

Physical distribution of recombination in B-genome chromosomes of tetraploid wheat

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Received August 5, 1992; Accepted September 3, 1992
Communicated by K. Tsunewaki

Summary. Several studies have indicated a non-correspondence between genetic and physical distances in wheat chromosomes. To study the physical distribution of recombination, polymorphism for C-banding patterns was used to monitor recombination in 67 segments in 11 B-genome chromosome arms of *Triticum turgidum*. Recombination was absent in proximal regions of all chromosome arms; its frequency increased exponentially with distance from the centromere. A significant difference was observed between the distribution of recombination in physically short and physically long arms. In physically short arms, recombination was almost exclusively concentrated in distal segments and only those regions were represented in their genetic maps. In physically long arms, while a majority of the genetic distance was again based upon recombination in distal chromosome segments, some interstitial recombination was observed. Consequently, these regions also contributed to the genetic maps. Such a pattern of recombination, skewed toward terminal segments of chromosomes, is probably a result of telomeric pairing initiation and strong positive chiasma interference. Interference averaged 0.81 in 35 pairs of adjacent segments and 0.57 across the entire recombining portions of chromosome arms. The total genetic map lengths of the arms corresponded closely to those expected on the basis of their metaphase-I chiasma frequencies. As a consequence of this uneven distribution of recombination there can be a 153-fold difference (or more) in the number of DNA base pairs per unit (centiMorgan) of genetic length.

Key words: Wheat – Recombination – Genetic mapping – Interference

Introduction

In both *Triticum turgidum* L. ($2n = 4x = 28$; genomic constitution AABB), and *T. aestivum* L. em Thell. ($2n = 6x = 42$; genomic constitution AABBDD) a consistent non-correspondence is observed between the physical and genetic locations of genes. Several genes which are genetically very close to the centromere have been shown to have physical locations in the distal halves of chromosome arms. On the other hand, in distal chromosome regions the genetic distances between genes are often greater than the corresponding physical distances (Dvorak et al. 1984; Sears 1984; Snape et al. 1985; Dvorak and Appels 1986; Curtis and Lukaszewski 1991). This suggests that recombination is not distributed evenly along the chromosome arms. Instead, it appears concentrated in distal chromosome segments and is infrequent or absent in the proximal segments. As a consequence, distal chromosome segments are disproportionately extended and proximal segments compressed on genetic maps (Jampates and Dvorak 1986; Curtis and Lukaszewski 1991). Similar observations have been made in barley (Linde-Laursen 1982) and rye (Lukaszewski 1992).

Uneven distribution of recombination along chromosome lengths may have implications for breeding since strong linkages may be due not only to the close physical proximity of genes but also to their location in chromosome regions where recombination is restricted or even absent. Also, an uneven distribution

of recombination would complicate chromosome walking studies as the same genetic distance would correspond to a widely different number of DNA base pairs, depending on the physical location of the markers.

In the present study, polymorphism for C-banding patterns among accessions of *T. turgidum* L. was used to study the distribution of recombination in 11 arms of six of the seven chromosomes of the B-genome. The results were combined to yield mathematical relationships between genetic and physical distances within the B-genome chromosomes. These results also permitted the estimation of chiasma interference.

Materials and methods

Genetic stocks

T. turgidum L. var. *dicoccoides* Korn accessions TTD03, TTD06, TTD49, TTD61, TTD95, TTD113, and TTD126 were chosen for this study following screening for C-banding polymorphism among the collection of M. Feldman, The Weizmann Institute of Science, Rehovot, Israel. They were selected because they exhibited clear differences along their B-genome chromosomes for the presence/absence or size of C-bands compared to the B-genome chromosomes of *T. turgidum* var. *durum* cv 'Langdon' (Ldn) or their corresponding telosomes in the 'Langdon' double ditelosomic (Ldn DDt) lines. All stocks of 'Langdon' used in this study were obtained from L. R. Joppa, USDA-ARS, Fargo, North Dakota.

