Theor Appl Genet (1989) 77:84–94

Heterochromatin differentiation and phylogenetic relationship of the A genomes in diploid and polyploid wheats *

X. M. Shang [1], H. T. Nguyen [1] and R. C. Jackson [2]

Departments of Plant and Soil Science [1] and Biological Sciences [2], Texas Tech University, Lubbock, TX, 79409, USA

Received May 16, 1988; Accepted July 30, 1988
Communicated by F. Mechelke

Summary. Heterochromatin differentiation, including band size, sites, and Giemsa staining intensity, was analyzed by the HKG (HCl-KOH-Giemsa) banding technique in the A genomes of 21 diploid (*Triticum urartu*, *T. boeoticum* and *T. monococcum*), 13 tetraploid (*T. araraticum*, *T. timopheevi*, *T. dicoccoides* and *T. turgidum* var. Dicoccon, Polonicum), and 7 cultivars of hexaploid (*T. aestivum*) wheats from different germplasm collections. Among wild and cultivated diploid taxa, heterochromatin was located mainly at centromeric regions, but the size and staining intensity were distinct and some accessions' genomes had interstitial and telomeric bands. Among wild and cultivated polyploid wheats, heterochromatin exhibited bifurcated differentiation. Heterochromatinization occurred in chromosomes $4A^t$ and $7A^t$ and in smaller amounts in $2A^t$, $3A^t$, $5A^t$, and $6A^t$ within the genomes of the tetraploid Timopheevi group (*T. araraticum*, and *T. timopheevi*) and vice versa within those of the Emmer group (*T. dicoccoides* and *T. turgidum*). Similar divergence patterns occurred among chromosome $4A^a$ and $7A^a$ of cultivars of hexaploid wheat (*T. aestivum*). These dynamic processes could be related to geographic distribution and to natural and artifical selection. Comparison of the A genomes of diploid wheats with those of polyploid wheats shows that the A genomes in existing diploid wheats could not be the direct donors of those in polyploid wheats, but that the extant taxa of diploids and polyploids probably have a common origin and share a common A-genomelike ancestor.

Key words: *Triticum* – Heterochromatin – Wheat evolution – Diploids – Polyploids

* Contribution of the College of Agricultural Sciences, Texas Tech Univ. Journal No. T-4-233.

Introduction

Wheat taxa (*Triticum*) include wild and cultivated diploid, tetraploid, and hexaploid species. The origin and ancestry of the cultivated wheats have been studied for almost five decades (Wagenaar 1966; Sears 1974; Johnson 1975; Peacock et al. 1981; Dhaliwal and Johnson 1982; Kimber and Feldman 1987 for review). It is generally accepted that the genomes in the wild diploids *Triticum boeoticum* Boiss., *T. urartu* Tum. and the cultivated *T. monococcum* L. were the A genome donors of polyploid wheats (Morris and Sears 1987; Gill and Kimber 1974; Chapman et al. 1976; Dvorak 1976; Konarev 1983; Furuta et al. 1986). However, using in situ hybridization to analyze the highly repetitive DNA sequences in wheats, Peacock et al. (1981) suggested that the sources of genomes in polyploid wheats are by no means known with certainty, and the genomes of *T. boeoticum*, *T. urartu*, and *T. monococcum* could not be the A genome donors of polyploid wheats by simple hybridization and chromosome doubling events. Johnson (1975) argued that, based on protein electrophoretic analysis, *T. urartu* could be the B genome donor of polyploid wheats.

Heterochromatin banding analysis is one of several methods of studying genome composition, differentiation, and evolutionary relationships among species, and banding sites are highly correlated with satellite-repeated DNA sequences (Gerlach 1977; Dennis et al. 1980; Dvorak and Appels 1982; Badaeva et al. 1986; Vega et al. 1987). However, detailed knowledge of the A genome structure and differentiation in diploid and polyploid wheats is still lacking. One of the reasons is that chromosomes of the diploids *T. boeoticum*, *T. urartu*, and *T. monococcum* are almost bandless, when previously reported banding techniques are used (Gerlach, 1977; Iordansky et al. 1978). Another reason is the small sample sizes that

Table 1. *Triticum* species and cultivars used in the present study. The Hornemannaii and the Sinskajae in the cultivated *T. monococcum* L. are considered as different cultivars. *T. boeoticum* Boiss. and *T. urartu* Tum. are wild diploid species. The wild *T. araraticum* Jakubz. and the cultivated *T. timopheevi* Zhak. are tetraploid species of the Timopheevi group; and the wild *T. dicoccoides* Korn. and the cultivated *T. turgidum* L. are the Emmer group (4 ×). The Dicoccon and Polonicum are treated as cultivars in *T. turgidum*

