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The ribosomal RNA genes in synthetic tetraploids of wheat

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Summary. The ribosomal RNA genes in the A genome of tetraploid (AABB) wheats are either absent or present at low levels. In four synthetic AABB tetraploids tested by in situ hybridization with a radioactive probe, the level of radioactive label at A and B NOR's corresponded to those of the parent species. There was no reduction after ten generations. In addition, the A chromosome rDNA is transcriptively active, the numbers of nucleoli being governed by the number of rRNA gene repeats in the smaller of the two A-genome NOR's. Since the wild tetraploid *Triticum dicoccoides*, as well as its domesticated derivatives, lack A-genome NOR's, their deletion is likely to have occurred prior to domestication, i.e. more than 10,000 years ago.

Key words: Wheat – Ribosomal RNA genes – Synthetic tetraploids – Evolution – Nucleolar activity

Introduction

In the polyploid wheat series there is a marked variation in the number of rRNA genes on A genome chromosomes. Diploid wheats, with genome designation AA, have rRNA genes on two chromosomes, 1A and 5A (Miller et al. 1983). Many hexaploid wheats have major sites of rRNA genes on two B genome chromosomes, 1B and 6B, and a minor site on chromosome 5D (Flavell and Smith 1974a; Flavell and O'Dell 1976). Chromosome 1A of some hexaploid wheats may have rRNA genes (Crosby 1957; Flavell and Smith 1974b; Miller et al. 1980), but in general the A genome of hexaploids does not have detectable numbers of rRNA genes. Tetraploid wheats, with genome designation AABB, can be considered as intermediates between the AA diploids and the AABBDD hexaploids. In a sample of tetraploids only two chromosomes had detectable rRNA genes (Hutchinson and Miller 1982). A small additional site is seen in the tetraploid *T. carthlicum* but this is likely to have been a secondary acquisition of rRNA genes from an introgression from *T. aestivum*, analogous to that presumed for the *Q* complex from the same source (Morris and Sears 1967).

We have attempted to gain some insight into the loss of rRNA genes from the A genome in the polyploid wheats. Recently deletion of rRNA genes from one rye chromosomal site has been reported by Brettell et al. (1986) in hybrids between wheat and rye. In this particular hybrid the rye rRNA genes are not active and any event which leads to reduction in number of rRNA genes would presumably not be selected against. We have asked whether the same situation holds for the polyploid wheats. When the A genome and B genome species intercross to form the tetraploid, are the A genome ribosomal DNA sites inactive, allowing for successive losses of the repeats on these chromosomes, or must we postulate there are other reasons for selective decrease of the ribosomal genes on the A chromosomes?

We have examined synthetic tetraploids to determine whether the A genome rDNA sites are suppressed. This is not the case and in synthetic tetraploids which have been raised for ten generations we find no evidence of change in the relative numbers of repeats in the two A genome sites and the two B genome sites. We have also found significant variation in repeat numbers in different accessions of one A genome species and conclude that this may be important in the apparent reduction of the A-genome rDNA sites in polyploids. The A genome parent of the polyploid wheats may initially have had low numbers of rRNA gene

repeats and not contributed significantly to the total rRNA gene repeat numbers.

Materials and methods

Location of the rDNA sites of tetraploids on B-genome chromosomes

Fourteen lines of four tetraploid subspecies (*T. dicoccoides, T. dicoccum, T. turgidum, T. carthlicum*) were examined using either in situ hybridization or N-banding (Table 1).

Three lines were investigated using in situ hybridization. Root-tip metaphase cells were examined after immersion of root tips in ice slurry for 20–26 h. In situ hybridization followed procedures described by Appels et al. (1978). As a probe we have used a highly repeated sequence DNA (the Ag^+ satellite) which can be isolated from wheat, barley or Drosophila. It can be used to identify each of the chromosomes of the B genome (Gerlach et al. 1979). We have also used the Ag^+ satellite probe 31, cRNA 1.705, from Drosophila which identifies the same sites as the wheat probe (Appels et al. 1978). Appels et al. (1980) had shown the sites of rDNA to be adjacent to the secondary constrictions, and since secondary constrictions frequently are obliterated by the hybridization procedure, the satellited chromosomes were identified prior to hybridization. The four satellite chromosomes were identified as the pairs of 1B and 6B in root-tip cells of each of the three genotypes.

