Genomic Instability in Wheat Induced by Chromosome $6B^s$ of *Triticum speltoides*

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ABSTRACT

A massive restructuring of chromosomes was observed during the production of a substitution of chromosome $6B^s$ from *Triticum speltoides* (Tausch) Gren. ex Richter for chromosome *6B* of Chinese Spring wheat (*Triticum aestivum* L.). Deletions, translocations, ring chromosomes, dicentric chromosomes and a paracentric inversion were observed. Chromosome rearrangements occurred in both euchromatic and heterochromatic regions. Chromosome rearrangements were not observed either in the amphiploid between Chinese Spring and *T. speltoides* or in Chinese Spring. No chromosome rearrangements were observed in the backcross derivatives; however, after self-pollination of a monosomic substitution ($2n = 41$) of chromosome $6B^s$ for wheat chromosome *6B*, 49 of the 138 plants carried chromosome aberrations. Chromosome rearrangements were observed in both wheat and *T. speltoides* chromosomes. The frequency of chromosome rearrangements was high among the *B*-genome chromosomes, moderate among the *A*-genome chromosomes, and low among the *D*-genome chromosomes. In the *B* genome, the rearrangements were nonrandom, occurring most frequently in chromosomes *1B* and *5B*. Chromosome rearrangements were also frequent for the $6B^s$ chromosome of *T. speltoides*. An intriguing aspect of these observations is that they indicate that wheat genomes can be subject to uneven rates of structural chromosome differentiation in spite of being in the same nucleus.

BREAD wheat owes its origin to interspecific hybridization of *Triticum urartu* Thum. (*AA* genomes) (KONAREV *et al.* 1978; NISHIKAWA 1983; DVORAK, MCGUIRE and CASSIDY 1988), *Triticum speltoides* (Tausch) Gren. ex Richter (B^sB^s genomes, usually designated *SS*) or some other very closely related species of section Sitopsis (SARKAR and STEBBINS 1956) and *Triticum tauschii* Coss. (KIHARA 1944; MCFADDEN and SEARS 1946). Bread wheat, therefore, contains three differentiated genomes. CHEN and DVORAK (1984) selected an inbred line of *T. speltoides* that lacked the ability to suppress the wheat *Ph1* gene which prevents heterogenetic chromosome pairing in polyploid wheat. A hybrid with *Triticum aestivum* cv. Chinese Spring that had essentially the same level of homoeologous pairing as wheat haploids was treated with colchicine and a 56-chromosome amphiploid was obtained. This amphiploid was used in substituting *T. speltoides* chromosomes for homoeologous chromosomes of Chinese Spring wheat according to the modified technique of KOTA and DVORAK (1985). In advanced backcross populations, a massive restructuring of both wheat and *T. speltoides* chromosomes was observed. This paper describes this phenomenon and its chromosomal control.

MATERIALS AND METHODS

Materials: The original hybrid was produced by crossing the selected *T. speltoides* inbred line of CHEN and DVORAK (1984) as a male parent with Chinese Spring wheat. Hybrid embryos were cultured on a modified B-5 medium (DVORAK 1981). The amphiploid was obtained by doubling the chromosome number of the hybrid by immersing the crown in a 0.25% colchicine solution for 5 h (JENSEN 1974). To substitute *T. speltoides* chromosomes for wheat homoeologous chromosomes the amphiploid was recurrently backcrossed with selected Chinese Spring monotelosomics. Each monotelosomic was developed by crossing a ditelosomic with the monosomic for the same chromosome and selecting a monotelosomic progeny. Seeds of Chinese Spring and ditelosomic and monosomic stocks were provided by E. R. SEARS, University of Missouri, Columbia.

To determine the chromosome constitution of plants during backcrossing, root tips were cut from 2-day-old seedlings germinated in Petri dishes in the dark. One root tip per plant was used for determining its chromosome number and the two or three remaining roots were used for C-banding analysis. For determination of chromosome number, root tips were pretreated at 2° for 24 hr in distilled water and fixed in 3:1 ethanol:acetic acid (v/v). These root tips were then stained in Schiff's reagent. The root tips for C-banding analysis were pretreated at 2° for 17 hr and fixed in 45% acetic acid. The C-bands were revealed according to a procedure described by DVORAK and APPELS (1982).

Nomenclature: The *T. urartu* genome is designated *A* and *T. tauschii* genome *D*. The designation of *T. speltoides* genome B^s differs from the customary designation *S*. This is done to emphasize its relationship to the wheat *B*-genome. Chromosomes for which homoeology is known are designated by arabic numerals specifying the homoeologous group followed by capital letter, specifying the genome of origin. The genomic designation of chromosome *4A* and *4B* are switched as proposed by DVORAK (1983). Chromosome

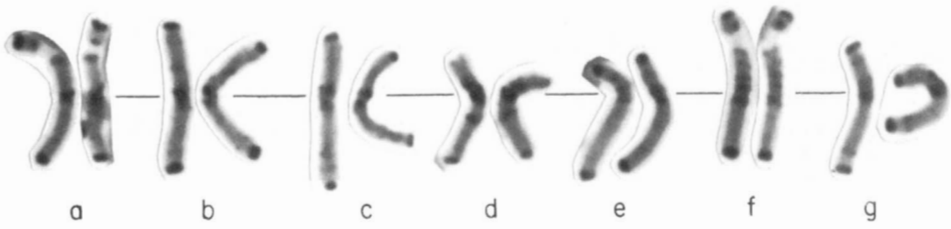

FIGURE 1.—C-banded karyotype of *Triticum speltoides* prepared from a single cell of the amphiploid Chinese Spring X *T. speltoides*.

