Rapid Elimination of Low-Copy DNA Sequences in Polyploid Wheat: A Possible Mechanism for Differentiation of Homoeologous Chromosomes

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ABSTRACT

To study genome evolution in allopolyploid plants, we analyzed polyploid wheats and their diploid progenitors for the occurrence of 16 low-copy chromosome- or genome-specific sequences isolated from hexaploid wheat. Based on their occurrence in the diploid species, we classified the sequences into two groups: group I, found in only one of the three diploid progenitors of hexaploid wheat, and group II, found in all three diploid progenitors. The absence of group II sequences from one genome of tetraploid wheat and from two genomes of hexaploid wheat indicates their specific elimination from these genomes at the polyploid level. Analysis of a newly synthesized amphiploid, having a genomic constitution analogous to that of hexaploid wheat, revealed a pattern of sequence elimination similar to the one found in hexaploid wheat. Apparently, speciation through allopolyploidy is accompanied by a rapid, nonrandom elimination of specific, low-copy, probably noncoding DNA sequences at the early stages of allopolyploidization, resulting in further divergence of homoeologous chromosomes (partially homologous chromosomes of different genomes carrying the same order of gene loci). We suggest that such genomic changes may provide the physical basis for the diploid-like meiotic behavior of polyploid wheat.

ALLOPOLYPLOIDY has played a major evolutionary role in the formation of many plant species (STEBBINS 1950, 1971; SOLTIS and SOLTIS 1993, 1995). Yet, little information exists about the nature of genomic changes that are required for successful speciation via allopolyploidy. In particular, the mechanism by which several genomes coexist in the same nucleus is largely unknown. This mechanism may involve adjustments in DNA sequences that differentiate between the constituent genomes of an allopolyploid plant. We have addressed this issue in wheat, which provides a classical example of evolution through allopolyploidy. Bread wheat is a hexaploid species ($2n = 6x = 42$; genomes *AABBDD*) that originated from hybridization events involving three different diploid progenitors classified in the genera Triticum and Aegilops (Figure 1) (for review see FELDMAN *et al.* 1995). On the basis of genetic similarities, the 21 pairs of homologous chromosomes of bread wheat (seven pairs of each genome) fall into seven homoeologous groups, each containing one pair of chromosomes from the *A, B,* and *D* genomes, respectively (SEARS 1954). Hence, homoeologous group 1, for example, contains the pairs *1A, 1B,* and *1D*. In each group, homoeologous chromosomes, being derived from a common ancestral chromosome, share a high level of gene synteny but differ from one another by a number of noncoding DNA sequences (FLAVELL 1982). On the basis of specificity and distribution in the constituent genomes of polyploid wheat, we classified the DNA sequences of these polyploid species into the following four categories: nonspecific sequences, group- or homoeologous-specific sequences, genome-specific sequences, and chromosome- or homologous-specific sequences (LIU *et al.* 1997). To study the nature of changes associated with the divergence of homoeologous chromosomes, we analyzed several low-copy chromosome-specific sequences (CSSs) and genome-specific sequences (GSSs) previously isolated from hexaploid wheat and studied their occurrence in different lines of tetraploid and hexaploid wheat, in lines of their diploid progenitors, as well as in a newly synthesized hexaploid wheat.

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MATERIALS AND METHODS

Plant materials: To confirm the chromosome specificity of the studied DNA sequences, several kinds of aneuploid lines were used. Hexaploid nullisomic-tetrasomic lines, each deficient for a given pair of chromosomes (nullisomic) and carrying four doses of one of its homoeologous chromosomes (tetrasomic), were produced by the late E. R. SEARS. The tetraploid nullisomic *5B*-disomic *5D* line carries *5D* chromosomes from hexaploid wheat substituting for the *5B* of the tetraploid. This line was produced and kindly provided by L. R. JOPPA (USDA-ARS Agronomy Department, North Dakota State University, Fargo, ND).