Species	Fig.	Symbols	Accession no.	Seed sources*	Genome symbols	Designated origin
T. monococcum	2	a	G3327	W	A^m	England
		b	G1483	W	A^m	England
		c	G3363	W	A^m	Germany
		d	G3302	W	A^m	Yugoslavia
		e	G3373	W	A^m	Lebanon
		f	Sinskajae	W	A^m	USSR
		g	Hornemannaii	K	A^m	USA
		h	PI306543	S	A^m	Rumania
		i	PI355541	S	A^m	Syria
		j	PI355547	S	A^m	Australia
T. boeoticum	3	a	G1004	W	A^b	Transcaucasia
		b	G2517	W	A^b	Iran
		c	TA553	G	A^b	Lebanon
		d	TA 580	G	A^b	England
		e	G2587	W	A^b	Iraq
		f	TA199	G	A^b	USSR
T. urartu	3	g	G3241	W	A^u	Lebanon
		h	G3247	W	A^u	Lebanon
		i	TA831	G	A^u	Iran
		j	TA851	G	A^u	USSR
		k	TA856	G	A^u	Iraq
T. timopheevi	4	a	CI11651	S	A^t	USSR
		b	PI282932	S	A^t	Argentina
		c	PI288033	S	A^t	Australia
		d	PI355705	S	A^t	Germany
T. araraticum	4	e	G2206	W	A^t	Iraq
T. turgidum	4	f	PI352531	S	A^e	Yugoslavia
T. dicoccoides	4	g	G2051	W	A^e	Turkey
		h	PI482125	S	A^e	Lebanon
		i	PI428024	S	A^e	Turkey
T. turgidum var.						
Dicoccon	4	j	PI352337	S	A^e	Spain
Dicoccon		k	PI94636	S	A^e	Iran
Polonicum		l	PI286547	S	A^e	Ethiopia
Polonicum		m	PI384345	S	A^e	Equador
T. aestivum	5	a	Chinese Spring		A^a	China
		b	Jinghua 1		A^a	China
		c	Wichita		A^a	USA
		d	Mustang		A^a	USA
		e	Sturdy		A^a	USA
		f	TAM W-101		A^a	USA
		g	Uniculm		A^a	Israel

* W, K, S, and G seed sources were generously provided by Drs. JG Waines (Univ. of California at Riverside, USA), J Kuspira (Univ. of Alberta, Edmonton, Canada), DH Smith (National Small Grains Collection, Beltsville), and BS Gill (Kansas State Univ. USA), respectively. Chinese Spring and Uniculm wheats were provided by Drs. ER Sears (Univ. of Missouri, Columbia) and D Atsmon (Weizmann Institute, Israel), respectively. Jinghua 1 cultivar, from anther tissue culture, was provided by Ms. Huang (Beijing Agric. Academy China).

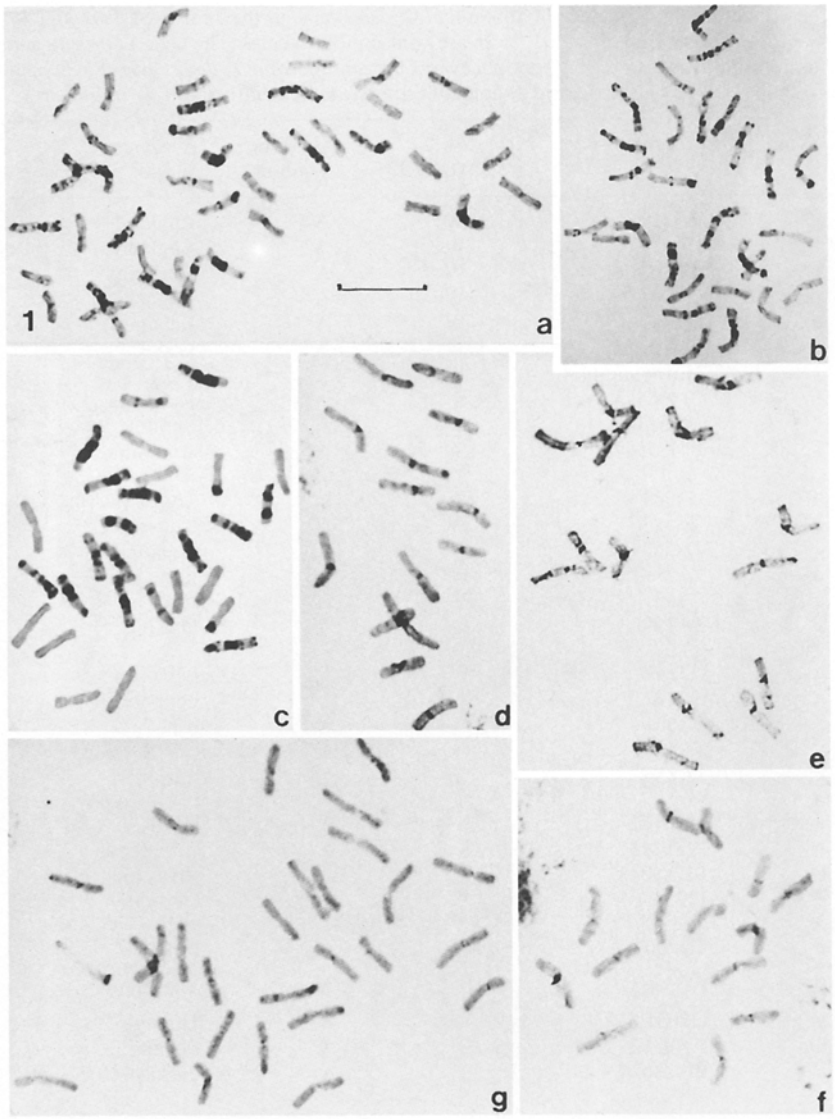

Fig. 1 a–g. The heterochromatin banding patterns of diploid and polyploid wheats. **a** TAM W-101 (*T. aestivum*), **b** Polonicum (PI 384345), **c** *T. timopheevi* (PI 288033), **d** *T. boeoticum* (TA199), **e** *T. urartu* (TA856), **f** *T. monococcum* var. Sinskajae, **g** Tetraploid of *T. monococcum* var. Hornemannaii; *bar* = 10 μm

have been used in most chromosome banding studies (Gill and Kimber 1974; Gerlach 1977; Badaeva et al. 1986); even the repeated DNA sequence analysis by in situ hybridization employed only one or a few accessions of diploid and polyploid wheats (Dennis et al. 1980; Peacock et al. 1981). Therefore, we have used larger sample sizes and a new chromosome banding method, and this has provided additional information of A genome heterochromatin differentation in diploid and polyploid wheats.

