DISTRIBUTION OF NONSTRUCTURAL VARIATION BETWEEN WHEAT CULTIVARS ALONG CHROMOSOME ARM *6BP*: EVIDENCE FROM THE LINKAGE MAP AND PHYSICAL MAP OF THE ARM

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ABSTRACT

Metaphase I (MI) pairing of homologous chromosomes in wheat intercultivar hybrids (heterohomologous chromosomes) is usually reduced relative to that within the inbred parental cultivars (euhomologous chromosomes). It was proposed elsewhere that this phenomenon is caused by polymorphism in nucleotide sequences (nonstructural chromosome variation) among wheat cultivars. The distribution of this polymorphism along chromosome arm *6Bp* (=*6BS*) of cultivars Chinese Spring and Cheyenne was investigated. A population of potentially recombinant chromosomes derived from crossing over between telosome *6Bp* of Chinese Spring and Cheyenne chromosome *6B* was developed in the isogenic background of Chinese Spring. The approximate length of the Chinese Spring segment present in each of these chromosomes was assessed by determining for each chromosome the interval in which crossing over occurred (utilizing the rRNA gene region, a distal C-band and the gliadin gene region as markers). The MI pairing frequencies of these chromosomes (only the complete chromosomes were used) with the normal Chinese Spring telosome *6Bp* were determined. These were directly proportional to the length of the euhomologous segment. The longer the incorporated euhomologous segment the better was the MI pairing. This provided evidence that the heterohomologous chromosomes are differentiated from each other in numerous sites distributed throughout the arm.——The comparison of the physical map of arm *6Bp* with the linkage map showed a remarkable distortion of the linkage map; no crossing over was detected in the proximal 68% of the arm. A population of 49 recombinant chromosomes was assayed for recombination within the rRNA gene region, but none was detected. No new length variants of the nontranscribed spacer separating the 18S and 26S rRNA genes were detected either.

WHEAT (*Triticum aestivum* L. em. Thell.) homologous chromosomes pair at metaphase I (MI) in hybrids between cultivars (heterohomologous chromosomes as defined by DVOŘÁK and MCGUIRE (1981) usually less regularly than within inbred parental cultivars (euhomologous chromosomes as defined by DVOŘÁK and MCGUIRE 1981). It was proposed that these reductions in MI pairing are caused by polymorphism in nucleotide sequences among wheat cultivars which reduces the likelihood of crossing over (DVOŘÁK and MCGUIRE 1981; APPELS and DVOŘÁK 1982; DVOŘÁK and APPELS 1982).

In a subsequent experiment CROSSWAY and DVOŘÁK (1984) obtained data

which, they argued, indicated that this polymorphism occurs in more than one site per chromosome arm. They produced F_1-substituted monotelodisomics for Cheyenne chromosomes *3A*, *6A* and *6B* in Chinese Spring by crossing Chinese Spring ditelosomics *3Aq*, *6Ap* and *6Bp* (for description of the ditelosomics see SEARS and SEARS 1979) with disomic substitutions of Cheyenne chromosomes *3A*, *6A* and *6B* in Chinese Spring, respectively. These F_1-substituted ditelosomics were then crossed with Chinese Spring monosomics *3A*, *6A* and *6B*, respectively, and monosomic or monotelosomic plants were selected in the B_1F_1 progeny. Due to crossing over, the monosome or telosome of some of the B_1F_1 plants was expected to be partly Chinese Spring and partly Cheyenne. In further work CROSSWAY and DVOŘÁK used only the monosomic plants (which will be called "recombinant," although some of them may have actually acquired an unrecombined chromosome). Each of these "recombinant" monosomics were then crossed with the respective Chinese Spring ditelosomic. The frequencies of the MI pairing (which is equivalent to the likelihood of at least one chiasma occurring in the arm) of the Chinese Spring telosome with the "recombinant" chromosomes were determined and compared with the frequency (= percentage of cells in which the telosome paired) of MI pairing of the same Chinese Spring telosome with the original Chinese Spring and Cheyenne chromosomes. In each of the three investigated chromosome arms the Chinese Spring telosome paired with the "recombinant" chromosomes with frequencies that varied between the extremes characterized by the pairing frequencies of the telosome with the original Chinese Spring and Cheyenne chromosomes. From this evidence CROSSWAY and DVOŘÁK (1984) concluded that the variation between the Chinese Spring and Cheyenne homologues is of a quantitative nature, *i.e.*, it occurs in more than one chromosome site.