The occurrence of the various CSSs and GSSs was studied in lines of the following diploid and polyploid species of wheat (Triticum) and in lines of their closely related genus Aegilops (classification after VAN SLAGEREN 1994): *T. urartu* Tumanian

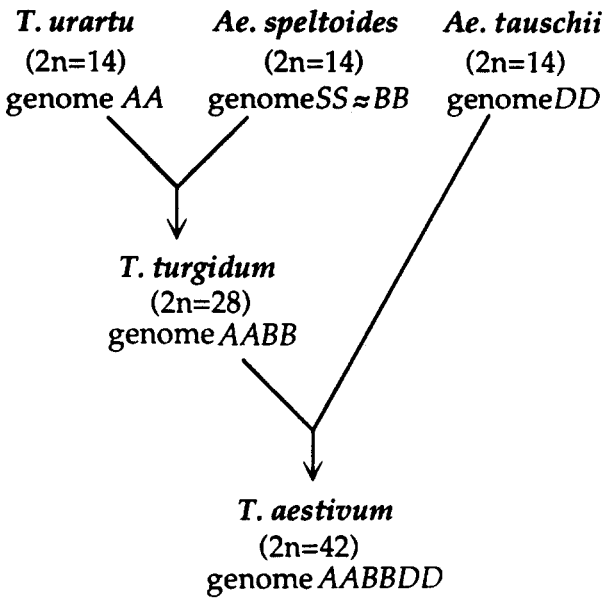

FIGURE 1.—A scheme describing the origin of hexaploid wheat, *Triticum aestivum*. Hexaploid wheat originated through hybridization, followed by chromosome doubling, between the tetraploid wheat *T. turgidum* and the diploid species *Ae. tauschii*. *T. turgidum* originated from hybridization, followed by chromosome doubling, between the diploid species *T. urartu* and a form closely related to *Ae. speltoides*.

ex Gandilyan, the putative diploid donor of the *A* genome of all tetraploid and hexaploid Triticum species (DVORAK 1976: CHAPMAN *et al.* 1976) (three lines); *Ae. tauschii* Coss., the diploid donor of the *D* genome to hexaploid bread wheat (KIHARA 1944; MCFADDEN and SEARS 1944) (four lines); *Ae. speltoides* Tausch, a diploid species whose genome is closely related to the *B* genomes of tetraploid and hexaploid Triticum species (RILEY *et al.* 1958; FELDMAN *et al* 1995) (six lines); *T. turgidum* L. ssp. *dicoccoides* (Körn, ex Asch. and Graebn.) Thell., the wild tetraploid progenitor of cultivated tetraploid and hexaploid wheat (four lines); *T. turgidum* L. ssp. *dicoccon* (Schrank) Thell., the primitive domesticated tetraploid wheat (one line); *T. turgidum* L. ssp. *durum* (Desf.) Husn., the domesticated tetraploid known as macaroni wheat (three lines); *T. aestivum* L. ssp. *aestivum*, hexaploid bread wheat (four lines); *T. aestivum* L. ssp. *spelta* L. Thell., hexaploid spelt wheat (one line); and *T. aestivum* L. ssp. *compactum* (Host) Mackey, hexaploid club wheat (one line). All these lines were selected from our germplasm collection.

A newly synthesized hexaploid wheat, *T. turgidum* ssp. *dicoccoides* (genomes *AABB*)-*Ae. tauschii* (genome *DD*), was produced by JIM WORSTELL and the late E. R. SEARS in 1979. Selfed seeds (S_3) of the synthetic hexaploid and its tetraploid and diploid parents were kindly provided by the late E. R. SEARS in 1980. This material was grown for two generations in our greenhouse, and S_5 plants of the synthetic hexaploid as well as its two parents were used for this study.

DNA sequences: Thirteen CSSs and three GSSs were used in this study (Table 1). Five CSSs and one GSS were isolated from a chromosome-arm DNA library developed in our laboratory. This library was produced by amplification and cloning of DNA derived from chromosome arm *5BL*, which was microdissected from the bread wheat cultivar Chinese Spring (VEGA *et al.* 1994, 1997). These sequences were characterized and mapped to specific chromosomal regions (LIU *et al.* 1997). Another set of sequences, including eight CSSs and two GSSs, was isolated from a genomic library of bread wheat (SHARP *et al.* 1989; GALE *et al.* 1995). This set was kindly provided by M. D. GALE (John Innes Centre, Norwich, UK).