TABLE 1

Chromosome constitution and frequency of rearrangements observed in plants during the production of chromosome substitutions *4B*^{s} and *6B*^{s} for *4B* and *6B* of wheat, respectively

Generation	Chromosome no.	Pedigree group[a]	Chromosome constitution[b]	Missing wheat disome	No. of plants	No. of plants with rearrangements	No. of rearrangements
F_1	48		*20″+4B′+7′spelt*		4	0	0
BC_1F_1	45	1	*20″+4B′+4′spelt*		6	0	0
	43	2	*20″+4B′+4B^{s}′+6B^{s}′*		1	0	0
	41+t	3	*19″+4B′+4B′p+6B′+6B^{s}′*		1	0	0
	41	4	*19″+4B^{s}′+6B^{s}′+6B′*	*4B*	4	0	0
BC_2F_1	41+t	3*1	*20″+6B′+6Bp′*		3	0	0
	41	3*2	*20″+6B′*		6	0	0
	42	3*3	*20″+6B^{s}′+6B′*		1	0	0
	41	4*1	*19″+4B′+4B^{s}′+6B′*		5	0	0
	41+t	4*2	*19″+4B′+4B^{s}′+6B′+6Bp′*		7	0	0
	41+t	4*3	*19″+4B′+4B^{s}′+6B^{s}′+6Bp′*		3	0	0
	41	4*4	*19″+4B′+4B^{s}′+6B^{s}′*		6	0	0
BC_2F_1	41	4*5	*20″+4B^{s}′*	*4B*	5	0	0
	42	4*6	*20″+4B′+4B^{s}′*		7	0	0
	41+t	4*7	*20″+4B′+4Bp′*		3	0	0
BC_2F_2	42	3*3-1	*20″+6B′+6B^{s}′*		18	17	31
	41	3*3-2	*20″+6B^{s}′*	*6B*	10	10	38
	42	3*3-3	*21″*		17	0	0
	41+t	3*3-4	*20″+4B′+4Bp′*		3	0	0
BC_2F_2	42	4*4-1	*19″+4B^{s}″+6B^{s}″*	*4B, 6B*	2	0	0
	43	4*4-2	*20″+4B^{s}′+6B^{s}″*	*6B*	4	1	4
	42	4*4-3	*19″+4B^{s}′+4B′+6B^{s}‴*	*6B*	7	3	5
	42	4*4-4	*19″+4B^{s}″+4B′+6B′^{s}*	*6B*	5	1	4
BC_2F_2	41	4*5-1	*20″+4B^{s}′*	*4B*	37	0	0
	42	4*5-2	*20″+4B^{s}″*	*4B*	10	0	0
BC_2F_3	42	3*2-1-1	*21″*		87	1	1
	42	3*3-1-1	*20″+6B′+6B^{s}′*		18	3	4
	42	3*3-2-1	*20″+6B^{s}″*	*6B*	6	0	0
	41	3*3-2-2	*20″+6B^{s}′*	*6B*	58	10	16
	41	4*4-4-1	*19″+4B^{s}″+6B^{s}′*	*4B, 6B*	7	2	2
	42	4*4-4-2	*19″+4B^{s}″+6B^{s}″*	*4B, 6B*	3	2	4
	40+t	4*4-4-3	*19″+4B^{s}″+6B^{s}′q*	*4B, 6B*	2	1	3
	40+t	4*4-4-4	*19″+4B^{s}″+6B^{s}′p*	*4B, 6B*	4	0	0
BC_2F_3	42	4*5-2-1	*20″+4B^{s}″*	*4B*	4	0	0

[a] The number following an asterisk designates an outcrossed family whereas the number following a dash designates a self-pollinated family.

[b] ′, ″ indicate a monosome and a disome, respectively.

4A is designated *4B* and chromosome *4B* is designated *4A*. Chromosome arms are designated p and q according to SEARS and SEARS (1979). Each chromosome arm is divided into euchromatic regions and C-bands, which are sequentially numbered in the proximal to distal orientation with arabic numerals which follow the arm designation. Since every arm begins with a centromeric C-band, all C-bands carry odd numbers and all euchromatic regions even numbers. This system was chosen for its simplicity over the one proposed by GILL (1987). Chromosome breaks and reunions are specified according to the cytogenetic nomenclature for human chromosomes (ISCN, 1985).

Statistical analysis: The distribution of chromosome breaks between genomes *B* and *D* was tested by the χ^2 test for 2 d.f. Distribution of breaks among the chromosomes within the *B* genome was tested by the χ^2 test for 6 d.f.

RESULTS

Derivation of Substitutions of *T. speltoides* Chromosomes *4B^s*, *6B^s*, and *7B^s*: The *T. speltoides* chromosomes from a single amphiploid plant were karyotyped (Figure 1). Chromosomes *A*, *C* and *E* were shown to be homoeologous to wheat chromosomes *1B*, *3B* and *5A*, respectively, and are designated *1B^s*, *3B^s* and *5B^s*, respectively (R. S. KOTA, unpublished data). The backcross procedure for substitution of an alien chromosome for a selected wheat homoeologue directly from the amphiploid, previously reported by KOTA and DVORAK (1985), was modified to use a single amphiploid as the nonrecurrent parent. The procedure is schematically shown in Figure 2 using as an example the substitution of *T. speltoides* chromosome *4B^s* for wheat chromosome *4B*. The development of substitution lines, *D* for *4B*, *F* for *6B*, and *G* for *7B*, which are relevant to this paper will be briefly described.