The present paper deals with an attempt to find in which chromosome interval the individual crossing over occurred and to ascertain whether or not the MI pairing frequencies of the "recombinant" chromosomes with the normal Chinese Spring telosomes were related to the lengths of the Chinese Spring euhomologous chromosome segment incorporated into the otherwise heterohomologous Cheyenne chromosome. Unfortunately, lack of suitable markers in two of the three chromosomes studied by CROSSWAY and DVOŘÁK permitted this analysis only for chromosome *6B*.

The Chinese Spring and Cheyenne *6B* chromosomes of the F_1-substituted monotelodisomic differed in the centromere, the rRNA gene region, the C-band located in the satellite and the gliadin gene region. The recombination among the four regions was used to orient them with respect to each other and with respect to the centromere and to find where in the arm each crossover occurred. Because the rRNA gene region and the C-band are cytologically identifiable, the linkage map of the arm could be compared with the physical map of the arm.

MATERIALS AND METHODS

Genotypes: The disomic substitution of Cheyenne chromosome *6B* for Chinese Spring chromosome *6B*, designated *CH6B(CS6B)*, was crossed with Chinese Spring ditelosomic *6Bp*, producing a

substituted monotelodisomic. The *6B* chromosomes of the substituted monotelodisomic *6B* differed in four loci (regions): centromere, rRNA gene region, C-band and gliadin gene region. These regions of the Chinese Spring chromosome will be designated *Ctr*^{t}, *rRNA*, C-band^{-} and *Gli*, whereas those of the Cheyenne chromosome will be considered a standard and designated +.

The substituted monotelodisomic was backcrossed in two independent attempts as a male parent to Chinese Spring monosomic *6B*. In the first attempt CROSSWAY and DVOŘÁK (1984) selected 36 B_1F_1 monosomic and eight monotelosomic plants. An additional ten monosomic plants and one monotelosomic plant were selected in a later attempt. These B_1F_1 plants were self-pollinated, producing thereby 55 B_1F_2 families. Plants of the B_1F_2 families having a complete *6B* chromosome were crossed with Chinese Spring ditelosomic *6Bp*, producing "recombinant"-substituted monotelodisomics. These plants were used in the chromosome-pairing study of CROSSWAY and DVOŘÁK (1984).

C-banding: Root tips were cut off from three seedlings per B_1F_2 family and pretreated at 2° for 18 hr. They were then fixed in 45% acetic acid for 12 hr, and C-bands were revealed following a procedure described by DVOŘÁK and APPELS (1982).

Gliadin electrophoresis: Embryos were removed from three seeds per B_1F_2 family, and the endosperm was ground in a pestle and mortar with the aid of acid-washed sand. The dust was extracted with 0.1 ml of 1.5 M aqueous solution of n,m-dimethylformamide (KASARDA 1980). The extracts were electrophoresed in 6% polyacrylamide vertical slab gels using a lactate buffer, pH system 3.1, according to a procedure of LAURIERE and MOSSE (1982) modified by D. LAFIANDRA (unpublished results).

DNA hybridization: DNA was isolated from one to ten seedlings per B_1F_2 family according to a procedure described by APPELS and DVOŘÁK (1983). These DNAs were then digested with *Taq*I endonuclease, and the fragments were separated according to their size in 1.5% agarose horizontal slab gels. The DNA was then denatured and transferred onto a gene screen (New England Nuclear) and hybridized with a ^{32}P-labeled probe of pTA 250.15 as described by APPELS and DVOŘÁK (1982). The clone pTA 250.15 is the 750-base pair (bp) long *Hha*I fragment of the nontranscribed spacer separating the 18S and 26S rRNA genes (APPELS and DVOŘÁK 1982). The gene screens were then washed, dried and autoradiographed.

MI chromosome pairing: The frequency of chromosome pairing at MI is equivalent to the probability that a pair of chromosomes form at least one chiasma, *i.e.*, at least one crossover, at prophase. The frequencies of MI pairing between the complete *6B* chromosomes and Chinese Spring telosome *6Bp* were determined by CROSSWAY and DVOŘÁK (1984) for 30 recombinant monotelodisomics. The MI pairing frequencies were expressed in percentages of pollen mother cells (PMCs) in which the telosome paired with the homologue.

