Recombination of Chromosomes *3A*^{m} and *5A*^{m} of *Triticum monococcum* With Homeologous Chromosomes *3A* and *5A* of Wheat: The Distribution of Recombination Across Chromosomes

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ABSTRACT

Recombination of chromosomes *3A*^{m} and *5A*^{m} of *Triticum monococcum* with closely homeologous chromosomes *3A* and *5A* of *T. aestivum* was compared with recombination across corresponding homologous chromosome pairs. Differentiation between the homeologues impacted recombination in the proximal regions of the long arms the most and in the distal regions of the long arms the least. It is concluded that this variation principally reflects allocation of multiple crossovers across an arm and positive crossover interference across chromosome arms. Recombination rates between homeologous chromosomes *5A*^{m} and *5A* differed in the opposite sexes.

ACCUMULATION of mutations during species divergence impairs the capacity of homologous chromosomes for meiotic crossing over, resulting in chromosome differentiation and, ultimately, conversion of homologous chromosomes to homeologous chromosomes. Originally, mutations in chromosome structure perturbing the linear order of gene loci across chromosomes were considered the primary cause of chromosome differentiation. If genomes differentiated structurally, genome differentiation would occur in discrete steps. Differentiated, closely related genomes would be composed of homologous and homeologous (structurally rearranged) chromosomes and homeologous chromosomes would be composed of homologous and structurally rearranged segments. This point of view is intrinsic to classical concepts such as segmental allopolyploidy and structural and cryptic structural differentiation (Stebbins 1971). However, studies in wheat have failed to find evidence consistent with this model (Dvořák and McGuire 1981; Crossway and Dvořák 1984; Dvořák and Chen 1984; Kota *et al.* 1986; Dubcovsky *et al.* 1995; Dvořák *et al.* 1995). As an alternative, it was suggested that chromosome differentiation is largely of a substructural nature, meaning that it is comprised of changes ranging from substitutions, deletions, and additions of base pairs to insertions, deletions, and rearrangements of stretches of nucleotides (Dvořák and McGuire 1981; Dubcovsky *et al.* 1995). The principal difference between the classical view and the substructural view of chromosome differentiation is that the gross linear order of gene loci may remain unaltered in substructurally differentiated genomes. Of course, the two mechanisms are not mutually exclusive; structural differentiation may be superimposed on substructural differentiation.

In allopolyploid plants, chromosome differentiation is the target of the activity of the suppressors of heterogenetic chromosome pairing, which prevent meiotic pairing and recombination between homeologous chromosomes and ensure disomic inheritance. The best-known suppressor of heterogenetic pairing is the wheat *Ph1* locus on the long arm of chromosome *5B* (Okamoto 1957; Riley and Chapman 1958; Sears and Okamoto 1958). The *Ph1* locus has a strong suppressive effect on heterogenetic pairing and almost entirely prevents recombination between homeologous chromosomes in polyploid wheats. In hexaploid wheat, *Triticum aestivum* L. (genomes *AABBDD*), meiosis regulated by the *Ph1* locus is highly discriminatory. Not only does the *Ph1* locus prevent pairing and recombination between homeologous chromosomes, but it also reduces metaphase I (MI) pairing between homologous chromosomes from different inbred lines (heterohomologous chromosomes) compared to identical homologues in an inbred line (euhomologous chromosomes; Dvořák and McGuire 1981; Kota *et al.* 1986; Dvořák 1988). The study of MI pairing between heterohomologous chromosomes led to a model that suggested that chromosome differentiation is initiated at a large number of sites across the genome (Crossway and Dvořák 1984; Dvořák and Chen 1984). In heterohomologous chromosome pairs, this differentiation is presumably synonymous with allelic variation. Extending the model of heterohomologous pairing to homeologous chromosome pairing, the homeologous chromosomes are expected to be differentiated across their entire lengths.

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A relevant question is whether differentiation impacts recombination between a pair of homeologous chromosomes across their lengths evenly, or if it reduces recombination to a greater extent in some regions than others. Lukaszewski (1995) employed segregation of polymorphic C-bands in a study of recombination among wheat and rye chromosomes of homeologous group *1* and between a recombined chromosome composed of segments of wheat chromosome arm *7AS* and chromosome *7S* of *Aegilops speltoides* Tausch with wheat chromosome *7A*. The distribution of exchanges between homeologues appeared to be similar to that between corresponding wheat homologues (Lukaszewski 1995). In contrast, recombination of molecular markers between wheat homeologous chromosomes *4B* and *4D* in the genetic background of tetraploid wheat, *T. turgidum* L. (genomes *AABB*), appeared to be disproportionately more reduced in the proximal region of the long arm and across the entire length of the short arm than in the distal region of the long arm. In a study of recombination between recombined *T. monococcum* L. ($2n = 14$, genomes A^mA^m) chromosome *1A*/*1A*^{m} and *T. aestivum* L. chromosome *1A*, recombination was virtually absent across the entire short arm and the proximal region of the long arm (Dubcovsky *et al.* 1995). Homeologous recombination of the distal region of the long arm could not be assessed, because the region was replaced by a segment of chromosome *1A* in the *1A*/*1A*^{m} chromosome.