To substitute a *T. speltoides* chromosome for wheat chromosome *4B*, the amphiploid was crossed with monotelosomic *4Bp*. Four F_1 plants with 48 chromosomes and therefore monosomic for chromosome *4B* were obtained. One was backcrossed as a male to monotelosomic *4Bp*. Twelve BC_1F_1 plants with chromosome numbers ranging from 41 to 45 were obtained. These 12 progeny were divided into four groups based on their chromosome constitution (Table 1). Plants from group 3 had 41 chromosomes plus a telosome. C-banding showed that they had 19 pairs of wheat chromosomes, one chromosome *4B*, telosome *4Bp*, monosome *6B*, and *T. speltoides* chromosome *F*. Plants from group 4 also carried monosome F but they lacked telosome *4Bp* and had *T. speltoides* chromosome *D* replacing wheat chromosome *4B* in addition to chromosome *F*. Chromosome *F* resembles chromosome *6B* of wheat in chromosome morphology and C-banding pattern (DVORAK 1983); thus, an attempt was made to substitute it for chromosome *6B* by crossing plants of groups 3 and 4 as males with monotelosomic *6Bp*.

Among ten BC_2F_1 progeny from crossing plants of group 3, one plant (number 3*3) with 42 chromosomes was obtained. This plant was a double monosomic for chromosomes *6B* and *F*. Plant 3*3 was self-pollinated.

When BC_1F_1 plants of group 4 were backcrossed again, 21 BC_2F_1 plants with 41 chromosomes or 41 + telosome were obtained (Table 1). Six 41-chromosome plants of group 4*4 were self-pollinated and plants with disomic substitutions of chromosome *F* for *6B* were selected in BC_2F_2 (groups 4*4-1, -2, -3, and -4). Two BC_2F_2 plants were double disomic substitutions of *D* for *4B* and *F* for *6B* (4*4-1). Nullisomics *4B* and *6B* have poor vigor and are sterile (SEARS 1954). Since both the disomic and double disomic substitutions were vigorous and fertile chromosome *D* and *F* must be related to wheat chromosomes of homeologous groups *4* and *6*, respectively, and they will be designated *4B^s* and *6B^s*.

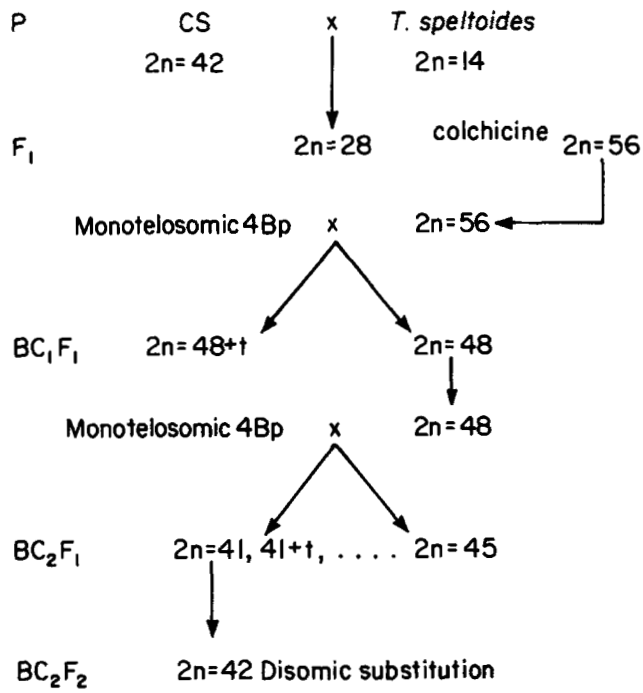

FIGURE 2.—Schematic presentation of the production of disomic substitutions of *T. speltoides* chromosomes into Chinese Spring (CS) wheat. The substitution of chromosome *4B^s* of *T. speltoides* for 4B of CS is shown as an example.

The C-band pattern of the chromosome *4B^s* that was substituted for *4B* was identical to *T. speltoides* chromosome *D* from the amphiploid (Figure 1) and chromosome *6B^s* was identical to *T. speltoides* chromosome *F*. Chromosome *6B^s* shows a secondary constriction in disomic substitutions for *6B* indicating that rRNA genes are being expressed (Figure 3). On the basis of that observation, the arm with the secondary constriction was tentatively designated *p*, to reflect presumable homeology with the satellited arm of wheat chromosome *6B* and the opposite arm was designated *q*.

A single F_1 plant with a chromosome number of 48 was obtained from the cross of monotelosomic *7Bq* with the amphiploid. This plant was used as a male in the next backcross. Three out of eleven plants were monosomic substitutions of chromosome *G* for chromosome *7B* of wheat (group 5, Table 2). Since in all three plants the chromosome *G* was substituted for *7B*, it is probably homoeologous to *7B* and will be designated *7B^s*. Additionally, a single monotelosomic addition (42 + t) was obtained (group 8). The telosome was identified as the long arm of chromosome *G*. All three monosomic substitutions and the single monotelosomic addition were self-pollinated, but only three seeds were obtained.