Materials and methods

There are different classifications for wheats (Wagenaar 1966; Sears 1974; Kimber and Feldman 1987; Waines and Payne 1987), but for this study we mainly used the original nomenclature supplied for seeds from different sources of germplasm collections (Table 1). Seeds of wheat were germinated on the surface of 30 ml water in 125 ml flasks at room temperature. Root tips were collected from 12:30–1:30 p.m. and pretreated for 2.5 h with 1-bromonaphthalene (prepared by 1/100 ml of stock solution per 10 ml water per vial; the stock solution was made by 1 ml pure 1-bromonaphthalene in 100 ml absolute ethanol).

Maceration. The root tips were washed twice in distilled water, directly hydrolyzed with 5 N HCl for 20 min at room temperature, washed twice in distilled water then stored in 45% acetic acid before squashing.

Slide preperation. The meristematic part of the root, about 1 mm long, was cut from the root trip with a razor blade on a clean slide in a drop of 45% acetic acid. A cover-glass was added, and the meristematic tissue spread by first tapping on the cover-glass with a dissecting needle and then by squashing. The slide was subsequently dipped in liquid nitrogen for 3 min and then the cover-glass was removed with a razor blade before thawing.

Banding. The slides were air-dried and stored for 3–7 days. The dried slides were then treated with 1 N HCl at 60°C ± 1°C for

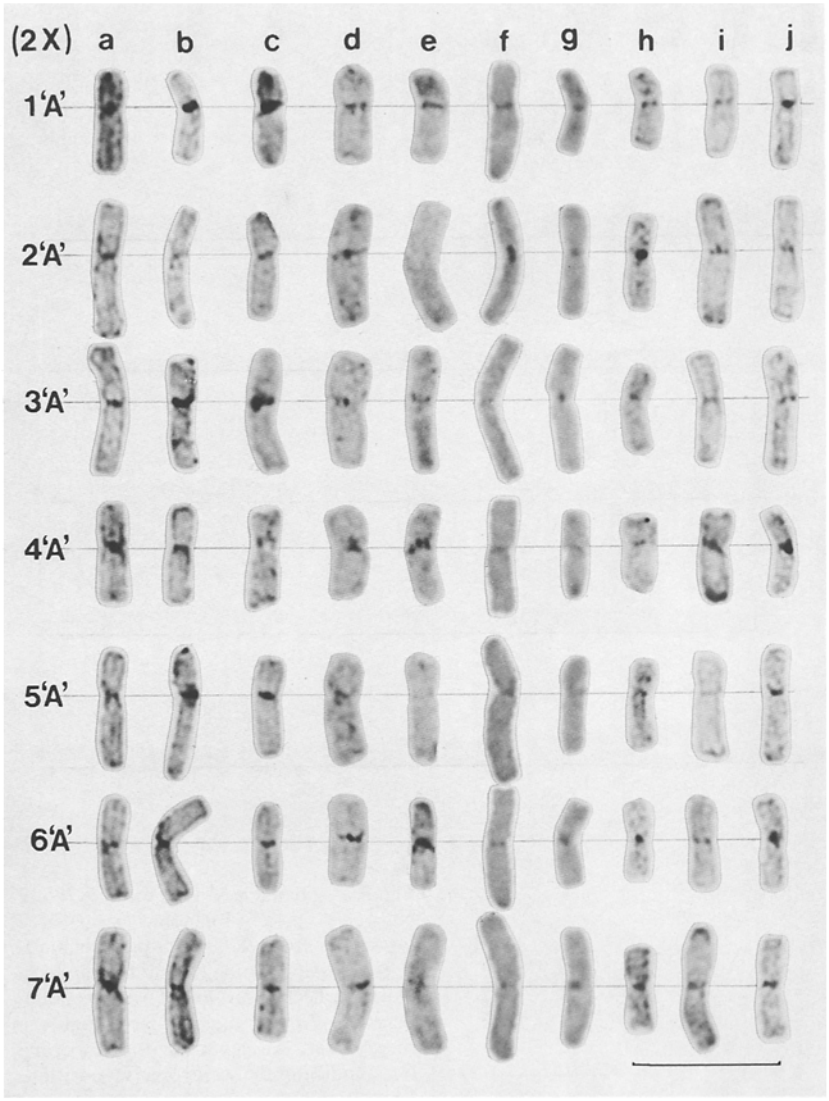

Fig. 2a–j. Banded A^m genome ($x=7$) of *T. monococcum* by the HKG banding technique; **a–j** accessions come from different germplasm collections (Table 1); arabic numerals *1A–7A* are the non-homologues in the genomes; the horizontal lines indicate the centromeric positions; *bar* = 10 μm

6 min, washed 4 times in distilled water for a total of 10 min at room temperature, and air-dried for half a day. They were then dipped into fresh 0.07 N KOH solution for 23 ± 3 s, followed by 1/15 M Sorenson's phosphate buffer shaken at room temperature, and stained in 3% Gurr's improved Giemsa stain solution (3 ml Gurr's improved Giemsa stock solution in 100 ml 1/15 M Sorenson's phosphate buffer, pH 6.8), until the clear and sharp band patterns appeared. The slides were rinsed in destilled water, air-dried, and mounted in a synthetic resin (Preserveaslide, Mathesin, Coleman, and Bell Co.). We designated this method as the HKG (HCl-KOH-Giemsa) banding technique.

