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Chromosomal location of genes for Rubisco small subunit and Rubisco-binding protein in common wheat

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Summary. The genes coding for the Rubisco small subunit (SSU) and for the α-subunit of the Rubisco-binding protein were located to chromosome arms of common wheat. HindIII-digested total DNA from the hexaploid cultivar Chinese Spring and from ditelosomic and nullisomic-tetrasomic lines was probed with these two genes, whose chromosomal location was deduced from the disappearance of or from changes in the relative intensity of the relevant band(s). The Rubisco SSU pattern consisted of 14 bands, containing at least 21 different types of DNA fragments, which were allocated to two homoeologous groups: 15 to the short arm of group 2 chromosomes (4 to *2AS*, 7 to *2BS*, and 4 to *2DS*) and 6 to the long arm of group 5 chromosomes (2 on each of arms *5AL*, *5BL*, and *5DL*). The pattern of the Rubisco-binding protein consisted of three bands, each containing one type of fragment. These fragments were located to be on the short arm of group 2 chromosomes. The restriction fragment length polymorphism (RFLP) patterns of several hexaploid and tetraploid lines were highly conserved, whereas the patterns of several of their diploid progenitors were more variable. The variations found in the polyploid species were mainly confined to the B genome. The patterns of the diploids *T. monococcum* var. *urartu* and *Ae. squarrosa* were similar to those of the A and D genome, respectively, in polyploid wheats. The pattern of *T. monococcum* var. *boeoticum* was different from the patterns of the A genome, and the patterns of the diploids *Ae. speltoides*, *Ae. longissima*, and *Ae. searsii* differed from that of the B genome.

Key words: Rubisco – Wheat – Restriction fragment length polymorphism (RFLP) – Binding protein – Gene allocation to chromosomes

Introduction

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (EC 4.1.1.39) is the most abundant enzyme in nature (Ellis 1979) and is the rate-limiting factor in both photosynthesis and photorespiration (Miziorko and Lorimer 1983). In cereals, this enzyme comprises more than 50% of the total leaf-cell proteins (Kawashima and Wildman 1970; Dean and Leech 1982) and functions as the main source of amino acids for the developing grain (Simmons 1987). Since degradation of Rubisco during post-anthesis reduces the rate of CO_2 fixation, the stability and relative activity of Rubisco in photosynthesis during that period largely determine the amount of assimilated carbohydrates and, consequently, grain protein percentage (Feldman et al. 1990).

The Rubisco holoenzyme is a hexadecamere, consisting of eight large subunits (LSU) and eight small subunits (SSU) (McIntosh et al. 1980). The LSU (M_r = 53,000–55,000) is encoded by the chloroplast genome (Coen et al. 1977) and is synthesized inside the organelle (Blair and Ellis 1973). The SSU (M_r = 12,000–15,000) is encoded by the nuclear genome (Kawashima and Wildman 1972) and is synthesized on free cytoplasmic ribosomes as a larger precursor containing a transit peptide (Dobberstein et al. 1977; Highfield and Ellis 1978; Chua and Schmidt 1978). The SSU precursor is then transported into the chloroplast where it is processed to the mature form (Highfield and Ellis 1978; Chua and Schmidt 1978).

While the LSU is coded by the chloroplast genome consisting of thousands of gene copies per cell, one on each copy of a chloroplast chromosome (Bowman 1986), the SSU is encoded by a small number of nuclear genes that are arranged in one or several multigene families (Coruzzi et al. 1983; Dean et al. 1985). The copy number of the SSU genes varies among different plant species.

Hexaploid wheat carries at least ten copies of the SSU genes (Broglie et al. 1983), although there is some evidence that the gene number may be as high as 36 (Chao et al. 1989). From the relative amounts of Rubisco in leaves of different aneuploid lines of common wheat, Jellings et al. (1983) identified homoeologous group 4 chromosomes as the major site that controls the level of this enzyme. Using DNA from wheat-barley addition lines for Southern hybridization analysis, Chao et al. (1989) located the Rubisco SSU genes to chromosomes of homoeologous groups 2 and 7. The location of some of the SSU genes on the short arm of group 2 chromosomes was confirmed by the use of wheat aneuploids (Chao et al. 1989).