To assess recombination rates across the entire length of wheat and *T. monococcum* homeologues, complete *T. monococcum* chromosomes *3A*^{m} and *5A*^{m} were substituted for chromosomes *3A* and *5A* of *T. aestivum*. Recombination rates between *3A*^{m} and *3A* and *5A*^{m} and *5A* were assessed and compared with those between corresponding homologous chromosomes.

MATERIALS AND METHODS

Disomic substitution lines: Chromosomes *3A*^{m} of *T. monococcum* accession no. G2203 and *5A*^{m} of *T. monococcum* accession no. G1777 were substituted for chromosomes *3A* and *5A* of *T. aestivum* "Chinese Spring" (henceforth, CS), respectively, following a procedure described by Kota and Dvořák (1985). Both *T. monococcum* accessions were collected and supplied by B. L. Johnson (University of California, Riverside). Briefly, *T. monococcum* was crossed with a respective CS monotelosomic, and 54-chromosome nullisomic amphiploids were produced by colchicine treatment of nullisomic hybrids. Each nullisomic amphiploid was recurrently backcrossed as a male to the corresponding monotelosomic, selecting plants devoid of a telosome in each backcross generation. In BC_5, plants were selfed and disomic substitutions (DS) were selected in the progeny. Disomic substitutions *3A*^{m}*(3A)* and *5A*^{m}*(5A)* will be designated as DS*3A*^{m} and DS*5A*^{m}, respectively.

The study of recombination between homologues involved DS*5Aspelta* and DS*3ACnn*. In the former line, chromosome *5A* of Iranian spelt (*T. aestivum* ssp. *spelta*) accession no. 407a (Kuckuck 1964) was substituted for CS *5A*. The substitution line was developed and supplied by E. R. Sears (Luo *et al.* 2000). In the latter line, chromosome *3A* of *T. aestivum* "Cheyenne" (henceforth, Cnn) was substituted for CS chromosome pair *3A* (Morris *et al.* 1966).

Mapping populations and their development: The maps employed in this work were constructed from segregating populations of single-chromosome recombinant substitution lines (RSLs). RSLs are lines in which a chromosome pair is replaced by a recombined monosome (monosomic RSL) or disome (disomic RSL). The strategy for the development of populations of wheat RSLs has been described (Luo *et al.* 1998). While individual lines in a population of RSLs differ in the recombined chromosome, they are expected to be isogenic for the remaining 20 chromosome pairs. In the monosomic RSL populations employed here, chromosome *5A* or *3A* was recombined, whereas the remaining 20 chromosome pairs were of isogenic CS (Table 1). Except for the DS*5A*^{m} × CS (F) mapping population and the DS*5A*^{m} × CS*ph1b* mapping population produced in the genetic background homozygous for the *ph1b* mutation (Table 1), all other RSL mapping populations were developed by crossing an F_1 from a cross of DS × CS with a respective CS monotelosomic (female) and selecting monosomics in the progeny (Table 1); only recombination in the male meiosis was consequently sampled in these RSL populations. The population DS*5A*^{m} × CS (F) was developed by backcrossing the F_1 as a female to CS; only recombination in the female meiosis was sampled in this RSL population. A total of five RSL populations were developed here; RSL population *DS5Aspelta* × CS was developed and described earlier (Luo *et al.* 2000) (Table 1). The DS5A^m × CS *ph1b* population was developed using a strategy described by Dubcovsky *et al.* (1995). A single *5A*^{m}*-5A* plant homozygous for the *ph1b* mutation was obtained. Since this plant was male sterile, it was backcrossed as a female to CS, and 38 F_1 plants were obtained.

Restriction fragment length polymorphism (RFLP) and map construction: Nuclear DNAs were isolated from individual plants of RSLs (Dvořák *et al.* 1988). Southern blotting and DNA hybridization were performed as described earlier (Luo *et al.* 1998). The clones used as probes for the detection of RFLPs were selected from the pool of probes used to construct the maps of chromosomes *5A*^{m} and *3A*^{m} in *T. monococcum* (Dubcovsky *et al.* 1996). RFLP maps were constructed with the computer program MAPMAKER/EXP 3.0 (Lander *et al.* 1987; Lincoln *et al.* 1992) using the Kosambi function (Kosambi 1943), with a LOD threshold of three. To test the statistical significance of differences in the lengths of individual intervals between maps, interval lengths in centimorgans were converted into percentage recombination, variances of the estimates were calculated according to Allard (1956), and the differences in the interval lengths between maps were tested by *z*-test.