Crossing scheme

T. turgidum var. *dicoccoides* accessions were crossed to Ldn or Ldn DDt lines to produce F₁ hybrids carrying polymorphisms for C-banding patterns along chromosome 1B, 2B, 3B, 5B, 6B, and/or 7B. Chromosome 1B was analyzed previously (Curtis and Lukaszewski 1991) and the data were included in the calculations employed in this study. Chromosome 2B was analyzed in three F₁ hybrids (Ldn × TTD06; Ldn DDt2B × TTD61; Ldn DDt2B × TTD126), as was chromosome 3B (Ldn × TTD06; Ldn DDt3B × TTD03; Ldn DDt3B × TTD95). The long arm of chromosome 5B was analyzed in two F₁ hybrids (Ldn × TTD06; Ldn × TTD126). TTD126 was homozygous for a reciprocal centric translocation 1BS.5BL, 5BS.1BL which allowed mapping of the centromere. Chromosomes 6B and 7B were analyzed in one F₁ hybrid each (Ldn DDt6B × TTD06 and Ldn DDt7B × TTD06, respectively). Mapping was performed either in F₂ or in backcross progenies to the appropriate Ldn (D)B substitution line.

Cytological procedures

All cytological procedures used in this study, including C-banding, chromosome measurements, and the development of physical maps of C-bands were as described previously (Curtis and Lukaszewski 1991). The physical locations of segments in which recombination was monitored are shown in Fig. 1.

Calculations

For each recombinant chromosome, the interband locations of the minimum number of crossovers necessary to generate its

observed banding pattern were determined. On this basis, recombination frequencies (percent of chromosomes recombined in a given segment in the total number of chromosomes analyzed) were calculated for each chromosome segment.

Distances from the centromere were calculated using the distal endpoints of chromosome segments, either in relative (%) or physical (arbitrary units, a.u.) terms. The relative (%) or physical (a.u.) distance of an endpoint from the centromere was calculated by the summation of relative or physical lengths of all segments proximal to that point. Similarly, genetic distances from the centromere were calculated by the summation of genetic lengths of individual segments proximal to the endpoint of a given segment. Genetic lengths of individual segments were calculated by converting their recombination fractions using the Kosambi (1944) mapping function. Data was analyzed to examine the following relationships: (1) the recombination frequency per relative length unit vs relative distance (%) from the centromere; (2) the genetic distance (cM) vs relative distance (%) from the centromere; (3) the recombination frequency per relative length unit vs physical distance (a.u.) from the centromere; and (4) the genetic distance (cM) vs physical distance (a.u.) from the centromere. Statistical analyses were performed using SAS general linear models (PROC GLM) and non-linear regression (PROC NLIN).

Coefficients of coincidence and interference values were calculated according to Sybenga (1972). These calculations were performed for all pairs of adjacent chromosome segments in which recombination was detected. To calculate the coefficients of coincidence and interference over the entire recombining regions of chromosome arms, adjacent segments in which recombination was observed (normally the three or four most distal segments per chromosome arm) were combined into two larger regions roughly equal in length.

Results

A total of 924 chromosomes were cytologically analyzed to determine the frequency of recombination between C-bands. These included 297 1B chromosomes, 189 2B chromosomes, 190 3B chromosomes, 128 5B chromosomes, 60 6B chromosomes, and 60 7B chromosomes. Crossing-over was monitored in 67 different interband segments distributed among 11 chromosome arms (1BS, 1BL, 2BS, 2BL, 3BS, 3BL, 5BL, 6BS, 6BL, 7BS, and 7BL) (Fig. 1). Frequently, the same segments of a chromosome were analyzed in more than one hybrid combination and significant differences in recombination frequencies were observed. Consequently, recombination frequencies in the same segment were treated individually, bringing the total number of observations to 90.

In each chromosome arm, recombination frequency per relative length unit increased with relative distance from the centromere. With one exception, in all chromosome arms analyzed along their entire lengths the highest proportion of recombination per relative length unit was found in terminal segments. In these most distal segments, the number of recombination events per unit relative length ranged from 1.10 to 2.56. The exception was chromosome arm 3BL in the

