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Comparisons of recombination frequencies in hybrids involving telocentric and bibrachial wheat chromosomes

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Abstract Telosomic stocks have been extensively used to map genes to chromosome arms and to determine gene-to-centromere genetic distances. It has been suggested that if a chromosome arm is present as a telosome, recombination frequencies will be drastically reduced in the centromeric region. However, previous studies have not considered the bias in recombination estimates due to selection against aneuploid gametes produced by failure of pairing at the first meiotic division. Formulas are derived here for adjusting recombination estimates for this bias. Adjusted recombination frequencies between markers located on both sides of the centromeres are analyzed in three different pairs of wheat (*Triticum aestivum*) isogenic segregating populations involving bibrachial and telocentric chromosomes. Recombination frequencies estimated from crosses involving telocentric chromosomes were not significantly different from recombination frequencies estimated from isogenic crosses involving bibrachial chromosomes. The implications of the present findings for karyotype evolution, and specifically for Robertsonian fissions and fusions, are discussed.

Key words *Triticum aestivum* · Recombination · Centromeric region · Telosomes · Gametic selection

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Introduction

Bread wheat (*Triticum aestivum* L., 2n=6*x*=42, genomes AABBDD) tolerates hypo-aneuploidy (nullisomy, monosomy and telosomy) and transmits it to its progeny (Sears 1954). Telosomy is a state in which a bibrachial chromosome is replaced by a chromosome with a single arm (a telosome). Telosomes are generated by misdivision of the centromere in unpaired meiotic chromosomes (Sears 1952). In wheat, they are maintained either in ditelosomic stocks (Dt) or double-ditelosomic stocks (dDt). In the former, a pair of bibrachial chromosomes is replaced by a pair of telosomes corresponding to one arm of the chromosome and, in the latter, it is replaced by two pairs of telosomes, a pair corresponding to the short arm and a pair corresponding to the long arm. Therefore, while Dt cells are nullisomic for one chromosome arm dDt cells are actually euploid. Wheat telosomic stocks have been extensively used to map genes to chromosome arms and to determine gene-to-centromere genetic distances (Sears 1962, 1966; Driscoll and Sears 1963). A relevant question is whether the distribution of crossovers across a chromosome arm is altered in telosomes relative to the bibrachial chromosome. This is important for gene mapping and for genome evolution, since bibrachial chromosomes have frequently been converted into telosomes, and vice versa, by Robertsonian fissions and fusion during evolution.

A few studies have attempted to address this question. Endrizzi and Kohel (1966) reported that recombination values between two morphological markers located at the centromeric region of cotton chromosome 6A were almost four times smaller in crosses involving telocentric chromosomes than in crosses involving bibrachial chromosomes. However, the 6AL telosome used in that study was poorly transmitted through the pollen (only 13%) in spite of its pairing with the bibrachial chromosome in 98.8% of the pollen mother cells. This indicates a strong gametic selection that could have potentially distorted recombination estimates.

Sears (1972) found a reduction of similar magnitude in recombination between markers flanking the centromere of wheat chromosome 6B. In that study, he employed a gene for reaction to *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* located on a large segment of an *Aegilops umbellulata* Zhuk. chromosome translocated to the short arm of wheat chromosome 6B. This alien segment exhibits nearly no pairing with its wheat homoeologue and its effect on recombination is not known. Sears (1972) was aware of the potential problems of the materials used in his study and suggested that markers which do not themselves have an effect on pairing, and which are located at close intervals on both sides of the centromere, should be used.

In a more recent study, Jones et al. (1990) analyzed genetic distances between a high-molecular-weight glutenin locus on the long arm of wheat chromosome 1DL and rust resistance loci on the short arm of the same chromosome. No significant differences were detected in that study between genetic distances calculated from bibrachial and telocentric chromosomes. However, the markers used by Jones et al. (1990) were too far apart (approximately 40 cM) to differentiate putative effects of the telocentric chromosomes on recombination in the centromeric regions. Lukaszewski and Curtis (1993) also found no evidence of distally shifted recombination patterns among C-bands in telocentric chromosomes compared with bibrachial chromosomes.