Chromosome analyses: DS*3A*^{m} and DS*5A*^{m} were crossed with CS, and the total number of bivalents per cell at MI of meiosis was assessed under microscope in the progeny using the acetocarmine squash technique.

RESULTS

Group 3 chromosomes: *T. monococcum* chromosome *3A*^{m} recombined with CS chromosome *3A* in the presence of the *Ph1* locus with a reduced rate (Figure 1). While the total length of the DS*3A*^{m} × CS map was only 45.6 cM, the total length of the same intervals on the map of chromosome *3A*^{m} constructed in *T. monococcum* was 144.5 cM (Figure 1). The *T. monococcum* map is similar to the map of *T. aestivum* chromosome *3A* (Dub-

TABLE 1

Characteristics of the mapping populations

Population	Type of population	Status of *Ph1*	No. of plants
DS*3A*^{m} × CS	RSL	+	68
DS*Cnn3A* × CS	RSL	+	67
DS*5A*^{m} × CS	RSL	+	93
DS*5A*^{m} × CS*ph1b*	RSL	−	38
DS*5A*^{m} × CS (F)	RSL	+	70
DS*5Aspelta* × CS[a]	RSL	+	87
T. monococcum[b]	F_2/F_3 families	Not applicable	74

[a] Luo *et al.* (2000).
[b] Dubcovsky *et al.* (1996).

covsky *et al.* 1996) reported by Gale *et al.* (1995). Only three polymorphic markers were found between DS*Cnn3A* and CS. The distances between them were similar to those on the *T. monococcum* map (Figure 1).

Recombination across the short arm was reduced to a half on the DS*3A*^{m} × CS map compared to that on maps based on recombination between homologues (Figure 1). A reduction of a similar size in recombination was observed in the distal region of the long arm. However, in the proximal region, *Xpsr909* to *Xwg110*, recombination was reduced to one-ninth (Figure 1).

Group 5 chromosomes: In the *Ph1* background, a map based on recombination between *5A*^{m} and *5A* in the male was 64.3-cM long (Figure 2). In contrast, a map based on recombination between wheat *5A* homologous chromosomes (also in the male) was 233-cM long, and the F_2 *T. monococcum 5A*^{m} map was 191-cM long.

In the short arm, recombination between *5A*^{m} and *5A* was 13.5- and 18.6-fold lower than recombination in the DS*5Aspelta* × CS population and the *T. monococcum* F_2 population, respectively. Compared to the maps of the short arm based on recombination between homologues, the distal intervals on the DS*5A*^{m} × CS map were reduced more than the proximal intervals (Figure 2).

In the long arm, recombination between *5A*^{m} and *5A* in the distal intervals was either comparable to recombination between homologues (intervals *XksuF1-Xwg114-Xwg199*) or was only slightly reduced. However, in the proximal interval, interval *Xbcd508-XksuH8*, recombination was manyfold lower than that between homologous chromosomes (Figure 2).

A map based on recombination between *5A*^{m} and *5A* in the female was only 26-cM long (Figure 3). This is less than half of the length of the map based on recombination between the same chromosomes in the male (compare Figures 2 and 3). The pattern of recombination rates across the map based on female recombination was similar to that on the map based on male recombination, with the exception that there was an absence of recombination in the *XksuF1-Xwg114* interval in the long arm. The same interval was 12.2 cM on the male map.

In the *ph1b* background (Figure 3), extensive recombination occurred between *5A*^{m} and *5A* in all intervals. The map was a total of 239.8-cM long, and in no interval did the map differ significantly from the corresponding maps based on recombination between homologues.

Segregation distortions: No segregation distortion was observed in RSL population DS*3A*^{m} × CS. In RSL populations DS*5A*^{m} × CS, segregation distortion occurred across the entire short arm and a proximal portion of the long arm (Figures 2 and 3). Chromosome *5A*^{m} was favored in the male, but CS *5A* was favored in the female.

Chromosome pairing and transmission of nullisomic gametes: In F_1 plants from crosses of DS*3A*^{m} and DS*5A*^{m} with CS, 80% of the investigated 63 PMCs and 90% of the investigated 67 pollen mother cells (PMCs) had 21 bivalents, respectively. These values represent a minimum pairing level of *3A*^{m} and *5A*^{m} with wheat chromosomes *3A* and *5A*, respectively, since other chromosomes may have occasionally failed at pairing at MI as well.

In the DS*5A*^{m} × CS (F) backcross population constructed in the *Ph1* background, 15.7% progeny were monosomic for *5A*. These plants originated from female nullisomic gametes, which in turn originated from the failure of chromosomes *5A*^{m} and *5A* to pair at MI. PMCs with nondisjunction produce, on the average, 3/4 nullisomic gametes (Sears 1954). From the frequency of monosomic plants, the frequency of meiocytes with regular *5A*^{m} and *5A* disjunction was calculated to be 79.1%. This estimate is only slightly lower than the observed 90% pairing in PMCs ($P > 0.05$).