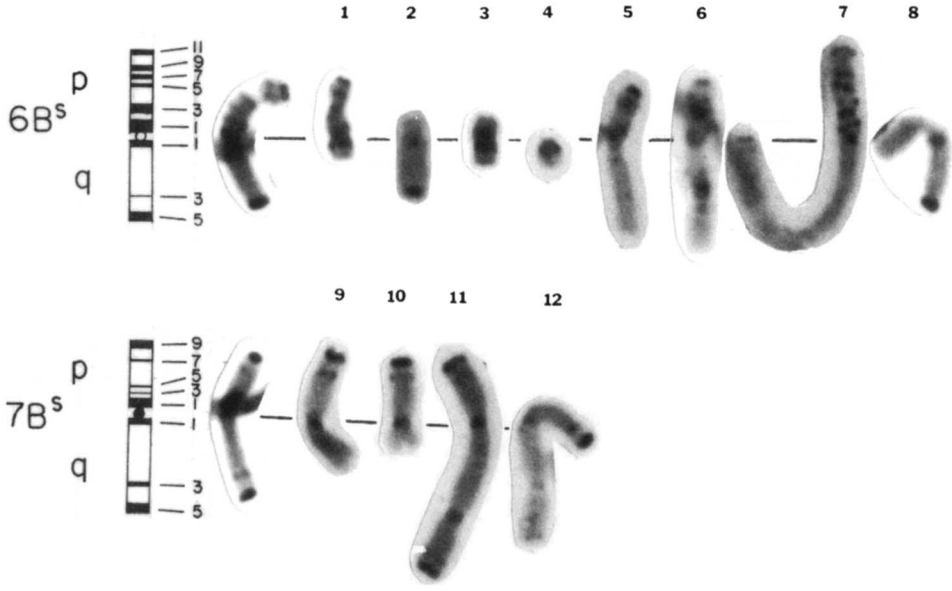

FIGURE 3.—C-banded rearranged *T. speltoides* chromosomes $6B^s$ and $7B^s$. The rearrangement types are designated above the chromosomes.

TABLE 2

Chromosome constitution and frequency of rearrangements observed during the production of chromosome substitution $7B^s$ for *7B* of wheat

Generation	Chromosome no.	Pedigree group[a]	Chromosome constitution[b]	Missing wheat disome	No. of plants	No. of plants with rearrangements	No. of rearrangements
F_1	48		*20″+7B′+7spelt′*		1	0	0
BC_1F_1	42-46				8	0	0
BC_2F_1	41	5	*20″+7B^s′*		3	0	0
	41+t	6	*20″+7B^s′+7Bq′*		4	0	0
	42+t	7	*20″+7B′+7B^s′+7Bq′*		3	0	0
	42+t	8	*21″+7Bq′*		1	0	0
BC_2F_2	42	5*1	*20″+7B^s″*	*7B″*	2	0	0
	41+2t	7*1	*20″+7B^s′+7Bq″*		4	1	4
	42	7*2	*21″*		6	0	0
	42+t	7*3	*21″+7B^{s}q′*		4	0	0
	42+2t	8*1	*21″+7B^{s}q″*		1	0	0
	42+t	8*2	*21″+7B^{s}q′*		1	0	0
	41+2t	8*3	*20″+7B′+7B^{s}q″*		2	0	0
	42	8*4	*21″*		2	0	0

[a] A number following an asterisk designates an outcrossed family whereas a number following a dash designates a self-pollinated family.
[b] ′, ″ indicate the monosome and disome, respectively.

Chromosome rearrangements: Chromosome rearrangements observed during this work are shown in Figures 3–7 and individually described in Table 3. No chromosome rearrangements were found in 40 amphiploid plants. Furthermore, no rearrangements were found in the four F_1 plants or in any of the 66 BC_1F_1 and BC_2F_1 plants (Table 1). Of the total of 251 BC_2F_2 and BC_2F_3 plants, 107 had no $6B^s$ chromosome, 124 were monosomic for $6B^s$ and 20 were disomic for $6B^s$. Except for one, plants that lacked $6B^s$ had no chromosome rearrangements. Forty-nine of 138 plants that were monosomic or disomic for $6B^s$ had rearrangements. None of the 51 BC_2F_2 or BC_2F_3 plants that were disomic for $4B^s$ but did not have $6B^s$ showed rearrangements. No rearrangements were observed in 6 BC_1F_1 monosomic *6B* plants. Yet, chromosome rearrangements were observed in 36 plants that were monosomic *6B* and simultaneously monosomic for $6B^s$ in BC_2F_2 and BC_2F_3, groups 3*3 and 3*3-1. This indicates that the rearrangements are not caused by the monosomy or nullisomy for wheat chromosome *6B* but are caused by chromosome $6B^s$ of *T. speltoides*. A single BC_2F_3 plant in group 3*2-1 was an exception since it had a deletion in chromosome *1B* (chromosome type 25, Table 3, Figure 5) but did not have any *T. speltoides* chromosomes. However, the parental BC_2F_2 plant had chromosome $6B^s$.

Four BC_2F_3 monotelosomic substitution plants for the *p* arm of $6B^s$ were obtained. These plants did not have any chromosome rearrangements (Table 1).