Southern analysis: Genomic DNA was isolated by the CTAB method (KIDWELL and OSBORN 1992) from young leaves of individual plants. DNA (10 μg) was digested with five restriction enzymes, *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV and *Hin*dIII, unless indicated otherwise. Southern blotting, probe labeling, hybridization and washing conditions were as described earlier (LIU *et al.* 1997).

RESULTS AND DISCUSSION

The CSSs and GSSs were hybridized to genomic DNA of several different genetic lines of tetraploid (*T. turgidum*) and hexaploid (*T. aestivum*) wheat and to lines of the three diploid progenitors, *T. urartu*, *Ae. speltoides* and *Ae. tauschii*. Each of the studied 16 sequences were found in at least one of the diploid taxa, providing a clear indication that none of them appeared *de novo* after polyploidization. Based on their occurrence in the diploid species, we have classified these sequences into two distinct groups (Table 1): group I, which occur in only one of the three diploid progenitors of hexaploid wheat, and group II, which occur in all three diploid progenitors. Group I includes only CSSs (seven sequences) and group II includes six CSSs and three GSSs.

Group I sequences exhibit high polymorphism at the diploid and polyploid levels (Figure 2a and data not shown). In many sequence-species combinations these sequences are present only in some lines and absent from others (Table 1 and Figure 2a, lanes 7 and 8). Evidently, group I sequences do not play an essential role. Their presence in only one diploid progenitor may indicate that they evolved at the diploid level during or after the divergence of the three diploid progenitors from one another. For this reason, additional studies on the distribution of group I sequences among a larger sample of lines from all the diploid species of the Triticeae may illuminate phylogenetic relationships among these species as well as between them and the polyploid species of Triticum and Aegilops.

The nine group II sequences appear to be relatively conserved, exhibiting little or no polymorphism at the diploid and polyploid levels (Figure 2b, and data not shown). One of these sequences, WPG15, was found non-polymorphic both in the present study as well as in a broader study that included 72 wild and domesticated lines of tetraploid wheat and 34 cultivars of hexaploid wheat (L. HUANG, E. MILLET and M. FELDMAN, unpublished data). Moreover, we also found the three group II CSSs isolated in our lab (WPG15, WPG79 and WPG90) in other species of Aegilops and in three closely related genera of the tribe Triticeae, *Secale cereale* (rye), *Agropyron intermedium* (wheat grass) and *Hordeum vulgare* (barley), as well as in the more remotely related grass species *Oryza sativa* (rice) (data not shown). The ubiquitous occurrence of these sequences strongly suggests an ancient origin, early in the development of

TABLE 1

Occurrence of chromosome-specific sequences and genome-specific sequences in hexaploid and tetraploid wheats and in their diploid progenitors

Sequences			Hexaploids	Tetraploids	Diploid progenitors			
Designation[a]	Size (kb)	Chromosome-arm location in common wheat	*T. aestivum* (*AABBDD*)	*T. turgidum* (*AABB*)	*T. urartu* (*AA*)	*Ae. speltoides* (*SS* ≈ *BB*)	*Ae. tauschii* (*DD*)	Sequence group[b]
PSR1202	0.500	*5AL*	+	+	+	−	−	I
PSR907	1.100	*3BS*	+	+/−	−	+/−	−	I
WPG118	0.250	*3BL*	+	+	−	+/−	−	I
PSR454	0.600	*3BL*	+/−	+/−	−	+/−	−	I
WPG35	0.211	*5BL*	+	+	−	+	−	I
PSR548	1.800	*7DL*	+/−	−	−	−	+	I
PSR560	2.700	*7DL*	+/−	−	−	−	+	I
PSR743	2.200	*7AX*[c]	+	+	+	+	+	II
PSR618	2.800	*5BS*	+	+	+	+	+	II
WPG15	0.279	*5BL*	+	+	+	+	+	II
WPG79	0.238	*5BL*	+	+	+	+	+	II
WPG90	0.279	*5BL*	+	+	+	+	+	II
PSR301	2.120	*6BX*[c]	+	+	+	+	+	II
PSR551	1.200	*2BS, 6BS*	+	+	+	+	+	II
PSR593	2.500	*2BS, 4BS, 7BL*	+	+	+	+	+	II
WPG176	0.206	*3BL, 4BX*[c]*, 5BL*	+	+	+	+	+	II

+, occurrence in all lines; −, absence from all lines; and +/−, occurrence in some lines.