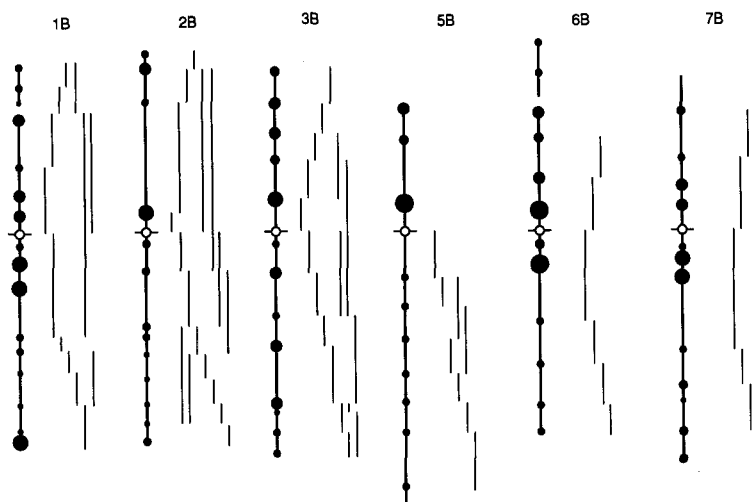


Fig. 1. Schematic diagram of C-band positions for chromosomes 1B, 2B, 3B, 5B, 6B and 7B of *T. turgidum* and the physical lengths and positions of 67 interband segments in which recombination was monitored. Centromere positions are indicated by open circles

Ldn DDt3B \times TTD95 hybrid where the proportion of recombination per unit relative length was slightly higher in the interband region immediately adjacent to its terminal segment. On the other hand, among all 924 chromosomes analyzed the single most proximal recombination event detected was in a segment ending at 37.4% of the relative arm length from the centromere. Among all chromosomes analyzed, recombination frequency per unit relative length in the proximal 50% of the arm lengths remained less than 0.2.

The relationship between recombination frequency per relative length unit and relative distance from the centromere did not differ significantly between arms [$F_{(20,68)} = 1.55$; $P > 0.1$]. When the results from all arms were combined, a significant exponential

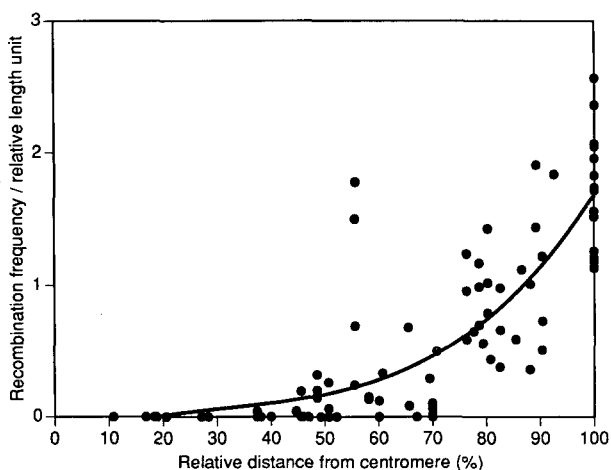


Fig. 2. Relationship between recombination frequency per chromosome arms' relative length unit and relative distance from the centromere (%), described by the function $f(x) = 0.022e^{0.0434x}$ ($R^2 = 0.696$)

relationship, described as $f(x) = 0.022e^{0.0434x}$, was found (Fig. 2). Approximately 70% of the variation in the data is explained by this function ($R^2 = 0.696$). A similar proportion of the data's variation ($R^2 = 0.689$) is also explained by a curved relationship, described as $f(x) = 0.299 - 0.0206x + 0.000338x^2$ [$F_{(2,87)} = 96.54$, $P < 0.0001$]. To test whether these relationships reflected a constraint imposed by the natural limit of the 100% relative arm length, the data set was re-analyzed excluding the endpoints of the arms. A significant relationship [$F_{(2,72)} = 3.36$; $P < 0.05$] was again found.

Similarly, for all hybrid arm combinations, an increase in the relative distance from the centromere was accompanied by an increase in the genetic distance from the centromere (Fig. 3). When the results from all arms were combined, a significant exponential

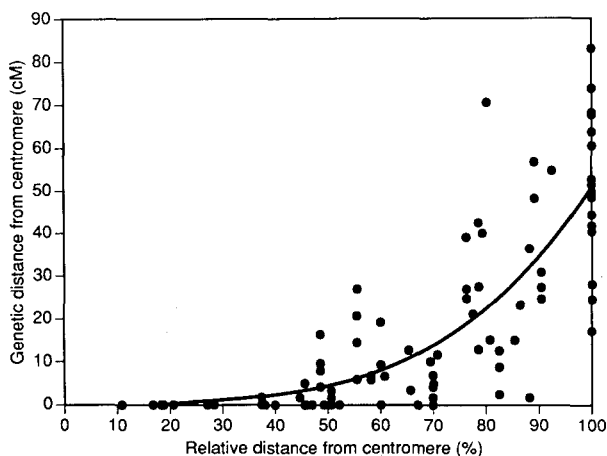


Fig. 3. Relationship between genetic distance from the centromere (cM) and relative distance from the centromere (%), described by the function $f(x) = 0.617e^{0.044x}$ ($R^2 = 0.677$)