RESULTS

Centromere-C-band: Chinese Spring telosome *6Bp* differed from the complete Cheyenne chromosome *6B* in the substituted monotelodisomic by the absence (or greatly reduced size) of a band distal to the nucleolus organizing region (NOR) (Figure 1c). A single crossover between the centromere and the C-band would generate a telosome in the B_1F_1 with the C-band and a complete chromosome without it. Of 49 B_1F_2 families investigated, only six showed the recombinant genotype (Table 1). Hence, the recombination fraction (r) between the centromere and the C-band site was estimated to be 12.2 ± 4.6 cM.

Centromere-gliadin region: The electrophoretic profile of Chinese Spring gliadins differed from that of *CH6B(CS6B)* by the presence of two extra bands (specified by arrows in Figure 1a). Electrophoretic profiles (data not shown) of Chinese Spring nullisomic *6B*-tetrasomic *6A* (designated *N6BT6A*), *N6BT6D*, *N6AT6B* and *N6DT6B* and disomic substitutions of *Elytrigia elongata* (Host) Nevski chromosome *6E* for Chinese Spring chromosome *6A*, designated

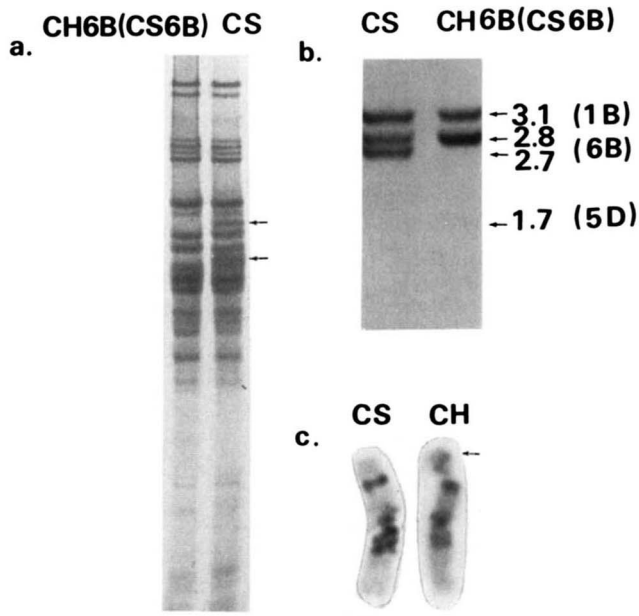

FIGURE 1.—a, Electrophoretic profiles of gliadins of Chinese Spring (CS) and disomic substitution of Cheyenne (CH) chromosome *6B* in Chinese Spring, *CH6B(CS6B)*. Bands specified by arrows in the Chinese Spring profile are absent in the profile of *CH6B(CS6B)*. b, Southern blots of Chinese Spring and *CH6B(CS6B)* genomic DNAs. The DNAs were digested with *Taq*I endonuclease, fractionated on 1.5% agarose gel, transferred onto a gene screen and hybridized with the 750-bp long sequence (pTA 250.15) cloned from the Chinese Spring nontranscribed spacer which separates 18S and 26S rRNA genes. The rRNA gene region of Chinese Spring chromosome *6B* has two equally frequent nontranscribed spacer length variants, 2.7 and 2.8 kb long. The former is absent in the Cheyenne chromosome. c, C-banded *6B* chromosomes in Chinese Spring and *CH6B(CS6B)*. The Cheyenne chromosome shows a band (arrow) in the satellite that is indiscernible in the Chinese Spring chromosome.

6E(6A), disomic substitution *6E(6B)* and disomic substitution *6E(6D)* unequivocally showed that these two bands were contributed by Chinese Spring chromosome *6B*. Gliadin electrophoretic patterns were determined for 55 B_1F_2 families. In 11 of them a crossover occurred between the centromere and the gliadin region; hence, the estimated r between the gliadin region (*Gli*) and the centromere was 20.0 ± 5.3 cM. Whether or not a crossover occurred between *Gli* and C-band could be determined in 49 B_1F_2 families. Since a crossing over occurred in this interval in five chromosomes, the estimated r between *Gli* and C-band was 10.2 ± 4.3 cM.

Six crossovers resulted in recombination between the centromere and the C-band, and five of these also resulted in recombination between the centromere and the gliadin region (Table 1). This fact and the larger distance from the centromere to *Gli* than to the C-band suggested that *Gli* is located distal to the C-band in the satellite.