TABLE 3

Description of restructured chromosomes showing in Figures 3 to 7 and the frequency of their occurrence

Chromosome type	Designation[a]	Frequency of independent occurrence
1	*del 6B^s pter→q2:*	21
2	*del 6B^s qter→p2:*	3
3	*del 6B^s p2→q2:*	3
4	*del 6B^s q2→q1:*	4
5	*T 6B^{s}pter→6B^{s}p1::5Aq1→5Aqter*	3
6	*dic 6B^{s}pter→6B^{s}p1::7Bp2→7Bqter*	1
7	*T 6B^{s}pter→6Bpl*::unknown::unknown	1
8	*T 6B^{s}qter→6Bq1::1Dp1→1Dpter*	2
9	*del 7B^s pter→q2:*	1
10	*del 7B^s pter→q2:*	1
11	*dic 7B^{s}pter→7B^{s}q2::7B^{s}q2→7B^{s}pter*	1
12	*dic 7B^{s}pter→7B^{s}q1::5Aq4→5Apter*	1
13	*del 3A p3→qter*	2
14	*del 4A pter→p9:*	2
15	*del 4A pter→q7:*	3
16	*T 4Aqter→4Ap1::5Aq2→5Aqter*	2
17	*T 4Aqter→4Ap2*::unknown	1
18	*del 5A pter→q2:*	4
19	*T 5Apter→5Aq2::1Bq12→1Bqter*	2
20	*dic 6Apter→6Aq::3Dq2→3Dpter*	1
21	*del 7A pter→q2:*	3
22	*del 1B pter→q12:*	2
23	*del 1B pter→q7:*	4
24	*del 1B qter→p5:*	4
25	*del 1B qter→p7:*	2
26	*T 1Bp7→1Bq10*::unknown	1
27	*dic 5Bpter→5Bq1*::unknown:: *1Bq1→1Bqter*	1
28	*dic 1Bqter→1Bp6::5Bq5→5Bpter*	1
29	*dic 1Bqter→1Bp2::5Bq2→5Bpter*	2
30	*T 1Bqter→1Bq1::5Bq4→5Bqter*	1
31	*T 1Bqter→1Bq1::5Bq2→5Bqter*	1
32	*del 2B qter→p8:*	1
33	*del 2B qter→p4:*	1
34	*del 2B qter→p3:*	1
35	*T 2Bqter→2Bp1::5Bq2→5Bqter*	1
36	*r 2Bq2::2Bq8*	1
37	*del 3B pter→q5:*	1
38	*dic 3Bpter→3Bq6::5Dq4→5Dpter*	1
39	*dic 3Bpter→3Bq6::5Dq4→5Dpter*	1
40	*T 3Bqter→3Bp1::7Bp1→7Bpter*	1
41	*dic 3Bqter→3Bp11::3Bp11→3Bq4:*	1
42	*T 3Bqter→3Bp4::5Bq2→5Bqter*	1
43	*del 4B pter→q7:*	1
44	*del 5B pter→q10:*	3
45	*del 5B pter→q7:*	2
46	*del 5B pter→q5:*	3
47	*del 5Bp3→5Bq7:*	2
48	*T 5Bpter→5Bq4*::unknown	1
49	*del 5B pter→q3:*	3
50	*r 5Bp3::5Bq5*	1
51	*T 5Bqter→5Bp3*::unknown	1
52	*T 5Bqter→5Bp3*::unknown	1
53	*dic 5Bpter→5Bq4::3Aq2→3Apter*	1
54	*T 5Bqter→5Bp6::5Bq2→5Bqter*	1
55	*Inv 5Bpter→5Bq9::5Bqter→5Bq9*	1
56	*del 6B qter→p5:*	1
57	*del 7B pter→q4:*	2
58	*del 3D pter→q2:*	2
59	*del 5D qter→p6:*	2

Symbols (→), (:), (::) indicate " from-to," a chromosome break, and a break and reunion, respectively. *del* = a deletion; *dic* = dicentric chromosome; *inv* = inversion; *r* = ring chromosome; *T* = translocation; *ter* = terminal region of a chromosome arm: p and q represent chromosome arms p and q, respectively.

[a] Designations describe the chromosome regions present in the chromosome after rearrangement.