function, $f(x) = 0.617e^{0.044x}$, was found between relative distance (%) from the centromere and genetic distance (cM) from the centromere. A majority of the data's variation ($R^2 = 0.677$) is explained by this function. A similar proportion of variation ($R^2 = 0.673$) is also explained by a curved relationship described as $f(x) = 9.455 - 0.659x + 0.0106x^2$ [$F_{(1,87)} = 27.99$; $P < 0.0001$].

To examine the effect of the physical chromosome arm length on the distribution of recombination, all arms analyzed were divided into two classes: physically short arms less than 25 a.u. in length (1BS, 2BS, 3BS, 6BS, 6BL, and 7BS) and physically long arms more than 25 a.u. in length (1BL, 2BL, 3BL, 5BL, and 7BL). In all 11 arms, recombination frequency per relative length unit increased with physical distance from the centromere. When data from all arms were combined, a significant exponential relationship was found, described as $f(x) = 0.061e^{0.123x}$. Approximately 58% of the data's variation ($R^2 = 0.58$) is explained by this equation. A higher proportion of variation ($R^2 = 0.635$) is explained by a curved relationship $f(x) = -0.115 - 0.006x + 0.003x^2$ [$F_{(2,87)} = 75.69$; $P < 0.0001$]. However, when data from physically short and long arms were analyzed separately, significant exponential relationships were found for each. Recombination in physically short arms was concentrated in the distal regions and virtually absent from proximal and interstitial regions. The distribution of recombination per unit relative length in physically short arms can be described by the function $f(x) = 0.017e^{0.203x}$ ($R^2 = 0.764$). In physically long arms, while recombination was again absent in regions immediately adjacent to the centromeres, some recombination in the interstitial regions was observed. This amount increased with distance from the centromeres, with the highest levels of recombination again in the most distal regions of the arms. The distribution of recombination per unit relative length in physically long arms can be described by the function $f(x) = 0.052e^{0.126x}$ ($R^2 = 0.606$). The difference between the short and long arm curves was determined mainly by their degrees of curvature [$F_{(1,84)} = 6.63$; $P < 0.0118$].

Genetic distance from the centromere and physical distance from the centromere were also found to increase simultaneously, though differences between physically short and physically long arms were again evident (Fig. 4). As recombination was virtually absent from the proximal and interstitial regions of physically short arms, their genetic maps were derived almost exclusively from recombination in the distal 25 to 30% of their physical lengths. The relationship between genetic and physical distance from the centromere in physically short arms can be described by the function $f(x) = 0.019e^{0.353x}$ ($R^2 = 0.789$). In contrast to the physically short arms, the interstitial regions of

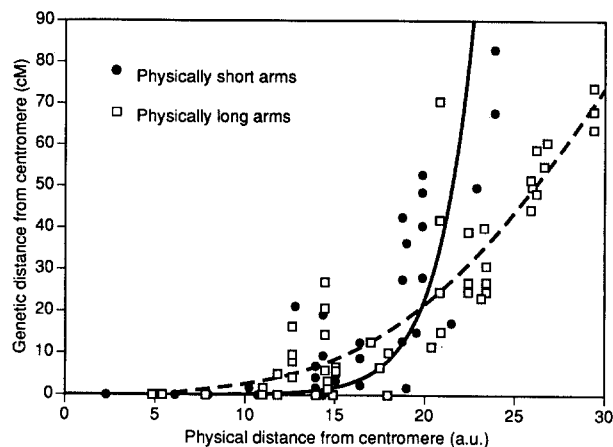


Fig. 4. Relationships between genetic distance from the centromere (cM) and physical distance from the centromere (a.u.) for physically short arms (1BS, 2BS, 3BS, 6BS, 6BL and 7BS) described by the function $f(x) = 0.019e^{0.353x}$ ($R^2 = 0.789$), solid line, and for physically long arms (1BL, 2BL, 3BL, 5BL, and 7BL) described by the function $f(x) = 1.357e^{0.136x}$ ($R^2 = 0.814$), broken line

physically long arms consistently showed some level of recombination and, consequently, contributed to their genetic lengths. Even so, a majority of the genetic maps of physically long arms were based on the much higher frequency of recombination in distal segments. The relationship between genetic distance and physical distance from the centromere in physically long arms can be described by the function $f(x) = 1.357e^{0.136x}$ ($R^2 = 0.814$).