As part of our study on the structure and expression of genes coding for Rubisco in common wheat, we used various wheat aneuploids to determine the chromosomal location of all Rubisco SSU genes, as well as the location of genes coding for the α-subunit of the Rubisco-binding protein; the latter has been implicated in the assembly of the holoenzyme (Barraclough and Ellis 1980; Ellis and Van der Vies 1988; Roy 1989). In addition, length polymorphism of DNA fragments containing sequences of genes coding for the Rubisco SSU and for the binding protein was studied in different lines of hexaploid and tetraploid wheat, as well as in their presumed diploid progenitors.

Table 1. Lines of hexaploid and tetraploid wheats and of related diploid species used in this study

Line	Species and varietas	Ploidy level	Genomic formula
TMB01	*T. monococcum* var. *boeoticum*	2x	A
TMU01	*T. monococcum* var. *urartu*	2x	A
TE10	*Ae. searsii*	2x	S^S
TL01	*Ae. longissima*	2x	S^l
TS01	*Ae. speltoides*	2x	S
TQ08	*Ae. squarrosa* var. *strangulata*	2x	D
TTD09	*T. turgidum* var. *dicoccoides*	4x	AB
TTC01	*T. turgidum* var. *dococcum* cv Farrum	4x	AB
TTR04	*T. turgidum* var *durum* cv Inbar	4x	AB
Tetra T	Extracted tetraploid from *T. aestivum* var. *aestivum* cv Thatcher	4x	AB
TAA01	*T. aestivum* var. *aestivum* cv CS	6x	ABD
TAA66	*T. aestivum* var. *aestivum* cv Bet-Lehem	6x	ABD
TAC01	*T. aestivum* var. *compactum*	6x	ABD
TAS03	*T. aestivum* var. *spelta*	6x	ABD

Materials and methods

The following plant materials were used: the standard laboratory hexaploid wheat cultivar Chinese Spring (CS) (2n = 6x = 42); nullisomic-tetrasomic (NT) lines of CS, each lacking a given pair of chromosomes and carrying an extra pair of one of their homoeologues; and ditelosomic (DT) lines of CS, each deficient for one chromosome arm. In addition, three hexaploid, four tetraploid, and six diploid lines (Table 1) were also used. All lines are maintained in our laboratory.

Total DNA from these lines was extracted from 2 g of plant leaves, as described by Dellaporta et al. (1983), using several modifications: after the first isopropanol precipitation, the DNA pellet was resuspended in 2 ml of 50 m*M* TRIS plus 10 m*M* EDTA, treated with 0.01 mg/ml RNase A at 37 °C for 30 min, and then ethanol-precipitated. The extracted DNA was digested with a restriction enzyme (HindIII), separated by electrophoresis (1.75 v/cm for 20–24 h) on 0.8% agarose TRIS-acetate gels (Maniatis et al. 1982), and then transferred to Gene-Screen plus filter (DUPONT) according to the Gene-Screen plus protocol. Radioactive labeling of DNA probes was performed by random primer kit (Prime-a Gene labeling system Promega), according to the protocol provided by the supplier. The Gene-Screen plus filters were prehybridized for 6 h in 5 × SSPE (1 × SSPE = 0.18 *M* NaCl, 10 m*M* NaH_2PO_4, 1 m*M* EDTA, pH 7.4), 5 × Denhardt's (1 × Denhardt's = 0.2 g/l of Ficoll, polyvinylpyrrolidone, bovine serum albumin) and 1% SDS, and then hybridized for 16–24 h in the same solution containing the DNA probe. Filters were washed once in 2 × SSC (1 × SSC = 0.15 *M* NaCl, 0.015 *M* Na_3 citrate, pH 7.0) and 1% SDS for 10 min at room temperature (ca. 25 °C), and then twice in 0.1 × SSC, 1% SDS at 55–65 °C. The filters were then exposed to Kodak filter (XAR-5) for 1–7 days.

Two common wheat cDNA clones were used as probes in this study. (1) pTS512 (Smith et al. 1983), kindly provided by Dr. Jim Speirs, CSIRO, was used as a probe for the Rubisco SSU genes. This clone contains the coding sequence for the mautre protein (without the 14 first codons) and lacks the coding sequence for the transit peptide. (2) The 300-bp XhoI-EcoRI fragment of pSV10 (Hemmingsen et al. 1988), kindly obtained from Prof. R. J. Ellis, was used to probe the α-subunit of the Rubisco-binding protein.

Bands were assigned to specific chromosomes or to chromosome arms, either by their disappearance or by their relative intensity: a decrease in intensity of a given band relative to that of the other bands in the same lane appeared in lines deficient for the relevant chromosome or chromosome arm; a similar increase in the relative intensity of a band signified lines carrying extra doses of that chromosome.