No recombination within the gliadin region was detected; the two Chinese Spring bands always segregated together. However, it would be unreasonable

TABLE 1

The genotypes of the B_1F_2 families produced by self-pollination of monosomic B_1F_1 plants from the cross: Chinese Spring monosomic 6B × *(Chinese Spring* 6Bp × *Cheyenne* 6B *substituted for Chinese Spring* 6B)

Genotype				No. of families
Ctr^1	rRNA	C-band$^-$	*Gli*	5
Ctr^1	?	?	*Gli*	2
Ctr^1	rRNA	C-band$^-$	+	2
+	+	+	+	34
+	?	?	+	3
+	+	+	*Gli*	2
+	+	?	*Gli*	1
+	+	C-band$^-$	*Gli*	4
+	?	C-band$^-$	*Gli*	1
+	+	C-band$^-$	+	1
Total				55

The question marks specify the characters for which genotype could not be determined due to the lack of seeds.

to expect a recombinant in such a small population as investigated here. Additionally, it is not certain that the two Chinese Spring bands were encoded by different genes; they could result from posttranslational processing of a primary gene product.

Centromere-rRNA gene region: The rRNA gene regions are composed of tandem repeats of 18S and 26S rRNA genes separated by a nontranscribed spacer. The nontranscribed spacers of the rRNA gene region of the Chinese Spring chromosome *6B* were characterized by two *Taq*I fragment length variants, 2.7 and 2.8 kb long, and those of Cheyenne chromosome *6B* by a single one 2.8-kb long (Figure 1b). The rRNA gene region is located in the NOR, which is proximal to the C-band (Figure 1c). This proximal location was clearly reflected by the lack of recombination between the centromere and the rRNA gene region. No crossing over was detected in this interval among 49 B_1F_2 families; the r between the centromere and the rRNA gene region from the present data is, hence, 0.0 cM. The maximum value for r between the centromere and the rRNA gene region was calculated (M. T. CLEGG, personal communication) by assuming that 5% or fewer samples of size 49 would give no recombinants when the true value of recombination fraction is r. The value of $r < 6.1$ cM satisfies this assumption.

As in the case of the gliadin gene region, no recombination was detected within the rRNA gene region. The Cheyenne chromosome does not have the 2.7-kb spacer variant present in the Chinese Spring chromosome. Recombination within the rRNA gene region could result in the transfer of some of the rRNA gene units from the Chinese Spring chromosome into the Cheyenne chromosome. This would result in the occurrence of a band with mobility equivalent to that of the 2.7-kb cleavage fragment of the Chinese Spring

chromosome. If the converse happened and some of the Cheyenne rRNA gene units were transferred into the Chinese Spring telosome, the 2.8-kb band would become more intense relative to the 2.7-kb band in the autoradiograms. Neither of the two outcomes nor any new spacer length variants were observed.

Length of the euhomologous segment and MI pairing: On the basis of these results chromosome arm *6Bp* was divided into four intervals as shown in Figure 2. The 30 B_1F_1 "recombinant"-substituted monosomics investigated by CROSSWAY and DVOŘÁK (1984) were divided into three groups on the basis of the interval in which crossing over occurred. No monosomic, as shown, had a crossover proximal to the rRNA gene region (interval 1). Four monosomics had crossovers in the interval between the rRNA gene region and the C-band (interval 2), three had crossovers in the interval between the C-band and the gliadin region (interval 3) and 23 had either crossovers distal to *Gli* (interval 4) or none at all.