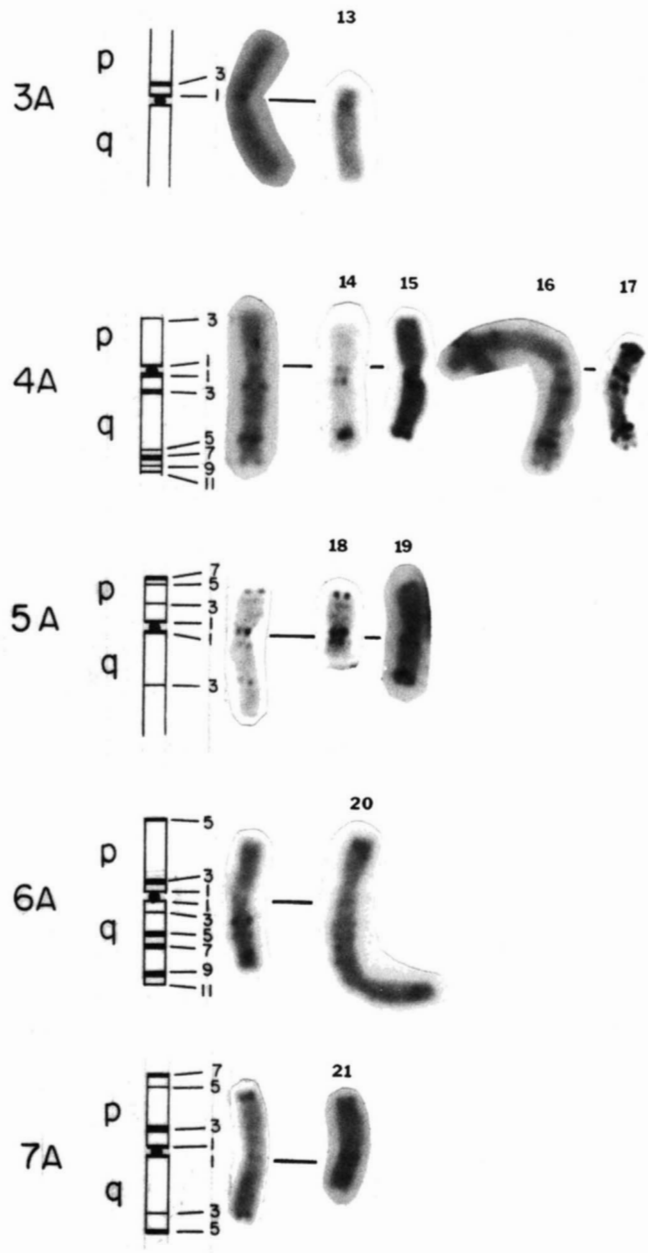

FIGURE 4.—C-banded rearranged Chinese Spring chromosomes of the *A* genome. The rearrangement types are designated above the chromosomes.

However, one of two BC_2F_3 plants that were monotelosomic substitutions of the *q* arm had rearranged wheat chromosomes (Table 1). Since chromosome rearrangements were observed in plants which had deletions in the euchromatic region of the *6B^{s}q* arm (chromosome type 1, Table 3, Figure 3), it appears that the factor that is causing chromosome rearrangements is located near the centromere in the q arm.

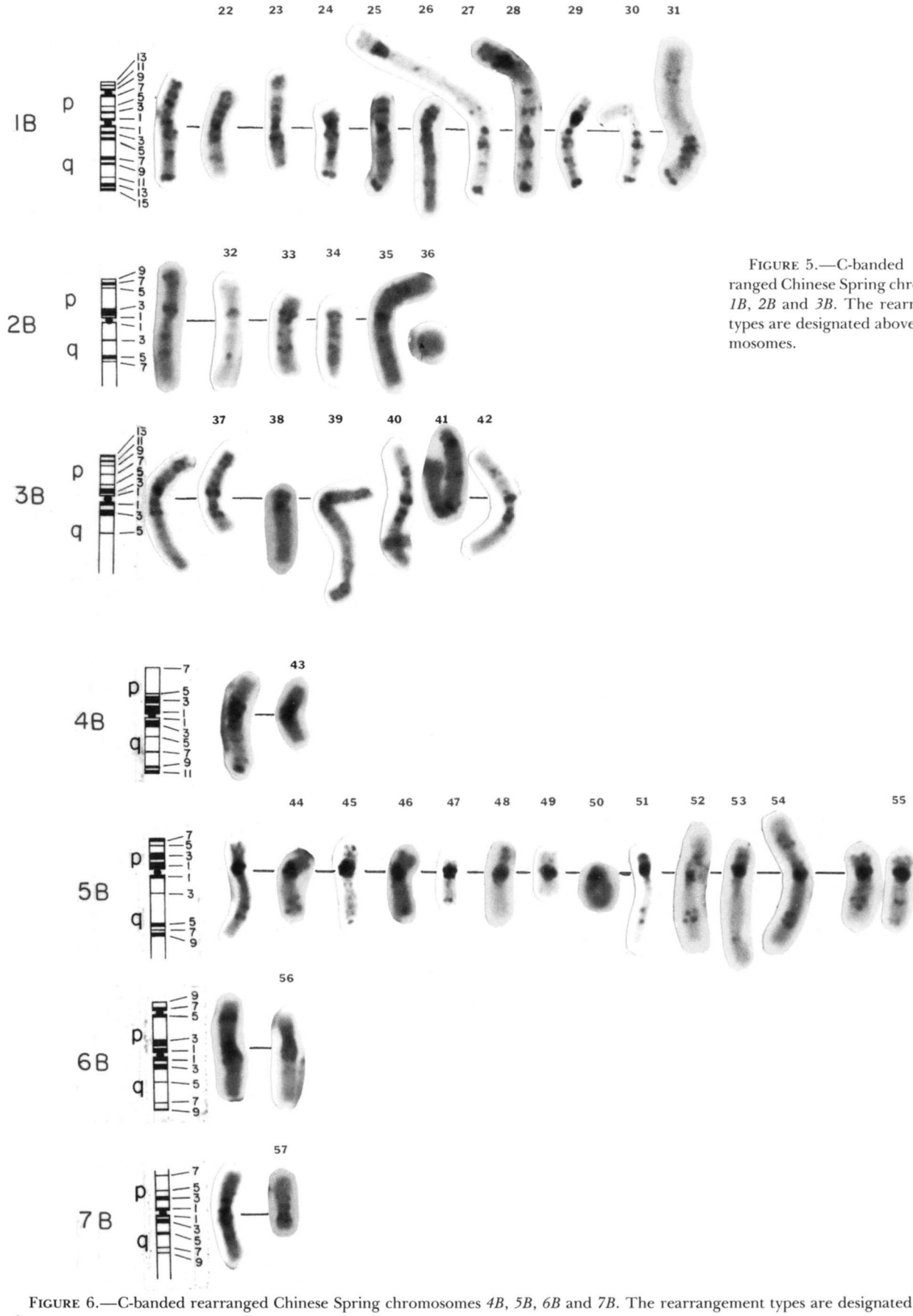

FIGURE 5.—C-banded rearranged Chinese Spring chromosomes *1B*, *2B* and *3B*. The rearrangement types are designated above the chromosomes.

