosomes were fluorescently labeled in hexaploid wheat and their behavior followed from early floral (anther development) through to meiotic prophase (118). These studies were undertaken using anther sections and confocal microscopy so that intact cells could be analyzed (7). The sections enabled the cells to be clearly classified. The study showed that early in anther development prior to the meiocytes being clearly recognizable from tapetal cells, some seven days prior to meiotic prophase, the centromeres in the developing anther associate in pairs (8, 10, 118). By five days prior to meiotic prophase, these associations are becoming homologous associations. Thus, the homologous chromosomes at this stage form a V-configuration. By three days prior to meiotic prophase, the stage at which meiocytes are in premeiotic interphase, 90% of the homologous chromosomes being visualized were associated via their centromeres (10). During premeiotic interphase, the homologous chromosomes colocalize along their length. However, the telomeres of the homologues do not associate as pairs (118). The meiocytes progress through S phase. The telomeres cluster to form a bouquet. The homologous chromosomes separate along their length and are associated by the centromeres and telomeres. The homologous chromosomes are visualized as sister chromatids at this stage (118). The sister chromatids then associate and the homologous chromosomes associate simultaneously. The homologous chromosomes are intimately aligned and then the telomere

bouquet declusters (118). A schematic representation of the chromosome pairing process in polyploid and diploid *Triticeae* is shown in Figure 4 (see color plate).

Hexaploid and tetraploid wheats (69, 90) and rice have not suffered major rearrangements following polyploidization. The maize genome, on the other hand, evolved through breakage and fusion events of centromeres and telomeres, followed by tetraploidization and then by further rearrangements (Figure 3). It is not yet known whether maize centromeres associate premeiotically, as happens in hexaploid wheat and polyploid *Aegilops* species. However, visualizing the maize heterochromatin knobs, Cande and colleagues showed no premeiotic association of these sites (46). This implies that maize chromosomes do not align along their length during premeiotic interphase. During the leptotene and zygotene transition of meiotic prophase, maize telomeres cluster to form a bouquet, and then the heterochromatin knobs associate (16, 46). The homologues intimately associate along their length with the telomeres still clustered (75, 76). If centromeres in maize associate premeiotically, chromosome behavior in maize and the timing of the telomere bouquet would resemble that described for hexaploid wheat lines lacking the *Ph1* locus.

The *Ph1* Locus

The requirement for breeding purposes to introgress chromosome segments carrying beneficial traits from wild relatives into polyploids such as wheat encouraged researchers to study the genomic relationships of wheat (*Triticum*) and its wild relatives (*Aegilops*) through chromosome pairing. F1 hybrids between diploid progenitors of hexaploid wheat or wild relatives are capable of pairing and recombining (14, 181). However, polyploidization and the subsequent premeiotic association of centromeres promotes homologous pairing and thereby reduces the ability to introgress chromosome segments from wild species. Both Riley and Okamoto observed that by deleting both 5B chromosomes, a level of homoeologous pairing could be induced (140, 146). Sears identified a deletion (*ph1b*) of the 5B chromosome that also produced the same effect (155). A deletion of the same region of 5B causes a similar effect in tetraploid wheat. Researchers termed the deleted locus *Ph1*. Sears noted that the fertility of the line was around 30% of that of the wild-type wheat (155). This implied that the majority of pairing configurations observed at metaphase I in this line resulted in infertility, possibly through gamete abortion. A number of studies have been undertaken to characterize the effect of the *Ph1* locus. Analysis of anther sections during floral development revealed that, in common with hexaploid wheat (and its polyploid relatives), centromeres associated during floral development in the absence of the *Ph1* locus (118). However, the centromere structure is affected when the *Ph1* locus is deleted (9). The nature of the premeiotic centromere associations has been determined. In similarly staged sections, when 90% of the homologues were associated via their centromeres in the presence of the *Ph1* locus, only 30% of the homologues were in the absence of the locus (10). This is also the level of fertility of the *ph1b* line (155). Analysis of the wild