In the DS*5A*^{m} × CS male backcross population constructed in the *Ph1* background, no plant indicating that a nullisomic gamete was transmitted was observed. This is expected because of severe selection against nullisomic gametophytes in the male. Unexpectedly, no nullisomic gametes were transmitted in the *ph1b* female backcross progeny, presumably due to lethal effects on

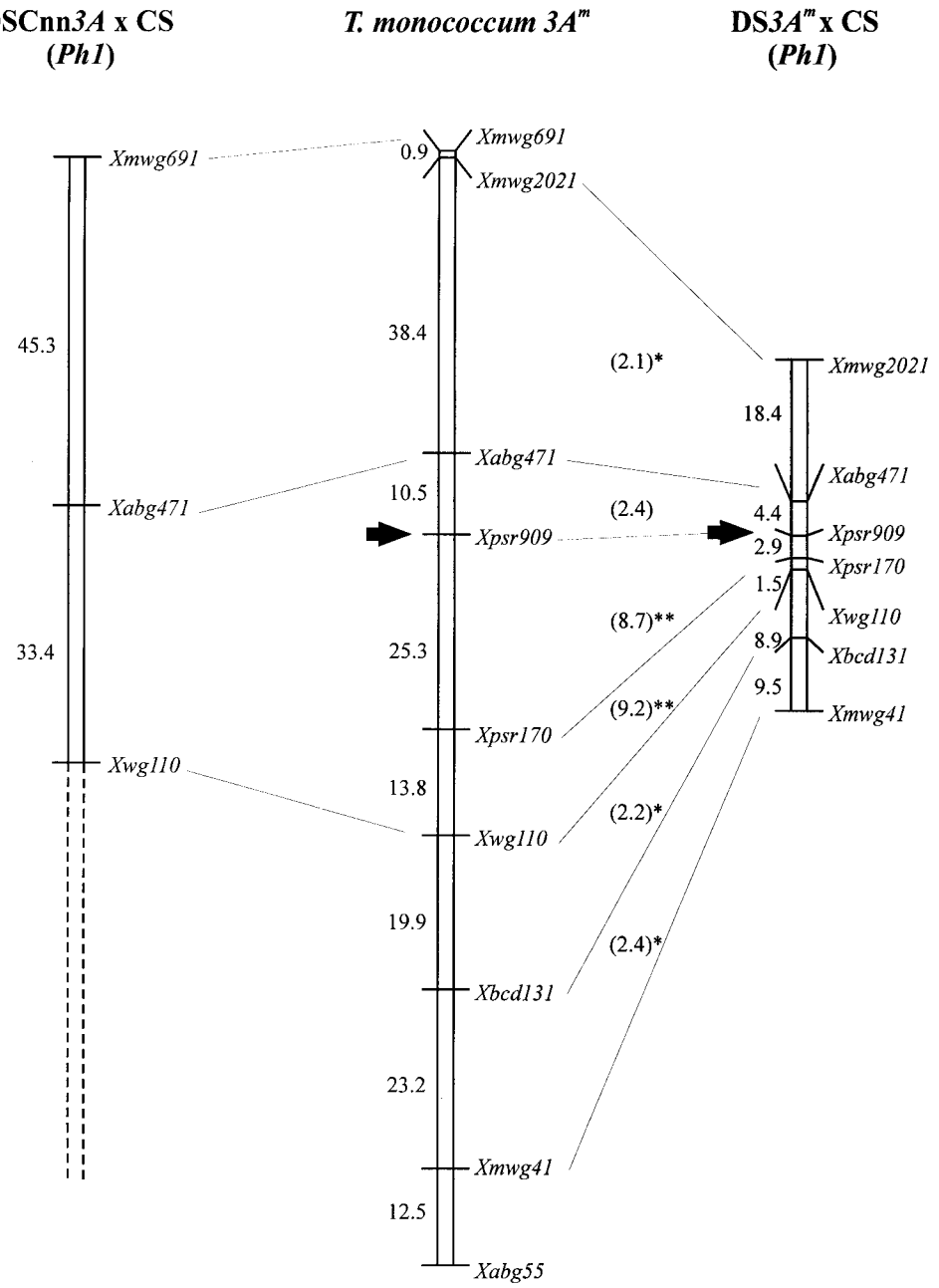

Figure 1.—Comparison of a genetic map constructed from recombination between *T. monococcum* chromosome *3A*^{m} and Chinese Spring chromosome *3A* in the *Ph1* background (*DS3A*^{m} × CS) with the map of chromosome *3A*^{m} in *T. monococcum* (Dubcovsky *et al.* 1996) and with a map of chromosome *3A* constructed from recombination between *Cnn3A* and *3A* of Chinese Spring (*DSCnn3A* × CS). The lengths of the intervals in centimorgans are to the left of each chromosome. Ratios of interval lengths in terms of recombination between homologous chromosomes relative to recombination between homeologous chromosomes are in parentheses. * and ** indicate significant differences between the intervals on compared maps at the 5% and 1% probability levels, respectively. The centromeres are indicated by arrows.

female gametophytes of simultaneous nullisomy for chromosome 5A and the *ph1b* deletion mutation.