An additional limitation of previous comparisons of recombination frequencies (*RFs*) involving telocentric and bibrachial chromosomes was that selection against aneuploid gametes was not taken into account. Wheat monotelodisomic F_1 plants with a bibrachial chromosome and a telosome (MtD, 2n=41 +t) transmit aneuploid gametes produced by failure of chromosome pairing at the first meiotic division (MI) to the progeny on the female side but seldom on the male side. The absence of transmission of these unrecombined chromosomes biases upward the recombination estimates based on male meioses (Dvorak and Appels 1986; Curtis et al. 1991). Dvorak and Appels (1986) presented a formula by which this bias in recombination estimates in male monotelodisomics can be corrected.

In the present paper, we report the derivation of formulas for the adjustment of recombination in male monotelodisomic and double-monotelotrisomic (dMtT, 2n=41 $+t_L$ $+t_S$) plants and employ them in comparisons of recombination in the centromeric regions between two bibrachial chromosomes and between a bibrachial chromosome and telosomes.

Materials and methods

Plant materials and crosses

The parental lines used to produce the segregating populations (Table 1) were cultivars of Chinese Spring; Chinese Spring double-ditelosomics (2n=40 $+2t_L$ $+2t_S$) dDt1A, dDt1D, dDt6B; substitution lines of cv Cheyenne chromosome 1A in Chinese Spring (DSCnn1A) (Morris et al. 1966), cv Sinvalocho M.A. chromosome 6B in Chinese Spring (DSSin6B) (Perez Camargo et al. 1984); and *Aegilops tauschii* chromosome 1D in Chinese Spring ($DSTt_{5405}$1D) (Jones et al. 1990). The source of *Ae. tauschii* chromosome 1D was Synthetic wheat RL5405 produced from 'Tetra-Canthatch' (genomes AABB)×*Triticum tauschii* (genome DD) accession RL5288 (Kerber and Dyck 1979).

Substitution lines DSCnn1A and $DSTt_{5405}$1D were crossed with Chinese Spring and with Chinese Spring double-ditelosomics dDt1A and dDt1D, respectively. Both the euploid (2n=42) and the double-monotelotrisomic F_1 plants were backcrossed as males to CS monotelosomics 1AL and 1DL, respectively. Monosomic (41 chromosomes) and double-monotelosomic plants (40+t_L+t_S chromosomes) were selected on the basis of root-tip counts from the progeny and were self-pollinated. Euploid and double-ditelosomic recombinant substitution lines (RSLs) were selected by root-tip chromosome counting.

Substitution line DSSin6B was crossed with Chinese Spring and with Chinese Spring dDt6B. The euploid and the double-monotelotrisomic F_1 plants were backcrossed as females to DSSin6B. Root tips of the resulting BC_1 plants were analyzed cytologically and details of the chromosome constitution of all progeny plants were obtained.

Genetic markers

The awn inhibitor locus *B2* and the aminopeptidase isozyme locus *Amp-B1* were used for chromosome 6B. The *B2* locus is located on the long arm of chromosome 6B, tightly linked to the centromere [Recombination Frequency (*RF*)=0.0044, Sears 1966], while the *Amp-B1* locus is on the short arm, also tightly linked to the centromere (*RF* <0.006, Sacco et al. 1992). Samples for aminopeptidase were extracted from second leaf-stage plants and analyzed on 11% starch gels using a discontinuous buffer system at pH 8.3 (Sacco et al. 1992).

For chromosome 1A, restriction fragment length polymorphism (RFLP) loci *XTri* (Singh et al. 1991) and *XGlu-A1* (Anderson et al. 1989) were analyzed. The *XTri* locus is on chromosome arm 1AS linked to the centromere (*RF*=0.04, Dubcovsky et al. 1995), and the *XGlu-A1* locus is on chromosome arm 1AL, also linked to the centromere (*RF*=0.17, Dubcovsky et al. 1995). For chromosome 1D, loci *Xcdo580* (Anderson et al. 1992) and *XGlu-D1* (Anderson et al. 1989) were used. The *Xcdo580* locus is on chromosome arm 1DS (*RF* with centromere=0.05, Dubcovsky et al. 1997), and the *XGlu-D1* locus is on chromosome arm 1DL (*RF* with centromere = 0.18, Dubcovsky et al. 1997). Additional RFLP markers outside the centromeric regions (Dubcovsky et al. 1996) were analyzed for chromosome 1A and 1D. Nuclear DNAs were isolated from leaves of single plants following the procedure of Dvorak et al. (1988). Southern hybridization was performed as described earlier (Dubcovsky et al. 1994).