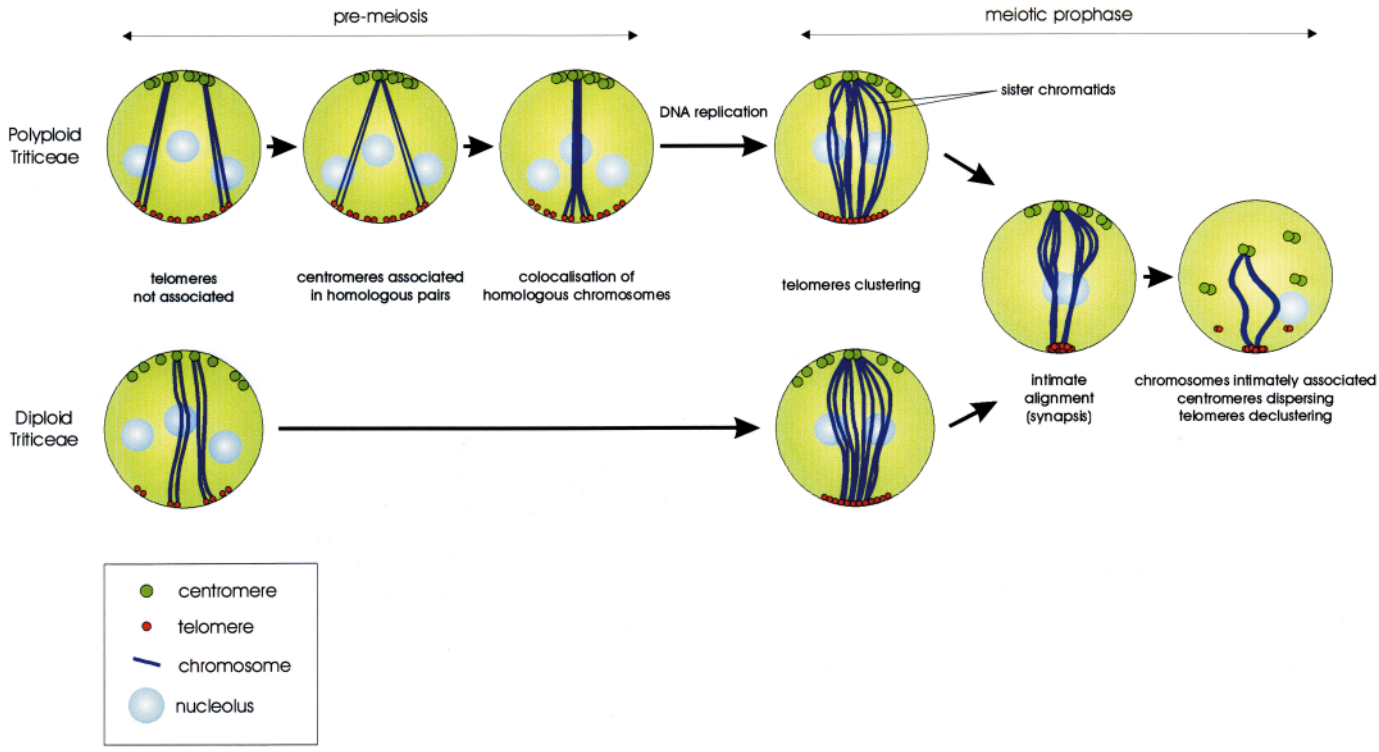

Figure 4 Diagram of chromosome-pairing events before and during meiosis in polyploid and diploid wheats. Polyploid and diploid *Aegilops* species within the *Triticeae* also exhibit similar pairing to the *Triticum* species.

relatives of wheat reveals that none of the chromosomes tested carry loci that can compensate for the loss of the 5B chromosome in hexaploid wheat (14). In the absence of the *Ph1* locus in wheat, centromeres still associate premeiotically as they do in polyploid *Aegilops* relatives (117, 118). The *Ph1* locus on chromosome 5B raises the fertility of wheat. It is quite possible therefore that the current 5B allele was not present in the original hybridization but was a mutation that arose and was then selected because it conferred increased fertility.