DISCUSSION

Since the *T. aestivum A* genome was contributed by *T. urartu* Thum., a diploid species closely related to *T. monococcum*, the *T. monococcum* genome and the *A* genome of *T. aestivum* exemplify genomes of two closely related diploid species (Dvořák *et al.* 1988). Diploid hybrids between *T. monococcum* and *T. urartu* show no irregularities of meiosis (Johnson and Dhaliwal 1976). Recombination of *T. monococcum* chromosomes *1A*^{m} and *5A*^{m} with wheat chromosomes *1A* and *5A*, respectively, was normal in all intervals in the *ph1b* background (present data; Dubcovsky *et al.* 1995). Detailed maps have been constructed for *T. monococcum* chromosomes and compared with those of the wheat *A* genome (Devos *et al.* 1995; Dubcovsky *et al.* 1996). No structural differences (see definition in Introduction), except for multiple rearrangements of wheat chromosome *4A* that happened during the evolution of polyploid wheat (Devos *et al.* 1995), have been detected between the two genomes. All these observations are consistent in providing no hint of differentiation between these two genomes.

Yet, in the *Ph1* background, recombination between the genetic material of *T. monococcum* and that of the *A* genome was reduced or absent in virtually all investigated intervals (present data; Paull *et al.* 1994; Dubcov-