[a] WPG (Weizmann Plant Genetics) sequences; PSR (Plant Science Research) sequences were kindly provided by M. D. GALE, John Innes Centre, Norwich, United Kingdom.

[b] Group I sequences are defined by their occurrence in only one diploid progenitor; group II sequences are defined by their occurrence in all three diploid progenitors. Sequences PSR743 and PSR551 were found in all diploid species only when some restriction enzymes were used.

[c] The sequence was not yet located to chromosome arm.

the grass family. The high conservation and ubiquity of group II sequences indicate that they are under some selection pressure.

Although group II sequences occur in all three diploid progenitors, they hybridized to chromosomes of a single genome in hexaploid wheat: CSSs hybridized to only one chromosome pair (Figure 3, lanes 1–4) and GSSs to several chromosome pairs of the same genome,

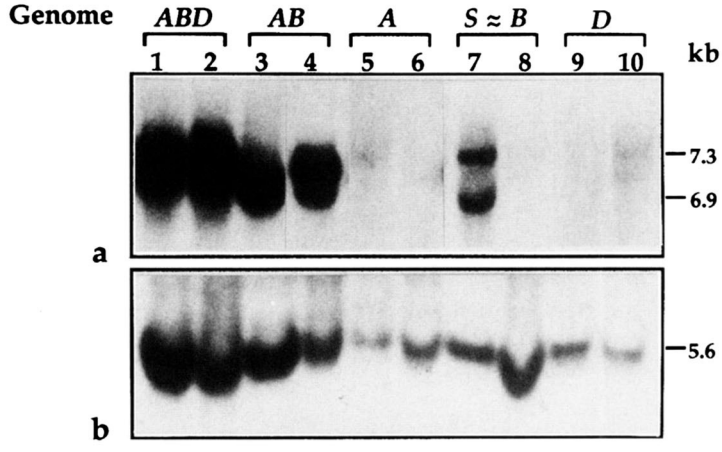

FIGURE 2.—Southern hybridization of chromosome-specific sequences to genomic DNA from different polyploid and diploid species. (a) A group I chromosome-specific sequence PSR907 (located on chromosome arm *3BS*) hybridized to *Eco*RI-digested genomic DNA. (b) A group II chromosome-specific sequence WPG15 (located on chromosome arm *5BL*) hybridized to *Hin*dIII-digested genomic DNA. Genomic DNA from two hexaploid wheats, *T. aestivum* var. *aestivum* cv. Chinese Spring (CS) (lane 1) and ssp. *spelta* (TAS03) (lane 2); from two tetraploid wheats, *T. turgidum* ssp. *durum* cv. Inbar (lane 3) and ssp. *dicoccoides* (TTD15) (lane 4); and from six diploid wheats: *T. urartu,* TMU01 (lane 5) and TMU41 (lane 6); *Ae. speltoides,* TS19 (lane 7) and TS27 (lane 8); and *Ae. tauschii,* TQ56 (lane 9) and TQ78 (lane 10). These lines are a representative sample of a larger number of lines that were analyzed in each species. Genomic formulae and size (in kb) are indicated.