Chiasma interference was observed in all chromosome arms studied. In 35 pairs of adjacent interband segments in which at least one recombination event was observed, coefficients of coincidence ranged from 0.00 to 1.08 and averaged 0.19. This means that only 19% of the double crossovers expected in these segments were actually observed, equivalent to an interference level of 0.81. The pair of segments in which the observed number of double crossovers was greater than expected (coincidence > 1.0) was in the long arm of chromosome 3B in the Ldn \times TTD06 hybrid combination.

To calculate a coefficient of coincidence across the entire recombining areas of the 11 chromosome arms, the shorter, adjacent segments in which recombination had been observed (normally the three or four most distal segments per arm) were consolidated into two longer regions of approximately equal physical length. Coincidence levels for these longer segments ranged from 0.00 to 2.35 and averaged 0.43. The corresponding average interference in these segments was 0.57. Coincidence values greater than 1.0 were found in four combinations: 1BS and 1BL in the hybrid Ldn \times TTD06, 2BL in the hybrid Ldn \times TTD06 and 6BL in the hybrid LdnDDt6B \times TTD06.

Discussion

Polymorphism for chromosomal banding patterns can be used in cytological studies of recombination in much the same way as genetic markers have been used in conventional linkage studies. Their advantages lie in the immediate integration of genetic and physical maps and, in species where allelic variation is minimal and gene mutations scarce, in a significant increase in the total number of available markers. In wheat, chromosomes of the B-genome provide the best opportunity for a detailed study of the physical distribution of recombination because they are more heavily banded than the A- and D-genome chromosomes.

In this study, in each of the combinations analyzed, recombination was absent in regions immediately adjacent to the centromere. In fact, the most proximal recombination event observed in the entire sample of 924 chromosomes occurred within a segment stretching from 18.4 to 37.4% of the relative arm length from the centromere. No recombination was detected in segments ending closer to the centromere. Recombination frequency, reported either per unit relative length or as a genetic map distance, increased exponentially with distance from the centromere (Figs. 2, 3). This observation is in agreement with earlier studies that indicated reduced recombination between the centromere and the *Nor-B1* and *Nor-B2* loci on the short arms of chromosomes 1B and 6B, respectively (Snape et al. 1985; Dvorak and Appels 1986), the *Ph1* gene on the long arm of chromosome 5B (Dvorak et al. 1984; Sears 1984), and the *Glu-B1* gene on the long arm of chromosome 1B (Payne et al. 1982). Alternatively, high levels of recombination have been detected between distally located markers. Snape et al. (1985) observed a genetic distance of 47 cM between the *Nor-B1* and *Gli-B1* loci within the satellite of chromosome 1B. A four-point linkage study of the short arm of chromosome 6B using the centromere, the *Nor-B2* and *Gli-B2* loci, and a C-band showed that a majority of the total recombination in the arm was distal to *Nor-B2*, that is, in the distal one-third of the arm (Dvorak and Appels 1986).

Reduced levels of proximal recombination have sometimes been observed in wheat when telocentric chromosomes have been used in mapping studies (Sears 1972). Gene-centromere distances derived from telocentric mapping may, as a result, appear shorter than those derived from recombination between two complete chromosomes. In this study combinations of complete-complete, complete-two telosomes, and complete-centric translocation were used in mapping and no evidence of distally shifted recombination patterns was observed in the combinations involving telocentric chromosomes. As a matter of fact, among four combinations of chromosomes 1B the one involv-

ing two complete chromosomes showed an overall lower recombination frequency and a higher proportion of distal to proximal recombination than any of the three combinations involving complete plus two telosomes (Curtis and Lukaszewski 1991). A similar effect was observed among the three combinations involving chromosome 2B.