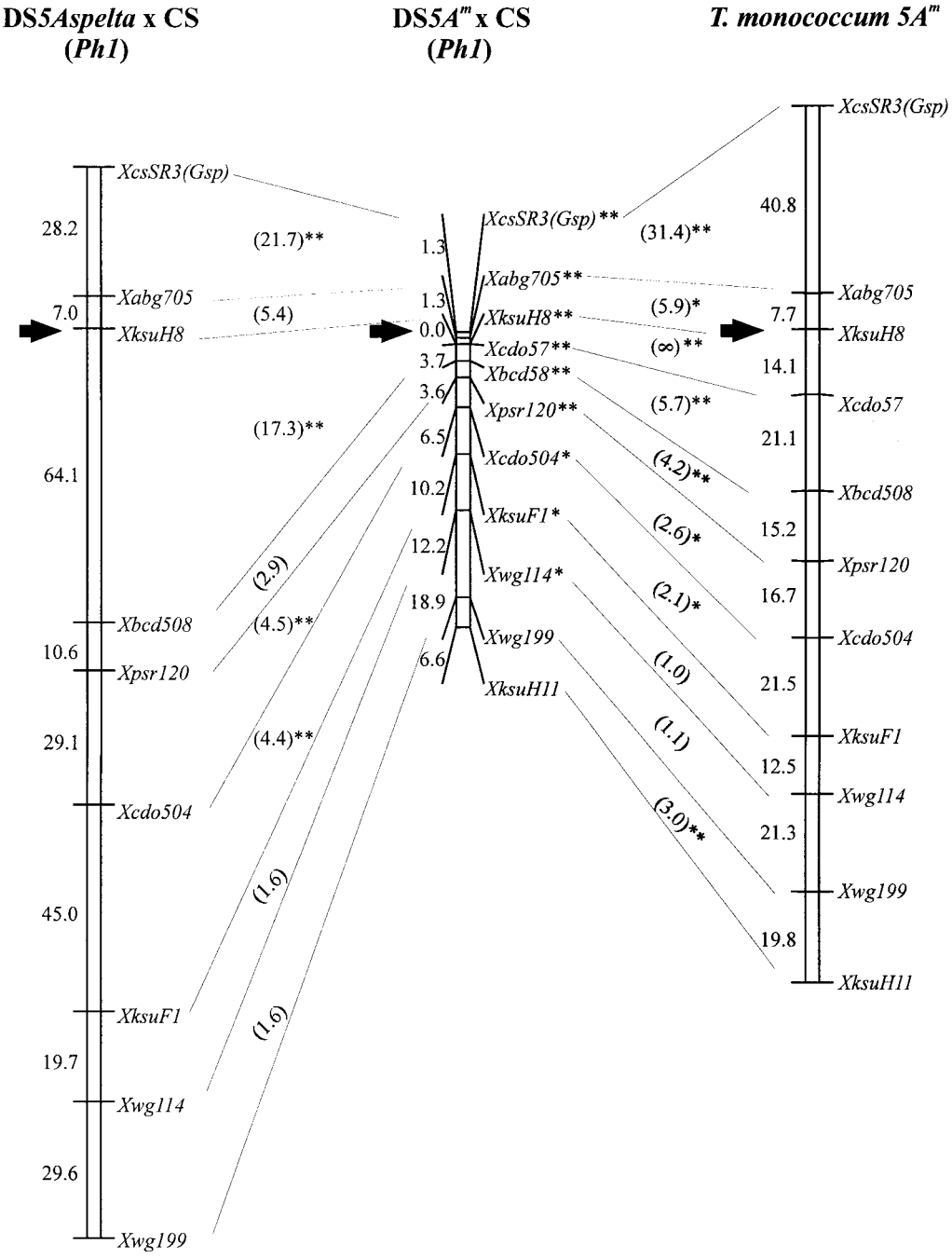

Figure 2.—Comparison of a genetic map constructed from male recombination between *T. monococcum* chromosome $5A^m$ and Chinese Spring chromosome *5A* (DS$5A^m$ × CS) in the *Ph1* background with the map of chromosome $5A^m$ in *T. monococcum* (Dubcovsky *et al.* 1996) and with a map of chromosome *5A* constructed from male recombination between DS*5Aspelta* and *5A* of Chinese Spring (DS*5Aspelta* × CS). The lengths of the intervals in centimorgans are to the left of each chromosome. In parentheses are ratios of interval lengths in terms of recombination between homologous chromosomes relative to recombination between homeologous chromosomes. The centromeres are indicated by arrows. * and ** next to a locus designation indicate a significant departure of allele segregation from the expected 1:1 ratio at the 5% and 1% probability levels (χ^2), respectively. * and ** next to parentheses indicate that the length of an interval in terms of recombination between homologous chromosomes is significantly different from the length of the same interval measured in terms of recombination between homeologous chromosomes at the 5% and 1% probability levels, respectively. No polymorphic marker was found within intervals *XksuH8-Xbcd508* and *Xcdo504-XksuF1*, which were ≥50 cM on the DS*5Aspelta* × CS map. The positions of these markers on the DS*5Aspelta* × CS map was inferred from the other two maps.

sky *et al.* 1995; Luo *et al.* 1996). To reconcile these realities, it is suggested that the differentiation between A^m and *A* genomes is minor and perceivable only by the highly discriminatory meiosis in the *Ph1* genetic background and that the differentiation is of a substructural nature. That is, differentiation appears to be present across the entire genome and is not associated with the perturbation of the linear order of loci.

In the study reported by Dubcovsky *et al.* (1995), the *T. monococcum* chromosome $1A^m$ had the distal region of the long arm replaced by the corresponding region of the wheat chromosome *1A*, and, hence, the distribution of recombination across the entire $1A^m/1A$ chromosome pair could not be assessed. In the present study, both *T. monococcum* chromosomes were apparently intact, which facilitated assessment of recombination across their entire lengths. Relative to homologous chromosomes, recombination was reduced more in the proximal regions of the long arms than in the distal regions of the long arms. A similar recombination pattern was