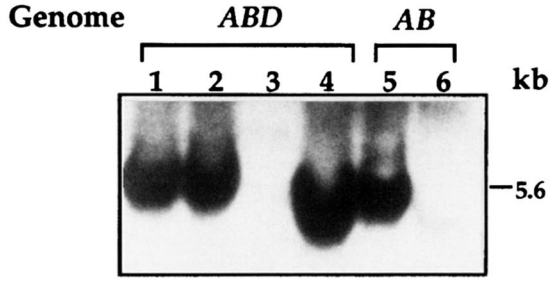

FIGURE 3.—Southern hybridization of the chromosome-specific sequence WPG15 to aneuploid lines of hexaploid and tetraploid wheat. *Hin*dIII-digested genomic DNA from the following lines: the hexaploid wheat cv. CS (lane 1), nullisomic *5A*-tetrasomic *5D* of CS (lane 2), nullisomic *5B*-tetrasomic *5D* of CS (lane 3), nullisomic *5D*-tetrasomic *5B* of CS (lane 4), the tetraploid cultivar Langdon (lane 5), and nullisomic *5B*-disomic *5D* of cv. Langdon (lane 6). The specificity of sequence WPG15 to chromosome arm *5BL* of hexaploid and tetraploid wheats is evident, indicating the elimination of this sequence from the *A* genome at the tetraploid level and from the *D* genome at the hexaploid level. Genomic formulae and size (kb) are indicated.

indicating elimination from the homoeologous chromosomes of the other two genomes. Probing a newly synthesized hexaploid wheat and its two parental lines with four group II sequences (two chromosome-specific, WPG90 and PSR301, and two genome-specific, PSR551 and PSR593), we further investigated this intriguing phenomenon of occurrence in all three diploid progenitors *vs.* elimination in the polyploid species. Each of these sequences exhibited a unique restriction fragment length polymorphism pattern in the parental tetraploid and diploid lines that were used to produce the synthetic hexaploid wheat, thus allowing to study their existence in the synthetic line. As shown in Figure 4, all four sequences of the tetraploid parent (genomes *AABB*) exist in the three different amphiploid plants analyzed, whereas those of the diploid parent (genome *DD*) are absent.

As a control to the elimination of the CSSs and GSSs, 42 group (homoeologous)-specific sequences, *i.e.,* sequences present in all three pairs of homologues of a given homoeologous group in hexaploid wheat, were hybridized to genomic DNA of the synthetic hexaploid wheat and of its parental lines. The 42 group-specific sequences were selected to represent the proximal and distal regions of the short and long arms of all seven homoeologous groups. It was found that some genomic changes, such as loss of parental hybridization fragment(s) and/or gain of novel fragment(s), occurred in the amphiploid with some of the sequence/enzyme combinations. However, these changes were not brought about by elimination since for every studied sequence in at least one of the enzyme digests (*e.g.,* Figure 5), the hybridization pattern of the synthetic hexaploid revealed the combination of its two parents. This finding confirmed the integrity of the chromosome complement of the amphiploid. We thus concluded that the observed elimination of CSSs and GSSs did not result from loss of a chromosome arm or segment.

The data obtained from the newly synthesized amphiploid strongly suggests that further differentiation of homoeologous chromosomes via elimination of low-copy DNA sequences occurs rapidly, soon after the polyploid speciation event rather than by a slow evolutionary process. Moreover, the elimination of a particular sequence is nonrandom, consistently targeting the same genome(s) in the polyploids. This elimination has presumably happened twice in the evolution of bread wheat: initially, with the formation of *AABB* tetraploid species, there has been an elimination of CSSs or GSSs from either the *A* or the *B* genomes at the tetraploid level; subsequently, with the formation of the hexaploid species, there has been an elimination of *D* or *A/B* sequences at the hexaploid level. Results with WPG15 (chromosomal arm *5BL*) clearly demonstrate this phenomenon. Although present in all three diploid progenitors, WPG15 is specific to chromosome arm *5BL* in polyploids, *i.e.,* it is absent from chromosome arm *5AL* in tetraploid wheat and from chromosome arms *5AL* and *5DL* in hexaploid wheat (Figure 3). (Unfortunately, WPG15 is not polymorphic and therefore could not be used for studying the newly synthesized hexaploid wheat). Such nonrandom elimination of DNA sequences may contribute to cytological diploidization by increasing the divergence of homoeologous chromosomes and might be an essential prerequisite for the successful formation of the new polyploid species.