Table 1 Segregating populations. (CS=Chinese Spring, dMtT=double-monotelotrisomic, RSL=recombinant substitution line, BC_1=testcross)

Chrom.	Type	Parental lines used in the initial cross	Recombination	Pop.	No.
1A	Bibrachial	CS, DSCnn1A[a]	Male	RSL	101
1A	dMtT	CS dDt1A, DSCnn1 A	Male	RSL	41
1D	Bibrachial	CS, $DSTt_{5405}$1D	Male	RSL	80
1D	dMtT	CS dDt1D, $DSTt_{5405}$1D	Male	RSL	87
6B	Bibrachial	DSSin6B, CS	Female	BC_1	136
6B	dMtT	DSSin6B, CS dDt6B	Female	BC_1	205

[a] From Dubcovsky et al. (1995)

Statistical analyses

The significance of the differences in *RF* between markers derived from crosses involving telocentric and bibrachial chromosomes was determined by *z*-tests. To perform these tests, variances of the estimated *RFs* were calculated according to Allard (1956). For telocentric chromosomes, the *RFs* between markers located on both sides of the centromere were obtained by addition of the short arm marker-centromere *RF* and the long arm marker-centromere *RF*. The goodness of fit of observed and the expected frequencies of plants with different chromosome constitutions were determined by χ^2 tests.

Results and discussion

Corrections for *RF* in backcrosses or RSLs derived from male dMt*T*

In meiosis of a dMtT plant, the bibrachial chromosome pairs with the two telosomes forming a trivalent at metaphase-I (MI), provided that at least one chiasma is present in each arm. If one telosome fails to pair (zero chiasma in that arm), it will segregate randomly to the poles or be lost. If both telosomes fail to pair with the bibrachial homologue at MI, all three will segregate randomly to the poles or be lost. Sears (1953) empirically determined that an unpaired chromosome has a $^1/_4$ probability to be incorporated into the nucleus of a microspore. Since the average univalent inclusion and exclusion rates for wheat are not necessarily valid for other species the general symbol *i* will be used for inclusion rate and (1-*i*) for exclusion rate ($=^3/_4$ in wheat) throughout the text. Another aspect that needs to be considered if these equations are used in species different from wheat, is the general orientation of the trivalent resulting from the pairing of a bibrachial chromosome with two telosomes. In wheat the orientation of these trivalents tends to be alternate, resulting in a normal disjunction. However, additional corrections would be necessary in species with different trrivalent orientation.

To facilitate the calculation of the expected gametic frequency of each of the resulting meiotic products in a dMtT plant, pairing configurations were divided into four different classes (Table 2, column one):

Class A: at least one chiasma is present in each arm.
Class B: at least one chiasma is present in the long arm and none in the short arm.
Class C: at least one chiasma is present in the short arm and none in the long arm.
Class D: no chiasma is present between the bibrachial chromosome and the telosomes.

The frequency of each of the four classes can be calculated from the estimated pairing frequency for the long arm telosome (*pl*) and the pairing frequency of the short arm telosome (*ps*) with the bibrachial chromosome at MI (Table 2, column 2). If only one telosome has a chiasma (Classes B and C), there will be only one univalent in the cell and $^1/_2$ of the gametes will be aneuploid (Table 2) irrespective of the value of inclusion and exclusion rates. If both telosomes fail to pair with the bibrachial chromosome (Class D), three univalents are present in such a cell and $(1–i+i^2)$ of the gametes (13/16 in wheat) are aneuploid and consequently eliminated from the population of gametes (Table 2).

In wheat, most of the nullisomic male gametes are excluded from fertilization by gametic selection (90%–99% depending on the nullisomic chromosome; Sears 1954, 1958). In most studies, including this one, the few aneuploid RSLs recovered are discarded based on chromosome counts, leading to 100% elimination of the aneuploid male gametes. Since most of these eliminated chromosomes were not recombined, the estimate of recombination frequency is biased upward as pointed out by Dvorak and Appels (1986). For example, unrecombined short arms are eliminated from classes B (1/2) and D $(1–i+i^2)$, while recombinant short arms are eliminated only from class C (1/2, Table 2).