Results

Allocation of the Rubisco SSU genes

In order to locate the wheat Rubisco SSU genes to chromosomes, HindIII-digested total DNA from CS and from all available ditelosomic lines of the D genome (DT7AL substituting for the unavailable DT7DL) was used for Southern hybridization analysis and probed

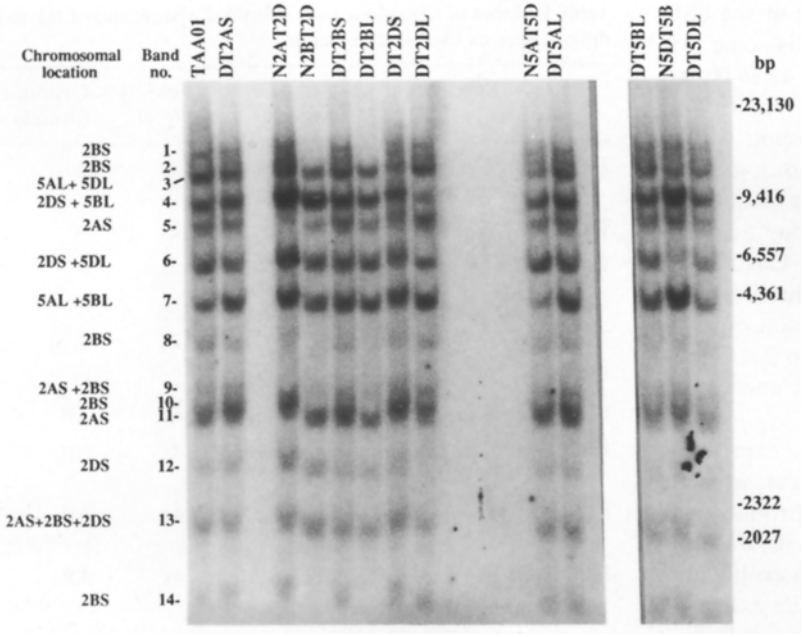

Fig. 1. Autoradiogram from Southern hybridization of HindIII-digested DNA from hexaploid wheat cv CS and aneuploid lines for groups 2 and 5 chromosomes hybridized with wheat Rubisco SSU probe. Band number and the deduced chromosomal location of each band is indicated on the *left*; molecular weight marker (λDNA HindIII digest) is on the *right*

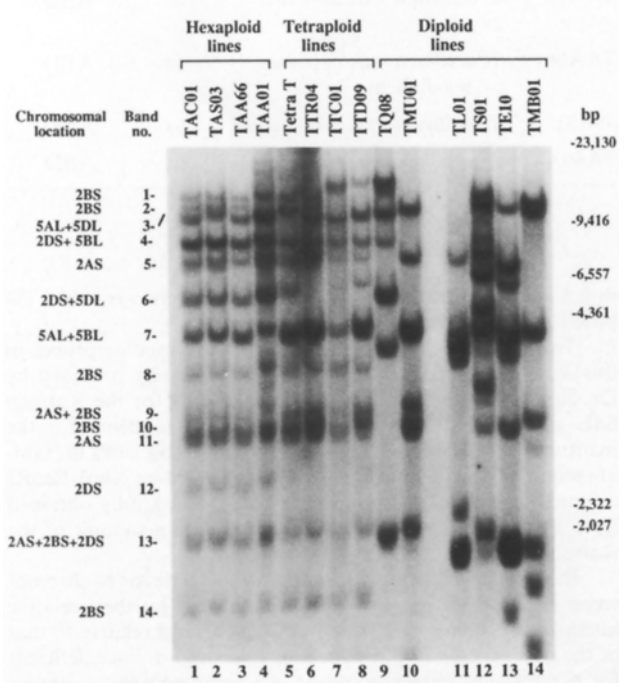

Fig. 2. Autoradiogram from Southern hybridization of HindIII-digested DNA from lines of hexaploid (*lanes 1–4*) and tetraploid (*lanes 5–8*) wheats and from their diploid progenitors (*lanes 9–14*), hybridized with wheat Rubisco SSU probe. Band number and the deduced chromosomal location of each band is indicated on the *left*; molecular weight marker (λDNA HindIII digest) is on the *right*