The remaining 11 genotypes (Table 1) were tested by N-banding, using the technique of Gerlach (1977) and its modification by Endo and Gill (1984). Satellited chromosomes were noted prior to treatment.

Diploid parents and synthetic tetraploids

There is general consensus that the A genome is derived from *T. boeoticum*, the wild ancestor of *T. monococcum*. Both these closely related species are the A-genome parents of the synthetic tetraploids we have used in our experiments.

One or more members of the *Sitopsis* group of *Aegilops* are most likely to have been involved as B-genome ancestors (Sears 1975). Accordingly, three species of the *Sitopsis* group, *Ae. speltoides, Ae. longissima,* and *Ae. sharonensis,* were used as B-genome parents for the synthetic tetraploids.

T. urartu, a wild diploid wheat which is sympatric with and closely related to *T. boeoticum,* has been proposed as an alternative source of the B genome (Johnson 1975; Johnson and Dhaliwal 1978; Dhaliwal and Johnson 1982). It was used to form a synthetic tetraploid with *T. boeoticum.*

A number of synthetic tetraploids were kindly made available by Drs. G. Waines and B. L. Johnson, University of California, Riverside (UCR), and Dr. T. E. Miller, Plant Breeding Institute, Cambridge (PBI) (Table 2). The material received from Riverside included representatives of the parent species, but not the parent lines used in the crosses. The Cambridge material included the actual parents. All synthetic tetraploids had been grown about 10 times since the original cross.

In situ hybridization of rDNA

In situ hybridization followed procedures described by Appels et al. (1978), using the ^{3}H-labelled cDNA probe prepared by nick translation of the plasmid pTA250 (Gerlach and Bedbrook 1979).

Nucleolus staining

The silver staining method of nucleoli followed von Kalm and Smyth (1980).

Table 1. Tetraploid wheats used for identification of satellite chromosomes. (1) Australian winter cereal collection; (2) Drs. Waines and Johnson, University of California, Riverside; IS: in situ hybridization; NB: N-banding

Code	Orig. name, no.	Source of supply	Orig. source, origin	B-genome chromosome identification
T. dicoccoides				
TP1	G278	(1) AUS19785	Volcani Centre, Israel	NB
TP3	9-15	(1) AUS20303	Feldman, Missouri	NB
TP5	6252	(1) AUS17903	Hebrew Univ, Jerusalem	IS
TP9	G2126	(2)	Karakadaj, Turkey	NB
TP10	G3034	(2)	Rosh Pinna, Israel	NB
TP15	–	(1) AUS17980	Vavilov Inst, Leningrad	NB
TP16	G25	(1) AUS17480	Israel	NB
T. dicoccum				
TP4	VIR19091	(1) AUS17968	Vavilov Inst	NB
TP8	Blue Heron	(1) AUS1969		IS
TP17	Bari 7493	(1) AUS18303	Ethiopia	NB
T. turgidum				
TP2	Durati	(1) AUS20577		IS
T. carthlicum				
C3	var. rubiginosum	(1) AUS3838		NB
C4	Persian Black	(1) AUS3158		NB
C6	K32510	(1) AUS17644	Vavilov Inst	NB

Results

Ribosomal DNA sites confirmed on B-genome chromosomes

Our first objective was to establish whether the rRNA genes in normal tetraploid wheats were located on chromosomes of the B genome. The 14 tetraploids (see Table 1) including 7 lines of *T. dicoccoides,* 3 of *T. dicoccum,* 3 of *T. carthlicum* and 1 of *T. durum,* are widely representative of tetraploids with an AABB genomic constitution.