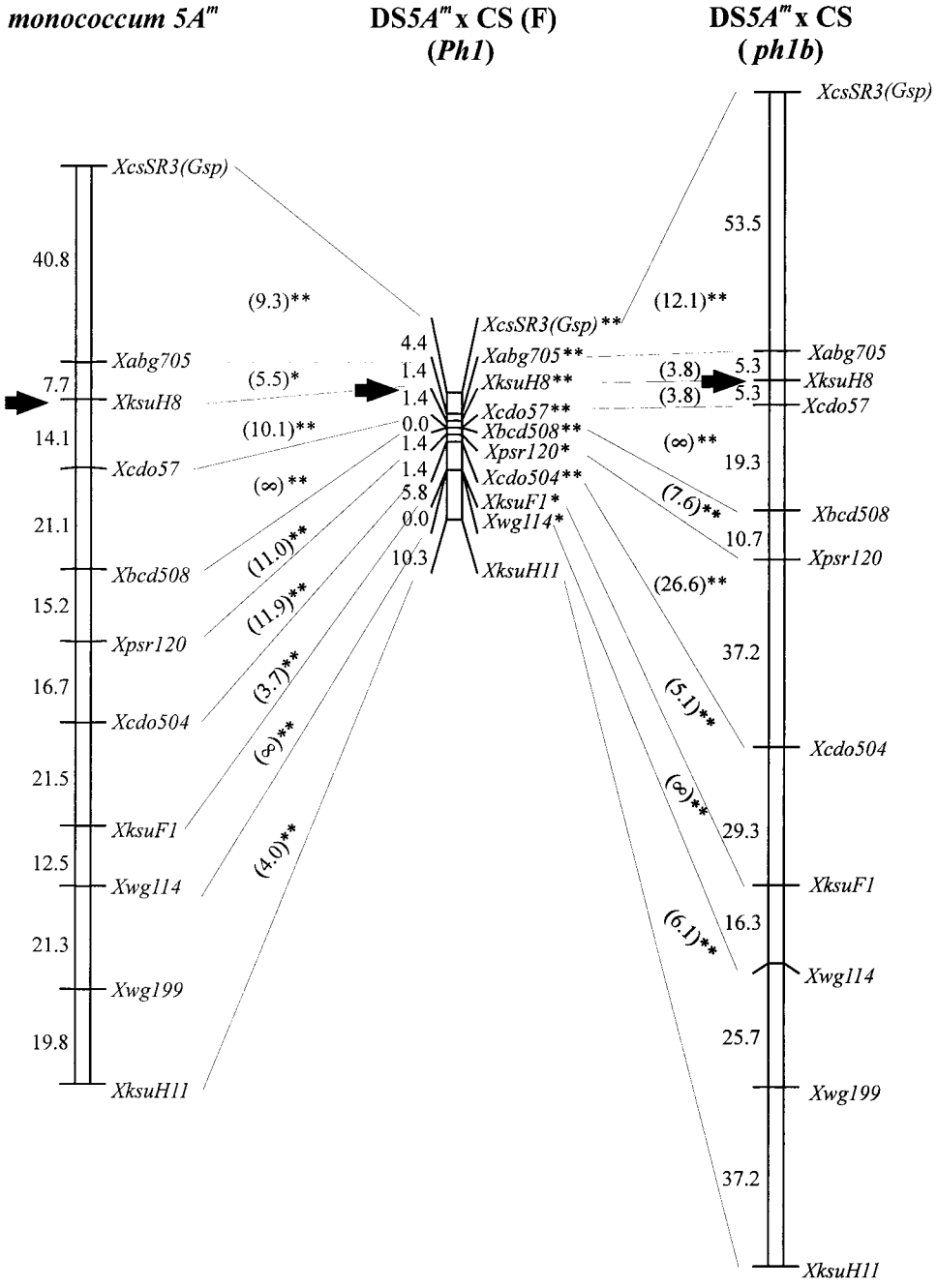

Figure 3.—Comparison of a genetic map constructed from female (F) recombination between *T. monococcum* chromosome $5A^m$ and Chinese Spring chromosome *5A* in the *Ph1* background (DS$5A^m$ × CS) with a map constructed from recombination between $5A^m$ and *5A* of Chinese Spring in the *ph1b* background (DS$5A^m$ × CS, *ph1b*) and with the map of chromosome $5A^m$ in *T. monococcum* (Dubcovsky *et al.* 1996). The lengths of the intervals in centimorgans are to the left of each chromosome. In parentheses are the ratios of interval lengths in terms of recombination between homologous chromosomes relative to recombination between homeologous chromosomes. The centromeres are indicated by arrows. * and ** next to a locus designation indicate a significant departure of allele segregation from the expected 1:1 ratio at the 5% and 1% probability levels (χ^2), respectively. * and ** next to parentheses indicate that the length of an interval in terms of recombination between homologous chromosomes that is significantly different from the length of the same interval measured in terms of recombination between homeologous chromosomes at the 5% and 1% probability levels, respectively.

observed between chromosomes *4B* and *4D* in the *ph1c* background (Dvořák *et al.* 1995). In that study, the cline of recombination across both arms was paralleled by the cline of segregation distortion preferring *4B* genetic material over *4D* genetic material. If the genetic material of chromosome *4D* compensated poorly for the genetic material of chromosome *4B*, gametophytic selection would prefer those 4B/4D recombinant chromosomes that acquired the least amount of 4D genetic material, *i.e.*, 4B/4D chromosomes with crossovers in the distal intervals (Dvořák *et al.* 1995). The potential for gametophytic selection introduced uncertainty as to the causes of the low levels of recombination between 4B and 4D in the proximal intervals. In the present study, no segregation distortion was observed in the population derived from recombination between $3A^m$ and *3A*, yet the pattern of recombination in the long arm was similar to that between *4B* and *4D*. The same pattern was also observed in both DS$5A^m$ × CS populations. Although both DS$5A^m$ × CS populations showed segregation distortion, it is unlikely that distortion caused the observed pattern of recombination across the long arm. Segregation distortion operated against $5A^m$ genetic material in the male, but for $5A^m$ genetic material in the female. Yet, the pattern of recombination across the chromosome was similar in both cases.