That newly formed polyploids undergo genomic changes at the molecular level was recently reported by SONG *et al.* (1995) who found extensive intra- and intergenomic changes at the DNA level in the F_2 to F_5 generations of amphiploids of Brassica. These changes involved loss and/or gain of parental restriction fragments as well as the appearance of novel fragments. Our data, showing differential and nonrandom elimination of DNA sequences from two of the three homoeologous chromosome pairs, point to a different type of genome change. Unlike the differences between individual plants observed in synthetic Brassica tetraploids (SONG *et al.* 1995), we found a similar pattern of sequence elimination in all plants tested, both of wild and cultivated species, as well as in a newly synthesized hexaploid wheat. Hence, we conclude that this pattern of sequence elimination occurs through a precisely orchestral mechanism and may be of adaptive value. According to SONG *et al.* (1995), the genomic changes observed in Brassica may have resulted either from chromosomal rearrangements due to intergenomic recombination or from DNA methylation. We can exclude the possibility of either intergenomic recombination or DNA methylation as an explanation for the hybridization patterns that we have found. Given the

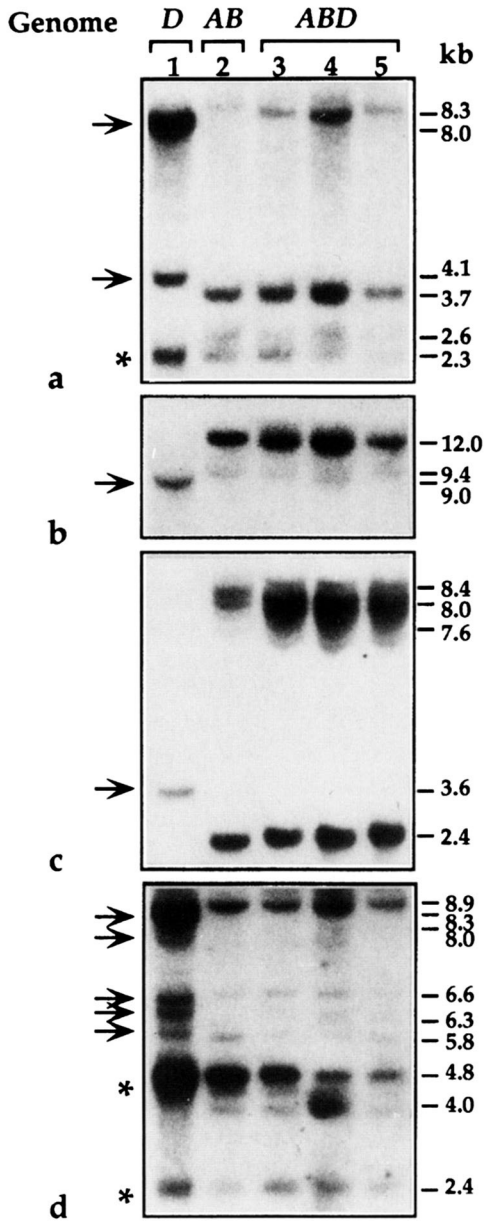

FIGURE 4.—Southern hybridization of chromosome- and genome-specific sequences to genomic DNA from a newly synthesized hexaploid wheat and from its two parents. (a) The chromosome-specific sequence WPG90 (located on chromosome arm *5BL*) hybridized to *Bam*HI-digested genomic DNA. (b) The genome-specific sequence PSR551 (located on chromosome arms *2BS* and *6BS*) hybridized to *Eco*RV-digested genomic DNA. (c) The chromosome-specific sequence PSR301 (located on chromosome *6B*) hybridized to *Bam*HI-digested genomic DNA. (d) The genome-specific sequence PSR593 (located on chromosome arms *2BS*, *4BS* and *7BL*) hybridized to *Eco*RV-digested genomic DNA. The genomic DNA was obtained from the amphiploid XX340 (genomes *AABBDD*) and from its two parental lines. The amphiploid (lanes 3–5) was produced by chromosome doubling of the F_1 hybrid between tetraploid wheat *T. turgidum* var. *dicoccoides* (TTD09; genomes *AABB*) (lane 2) and the diploid *Ae. tauschii* (TQ01; genome *DD*) (lane 1). Each of the lanes 3–5 represents a different amphiploid plant. The hybridization fragment(s) found in the *D* genome of the diploid parent that are marked by arrows are polymorphic to the corresponding fragments of the *AB* genomes and are absent from the amphiploid. The third fragment of *Ae. tauschii* in Figure 4a, and the sixth and seventh fragments of this species in Figure 4d (marked by asterisks) are not polymorphic to the corresponding fragments of var. dicoccoides. However, judging by the intensity of these bands in lanes 3–5, these *D*-genome sequences appear to be absent in the amphiploid. Similar results were repeatedly obtained following digestion with other enzymes. Genomic formulae and size (kb) are indicated.