The timing of formation of the telomeric bouquet in the *ph1b* line is also delayed in meiotic prophase, thereby lengthening the whole stage (19, 118). The level of association between homologues via the centromeres observed during premeiotic interphase may increase further during meiotic prophase until the telomeric bouquet is formed. The change in timing of the telomeric bouquet will change the timing of synapsis, which ultimately could affect the recombination between chromosomes in the presence and absence of the *Ph1* locus. The *Ph1* locus appears to indirectly affect synapsis (78). Gillies noted that it was difficult to prepare synaptonemal complex spreads from wheat carrying the *Ph1* locus (78). Most preparations revealed short fragments of associated lateral elements. This is consistent with the observation that sister chromatids and homologues are associating at the same time, implying that lateral element formation is not complete before the central element formation occurs. In wheat hybrids in which only homoeologous chromosome pairing could occur, the chromosomes were correctly synapsed in the presence or absence of the *Ph1* locus (78). The homoeologous chromosomes differ in size, yet synapse via lateral elements of similar length. This implies that the chromosomes are associated prior to synapsis, which is consistent with the occurrence of centromeres in pairs and telomeres in the bouquet. Analysis of pairing in autotetraploids described above indicates that centromeres can be involved in multivalent formation (118). The observation that centromeres are in pairs in the *Ph1* mutant is consistent with a low level of chromosomes present as multivalents at metaphase I. In the *ph1b* line, only four chromosomes per nucleus on average are engaged in higher-order associations; the rest are bivalents or univalents.

Recombination and the *Ph1* Locus

Deleting one of the telomere regions of the pair of homologous chromosomes results in the failure of the pair of homologous chromosomes to recombine in hexaploid wheat and therefore to be found associated at metaphase I (43, 113). Deleting the telomere regions of both chromosomes to the same extent does not reduce recombination between homologues in hexaploid wheat (113) nor does the possession of nonhomologous centromeres, provided the telomere/subtelomeric regions exhibited homology (43). The *Ph1* locus affects recombination (55, 61, 78, 114). In wheat hybrids in which homoeologous chromosomes had synapsed in the presence of the *Ph1* locus, the chromosomes failed to recombine (78). Even homoeologous interstitial segments within a homologous chromosome fail to recombine despite the occurrence of recombination within the homologous segments (113).

However, in the absence of *Ph1* locus, homoeologous chromosomes and interstitial homoeologous segments within homologous chromosomes recombine. This implies that either the *Ph1* locus is a complex containing genes that affect the premeiotic alignment through centromere association and other genes affecting recombination, or that the high level of association of homologues during floral development leads to an early association of telomeres and synapsis. The expression levels of genes preventing homoeologous recombination may be comparable in similar staged floral tissues of wheat with and without the *Ph1* locus. However, at the time the telomeric bouquet and chromosome synapsis occur in wheat lacking the *Ph1* locus, the expression levels may be in decline, resulting in homoeologous recombination.

Pairing Models

Three hypotheses have long dominated the field of cereal chromosome pairing. How do these hypotheses stand in the light of recent data?

As researchers studying pairing in autotetraploid plants were to show, the chromosomes associate in these species as multivalents that later resolve as bivalents by metaphase I. Researchers at Carlsberg performed some of the initial studies using Bombyx (silkworms), and observed the initial multivalent formation and later bivalents. They proposed that a similar mechanism operated in the case of allopolyploids, such as hexaploid (bread) wheat. The initial studies seem to support this proposal (88, 93). However, a more detailed analysis by Holm revealed mostly bivalent formation (89). Although Holm concluded that "most chromosomes are at mid zygotene present as partially paired bivalents and only few have engaged in multiple associations," he nevertheless argued that multivalent formation and their resolution were important (89). Thus it is generally perceived in the literature that chromosomes in hexaploid wheat are involved in a searching process at synapsis through associating at a number of sites along their chromosome arms. This hypothesis is, however, problematic. First, most multivalents claimed from analyses of synaptonemal complexes were based on a single site association between two chromosomes that were synapsed as partially paired bivalents with another partner. If there is generalized searching operating, it would be expected that a number of sites would be involved along their chromosome arms visualized as multiple interactions. This is not the case. Moreover, the process of squashing and spreading to analyze the synaptonemal complex structures will result in some chance associations between partially paired bivalents. Clearly, these two types of association need to be differentiated. Autotetraploids of the progenitors of wheat do not exhibit interstitial multivalent associations (as described above) between identical chromosomes (79). Thus, why would multivalent associations at synapsis occur between nonidentical and not between identical chromosomes? Subsequent synapsis studies of an autotetraploid of rye (152) and *Triticum monococcum* (79) show that one site is engaged in multivalent associations. Recent data indicate that such sites are now likely to be the centromere regions. However, centromere sites