The biased recombination frequency for a testcross or RSL (*RF=R/N*) can be adjusted by replacing the observed number of chromosomes (*N*) by the total number of chromosomes that would have been observed if no aneuploid gametes were eliminated (*N′*), and the number of recombined chromosomes obtained (*R*) by the total number of recombined chromosomes that were originally produced (*R′*).

If the pairing frequency of the short arm is *ps* and that of the long arm *pl*, *N′* can be calculated from *N=N′* – total number of lost chromosomes.

If $N=N'-[N' \,^1/_2\, pl(1-ps)+N' \,^1/_2\, ps(1-pl)+N'(1-i+i^2)(1-ps)(1-pl)]$ then,

$$N' = \frac{N}{1-\frac{1}{2}pl(1-ps)-\frac{1}{2}ps(1-pl)-(1-i+i^2)(1-ps)(1-pl)}. \quad (1)$$

A similar relationship can be used to calculate *R′* from *R = R'* - lost recombinant chromosomes. For the short arm $R = R'-[R' \,^1/_2\, ps(1-pl)]$ (Table 2, Classes C_2 and C_3) and

$$Short\ arm\ R' = \frac{R}{1-\frac{1}{2}ps(1-pl)}. \quad (2)$$

For the long arm $R=R'-[R'^1/_2 pl(1-ps)]$(Table 2, Classes B_2 and B_3) and

$$Long\ arm\ R' = \frac{R}{1-\frac{1}{2}pl(1-ps)}. \quad (3)$$

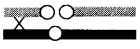
Hence, *RF* adjusted for eliminated chromosomes (RF_{adj}) can be calculated from equations (1) and (2) for the short arm or (1) and (3) for the long arm as:

$$RF_{adj} = \frac{R'}{N'}. \quad (4)$$

The formula derived here for dMtT differs from that reported by Dvorak and Appels (1986) which did not take into account the loss of recombined chromosomes in Classes B and C.

For a dMtT with complete pairing of one arm, the equation for adjusted recombination frequency is simplified. For example, if *pl*=1, the adjusted *RF* for the short

Table 2 Frequency of meiotic configurations and aneuploid gametes (*ps*=pairing frequency of the short arm, *pl*=pairing frequency of the long arm, *i*=average univalent inclusion rate, (1–*i*)=average univalent exclusion rate)

Pairing configurations	Config. frequency	Gametic chromosome constitution	Expected gametic frequency	Elim-inated	Frequency
Class A: at least one chiasma in each arm 	*pl ps*	**A**$_1$	½ *pl ps*		
		A$_2$	½ *pl ps*		
Class B: at least one chiasma in the long arm 	*pl*(1-*ps*)	**B**$_1$	½ (1-*i*) *pl*(1-*ps*)		
		B$_2$	½ (1-*i*) *pl*(1-*ps*)	X	½ *pl*(1-*ps*)
		B$_3$	½ *i pl*(1-*ps*)	X	
		B$_4$	½ *i pl*(1-*ps*)		
Class C: at least one chiasma in the short arm 	*ps*(1-*pl*)	**C**$_1$	½ (1-*i*) *ps*(1-*pl*)		
		C$_2$	½ (1-*i*) *ps*(1-*pl*)	X	½ *ps*(1-*pl*)
		C$_3$	½ *i ps*(1-*pl*)	X	
		C$_4$	½ *i ps*(1-*pl*)		
Class D: no chiasma 	(1-*ps*)(1-*pl*)	**D**$_1$	$i(1-i)^2$ (1-*ps*)(1-*pl*)		
		D$_2$	i^2(1-*i*) (1-*ps*)(1-*pl*)	X	(1-*i*+i^2) (1-*ps*)(1-*pl*)
		D$_3$	i^2(1-*i*) (1-*ps*)(1-*pl*)	X	
		D$_4$	i^3 (1-*ps*)(1-*pl*)	X	
		D$_5$	$(1-i)^3$ (1-*ps*)(1-*pl*)	X	
		D$_6$	$i(1-i)^2$ (1-*ps*)(1-*pl*)	X	
		D$_7$	$i(1-i)^2$ (1-*ps*)(1-*pl*)	X	
		D$_8$	i^2(1-*i*) (1-*ps*)(1-*pl*)		