FIGURE 6.—C-banded rearranged Chinese Spring chromosomes *4B*, *5B*, *6B* and *7B*. The rearrangement types are designated above the chromosomes.

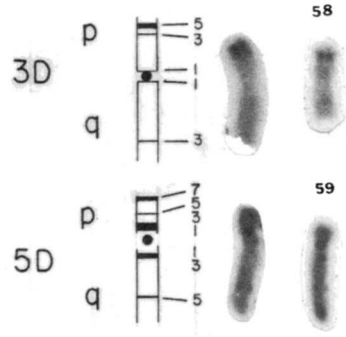

FIGURE 7.—C-banded rearranged Chinese Spring chromosomes of the *D* genome. The rearrangement types are designated above the chromosomes.

Chromosome rearrangements also occurred in the plants produced in attempt to substitute *T. speltoides* chromosome $7B^s$ for *7B*. No chromosome rearrangements were observed in the F_1, BC_1F_1, or BC_2F_1 generation plants (Table 2). Among 22 BC_2F_2 plants one plant was chimeric and had rearranged chromosome types 9, 10, 11, and 12, all involving the *T. speltoides* chromosome (Table 2, Figure 3).

Types of chromosome rearrangements: Chromosome rearrangements were observed in both wheat and *T. speltoides* chromosomes. Deletions, translocations, dicentric chromosomes, a ring chromosome, and a paracentric inversion were observed (Figures 3–7). The most frequent were chromosome deletions and translocations. All deletions were terminal. The location of breakpoints and reunions for every chromosome in Figures 3–7 is described in Table 3. The place in which a specific breakpoint is observed may not necessarily represent the exact place where a lesion occurred, because the primary breakpoint can move in the proximal direction if it is followed by fusion and bridge formation.

Uneven distribution of rearrangements among chromosomes: Among the three wheat genomes, the most rearrangements were observed in the B-genome chromosomes, fewer in the A-genome chromosomes, and the least in the D-genome chromosomes (Table 4). If the rearrangements were homogeneously distributed among the genomes, they would be expected to occur in a 1:1:1 ratio. The observed ratio was 22:62:5 in the *A*, *B*, and *D* genomes of wheat, respectively (Table 4), indicating a nonhomogeneous distribution of breaks among the genomes ($\chi^2 = 59.3$, $P < 0.01$). In the *B* genome, the higher number of rearrangements allowed a statistical test of homogeneity of the distribution of the breaks among chromosomes. It was assumed that if the breaks were distributed homogeneously among the seven chromosomes, they should occur in a 1:1:1:1:1:1:1 ratio. The actual ratio (Table 4) differed highly significantly from the expected ratio ($\chi^2 = 76.9$, $P \leq 0.01$). The most frequently affected chromosomes were *1B* and *5B* and the least affected were *4B* and *6B*. Data for chromosomes *4B* and *6B* may be somewhat underestimated because these chromosomes were not present in all plants that had $6B^s$. The same uneven distribution of breaks is also apparent among *T. speltoides* chromosomes. Thirty-six breaks were observed in chromosome $6B^s$ but none in $4B^s$ even though $4B^s$ was present in 28 BC_2F_2 or BC_2F_3 plants simultaneously with chromosome $6B^s$.

TABLE 4

Distribution of chromosome rearrangements per individual chromosome among the three wheat genomes

Chromosome	No. of rearrangements
3A	2
4A	8
5A	8
6A	1
7A	3
Total	22*
1B	19
2B	5
3B	4
4B	1
5B	28
6B	1
7B	4
Total	62*,**
1D	1
3D	2
5D	2
Total	5*

* The distribution of aberrations among the three genomes is nonhomogeneous ($P < 0.01$).

** The distribution of aberrations among the *B*-genome chromosomes in nonhomogeneous ($P \leq 0.01$).

The distribution of breaks appears uneven within chromosomes which is indicated by the frequency of occurrence of chromosome types listed in Table 2. Because of the uncertainty of the location of the original breakpoints and the relatively low numbers of each type of rearrangement, it is difficult to subject those data to statistical tests. A deletion with a breakpoint in the euchromatic region 2 of the *q* arm of $6B^s$ (chromosome type 1, Figure 3) was observed independently 21 times (Table 3). The same breakpoint also occurred in rearranged chromosomes of types 3 and 4 (Table 3, Figure 3) in BC_2F_3 generation. In most chromosomes, the breaks were in both euchromatin and heterochromatin (Figures 3–7).

The *B*-genome chromosomes have more C-bands than either the *A*- or *D*-genome chromosomes, and therefore it is easier to detect a rearrangement among the *B*-genome chromosomes. It could be, therefore, argued that some of the rearrangements involving *A*- and *D*-genome chromosomes were missed and that accounts for the observed uneven incidence of rearrangements among the three genomes. To minimize

this possibility the conclusions were based on analyses of metaphase cells in which all chromosomes were identified. Additionally, an idea of the incidence of chromosome breaks among the wheat genomes can be obtained from frequencies of translocations. Because of the abundance of C-bands it is unlikely to miss a translocation when it involved a *B*-genome chromosome. There were ten translocations involving two *B*-genome chromosomes and five translocations between *B*- and *A*- or *D*-genome chromosomes. Additionally, there were six translocations involving a *B*-genome chromosome and an unidentified chromosome. If this unidentified chromosome were an *A*- or *D*-genome chromosome in each case the number of the translocation between *B* and *A* or *D* chromosomes would be 12, a number close to the number of the translocations between two *B*-genome chromosomes. However, if the breaks are equal in all chromosomes, there should be twice as many *B-A* or *B-D* translocations than *B-B* translocations. Thus, the disproportionally high incidence of *B-B* translocations also suggest that the number of breaks had to be higher among the *B*-genome chromosomes than the *A*- or *D*-genome chromosomes.