with the Rubisco SSU gene. Since only ditelosomic lines of homoeologous groups 2 and 5 differed in their patterns from CS (data not shown), further studies with aneuploids of the A and B genomes were confined to these homoeologous groups. The Southern hybridization patterns of CS and of aneuploids of group 2 and group 5 chromosomes are shown in Fig. 1. The pattern of CS consisted of 14 bands. Of these, 8 bands (nos. 1, 2, 5, 8, 10, 11, 12, and 14) were allocated to single chromosome arms, 5 bands (nos. 3, 4, 6, 7, and 9), each containing two types of fragments, were allocated to two different chromosome arms, and 1 band (no. 13), containing three types of fragments, was allocated to three different chromosome arms (Table 2). Thus, altogether 21 DNA fragments were found to hybridize with the SSU probe. Out of these, 15 were located on the short arm of group 2 chromosomes (4 on *2AS*, 7 on *2BS*, and 4 on *2DS*) and 6 on the long arm of group 5 chromosomes (2 on *5AL*, 2 on *5BL*, and 2 on *5DL*).

The restriction fragment length polymorphism (RFLP) pattern of genes coding for the Rubisco SSU was also analyzed in different lines of hexaploid and tetraploid wheats and in their diploid progenitors (Fig. 2). The four tested hexaploid lines (lanes 1–4) showed identical patterns. The patterns of the tetraploid lines (lanes 5–8) were also highly conserved, resembling that of the hexaploids, with the following exceptions: the expected lack of bands controlled by the D genome; the absence of bands 1 and 2 in lines TTD09 and TTC01 of *Triticum* varieties *dicoccoides* and *dicoccum;* and the presence of an additional band in lines TTD09 and TTC01 (between bands 5 and 6 of CS), which was absent in the tetraploid line TTR04 and in the hexaploid lines. The diploids were more variable. The band pattern of *T. monococcum* var. *urartu* (lane 10) was similar to that of the A genome of the tetraploid and hexaploid wheats, while the pattern of *T. monococcum* var. *boeoticum* (lane 14) was different. The pattern of line TQ08 of *Ae. squarrosa* (lane 9) was

Table 2. The chromosomal location of Rubisco SSU genes as deduced from the disappearance or differential intensity of restriction fragments hybridized with the SSU probe in nullisomic-tetrasomic (NT) and ditelosomic (DT) lines of the common wheat cultivar Chinese Spring

Band no.[a]	Lines with missing bands	Lines with reduced bands intensity	Lines with increased bands intensity	Chromosomal location
1	N2BT2D DT2BL			*2BS*
2	N2BT2D DT2BL			*2BS*
3		N5AT5D[b] N5DT5B		*5AL*[c]+*5DL*[c]
4		DT2DL	N2AT2D N2BT2D N5DT5B	*2DS*+*5BL*[c]
5	N2AT2D		N2DT2A[e]	*2AS*[d]
6		DT2DL N5DT5B	N2AT2D N2BT2D N5AT5D	*2DS*+*5DL*[c]
7		N5AT5D	N5DT5B	*5AL*[c]+*5BL*[c]
8	N2BT2D DT2BL			*2BS*
9		N2AT2D N2BT2D DT2BL		*2AS*[d]+*2BS*
10	N2BT2D DT2BL			*2BS*
11	N2AT2D			*2AS*[d]
12	DT2DL		N2BT2D	*2DS*
13		N2AT2D[f] N2BT2D DT2BL DT2DL		*2AS*[d]+*2BS*+*2DS*
14	N2BT2D DT2BL			*2BS*

[a] Band number is according to Fig. 1

[b] The contribution of *5A* to the intensity of band 3 was larger than that of *5D*

[c] DT5AL did not exhibit differential intensity in bands 3 and 7; neither did DT5BL in bands 4 and 7, nor DT5DL in bands 3 and 6. It was deduced, therefore, that the fragments of all these bands were located on the long arm of these chromosomes

[d] Since DT2AS showed bands 5 and 11 and did not exhibit differential intensity in bands 9 and 13, it was deduced that the fragments of these bands were located on the short arm of this chromosome

[e] Data not shown

[f] Band 13 consisted of three types of fragments that were allocated to *2AS*, *2BS*, and *2DS*. Therefore, the relative intensity of this band in N2AT2D and in N2BT2D was similar to that of CS

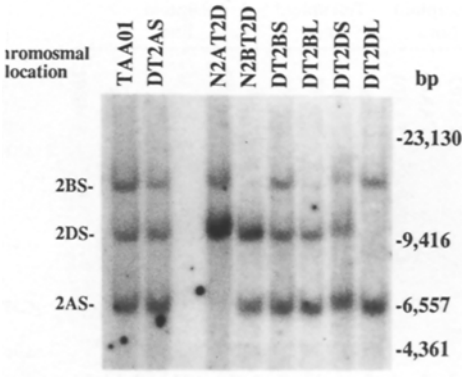

Fig. 3. Same as Fig. 1, hybridized with 300-bp XhoI-EcoRI fragment of the α-subunit of Rubisco-binding protein

only somewhat different from that of the D genome of hexaploid wheat. The patterns of *Ae. longissima*, *Ae. speltoides*, and *Ae. searsii* (lanes 11, 12, and 13, respectively) were different from that of the B genome of polyploid wheat.