The more proximal crossing over occurred, the longer was the Chinese

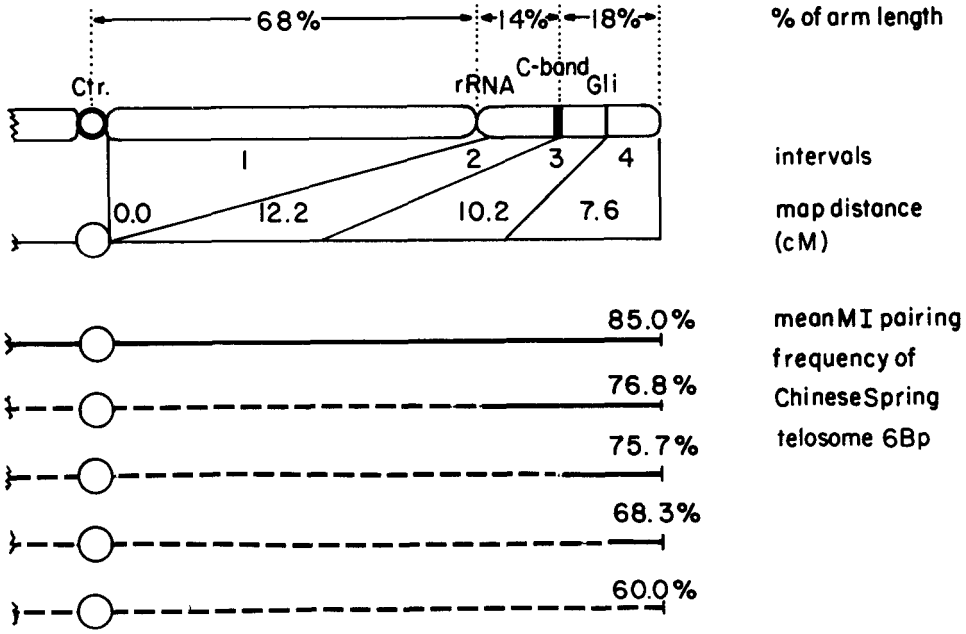

FIGURE 2.—Comparison of the physical chromosome map (in percentage of the arm length) with the linkage map of chromosome arm *6Bp*. The lengths of intervals 2 and 3 were derived from the recombination data in Table 1. The length of interval 4 (7.6 cM) was derived by subtracting the lengths of intervals 2 and 3 from the estimated arm length of 30 cM derived from the frequency of pairing of Chinese Spring telosome *6Bp* with the complete Cheyenne chromosome. The bottom part of the figure shows graphically the relationship between the length of the euhomologous Chinese Spring segment in arm *6Bp* and the pairing frequency of the arm with Chinese Spring telosome *6Bp* expressed as percentage of PMCs in which the telosome paired with the complete chromosome. The Chinese Spring chromatin is designated by a solid line and that of Cheyenne by an interrupted line.

Spring chromosome segment incorporated into the Cheyenne chromosome. Thus, if variation between the Chinese Spring and Cheyenne chromosome is distributed throughout the arm, the MI pairing frequencies of the complete *6B* chromosomes with the Chinese Spring telosome *6Bp* (expressed in percentages of PMCs in which the telosome paired at MI) in the substituted "recombinant" monotelodisomics studied by CROSSWAY and DVOŘÁK should reflect the length of the incorporated Chinese Spring chromosome segment. Hence, the chromosomes in which crossing over occurred in interval 2 should pair at MI better than those in which crossing over occurred in interval 4 or did not occur at all. The latter chromosomes should be identical with the parental Cheyenne chromosome, and their mean pairing frequencies with the Chinese Spring telosome should approximate 60% (DVOŘÁK and MCGUIRE 1981; CROSSWAY and DVOŘÁK 1984). The mean of the MI pairing frequencies of the chromosomes with crossovers in interval 2 (76.8%) was indeed the highest, whereas the mean of the pairing frequencies of the chromosomes with crossovers in interval 4 or none at all (68.3%) was the lowest (Figure 2). To test statistical significance, MI pairing data for families with crossovers in intervals 2 and 3 were combined (to increase the sample size) and compared with those of interval 4. The former mean pairing frequency was significantly higher at the 0.01 level of probability (one-tailed t-test) than the latter mean pairing frequency.

DISCUSSION

The use of cytologically identifiable markers in this study facilitated comparison of the linkage map with the physical chromosome map. This comparison showed a distortion of the linkage map similar to the distortion observed in Drosophila (LINDSLEY and GRELL 1968; BECKER 1976), corn (PHILLIPS 1969), tomato (RICK 1971) and barley (LINDE-LAURSEN 1982). The distortion observed here is more extreme than in these organisms; no crossing over was detected within the proximal 68% of the arm. However, because of the small sample size, the linkage data presented are burdened with substantial error. Additional uncertainty in the magnitude of this distortion is introduced by the use of a telosome in mapping. SEARS (1972) showed for wheat and ENDRIZZI and KOHEL (1966) for cotton that the estimated linkage distances among proximal markers become shorter when a telocentric, instead of a normal, bibrachial, chromosome is used in mapping. If this is generally true the actual linkage distance between the centromere and the rRNA genes should be longer than reported here. However, this may be partly offset by the fact that the linkage distances reported here are overestimated because the F_1 monotelodisomic was used as a male, instead of a female, parent in the test cross to the *6B* monosomic (to facilitate isolation of "recombinant" monosomes). The noncrossover chromosomes lack a chiasma and, consequently, form univalents in the monotelodisomic. The nullisomic gametes that predominantly result are seldom transmitted through the male. Thus, a male monotelodisomic is likely to show more recombination than actually occurred (DVOŘÁK and MCGUIRE 1981). Although these sources of experimental error create uncertainty about