The arrangements of non-homologous chromosomes of the A genomes in diploid, tetraploid, and hexaploid wheat species (Figs. 2–5) were based on chromosome size, arm ratio, heterochromatin banding size, and distribution and Giemsa staining intensity. They were also matched with those of the genomes previously described by Gill and Kimber (1974), Seal (1982), Endo and Gill (1984), and Badaeva et al. (1986). The banded A genomes were determined from at least five cells of each accession in which all chromosomes were characterized. Chromosome arm description is p = short arm, q = long arm. The percent of heterochromatin per genome ($x=7$) was determined by diving total length of all bands by total genome length of mitotic metaphase chromosomes.

Results

Heterochromatin differentation in the A genomes of diploid wheats

For the genomes of cultivated *T. monococcum* and the wild *T. boeoticum* and *T. urartu* diploid wheats, heterochromatin is mainly at centrometric region. But diversity in band size and Giemsa staining intensity is evident, and also some accessions from different germplasm collections have interstitial and telomeric bands in the A genomes (Figs. 1d–f, 2a–j and 3a–k; Table 1).

Chromosome 1A of accessions a, b, c, and j of *T. monococcum* (Fig. 2), b, c, and f of *T. boeoticum* (Fig. 3), and accession k of *T. urartu* (Fig. 3) has the

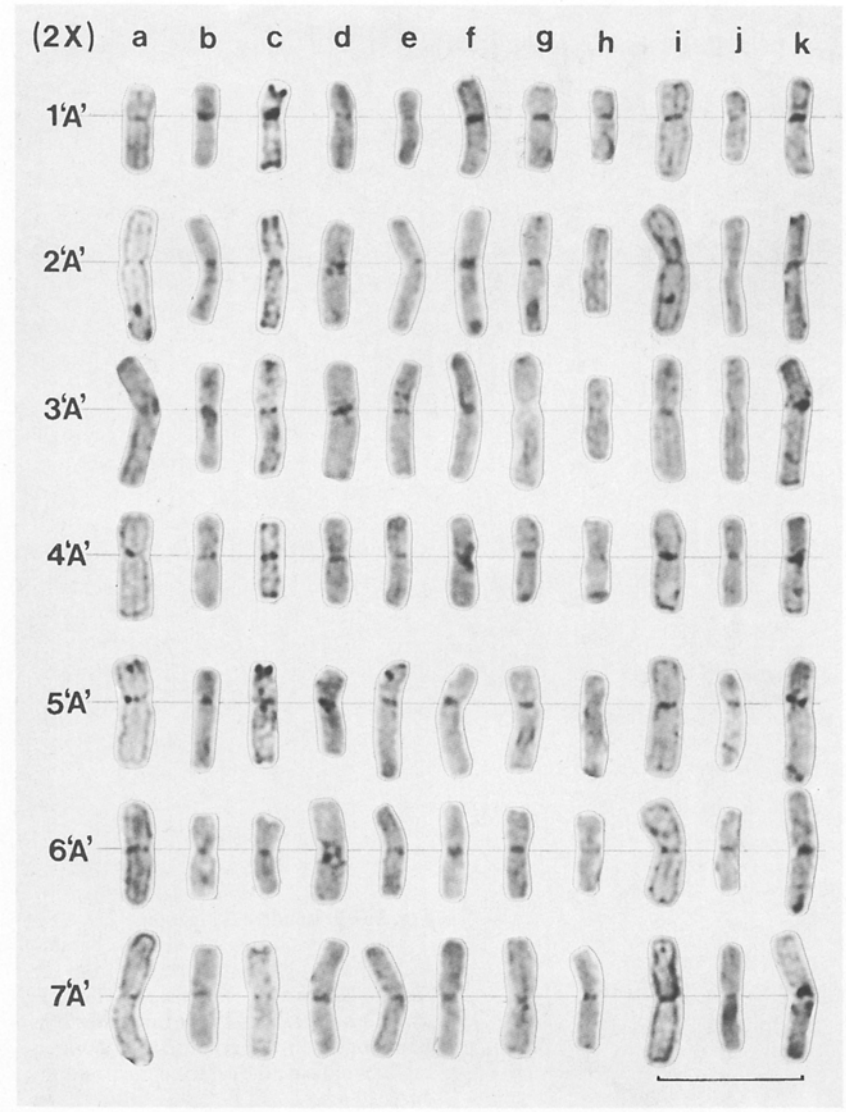

Fig. 3. a–g banded A^b genome ($x=7$) of *T. boeoticum*, **g–k** A^u genome ($x=7$) of *T. urartu* by the HKG banding technique; **a–k** accessions come from different germplasm collections (Table 1); arabic numbers *1A–7A* are the non-homologues in the A^b and A^u genomes; the horizontal lines indicate the centromeric positions; *bar* = 10 μm

largest and the darkest centric band, but other accessions from different collections have a small, faint centric band (Figs. 2 and 3). Only in accession c of *T. boeoticum*, does chromosome 1A have telomeric bands on both arms.