DISCUSSION

The chromosome rearrangements reported here were observed in the BC_2F_2 and BC_3F_2 progeny having chromosome $6B^s$ but not in either the amphiploid, the F_1, BC_1F_1, and BC_2F_1 generations. To obtain substitutions of *T. speltoides* chromosomes for specific wheat homoeologues all crosses were made using the recurrent wheat parents as females. However, during the substitution of *T. speltoides* chromosome $3B^s$ for *3B*, the recurrent wheat parent was used as a male in the second backcross. In this instance chromosome aberrations were observed in a BC_2F_1 generation (R. S. KOTA, unpublished data). This can be accounted for by assuming that chromosome aberrations are induced after chromosome disjunction at meiosis but prior to syngamy and are seldom transmitted through the gametophyte if the parent is used as a male. Another possibility is that the factor responsible for the genomic instability is active only in the maternal germ line.

Additionally, hybridization seems to activate the instability. The progeny of the double disomic substitution $4B^s(4B)$ $6B^s(6B)$ were self-pollinated for two generations. No chromosome rearrangements were observed in eight BC_2F_5 plants. The substitution line was then crossed to an unrelated wheat variety. While none of the ten F_1 plants showed a rearrangement, four of ten F_2 progeny from this cross again showed chromosome rearrangements. This suggests that the instability is activated by the hemizygosity of the $6B^s$ factor. In this way, the current observations resemble the behavior of several transposition systems in *Drosophila* and maize in which transposition is activated by hybridization (WOODRUFF and THOMPSON 1985; BREGLIANO and KIDWELL 1983; WALBOT 1984.

Even though chromosome restructuring coincided with the presence of chromosome $6B^s$ in 51 of 248 plants, there were two exceptions. One was a BC_2F_2 plant (group 7*1) which did not have $6B^s$ but had chromosome $7B^s$. In this case three arrangements involved $7B^s$ only and one was a $7B^s$-*5A* translocation. The other exception was a BC_2F_3 plant of Chinese Spring type (group 3*2-1-1). The parental plant had chromosome $6B^s$. The specific progeny had a rearranged chromosome *5B* (chromosome type 49, Figure 6) but did not have chromosome $6B^s$. It is possible that this aberration arose independently of $6B^s$ or that the factor causing chromosome rearrangements was translocated (or transposed) into a wheat chromosome. The latter possibility is currently being investigated.

Several other cases of genomic instabilities have been reported in wheat. Rearranged wheat chromosomes were found in intercultivar (ENDO and GILL 1984) and interspecific chromosome substitution lines (KOTA and DVORAK 1986) and in the progenies from interspecific hybridization (MILLER and READER 1982), but no definite genetic causes could be identified. FELDMAN and STRAUSS (1983) reported the existence of a recessive gene causing massive chromosome rearrangements in *T. longissimum*. Chromosome instability was also associated with gametocidal effects caused by several alien chromosomes of homoeologous group *4* in the monosomic state (MAAN 1975; FINCH, MILLER and BENNETT 1984; TSUJIMOTO and TSUNEWAKI 1984; ENDO 1985). It was concluded that this instability is similar to the hybrid dysgenesis of *Drosophila* (TSUJIMOTO and TSUNEWAKI 1985). It is possible that the elements causing chromosome instability are normally cryptic in wheat but are activated by hybridization or by autonomous factors introduced by alien chromosomes.

Constitutive heterochromatin is more susceptible to chromosome breakage than euchromatin (GILL *et al.* 1980; MCCOY and PHILLIPS 1982). Although the highest breakage occurred in the B genome which is more heterochromatic than the other two wheat genomes, it is hard to attribute the current observations entirely to the effect of heterochromatin. No chromosome aberrations were observed in the amphiploid and in advanced self-pollinated disomic substitutions involving chromosome $6B^s$ indicating that they are probably rare in these plants. If late replicating heterochromatin were the cause of chromosome instability, aberrations would be expected to occur in all generations. Additionally, heterochromatic regions should show a high frequency of chromosome breaks. The chromo-

some breaks caused by chromosome *6B*^{s} were, however, in both the euchromatic and heterochromatic regions.

Whatever is the cause of the chromosome instability described here, an evolutionarily intriguing aspect of these observations is that they show that in an alloploid one genome can have a greater potential for structural chromosome evolution than the other genomes despite being in the same nucleus and presumably exposed to the same selection pressures. Under the influence of the *T. speltoides* chromosome *6B*^{s}, the number of chromosome rearrangements in the *B* genome greatly outnumbered those in the *A* and *D* genomes. LARSEN (1974) catalogued the cytologically identified spontaneous translocations in *T. aestivum*. If the chromosome designated '*4A*' in his data is reallocated to the *B* genome (DVORAK 1983) the *B*-genome chromosomes are involved 17 times in different translocations, whereas the chromosomes of the *A* and *D* genomes are each involved five times. Likewise, in the wild tetraploid wheats *Triticum turgidum* Bowden em. Morris et Sears ssp. *dicoccoides* and *Triticum timopheevi*, ssp. *araraticum*, the *B*-genome chromosomes are involved in many more translocations than the *A*-genome chromosomes (KAWAHARA 1984).

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