Satellited chromosomes were noted prior to treatment, and 1B and 6B identified by in situ hybridization and N-banding, respectively. Secondary constrictions of 6B were invariably seen, but in some lines those of 1B were small or, as in line TPI, seldom discernible. With this one exception it was clear that the two major rDNA sites are situated on 1B and 6B across the range of tetraploid wheats.

Synthetic tetraploids

Our survey included the synthetics ST3, ST4, ST6 and ST1, *T. boeoticum* and *T. monococcum* as the A-genome parents, and three *Sitopsis* species and *T. urartu* as putative "B"-genome parents (Table 2). Although the *Sitopsis* genome is designated S, we are using the symbol B because of the putative connection as B-genome donor.

A-genome parents. 1A and 5A chromosomes (see "Materials and methods") cannot be distinguished morphologically, but in all our observations one pair was more heavily radioactively labelled than the other. We have designated the heavily labelled site A^1 and the lightly labelled one A^2. The rDNA sites in these species are near-terminal, and since nucleolar constrictions are not discernible, the radioactive label was invariably terminal (Fig. 1 a).

B. genome parents. Ae. speltoides has marked constrictions in both pairs of nucleolar organizer chromosomes, and satellite 1B is only slightly smaller than 6B. In *Ae. longissima* the 1B satellite is very small, yet the constriction is distinct. The radioactivity after in situ hybridization appears terminal (Fig. 1 b), as it does in *Ae. sharonensis* where the 1B satellite is even smaller. Unless the 1B chromosome is identified prior to hybridization it may be indistinguishable from the A chromosomes after hybridization. In these three species the labelling of 6B is less than that of 1B.

That *T. urartu* could be the B-genome parent, as suggested by Johnson (1975), was first disputed on

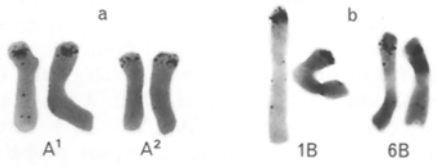

Fig. 1 a, b. Nucleolar organizer chromosomes of diploid species, **a** A-genome, *T. boeoticum;* **b** B-genome, *Ae. longissima;* both showing radioactive label at NOR regions after in situ hybridization

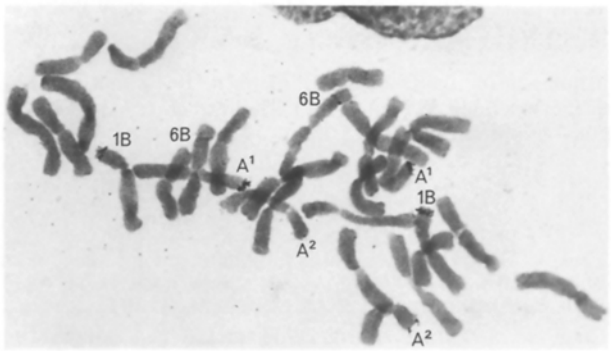

Fig. 2. Mitotic metaphase of synthetic tetraploid ST4 (*T. boeoticum-Ae. longissima*) showing radioactive label at NOR regions on A and B genome nucleolar organizer chromosomes, after in situ hybridization

Table 2. Synthetic tetraploids and parent species. 1: University of California, Riverside, USA; 2: Plant Breeding Institute, Cambridge, UK; 3: origin unknown

Class	Code	Line	Origin	Source
Synthetic 4×	ST3	*Ae. speltoides* (G366) – *T. monococcum* (G496)		1
	ST4	*T. boeoticum* (G640) – *Ae. longissima* (G945)		1
	ST6	*T. boeoticum* (G982) – *Ae. sharonensis* (G614)		1
	ST1	*T. boeoticum* (G2587) – *T. urartu* (G1734)		1
2× species	PA1	*T. boeoticum* (G1854)	Kiziltepe, Turkey	1
	PA2	*T. urartu* (G1868)	Kiziltepe, Turkey	1
	PA4	*T. monococcum* (G2927)	Turkey, cultivated	1
	PA5	*Ae. sharonensis* (G946)	Kyoto University	1
	PA7	*Ae. speltoides* (typica) (G1062)	Urfa, Turkey	1
	PA8	*T. monococcum* (G3373)	Germany, cultivated	1
	PA12	*Ae. longissima* (G609)	Gilat, Israel	1
Synthetic 4×	ST7	(PA13) *Ae. speltoides* (A) (3) × (PA14) *T. monococcum* (TA396) (3)		2