the actual map distances among the markers, it seems, nevertheless, improbable that they could be responsible for the distortion of the linkage map observed.

Of the 21 chromosome pairs present in each MI cell of the substituted monotelodisomics studied by CROSSWAY and DVOŘÁK (1984) only the heterohomologous chromosomes paired poorly, whereas the remaining 20 euhomologous Chinese Spring chromosome pairs paired as well as they did in the Chinese Spring monotelodisomic (CROSSWAY and DVOŘÁK 1984). This lack of influence of Cheyenne chromosome *6B* on the MI pairing of the other chromosome pairs was interpreted by CROSSWAY and DVOŘÁK as evidence that the poor pairing of the heterohomologues was caused by their incomplete homology rather than by a gene with a general effect on chromosome pairing at MI; if the latter were true, MI pairing of other chromosome pairs should have been reduced as well.

DVOŘÁK and MCGUIRE (1981) argued that the peculiar MI pairing behavior of wheat homologous chromosomes from different cultivars is best explained if it is assumed that they are polymorphic in numerous sites (presumably in noncoding nucleotide sequences) and this incomplete homology interferes with crossing over. APPELS and DVOŘÁK (1982) later demonstrated that molecular hybrids between nontranscribed spacers separating the 18S and 26S rRNA genes in Chinese Spring and Cheyenne are less thermostable than molecular hybrids between these sequences of Chinese Spring. A similar result was obtained in two of three other cultivar combinations that were investigated (APPELS and DVOŘÁK 1982). If it could be assumed that these nucleotide sequences are not exceptional in the magnitude of their polymorphism from other noncoding nucleotide sequences of wheat genomes, then a substantial portion of each wheat chromosome would be polymorphic among wheat cultivars. This polymorphism could cause the observed reduction in MI pairing between heterohomologous chromosomes.

The observation that the reductions in MI pairing between heterohomologous chromosomes were not the same among the three genomes, however, was puzzling (DVOŘÁK and MCGUIRE 1981). In every intercultivar hybrid investigated the reductions in MI pairing were largest in the *B* genome, smaller in the *A* genome and virtually absent in the *D* genome. It was shown here that crossing over is distally localized in the *6Bp* arm; all crossover points detected in the population of 49 chromosomes were in the satellite. Due to positive interference this localization of crossing over must result in a relatively low likelihood of double crossovers. The *B* genome chromosomes indeed showed the lowest chiasma frequencies (SALEE and KIMBER 1979) and the lowest MI pairing frequencies (DVOŘÁK and MCGUIRE 1981) among the three wheat genomes, even when pairing occurred between euhomologous, Chinese Spring chromosomes. If these already restrictive circumstances under which crossing over must occur in the *B* genome chromosomes are considered, it would not be surprising if differences in nucleotide sequences present in heterohomologous chromosomes had more effect on MI pairing of these chromosomes than differences of a similar magnitude in, *e.g.*, the *D* genome chromosomes.

Let us consider in this context arm *6Bp*. Telosome *6Bp* paired with the euhomologous Chinese Spring chromosome *6B* in 85% of the PMCs (see Figure

2). If the chiasmata were due to single crossovers, the entire arm would be 42.5 cM long (for the sake of simplicity the mapping function is not being considered). With the Cheyenne chromosome, Chinese Spring telosome *6Bp* paired in 60% of the PMCs, yielding under the same assumption an estimate of 30.0 cM for the arm. Although this reduction of 12.5 cM is quite apparent in a 30-cM arm, it would hardly be noticeable were the arm longer than 50 cM. It is quite feasible that the observed differences among the three genomes of wheat in the magnitudes of reductions of MI pairing between heterohomologous chromosomes reflect inherent differences in crossover frequency which evolved in the diploid ancestors before the formation of polyploid wheat.

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