arm can be calculated as $RF_{adj}=R[1-{}^1/_2(1-ps)]/N$ and no adjustment is needed for *RF* in the long arm ($RF_{adj}=R$/N). This is because the proportion of recombined chromosomes lost from *R* is the same as the proportion of chromosomes lost from *N* and they cancel in the calculation of *RF* (classes C and D, Table 2, are absent when *pl*=1).

No adjustment of recombination values is necessary for recombination between bibrachial chromosomes, unless the MI pairing frequencies of both arms are low and the frequency of eliminated aneuploid gametes, $[i^2+(1-i)^2](1-ps)(1-pl)$, becomes significant ($i^2+(1-i)^2=10/16$ in wheat). This adjustment is particularly useful when *RFs* are estimated from crosses involving homoeologous chromosomes with reduced pairing, or translocated chromosomes with reduced homologous segments.

Since only unrecombined chromosomes are lost in this case, only the total number of chromosomes (*N*) needs to be adjusted. The equation to correct *RF* for the lost unrecombined chromosomes due to nondisjunction in the male in backcrosses or RSLs is

$$RF_{adj}=\frac{R\{1-[i^2+(1-i)^2](1-ps)(1-pl)\}}{N}. \quad (5)$$

Table 3 Comparison of adjusted and unadjusted *RFs* between markers located an both sides of the centromere in crosses involving dMtT and bibrachial chromosomes. For the dMtT, *RFs* were obtained by addition of the short arm and long arm *RFs*. The probability values of the *z*-test between the *RFs* calculated from the complete chromosome and dMtT are indicated in parenthesis

Chrom	Interval	Bibrachial chromosome			dMtT chromosomes (*z*-test between complete chromosome and dMtT *RF*)		
		No.	*RF*	RF_{adj}	*RF*	RF_{adj}	No.
1A	*XTri–XGlu-A1*	101	0.198[a]	0.197	0.146 (*P*=0.45)	0.137 (*P*=0.37)	41
1D	*Xcdo580–XGlu-D1*	72	0.222[a]	0.207	0.184 (*P*=0.55)	0.147 (*P*=0.33)	87
6B	*Amp-B1–B2*	136	0.022	0.021	0.011 (*P*=0.48)	0.009 (*P*=0.41)	205

[a] The physical distance between these two markers represents approximately 50% of the length of the chromosome (Gill et al. 1996). No estimate is available for the physical distance between *Amp-B1* and *B2*

Table 4 Comparison of *RFs* between markers that do not include the centromere in crosses involving dMtT and bibrachial wheat chromosomes. Probability values of the *z* tests are indicated in parentheses

Chrom	Interval	Bibrachial chromosome			dMtT (*z*-test between bibrachial chromosome *RFs* and dMtT *RFs*)		
		No.	*RF*	RF_{adj}	*RF*	RF_{adj}	No.
1A	*XGli1-XGlu3*	101	0.030	0.030	0.122 (*P*=0.09)	0.109 (*P*=0.12)	41
1A	*XGlu3-XGli3*	101	0.228	0.227	0.143 (*P*=0.24)	0.128 (*P*=0.16)	35
1A	*XGli3-Xbcd98*	101	0.127	0.127	0.057 (*P*=0.17)	0.051 (*P*=0.13)	35
1A	*Xbcd98-XTri*	101	0.089	0.089	0.098 (*P*=0.88)	0.087 (*P*=0.98)	41
1A	*XGlu1-Xmsu433*(*Lec*)	93	0.020	0.020	0.049 (*P*=0.43)	0.048 (*P*=0.44)	41
1A	*Xmsu433*(*Lec*)*-Xpsr162*	93	0.040	0.040	0.049 (*P*=0.82)	0.048 (*P*=0.84)	41
1A	*Xpsr162-XAdh3*	101	0.108	0.108	0.216 (*P*=0.15)	0.212 (*P*=0.16)	37
1A	*XAdh3-XksuG34*	100	0.079	0.079	0.029 (*P*=0.21)	0.029 (*P*=0.20)	34
1A	*XksuG34-Xcmwg710*	97	0.112	0.112	0.125 (*P*=0.85)	0.123 (*P*=0.87)	32
1A	*Xcmwg710-Xmwg912*	85	0.278	0.277	0.393 (*P*=0.27)	0.386 (*P*=0.29)	28
1D	*Xcdo580- XTri*	79	0.013	0.012	0.012 (*P*=0.95)	0.008 (*P*=0.78)	86
1D	*XTri-X5SDna*	79	0.076	0.071	0.113 (*P*=0.44)	0.073 (*P*=0.95)	71