cytological grounds by Chapman et al. (1976). In situ hybridization identified four terminal NOR's.

Synthetic tetraploids. ST4 (*T. boeoticum-Ae. longissima*) is an example of the *Sitopsis* hybrids (Fig. 2). The levels of radioactive label of both A and B nucleolar chromosomes corresponded to those of the parental species. The A genome rRNA genes appeared unchanged by the association with the B genome. Indeed, in ST_4, A^1 is more strongly labelled than 6B. A^2 is invariably less labelled than A^1, although there are clear differences between the synthetic tetraploids (and also their parental diploids). The rDNA level of A^2, being the lowest, serves as a useful indicator. According to A^2 levels, the three *Sitopsis* synthetic tetraploids form two groups:

$$ST3 \sim ST6 < ST4$$

These differences could be due to the numbers of rRNA genes in their individual (unknown) A-genome parents. This was supported in an experiment reported in the next section. Over the four NOR's of the three synthetic tetraploids the average relative level of label was:

$$1B > 6B \sim A^1 > A^2$$

ST1, the *T. boeoticum-T. urartu* combination, had eight terminal sites; all were strongly labelled. This result is consistent with *T. urartu* having an A genome.

This series of experiments has shown that the parental A genome rDNA (rA) persists in newly synthesized tetraploid wheats.

Ribosomal DNA levels in the A genome of a synthetic tetraploid and its diploid parent strains

In all four synthetic tetraploids described above the A-genome rDNA sites were labelled but they did vary in rDNA levels. It is clear that comparisons with the parental strains used in the production of synthetic tetraploids is necessary to provide information on the dynamics of the A genome rRNA genes. Moreover, the low levels of radioactive label, due to the short exposure times used in the first experiment (14–31 days) did not facilitate accurate comparisons.

In a second experiment restricted to a single synthetic tetraploid, the parental strains were available and exposure times were doubled. The synthetic tetraploid, ST7, and its parents, PA13 (*Ae. speltoides*) and PA14 (*T. monococcum*) were provided by T. Miller, Plant Breeding Institute, Cambridge (Table 2). ST7 had the same parent species as ST3 (see above), though in all probability from different sources. The autoradiographic exposure time in this experiment was 44 days, almost twice that used in the initial experiment. The rDNA of the B chromosomes (rB) is more heavily labelled in ST7 than in ST3, consistent with the already mentioned difference in exposure times. However, the rA label of ST7 is on a level with that of ST3 and thus, by comparison with rB, substantially weaker. The comparative levels are shown in Table 3, rows 1 and 2. A^1 was readily identified by its stronger label, while the A^2 label was so weak that in half the observed cells either one or both A^2 sites had no label at all.

A critical test was provided by combined hybridization of the synthetic ST7 and its parents, PA13 and PA14, applied to slides in pairwise combinations. The rDNA levels in A^1 and A^2 of ST7 corresponded to those of the A parent, PA14. A^1 is always well labelled, at about the level of 6B; the A^2 label is weak or absent (Fig. 3a). The comparative levels of the four NOR's are clearly seen when the two parents are combined on the same slide (Figs. 3b, c). The A^2 label in Figs. 3a, b is low by comparison with A^1.

In independent tests two other lines of *T. monococcum*, PA4 and PA8 (Table 2), appeared to have substantially larger numbers of rRNA genes than PA14, the A-genome parent of ST7. This was examined by combined in situ hybridization of PA8 and PA14, using the B parent, PA13, as comparative standard. While A^1 levels appear similar, it is clear that the A^2 label of PA14 is distinctly less than that of PA8 (Figs. 3b, d).