Large and dark centromeric bands on chromosome 2A are shown in accession d, f, and h of *T. monococcum*, b, d, and f of *T. boeoticum*, and g and k of *T. urartu*. A band on arm q close to the centric region is shown in accessions a, b, and f of *T. monococcum*, c and d of *T. boeoticum*, and k of *T. urartu*. A faint subterminal band is on arm q in accession b, c, and d of *T. monococcum*, a and c of *T. boeoticum*, and g and i of *T. urartu*. A telomeric band on arm q is shown only in accession a, d, and i of *T. monococcum* and a, c and f of *T. boeoticum*. No bands were seen in accession e of *T. boeoticum* and h of *T. urartu*.

Chromosome 3A in accession b has the largest and darkest centromeric band among the 10 accessions of *T. monococcum* (Fig. 2a–j), and similar banding patterns occur in b, d, and f among 6 accessions of *T. boeoticum* (Fig. 3a–f) and k of 5 accessions of *T. urartu* (Fig. 3g–k). In accession c of *T. monococcum*, e of *T. boeoticum* and k of *T. urartu*, the chromosome has a proximal band on arm p. No bands were seen in accession f of *T. monococcum* or g, h, and j of *T. urartu*.

Chromosome 4A of accessions a, b, d, e, and j (*T. monococcum*) in Fig. 2 and c, f (*T. boeoticum*), i, and k (*T. urartu*) in Fig. 3 has a large, dark centromeric band. In accessions c and i of *T. monococcum*, c of *T. boeoticum*, and most accessions of *T. urartu* (g, h, i, and k), this chromosome has a faint subterminal and a telomerical band on arm q.

Chromosome 5A accessions c, f, g, and i of *T. monococcum* usually lack bands, but b and c of the same species, c and d of *T. boeoticum*, and i and k of *T. urartu* have a large, dark centromeric band. An arm p telomeric

band is in accession b of *T. monococcum* and a, c, and e of *T. boeoticum*, but only in accession e of *T. boeoticum* is there a dark subterminal band on arm p. Accession b, d, and h in Fig. 1 and c and d in Fig. 3 have proximal bands, and only accession k of *T. urartu* has a dark subterminal band on arm q.

In most accessions of *T. monococcum*, chromosome 6A has a dark, centromeric band (Fig. 2). Accession d has the largest and darkest centromeric band in *T. boeoticum* and, similarly in accession k, this chromosome has the darkest and largest centric band in *T. urartu* and also has a large, dark telomeric band on arm q.

Heterochromatin banding patterns on chromosome 7A are similar in the cultivated and the wild diploid wheats. However, in accession i of *T. monococcum* it has faint telomeric bands on both arms, and in accession k of *T. urartu* it has the largest and darkest centric, proximal, and telomeric bands on arm q.

For the whole genome, heterochromatin banding size and Giemsa staining intensity in accessions b (G1483) and c (G3363) of *T. monococcum* (Fig. 2) from England and Germany are larger and darker than those of accessions f and g (Sinskajae and Hornemannaii). Heterochromatin banding patterns of accessions c (TA553), d (TA580), and e (G2587) of *T. boeoticum* (Fig. 3) from Lebanon, England, and Iraq are distinct from each other and from other accessions of the same and different species. Lack of banding in accession h (G3274) and j (TA851) from Lebanon and the USSR and the large, dark banding pattern in k (TA856) from Iraq occur in the wild diploid *T. urartu* (Fig. 3). However, in other accessions of the three diploid wheats there is no clear-cut difference (Figs. 2 and 3). The range of the amount of banded heterochromatin in the wild diploid *T. urartu*, in the wild diploid *T. boeoticum*, and the cultivated *T. monococcum* is 3%–16%. The greatest amount of heterochromatin is found in the genome of *T. urartu* (TA856) collected in Iraq.

Heterochromatin differentiation in the A genomes of tetraploid wheats

The banding pattern of chromosome 1A is similar in tetraploids, but heterochromatin differentiation occurs in 2A–7A among all the studied accesions. Heterochromatin distribution is uneven. Large amounts of heterochromatin are located in chromosome 4 and 7 in the Timopheevi group and in chromosomes 2 and 4 in the Emmer group (Fig. 4a–m; Table 1).

Timopheevi group. In the wild *T. araraticum* tetraploid wheat (Fig. 4e), chromosomes $1A^t$, $2A^t$, $3A^t$, $5A^t$ and $6A^t$ mostly lack bands, but $5A^t$ has a subterminal band on arm q similar to that of $5A^u$ of diploid *T. urartu* (Fig. 3, j and k). Chromosome $4A^t$ has a large pericentric and two interstitial bands on arm q, and chromosome $7A^t$ has a proximal band on arm p and another subterminal band on arm q. In the tetraploid-cultivated *T. timopheevi* (Fig. 4a–d) chromosomes $1A^t$, $2A^t$, $3A^t$, $5A^t$, and $6A^t$ are similar to those of *T. araraticum*, but the band sizes and sites of chromosomes $4A^t$ and $7A^t$ are different; $4A^t$ has three bands on arm q, one of which is telomeric, and the amount of heterochromatin (60%–70%) for this chromosome is significantly different from that of *T. araraticum* (55%–62%) The band sizes of $7A^t$ of *T. timopheevi* are larger than those of *T. araraticum* (Fig. 4a–e).