The distribution of recombination differed between physically short and physically long arms. The proportion of distal recombination was higher, and that of proximal and interstitial recombination was lower, in short arms than in long arms. In physically short arms, recombination was overwhelmingly concentrated in terminal regions and virtually absent in proximal and interstitial regions (Fig. 4). This suggests that, in wheat, genetic maps of physically short arms are derived almost exclusively from crossing over occurring in the most distal regions of those arms. Because of an apparent absence of crossing-over, the proximal 70 to 75% of short arms are largely unrepresented in genetic maps. In physically long arms, while recombination was again absent in regions adjacent to the centromere and was concentrated in the terminal regions, low, though consistently detectable, levels of recombination were observed in the interstitial segments (Fig. 4). The most proximal 35 to 40% of physically long arms did not appear to contribute to the genetic maps of those arms while the interstitial 35 to 40% of their length made a minor but clearly identifiable contribution. Most of the total genetic map lengths of physically long arms, however, are derived from recombination events in the most distal 20 to 30% of the arms. Though conclusions in this study have been confined to arms of either of two lengths, an even greater proportion of the variation in the data (R^2) could have been accounted for if the 11 chromosome arms were divided into three groups based on length – physically short, medium, and long arms (data not shown). In actuality, the physical distribution of recombination appears to be a continuous rather than static variable, with the distribution within each individual arm reflecting its particular physical length.

It seems reasonable to conclude that, for all practical purposes, the proximal halves of the B-genome chromosome do not recombine. However, since proximal regions of wheat chromosomes appear fully capable of meiotic pairing and chiasma formation (Curtis et al. 1991), such a skewed distribution of recombination is more likely a consequence of the time course of chromosome pairing rather than an inherent inability of proximal regions to recombine. Holm (1986) observed primary initiation of the synaptonemal complex (SC) at or near the telomeres of wheat homologues, with multiple secondary initiation sites appearing later along the lengths of the

arms. The meiotic behavior of deficient wheat chromosomes also suggested the importance of a proper telomeric alignment of homologues for successful metaphase-I pairing (Curtis et al. 1991). As a consequence of telomeric pairing initiation, a longer time period, and hence a greater opportunity, may exist for the establishment of distal rather than interstitial chiasmata. Formation of additional, interstitial chiasmata could then be greatly restricted by positive chiasma interference.

Such strong positive interference was observed in this study. In 35 pairs of segments distributed over the 11 arms for which coincidence and interference could be calculated, the average interference value was 0.81. When the individual shorter segments of each arm were combined into pairs of longer segments encompassing the entire regions in which recombination was observed, the interference value averaged 0.57. This indicates that, in the entire recombining portions of the B-genome chromosomes used in this study, less than one-half of the expected double crossovers actually occurred. The data also reflect the inverse relationship between interference and physical distance. Reduced interference over longer physical distances may partially explain the differences in the distribution of recombination between physically short and long arms. In long arms, sufficient physical distance exists for interference to weaken to the point where a second, interstitial chiasma can occasionally be established.

Five pairs of segments involving chromosomes of *T. turgidum* var. *dicoccoides* accession TTD06 had coincidence values above 1.0. While this suggests negative interference, it is more likely that these five instances were the result of the large sampling error inherent in observations of low frequency events. For many pairs of segments, particularly those located interstitially where recombination was minimal, a difference of one recombination event would be sufficient to cause a drastic change in the coefficient of coincidence. The high coincidence values are probably not a consequence of an unusual pattern of recombination in hybrids with TTD06. Meiotic pairing in the Langdon × TTD06 F₁ hybrid was normal (average of 89% of arms paired, data not shown). Moreover, in a study of recombination in four 1B chromosomes (Curtis and Lukaszewski 1991), the 'Langdon' × TTD06 hybrid had the fewest number of crossovers per chromosome. Also, because of its extensive C-band polymorphism as compared to 'Langdon', TTD06 was the most frequently crossed accession; one half of all hybrids involved TTD06.

In this study, recombination was monitored along the complete lengths of eight chromosome arms (1BS, 1BL, 2BS, 2BL, 3BS, 3BL, 6BL, and 7BL), from centromere to telomere, in one or more hybrid combinations. Genetic maps of these arms, calculated by the

summation of the genetic lengths of individual interband segments, were 50.7, 88.1, 42.4, 54.1, 70.1, 65.9, 49.9, and 60.6 cM, respectively. These values are, on average, 10.2% lower (ranging from 19.1% lower to 30.3% higher) than the genetic map lengths of the same arms calculated on the basis of their cytologically observed chiasma frequencies (Sallee and Kimber 1978). Notwithstanding that the chiasma frequencies may have been overestimated to some degree and that several interband segments in this study were of considerable length, agreement between the map lengths derived by these two approaches is surprisingly close.