A formula for the adjustment of *RF* in a monotelodisomic for pairing failure between the telosome and the bibrachial chromosome is a special case of equation (5). Since the monosomic arm from the bibrachial chromosome in a monotelodisomic does not have a homologue at MI, either *ps* or *pl* is zero and the corresponding term (1–*ps*) or (1–*pl*) becomes 1 in equation (5). This special case of equation (5) is just a different form of the formula given for the adjustment of *RF* in monotelodisomics by Dvorak and Appels (1986).

Comparison between *RFs* based on telocentric and bibrachial chromosomes

For each of the three chromosomes analyzed in this paper crosses involving telocentric and bibrachial chromosomes were isogenic, differing only in the structure of the targeted chromosome.

In chromosome 1A, Chinese Spring telosomes 1AS and 1AL paired with Cheyenne chromosome 1A with frequencies of 0.794 (*ps*) and 0.971 (*pl*) respectively (Dvorak and McGuire 1981). These values were used to adjust *RFs* in Tables 3 and 4. The adjusted *RF* between *XTri* (1AS) and *XGlu-A1* (1AL) in the population derived from dMtT did not significantly differ (*P*=0.37) from that derived from bibrachial chromosomes (Table 3). Unadjusted *RFs* were also not significantly different (*P*=0.45). The number of plants analyzed in these two populations would have been sufficient to detect a significant difference if there had been a reduction in RF in the centromeric interval from 0.20 to 0.08 (58%). The *RF* between *XTri* and *XGlu-A1* found here is similar to the *RF* reported for an F_2 populations derived from a cross between Chinese Spring and Cheyenne chromosome 1A (*RF* = 0.213, Luo et al. 1998) and between two *Triticum monococcum* chromosomes $1A^m$ (*RF*=0.229, Dubcovsky et al. 1996). Additionally, no significant differences were found between the *RFs* for ten other intervals between the two 1A mapping populations (Table 4). The correlation between the distance to the centromere and the difference in RFs between bibrachial and telocentric chromosomes was also not significant for these ten intervals (*P*=0.17). The numbers of bibrachial and ditelocentric chromosomes found in the dMtT population did not differ significantly from the numbers expected from the observed frequencies of MI pairing (χ^2, *P*=0.23).

In chromosome 1D, Chinese Spring telosomes 1DS and 1DL paired with *Ae. tauschii* chromosome 1D with frequencies of 0.40 and 0.82, respectively (based on metaphase-I pairing data from 102 pollen mother cells). The adjusted *RF* for the interval *Xcdo580* (1DS)–*XGlu-*

Table 5 Observed and expected frequencies of aneuploid BC_1s from female meiosis of double-telotrisomic for chromosome 6B

BC1	Chromosome count		
	Observed	Expected based on *ps*=0.49 *pl*=0.87	Expected based on *ps*=0.60 *pl*=0.81
42	96	86.8	87.8
$41+t_L+t_S$	63	59.4	63.3
$41+t_L$	24	36.1	27.8
$41+t_S$	5	6.9	11.2
41	9	5.7	6.7
$42+t_L+t_S$	1	0.2	0.2
$42+t_L$	4	2.3	3.7
$42+t_S$	8	12.1	9.3
χ^2		13.1 (*P*=0.06)	7.9 (*P*=0.34)

D1 (1DL) in the population derived from the dMtT did not significantly differ (*P*=0.33) from the adjusted *RF* value in the population derived from the F_1 with bibrachial 1D chromosomes (Table 3). Unadjusted *RFs* were also not significantly different (*P*=0.55). The number of plants analyzed in the 1D populations would have been sufficient to detect a significant difference if there had been a reduction in RF in the centromeric interval from 0.21 to 0.10 (54%). Recombination fractions in the *XTri-5SDna* and *Xcdo580-XTri* intervals were also not significantly different between these two segregating populations (Table 4). In the population derived from the dMtT, the number of transmitted bibrachial and ditelocentric chromosomes conformed to the expected numbers (χ^2, *P*=0.54).