Emmer group (Fig. 4f–m). In most cases, chromosomes $2A^e$, $3A^e$, $5A^e$, and $6A^e$ in the Emmer group have larger and darker bands than those in the Timopheevi group, but the band sizes, sites, and staining intensity of chromosomes $4A^e$ and $7A^e$ are much smaller, different, and weaker than those of the Timopheevi group. In wild *T. dicoccoides* (4×) accessions (Fig. 3g–i), the heterochromatin banding patterns of h (PI428125) from Lebanon are distinct from those of g (G2051) and i (PI428024) from Turkey, except chromosome $1A^e$ and $2A^e$. In accession h, chromosome $3A^e$ has the largest and darkest centromeric band but lacks the proximal band on arm p; $4A^e$ has the smallest centric and pericentric bands (30%–34%), but in accession g and i the amounts are 36%–42%; $5A^e$ has no bands and is more similar to the *T. timopheevi* group in lacking the dark, proximal band on arm q; $6A^e$ has two interstitial bands on arm q but only one in accessions g and i; $7A^e$ has a faint subterminal and a dark, telomeric band on arm q but only a faint, subterminal band in g and i. The faint subterminal banding site is similar to that of $7A^t$ of the Timopheevi group, but the band size and staining intensity of $7A^e$ are much smaller and weaker.

Heterochromatin diversity occurs in cultivated *T. turgidum* (4×), including Dicoccon and Polonicum, (Fig. 4f and j–m). It is interesting to note that chromosome $4A^e$ in accession f (PI352531) from Yugoslavia has a subterminal band on arm q that is lacking in all other Emmer groups but is equivalent to one of those in the Timopheevi group. This chromosome also has a telomeric band on arm p. Another point is that both accessions l (PI286547) and m (PI384345) are Polonicum (Table 1), but from different areas (Equador l and Ethiopia m). The heterochromatin banding patterns of chromosomes $2A^e$, $5A^e$, $6A^e$, and $7A^e$ of both accessions are distinct from each other (Fig. 4 l and m). Chromosome $2A^e$ has a dark telomeric band on arm q in accession l but lacks the band in accession m. In contrast, the latter has a dark subterminal band on arm q. Chromosome $5A^e$ has a proximal band on arm q in accession l but a proximal band on arm p in accession m. Chromosome $6A^e$ has a large band on arm q in accession l but lacks the band in m; the lack of

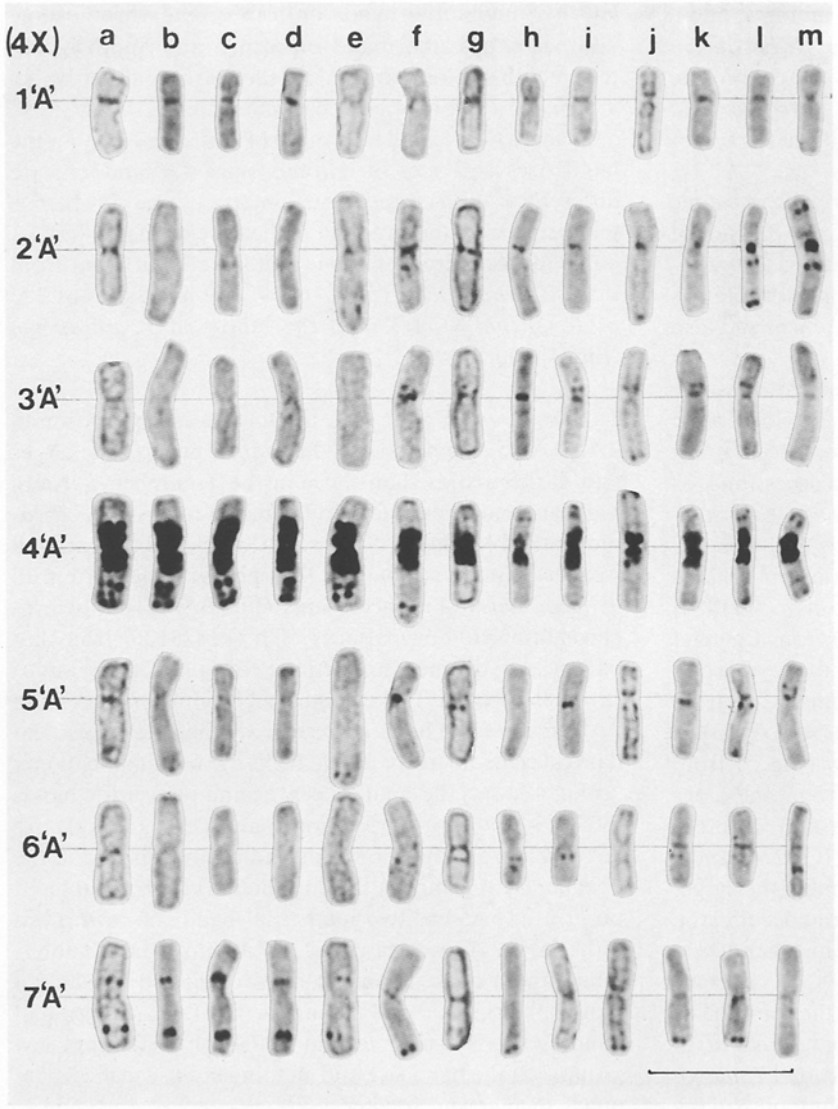

Fig. 4. **a–e** banded A^t genomes of Timopheevi group, **f–m** A^e genomes of Emmer group by the HKG banding techniques; **a–m** accessions come from different germplasm collections (Table 1); arabic numerals *1A–7A* are the non-homologues in the A^t and A^e genomes; the horizontal lines indicate the centromeric positions; *bar* = 10 μm

bands in the latter is typical of 7A in most diploid wheats (Figs. 2 and 3).