The lengths of genetic maps calculated in this study, however, are in stark contrast to recently published RFLP maps of wheat chromosomes (Gale et al. 1990; Gill et al. 1991). These RFLP maps, which do not yet have endpoints, are considerably longer than expected from cytological observations of chiasma frequency (Sallee and Kimber 1978), with some as long as 405 cM. A map of this length would require an average of eight crossover events per chromosome, which is inconsistent with the level of interference observed in the present study. Genetic mapping in wheat is not particularly precise. The wheat gene catalog (McIntosh 1988) lists 63 pairs of markers which have been genetically mapped relative to each other more than once. The average difference between the low and high estimates of these 63 genetic distances is 380% (taking the low estimate as 100%). This relatively imprecise genetic mapping is then probably compounded in RFLP mapping by an inherent conflict between efficiency and accuracy. For the sake of efficiency in laboratory procedures, maximum polymorphism is often desired in the segregating progenies to be analyzed. This then influences the selection of parental lines which, in wheat, where RFLP polymorphism is low (Gale et al. 1990), is strongly in favor of very distantly related lines. Chromosomes of such distantly related parents may reasonably be expected to have reduced pairing that results in the production of aneuploid gametes. Selection against aneuploid gametes, particularly on the male side, leads to serious overestimations of recombination frequencies and, consequently, genetic distances (for discussion and calculations see Dvorak and Chen 1984; Curtis et al. 1991). Another possibility, however unlikely, is that a combination of negative-positive interference may operate in wheat. A single cytologically observable chiasma could be the site of several recombination events. In this study, two short interstitial segments, 7% of the relative length of 1BL and 3% of the relative length of 3BL, are consistently off the recombination distribution patterns (Fig. 2), showing higher recombination frequencies than their lengths and relative arm positions would suggest.

The pattern of recombination in B-genome chromo-

somes detailed in this study has been observed in other studies in wheat (Jampates and Dvorak 1986), as well as in rye (Lukaszewski 1992) and barley (Linde-Laursen 1982). Fragmentary data for A- and D-genome chromosomes support further a suggestion that this is common for most species in the Triticeae. These species show distinctly terminal chiasmata at metaphase-I. A detailed study of the relationship between chiasma position in metaphase I and the distribution of recombination in wheat is underway but even a casual observation of MI squashes shows clearly that the physical distribution of chiasmata corresponds closely to that of recombination as observed in this study, suggesting there is no chiasma terminalization in these species. It appears that chiasma terminalization cannot be easily invoked to explain the differences in total map lengths derived by cytological and molecular approaches.

The disparities between genetic and physical distances as observed in this study can be complicating factors in chromosome walking studies in which linked markers are used in the isolation of genes of interest. This is because, even though two markers may be tightly linked genetically, the physical distance between them (in DNA base pairs) could vary enormously, depending upon their location relative to the centromere. Using the data from Flavell et al. (1987) on the DNA content and arm ratios of individual wheat chromosomes, assuming equal density of DNA along chromosome arms, and using the genetic distances between the telomeric and sub-telomeric C-bands in the most distal 17.5% of the short arm of chromosome 1B (Curtis and Lukaszewski 1991) and between the centromere and the breakpoint of chromosome 5B deficient for 49% of the long arm (Curtis et al. 1991), the number of DNA base pairs that correspond to a genetic distance of one centimorgan (1 cM) may vary from about 1,530 kbp in the distal chromosome regions to about 234,000 kbp in regions adjacent to the centromere. This 153-fold difference may still underestimate the possible range in variation by factor of two or three. With the exponential relationship between physical and genetic distances (Fig. 4), a shorter terminal segment would be expected to have an even greater proportion of recombination per unit length and thus an even smaller proportion of physical to genetic length.

Acknowledgements. The authors wish to thank Dr. M. Feldman, The Weizmann Institute of Science, for making possible the screening of his collection of *T. turgidum* var. *dicoccoides*, and Mr. R. Podolsky for performing statistical analyses of the data.

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