are not engaged in multiple associations at meiotic prophase in allopolyploids such as hexaploid wheat. They associate mostly in pairs early in floral development and remain in pairs through meiotic prophase (118). Importantly, a number of spreads of partially synapsing wheat chromosomes show no associations that can be interpreted as multivalent formation (89). If all chromosomes had to go through the multivalent formation as part of synapsis, multivalents would be observed in all spreads. The close polyploid relatives of hexaploid wheat, *Aegilops* and *Avena*, have recently been shown not to exhibit multivalent formation at synapsis but simply bivalent formation (41, 42). Moreover, as stated previously, homoeologous chromosomes are synapsed by lateral elements of similar lengths, which implies that these chromosomes were already committed to pair prior to completion of lateral element formation (78). All data indicate that chromosomes in hexaploid wheat synapse as bivalents, as is in the case for its wild polyploid (*Aegilops*) relatives.

Early studies on *Drosophila* observed that chromosomes associate in somatic tissues during embryo development (123). Based on these *Drosophila* observations, Feldman proposed that most plant species associate their chromosomes premeiotically. Because he had observed the presence of univalents, multivalents and interlocking of bivalents in hexaploid wheat with increased doses of the 5BL arm, Feldman argued that the presence of the *Ph1* locus on 5B suppresses this premeiotic chromosome pairing "causing random distribution of chromosomes in the premeiotic nucleus." Premeiotic association was concluded to be partially suppressed at two doses of the *Ph1*, which eliminated pairing between homoeologues and led exclusively to homologous pairing at meiosis. The presence of extra *Ph1* doses even suppressed homologous chromosome pairing. Feldman and colleagues therefore used squashed preparations to assess whether there was somatic chromosome association in root cells (64, 65). This strategy would provide evidence of somatic association leading up to premeiosis, which then would be disrupted premeiotically by the *Ph1* locus. From the squashed preparations, Feldman and colleagues concluded that there was somatic chromosome association in roots. From further studies using colchicine treatment, they concluded that microtubule interactions with the centromeres were involved in this somatic pairing (12, 13). The cloning of sequences at centromeres now permits the question of whether centromeres associate in roots to be addressed (8). There is no evidence for centromere association in roots nor association of homologues as proposed (87, 118). Furthermore, homologous chromosomes are not randomly organized in the premeiotic nucleus but homologues are associated via their centromeres (117, 118). Therefore, although the principle that association of homologues involved centromeres proved to be correct, current data do not support the experimental evidence on which this proposal was based.

Finally, Watanabe proposed from studies on polyploid Chrysanthemum that obligate bivalent formation in polyploids is achieved by initiating chromosome pairing at two sites (174). He concluded that there would be two sites under independent and fundamentally different genic control and that the pairing of one site always precedes the pairing at the other. These proposals are entirely

consistent with chromosome behavior of the *Triticum* and *Aegilops* (10, 117, 118). The analyses described above of autopolyploids and allopolyploids suggest that centromeres and telomeric regions are these two sites.

CONCLUDING REMARKS

In summary, centromeres and telomeres have been important in influencing cereal chromosome evolution and the pairing of cereal chromosomes. The development of new vector systems, particularly cereal artificial chromosomes for the biotech industry, is likely to promote centromere- and telomere-based studies. The better understanding of the structure of this regions and the proteins that interact with them will, in turn, help chromosome-pairing studies. The future characterization of the *Ph1* locus itself may well identify some of the key proteins/factors that interact at these sites.

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