It is also important to note that chromosome $2A^e$ of Polonicum has the largest, darkest centric and proximal bands of all diploid and tetraploid wheats, and the telomeric (accession l) and the subterminal (accession m) bands are also distinctive. It is interesting that the range of amount of heterochromatin in tetraploid wheats is 10%–17%. This is close to the amount of heterochromatin in some of the diploid wheat genomes, and both tetraploid groups contain almost the same amount of total heterochromatin in their genomes. However, heterochromatin distribution in the two tetraploid groups is distinct.

Heterochromatin differentiation in the A^a genomes of hexaploid wheats.

Banding patterns of chromosomes $1A^a$, $2A^a$, $3A^a$, and $5A^a$ in seven cultivars (Chinese Spring, Jinghua 1, Wichita, Mustang, Sturdy, TAM W-101, and Uniculm) are similar (Fig. 5a–g.). Chromosomes $1A^a$ is also similar to those of diploid and tetraploid wheats (Figs. 2–4). The banding patterns of $3A^a$, $4A^a$, and $5A^a$ are closer to those of most Emmer group accessions of tetraploid wheats. However, the banding sites and the amount of heterochromatin in chromosome $4A^a$ are significantly different among these cultivars. The amouns in Jinghua 1, Wichita, Mustang, and TAM W-101 are significantly greater than in Chinese Spring, Sturdy, and Uniculm. The highest amount is in TAM W-101 (47%–55%) which is close to that of *T. araraticum* of the Timopheevi group of tetraploid wheats, and the lowest amount (30%–35%) is that of Uniculm, which is close to that of accession h of the Emmer group. The banding pattern of chromosome $6A^a$ of Chinese Spring is similar to that of the Emmer group, but bands are lacking in $6A^a$ in the other six cultivars; it is more like those of 6A in diploid wheats and in the tetraploid Timopheevi group. Chro-

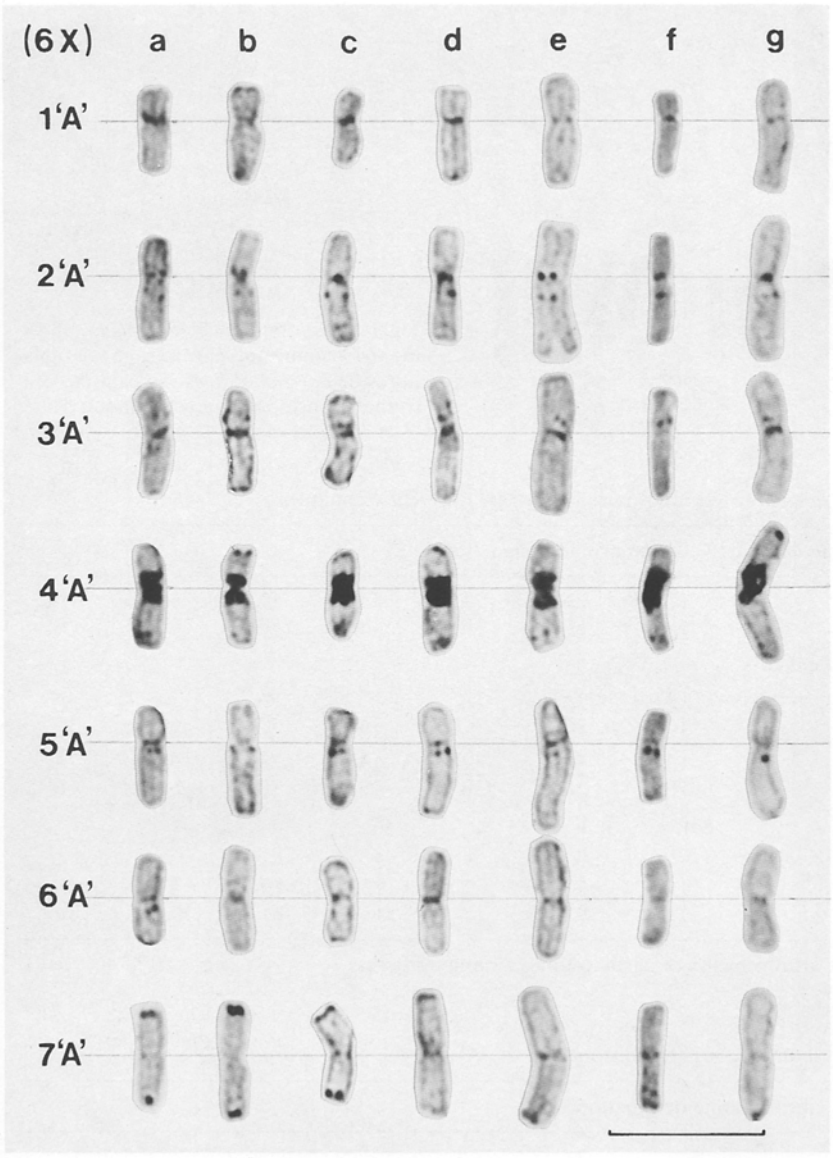

Fig. 5a–g. Banded A^a genome of *T. aestivum* by the HKG banding technique; **a–g** are different cultivars (Table 1); arabic numerals *1A–7A* are the non-homologues in the A^a genome; the horizontal lines indicate the centrometric positions; *bar* = 10 μm