In chromosome 6B, recombination fractions between the awn inhibitor locus *B2* and the aminopeptidase isozyme locus *Amp-B1* were based on female recombination. Since wheat aneuploid female gametes are viable, all aneuploid gametes could be recovered from the cross between dDt6B and bibrachial chromosome Sin6B (Table 5). To compare the observed frequencies of the various aneuploid classes with those given in Table 2, pairing of the Chinese Spring 6BS and 6BL telosomes with the Sinvalocho M. A. bibrachial chromosome 6B must be known. Since chromosome 6B is metacentric, these values could not be reliably estimated from meiotic pairing in dMtT, and crosses with the Dt6BS and Dt6BL were not available. Instead, an average pairing of 0.49 for 6BS and 0.87 for 6BL, estimated from the pairing data of Chinese Spring telosomes 6BS and 6BL with bibrachial chromosomes of three different cultivars (Dvorak and McGuire 1981) was used. These average values of *ps* and *pl* generated expected frequencies of individual classes of female aneuploid gametes (Table 2) which did not differ significantly (χ^2, *P*=0.06) from observed values, although the probability was close to the significance level (Table 5). Different combinations of *ps* and *pl* were tested and values *ps*= 0.6 and *pl*= 0.81 were found to minimize the χ^2 value (χ^2, *P*=0.34) (Table 5). These optimum *ps* and *pl* values derived from the observed frequencies of aneuploids were used to adjust the *RF* values for chromosome 6B in Table 3.

Neither the adjusted *RF* nor the unadjusted *RF* between *B2* and *Amp-B1* in Chinese Spring×DSSin6B and dDt6B×DSSin6B differed significantly (*P*=0.41 for RF_{adj} and *P*=0.48 for *RF*). The 341 chromosomes analyzed for chromosome 6B would have been sufficient to detect a significant difference if there had been a 0.02 RF reduction in recombination in the *B2–Amp-B1* interval. Recombination frequencies between *B2* and *Amp-B1* (0.009–0.021) were similar to those previously reported (*RF*=0.0044–0.0104, Sacco et al. 1992; Sears 1966).

In the three mapping populations derived from dMtT, the observed numbers of transmitted bibrachial and ditelocentric chromosomes did not differ from the expected numbers (χ^2>0.05), indicating the absence of additional factors that could perturb the assessment of *RFs*. This good fit also suggests that the assumptions used to calculate the adjusted *RFs* were appropriate.

None of the adjusted *RFs* in the centromeric intervals in the mapping populations derived from dMtT differed significantly from *RFs* in the same intervals in corresponding isogenic populations derived from F_1s with bibrachial chromosomes. Since all three *RFs* derived from dMtT were slightly smaller (*P*>0.30) than the corresponding *RFs* from bibrachial chromosomes, it is difficult to rule out the possibility that very small reductions in recombination may be produced by the presence of the telocentric chromosomes. However, even a reduction of approximately 50% of the length of the centromeric interval in the bibrachial chromosome would have been detected with the sizes of the populations analyzed here. Differences that would corroborate the four-fold reductions in recombination attributed by Endrizzi and Kohel (1966) and Sears (1972) to the telosomic state were not found in any of the three pairs of mapping populations studied here.

Since recombination between a telocentric and a bibrachial chromosome is similar to recombination between two bibrachial chromosomes, it is reasonable to assume that recombination between two telocentric chromosomes will also be similar. If this assumption is correct, and these results can be corroborated in other organisms, then evolutionary changes in the karyotype due to Robertsonian fissions and fusions are not expected to significantly impact on intra-arm recombination patterns.

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