Allocation of the genes coding for the α-subunit of Rubisco-binding protein

It has been suggested that the assembly of Rubisco holoenzyme from its monomers is mediated by a molecular chaperone, the so-called Rubisco-binding protein (Barraclough and Ellis 1980; Ellis and Van der Vies 1988; Roy 1989). This protein, which is not part of the Rubisco holoenzyme, consists of two nuclear encoded subunits (α and β) of 61 and 60 kDa, respectively (Musgrove et al. 1987). Figure 3 demonstrates the Southern hybridization pattern of CS and several aneuploid lines for group 2 chromosomes, following digestion with HindIII and hybridization with the α-subunit probe. Three DNA fragments hybridized with this probe. These fragments were located on the short arms of group 2 chromosomes *2AS*, *2BS*, and *2DS*.

The RFLP of the genes coding for the α-subunit of Rubisco-binding protein was also studied in several hexaploid and tetraploid lines and in their diploid progenitors (Fig. 4). In the hexaploid lines, bands of the A and D genomes were highly conserved. However, the uppermost band, located to the B genome, was found as a doublet in all hexaploids except CS (singlet). The tetraploid lines were much more conserved, showing the CS pattern but lacking the middle fragment that was located on the D genome. In all tetraploids, except for tetra T, the band corresponding to the A genome (the lowest one) appeared at a lower intensity than in the hexaploids. The diploids differed from one another but, as in the case of Rubisco, the pattern of *T. monococcum* var. *urartu* was similar to that of the A genome and the pattern of *Ae. squarrosa* was similar to that of the D

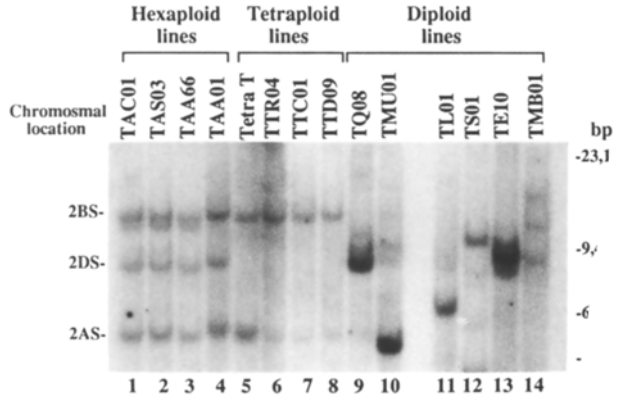

Fig. 4. Same as Fig. 2, hybridized with 300-bp XhoI-EcoRI fragment of the α-subunit of Rubisco-binding protein

genome. The pattern of *T. monococcum* var. *boeoticum* was different from that of the A genome. The band patterns of *Ae. speltoides, Ae. longissima,* and *Ae. searsii* differed from one another as well as from that of the B genome.

Discussion

The Rubisco SSU probe used in this study hybridized with 14 different bands of HindIII-digested total DNA of common wheat (cv CS). A similar number of bands was found when the same probe hybridized with CS DNA digested either with DraI (15 bands) or Eco RI (12 bands) (data not shown), neither of which cut within the coding region. The size of the bands obtained with HindIII ranged approximately from 1.5 to 23.0 kb. The smallest band is large enough to contain the entire SSU gene, which agrees with the fact that HindIII, too, does not cut within the coding sequence for the mature SSU, nor is it interrupted by an intron, which may contain such a site. We therefore assume that each band consists of at least one copy of the sequence that codes for the mature Rubisco SSU.

Using wheat aneuploid lines, we identified the chromosomal location of the DNA fragments of each band. Out of the 14 bands, 8 contained only one type of fragment and, consequently, each of them was located on a single chromosome arm. Of the remaining 6 bands, 5 contained two types of fragments, each assigned to a different chromosome arm, and 1 contained three types of fragments, each assigned to a different chromosome arm. Altogether, 21 different fragments were revealed and located on two groups of chromosomes: the short arm of chromosomes of homoeologous group 2 (*2AS, 2BS,* and *2DS*), and the long arm of chromosomes of homoeologous group 5 (*5AL, 5BL,* and *5AL*).