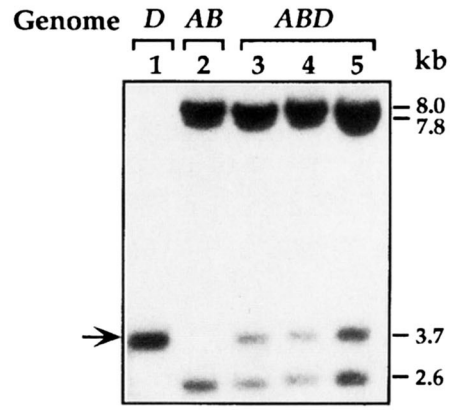

FIGURE 5.—Southern hybridization of a group (homoeologous)-specific sequence to genomic DNA from a newly synthesized hexaploid wheat and from its two parents. *Dra*I-digested genomic DNA from three individual plants of the newly synthesized hexaploid wheat (XX340) (lanes 3–5) and from its two parents, tetraploid *T. turgidum* ssp. *dicoccoides* (TTD09) (lane 2) and diploid *Ae. tauschii* (TQ01) (lane 1) was hybridized to sequence PSR370. This group-specific sequence locates at distal regions of the long arm of chromosomes of group 5 (*5AL*, *5BL* and *5DL*). Arrow indicates the *5DL* fragment. Genomic formulae and size (kb) are indicated.

presence of the tetraploid parent (ssp. dicoccoides) gene system, which suppresses homoeologous pairing (RILEY 1960; SEARS 1976), chromosome pairing leading to intergenomic recombinations would not have occurred in our synthetic amphiploid. With respect to methylation, we digested DNA of the newly synthesized amphiploid and its parental lines with the isoschizomers *Hpa*II and *Msp*I, which recognize a predominant DNA methylation site (CCGG) in plants but differ in methylation sensitivity (SAMBROOK *et al.* 1989). The blot was then probed with the four group II sequences mentioned above (WPG90, PSR301, PSR551 and PSR593). Only two of the four sequences, namely, WPG90 and PSR551, detected informative polymorphism between the two parental lines in *Msp*I/*Hpa*II digests, and for these two sequences the hybridization fragment(s) of the *D* genome parent (TQ01) was absent from the amphiploid in both of the enzyme digests (Figure 6). This finding implies that absence of parental hybridization fragment(s) in the amphiploid is not due to methylation changes in a CCGG site within or immediately adjacent to the group II sequences.

Homoeologous chromosomes of the different diploid species of Triticum and Aegilops retain a relatively

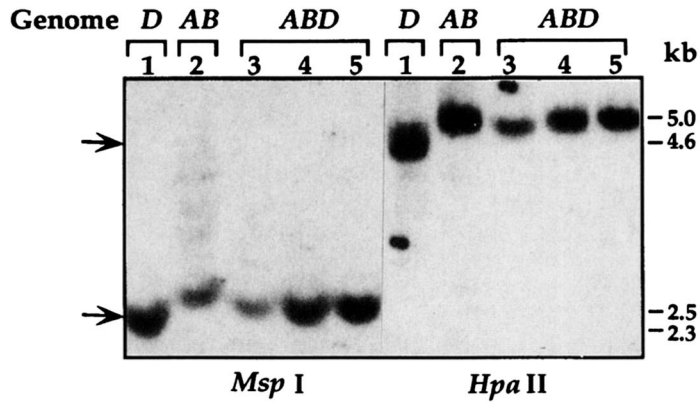

FIGURE 6.—Southern hybridization of group II genome-specific sequence PSR551 (located on *2BS* and *6BS*) to *Msp*I/*Hpa*II-digested genomic DNA of the newly synthesized hexaploid wheat and its two parental lines. In both enzymes, which differ in methylation sensitivity, hybridization patterns of all three individual amphiploid plants are monomorphic with those of the *AB*-genome parent (TTD09). This suggests that the absence of the *D*-genome parental (TQ01) hybridization fragment (arrowed) in the amphiploid is not due to methylation changes but the result of sequence elimination. Genomic formulae and size (kb) are indicated.