A possible cause of these patterns is the hierarchy of crossovers within an arm. In general, the preferred position of the first crossover is distal in wheat chromosomes. This accounts for the great distortions of wheat linkage maps relative to metaphase chromosome maps (Dvořák and Chen 1984; Werner *et al.* 1992; Gill *et al.* 1993, 1996; Lukaszewski and Curtis 1993; Hohmann *et al.* 1994; Delaney *et al.* 1995a,b; Mickelson-Young *et al.* 1995). Markers that are within the distal 50 cM on the homologous recombination maps tend to show similar levels of reduction in recombination between homeologues. The level of recombination between homeologues was found here to drop abruptly in the proximal regions of linkage maps if an arm was longer than 50 cM in terms of homologous recombination. Recombination in the proximal regions of such chromosome arms is largely dependent on multiple crossovers. A marked characteristic of recombination between differentiated chromosomes in the wheat genetic background is the reduction or complete absence of intraarm multiple crossovers (Dvořák *et al.* 1995; Lukaszewski 1995), indicating that chromosome differentiation, for an unknown reason, impacts disproportionately the probability of the second crossover compared to the probability of the first crossover. This accounts for the observation that 50-cM long arms (in terms of homologous recombination) show more or less even reduction in recombination across the arm, whereas those that are significantly longer show disproportionately reduced recombination in the proximal regions of linkage maps.

The linkage map of the long arm of chromosome 5 is longer than that of any other chromosome arm within each of the wheat genomes. On the *T. monococcum* linkage map, the interval *XksuF1-Xwg114*, which is in the middle of the long arm, is in a region showing compression of markers (Dubcovsky *et al.* 1996). This compression indicates the presence of an interstitial crossover minimum and very likely represents an interference zone of the distal crossovers. No crossover was detected in this interval in the population based on recombination between $5A^m$ and *5A* in the female. The same absence of recombination was also observed in the interval *Xcdo57-XksuH8*, which is juxtaposed to the centromere on the linkage map of the long arm, and which also shows marker compression on homologous maps. Hence, it appears that there is an additional reduction in these, normally crossover-poor, regions of linkage maps above that caused by the reduction or loss of multiple intraarm crossovers.

The centromeric interval *Xcdo57-XksuH8* showed no recombination in both the male and female. However, interval *XksuF1-Xwg114*, which did not recombine in the female, recombined in the male at the same rate as other distal intervals, suggesting a difference in the perception of chromosome differentiation between male and female meioses.

Another difference in the perception of chromosome differentiation between male and female meioses in the *Ph1* background is apparent from the total map lengths. The male map was more than twice as long as the female map. It is very unlikely that the difference was caused by the lack of transmission of nullisomic male gametes originating from incomplete pairing between $5A^m$ and *5A*. Since the $5A^m$ and *5A* chromosomes paired in close to 90% PMCs, the overestimation of recombination in the male backcross would account for only a few percent (Dvořák and Appels 1986), and not the twofold difference that was observed. These data suggest chromosome differentiation may have greater impact on recombination in the female meiosis than in the male meiosis in wheat.

Our conclusions about the distribution of recombination between homeologous chromosomes as compared to homologous chromosomes reported here and previously (Dvořák *et al.* 1995) differ from conclusions drawn by Lukaszewski (1995) from recombination of C-band polymorphisms. He concluded that the pattern of the distribution of recombination across homologues and homeologues is basically the same. Since the pattern of recombination between homeologues is affected by the arm length and potentially other confounding factors, it is possible that this disagreement simply reflects variation among different pairs studied. That this may be the case is hinted by another study by Lukaszewski (1992) in which recombination pattern across rye chromosome 1R in the wheat *Ph1* genetic background was compared with that in diploid rye. Recombination in the NOR-bearing short arm and the proximal region of the long arm of chromosome 1R was greatly reduced in the *Ph1* genetic background compared to that in rye. Reduced recombination in the proximal region of the long arm of rye heterohomologous chromosomes in the *Ph1* background of wheat is consistent with similar reductions in recombination between the long arms of the closely related homeologous chromosomes $3A^m$ and *3A* and $5A^m$ and *5A* in the *Ph1* genetic background.

An example illustrating that confounding factors may modify the basic pattern in specific chromosome pairs is provided by the distribution of recombination between $5A^m$ and *5A* across the short arm. In this arm, the recombination rate in the distal region was lower than the recombination rate in the proximal region when compared to homologous recombination. This anomaly could simply be sampling error (although the same pattern was observed in two different DS$5A^m$ × CS populations) since the observed recombination pattern was generated by a single crossover in the proximal interval (*XksuH8-Xabg705*) in each population. It is also possible that the deletion of the *Nor-11* locus from the terminus of the wheat chromosome arm *5AS* (Jiang and Gill 1994) or, conversely, the presence of the major *Nor11* locus on the $5A^mS$ arm may be responsible for poor recombination of the short arm in the region near the

Nor11 locus. Luo *et al.* (1998) demonstrated that the presence of a major *Nor* locus on a chromosome arm leads to redistribution of recombination, away from the locus. Since *Nor11* is terminally located on the $5A^mS$ arm, recombination along the arm is expected to take place in more proximal regions compared to a chromosome pair homozygous for the absence of the locus, such as chromosome *5A* of wheat.

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