Our data confirm the finding of Chao et al. (1989) for the location of Rubisco SSU genes on the short arm of group 2 chromosomes, and provide evidence for the existence of another cluster of genes on the long arm of chromosomes of group 5. All the DNA fragments located on group 5 were found in bands that contained two types of fragments. Therefore, the location of these fragments could be deduced only from changes in the relative intensity of bands in aneuploids that were either deficient or had an extra dose of the critical chromosome arm.

Using wheat-barley addition lines, Chao et al. (1989) found that the barley chromosome which is homoeologous to wheat group 7 carries Rubisco SSU genes. However, confirmation of these findings by the use of wheat aneuploids, as was done for group 2, was not reported. We also did not find evidence for the presence of Rubisco SSU genes on chromosomes of group 7. Taking into consideration the involvement of group 4 chromosomes with the total amount of Rubisco (Jellings et al. 1983), we propose that these chromosomes carry regulating genes rather than SSU structural genes.

Thus, the Rubisco SSU genes of common wheat are arranged in each genome in at least two clusters: a large one on the short arm of the chromosomes of group 2 (*rbcs-2A, rbcs-2B,* and *rbcs-2D*) and a smaller cluster on the long arm of the chromosomes of group 5 (*rbcs-5A, rbcs-5B,* and *rbcs-5D*).

Using the clone PW9 to probe total common wheat (cv CS) DNA digested with HindIII, Chao et al. (1989) found about 33–36 fragments (genes) or 11–12 per genome. Our probing with pTS512 revealed only 21 fragments. This discrepancy can be explained by the fact that the PW9 probe contains sequences for both the mature SSU and the transit peptide (Broglie et al. 1983), while pTS512 contains only the sequence for the mature SSU (Smith et al. 1983). Hence, PW9 can also hybridize to fragments that lack the coding DNA sequence for the mature SSU but contain the sequence for the transit peptide. Actually, since the intron, located between the coding sequence for the mature SSU and the sequence for the transit peptide, contains a HindIII site (Broglie et al. 1983), digestion within this site would form two fragments and thus confuse the results. The smaller number of probed fragments in our work, i.e., 21, indicates that this is the minimal number of the SSU genes in common wheat.

The three genomes contain different number of fragments: nine on the B genome and six on each of the A and D genomes. This reflects the higher number of genes on chromosome arm *2BS,* whereas the group 5 cluster contains two genes in each genome.

While the Rubisco SSU genes were allocated to two chromosome arms on each of the three genomes, the genes coding for the α-subunit of the Rubisco-binding protein were allocated to a single chromosome arm per

genome. These genes are located on the short arm of group 2 chromosomes (*2AS*, *2BS*, and *2DS*). The finding that the same chromosome arm carries genes both for the binding protein and for the Rubisco SSU may have some significance for the coordinated expression of these genes.

Examining the RFLP patterns for Rubisco SSU genes and for the Rubisco-binding protein genes in the different species revealed a higher degree of conservation among the hexaploids and the tetraploids, as well as between those two groups, than among the diploids (Figs. 2 and 4). A similar pattern of conservation was shown for phosphoribulokinase (Chao et al. 1989). The variation found in this work between the hexaploids and the tetraploids was mainly in fragments of the B genome. Unlike *T. monococcum* var. *boeoticum*, the pattern of *T. monococcum* var. *urartu* was identical to that of the A genome, confirming data from other studies (Nishikawa 1983; Dvorak 1988) that the A genome was derived from this variety and not from *T. monococcum* var. *boeoticum*. The pattern of *T. monococcum* var. *urartu* confirms the number of Rubisco SSU genes of the A genome of hexaploid wheat and their chromosomal location. The Rubisco SSU pattern of line TQ08 of *Ae. squarrosa* was similar but not identical to that of the D genome of hexaploid wheat, while the patterns of the Rubisco-binding protein in this diploid and in the D genome of the hexaploids were identical. The pattern of the B genome was different from that of the S genome diploids, *Ae. speltoides*, *Ae. longissima*, and *Ae. searsii*.

Further analysis of the Rubisco SSU genes, using more specific probes, may shed more light on the chromosomal location as well as on the evolutionary relationship of these genes.

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