These results show (a) that the DNA of the A chromosomes has not noticeably declined in this synthetic tetraploid and (b) that there are marked differences in the rDNA's of different strains of *T. monococcum*.

Nucleolus organizing activity in synthetic tetraploids

The question has to be asked whether the A-genome rRNA genes are transcriptionally active in the synthetic tetraploids. A positive answer would be indicated by the formation of A chromosome nucleoli and this can be determined from the frequency of nucleoli in synthetics by comparison with normal tetraploids.

Nucleoli tend to merge early in interphase, so that accurate counts can be obtained only in telophase or

Table 3. Levels of radioactive label in synthetic tetraploids and in diploids; 5 strong, 1 weak label. Exposure time of line ST3 was half that of other lines (44 days)

	Line	Level of radioactivity			
		1B	6B	A^1	A^2
ST3	(*Ae. speltoides–T. monococcum*)	3	2	2	1–0
ST7	(*Ae. speltoides–T. monococcum*)	5	3	2	1–0
PA13	(*Ae. speltoides* parent of ST7)	5–4	3	–	–
PA14	(*T. monococcum* parent of ST7)	–	–	2–1	1
PA8	(unrelated *T. monococcum*)	–	–	4	3

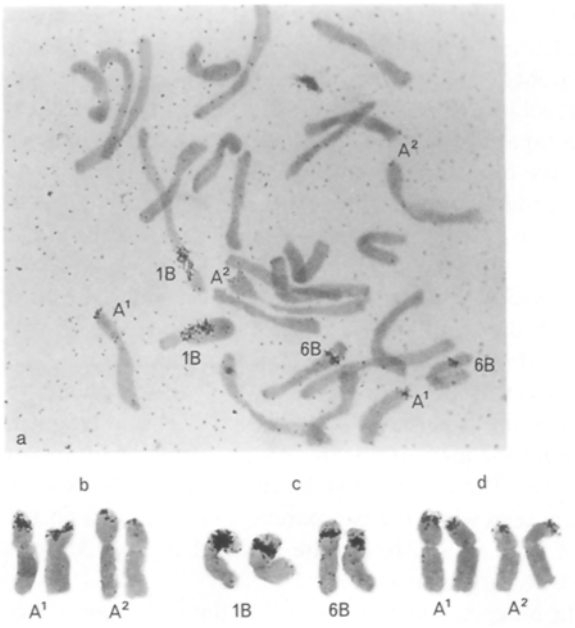

Fig. 3. **a** Mitotic metaphase of synthetic tetraploid ST7 (*Ae. speltoides-T. monococcum*) with labelled NOR regions of A and B nucleolar organizer chromosomes, the designation of A^2 to be accepted with caution because of its low level, **b** nucleolar chromosomes of A-genome parent strain *T. monococcum*, **c** B genome parent strain (*Ae. speltoides*) and **d** an unrelated strain of *T. monococcum* showing differences in the number of rDNA genes in the A^2 chromosomes of two strains of *T. monococcum* (**b, d**). All examined in multiple-strain in situ hybridization

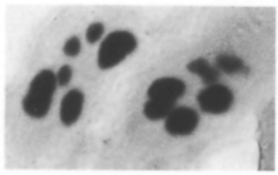

Fig. 4. Nucleoli in two late telophase cells of synthetic tetraploid, ST4 (*T. boeoticum-Ae. longissima*), showing nucleoli of both diploid parent species in each cell

soon thereafter (Fig. 4). In normal tetraploids there should be four nucleoli/cell arising from the two pairs of B-genome NOR's; additional nucleoli can be assumed to have arisen from A-genome NOR's. Therefore we determined the frequency of newly divided cells with more than four nucleoli in four synthetic tetraploids, with the cultivar 'Pentad' (*T. turgidum*) for comparison (Table 4).