high degree of homology (RILEY 1960; SEARS 1976). Thus, to prevent intergenomic pairing and ensure proper chromosome segregation and, hence, full fertility and disomic inheritance in the polyploid species, an exclusive bivalent pairing of homologous chromosomes is essential. We propose here that such bivalent pairing in polyploid wheat is brought about by two independent systems that complement each other. The first system is based on nonrandom elimination of DNA sequences from one of the two pairs of homoeologous chromosomes in the initial tetraploid wheat and, subsequently, from the third pair of homoeologous chromosomes in the initial hexaploid wheat. These sequences are assumed to be noncoding because sequencing data of clones WPG15, WPG79, WPG90 and WPG176 (not shown) indicate several stop codons and relatively short open reading frames. These elimination events occur instantaneously or soon after the formation of the polyploids and result in accentuating the differentiation among homoeologues, and thus provide the physical basis for the diploid-like meiotic behavior of these polyploids, a critical trait that has contributed to the successful establishment of the polyploids as new species. Preliminary data (LIU *et al.* 1997 and unpublished data) indicate that the CSSs and GSSs on chromosome arm *5BL* are clustered in several regions, interstitial, subterminal and terminal (subtelomeric), which exhibit high homologous specificity (in contrast to other regions that contain group-specific and nonspecific DNA sequences, *e.g.*, retrotransposons). Hence, it is tempting to suggest that these highly chromosome-specific regions may correspond to the chromosomal sites (pairing initiation sites) that play a critical role in homology search and initiation of pairing at first meiotic prophase (HAWLEY and ARBEL 1993). The second system involved in the exclusive bivalent pairing in polyploid wheat is a genic one consisting of the genes *Ph1* and *Ph2*, which suppress pairing of homoeologues while allowing homologues to pair regularly (RILEY 1960; SEARS 1976; FELDMAN 1993). This system has probably evolved later, superimposing itself on and thereby reinforcing the already existing system of homoeologous differentiation.

The multiplication of genetic material in polyploid species can lead to overexpression and inefficiency. To reduce redundancy of gene expression, many coding DNA sequences undergo dosage compensation (GALILI *et al.* 1986) or genetic diploidization (FELDMAN *et al.* 1986; SOLTIS and SOLTIS 1993); the latter is brought about mainly by a slow process of gene inactivation (SOLTIS and SOLTIS 1993) (via mutations and/or methylations). Our findings, assumed to be concerned with noncoding DNA sequences, suggest another type of diploidization: rapid elimination soon after the formation of the polyploid. CSSs and GSSs that are targeted for elimination might exert a regulatory control on the physical behavior of chromosomes.

As proposed by others (SONG *et al.* 1995; SOLTIS and SOLTIS 1993, 1995; TEUTONICO and OSBORN 1994; WENDEL *et al.* 1995; RIESEBERG *et al.* 1995, 1996; WALBOT and CULLIS 1985), our work supports the idea of considerable plasticity of plant genomes. It suggests that production of new polyploid species often is accompanied by extensive genomic modifications in a short period of time and that polyploid speciation *per se* may act as an accelerating evolutionary factor. Based on the example offered by the wheat model, rapid sequence elimination may be a mechanism promoting successful polyploid speciation events. Since several amphiploids that were produced by reciprocal crosses exhibited similar pattern of sequence elimination (unpublished data), and since we found in hexaploid wheat also CSSs and GSSs that are located on chromosome *5AL* and *5DL* (unpublished data), a possible major role for the cytoplasm in this specific elimination is ruled out. Un-

doubtedly, more studies are required to elucidate the mechanism by which nonrandom elimination of DNA sequences occurs in a short period of time.

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