All four synthetic tetraploids had some cells with more than four nucleoli and, correspondingly, fewer single nucleoli than the normal tetraploid. They fell into two distinct groups: ST7 ~ ST3 < ST4 ~ ST1 (Table 4). This corresponds with the levels of label of chromosome A^2. As we have seen, the number of rRNA genes in chromosome A^2 of ST7 is so low that in half the cells surveyed one or both A^2 chromosomes fail to

Table 4. Frequencies of nucleoli per cell in a tetraploid cultivar, Pentad (PE), and synthetic tetraploids

Line	No. of nucleoli					Probability level of significance	
	>4	4	3	2	1		
PE	–	6	29	42	23	0.05 level	0.01 level
ST7	4	9	36	35	16		
ST3	4	17	36	35	8		
ST4	13	22	31	26	8	0.10 level	
ST1	25	23	23	24	5		

have detectable label. By way of contrast, all observed cells of ST4 have well labelled A^2 rDNA. This evidence suggests a threshold of gene copies for the formation of a nucleolus, and that when the number is marginal, as it appears to be in A^2 of ST7, nucleoli may fail to form or are too small to be identified or merge too rapidly to be observed.

We conclude (a) that the rRNA genes in the A-genome chromosomes of the syntetic tetraploids are transcriptively active and (b) that there is correspondence between the number of rRNA genes in weakly labelled A chromosomes and the number of nucleoli observed in A-B genome synthetic tetraploids.

Discussion

The objective of this study was to shed some light on the process which led to the elimination or inactivation of the rRNA genes in the A genome of tetraploids. The first interaction of A and B genomes must have occurred in the amphiploid crosses that were to evolve into tetraploid species. We have attempted to study this early stage in the evolution of the tetraploid wheats using synthetic tetraploids derived from known A and putative B diploid parent species. The evidence we have obtained leads to the following conclusions:

1) In each of the four synthetic tetraploid combinations, rDNA sites have been positively identified on two chromosomes of the A genome, corresponding with the parental species in position and level of labelling.

2) There is no apparent diminution of the rDNA sites after approximately ten generations.

3) Of the two A chromosome rDNA sites, one consistently has less label than the other; in ST7 and its *T. monococcum* parent it is frequently without label. Such low levels are not characteristic of *T. monococcum* as a whole, since another (unrelated) line has strong label. Rather, it is indicative of considerable variation in the rDNA levels of *T. monococcum* strains.

4) The A-genome chromosome rDNA is transcriptively active, the number of nucleoli reflecting the rDNA level in the least-labelled chromosome, A^2.

These results have shown no detectable changes in numbers of copies of the rRNA genes in either the A or B genomes nor is there evidence of suppression of activity of the NOR's in either genome. Diminution of A-genome rDNA sites in the tetraploids is likely to have been a slow process if it occurred at all. There are examples of diminution of NOR's in the literature, especially where a NOR is not transcriptionally active (Brettell et al. 1986). An increase in NOR repeat numbers to a needed level has been well documented in *Drosophila* (Ritossa 1976). Our finding that there is considerable variation in the copy numbers of ribosomal genes in an A-genome species suggests that the lack of A-genome NOR's in polyploid wheats may be due to a participation of low NOR A-genome parents in the original hybrids. This may have been a preferred situation with regard to survival of the various amphiploids which were formed. Also, if the A genome was contributing relatively few of the total copies then successive accidental diminutions may have been readily tolerated. Low numbers of A-genome rDNA repeats could be due to loss or to the involvement of A-genome parents with low rDNA copy numbers.

Finally, what is the evidence on the timing of the deletion of A-genome NOR's? From this study of synthetic tetraploids we know that it is not an immediate consequence of hybridization, nor is it a short-term phenomenon. From the absence of A-genome NOR's in the tetraploid wild ancestor as well as in the domesticated species it seems plausible that their deletion predates domestication which the evolutionary history of wheat places some 10,000 years ago.

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