mosome $7A^a$ in Chinese Spring, Jinghua 1, and Wichita has two dark telomeric bands on both arms, but in Mustang, Sturdy, TAM W-101, and Uniculm there is only one telomeric band. The faint subterminal band on arm q in Jinghua 1, Mustang, and TAM W-101 is similar to that of $7A^e$ of *T. dicoccoides* (Fig. 4g–i). The site is also equivalent to that of $7A^t$ of the Timopheevi group, but size and staining intensity are distinct. Chromosomes $7A^a$ of hexaploid wheats are obviously different from those of diploid wheats. The amount of heterochromatin in the genome of hexaploid wheat is 12%–17%.

Discussion

The A genome differentiation among the wild and cultivated diploid wheat taxa has been identified by DNA content (Bennet and Smith 1976), protein and isozyme electrophoresis (Johnson 1975; Knonarev 1983; Asins and Carbonell 1986; Waines and Payne 1987), and hybridization studies (Sharma and Waines 1981; Dhaliwal and Johnson 1982). Our data provide the first evidence of heterochromatin differentiation as judged by banding size, site, and staining itensity. Heterochromatin differentiation has also occurred in the closely related genomes of wild and cultivated polyploid wheats. This dynamic process may be correlated with geographic distribution and natural and artificial selection.

Comparative identification of the seven non-homologous chromosomes in the A genomes of diploid and polyploid wheats is generally not difficult. However, in the tetraploid Timopheevi group, the chromosome designations, especially for $2A^t$, $3A^t$, $4A^t$, $5A^t$, and $7A^t$ in our system (Figs. 4a–e and 6; Tables 2 and 3), are differ-

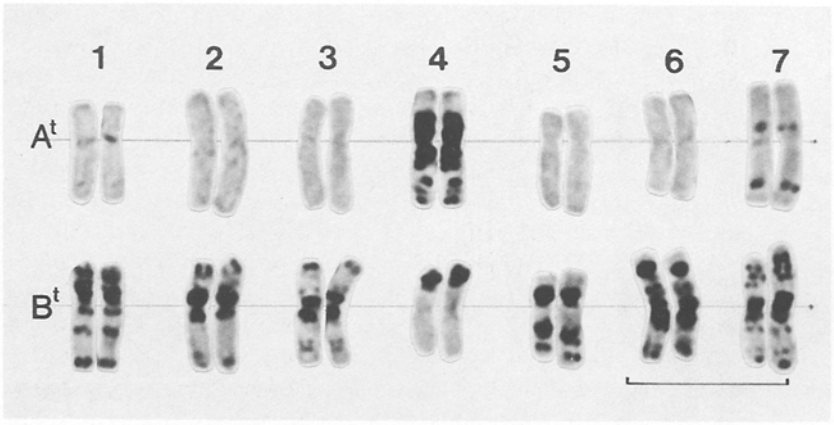

Fig. 6. Karyotype of *T. timopheevi* showing the genome and chromosome designation; the *horizontal lines* indicate the centromeric positions; *bar* = 10 μm

Table 2. Comparison of the designation of *T. timopheevi* chromosomes banded by different techniques

Authors	Genome name	Chromosome designations*						
This work	A^t	$1A^t$	$2A^t$	$3A^t$	$4A^t$	$5A^t$	$6A^t$	$7A^t$
	B^t	$1B^t$	$2B^t$	$3B^t$	$4B^t$	$5B^t$	$6B^t$	$7B^t$
	Equivalent to							
Badaeva et al. (1986)	A	1A	2A	3A	4G	5A	7A	4A
	G	1G	2G	7G	6A	5G	6G	3G
Dvorak (1983)	A^t	$1A^t$	$7A^t$	$5A^t$	$4A^t$	$3A^t$	$6A^t$	$2A^t$
	B^t	$1B^t$	$2B^t$	$3B^t$	$4B^t$	$5B^t$	$6B^t$	$7B^t$
Hutchinson et al. (1982)	A	f	b	a	h	d	e	c
	G	m	j	l	g	n	k	i
Zurabishvili et al. (1978)		14	3	7	12	10	6	4
		1?	9	12	13	11	5	8

* The numbers with underlines show different arrangements of chromosomes among authors

Table 3. Comparison of the designation of non-homologous chromosomes in the A^t genome of *T. araraticum*

Information	Genome	Chromosome designation*						
Our present results	A^t	1	2	3	4	5	6	7
and the arm ratio		1.5–1.6	1.4–1.7	1.2–1.4	1.2–1.3	1.8–2.0	1.0–1.1	1.0–1.1
Chen and Gill (1983)	A	1	7	5	4	3	6	2
and the arm ratio		1.5	1.1	1.9	1.2	1.4	1.2	1.7
Hutchinson et al. (1982)		f	b	a	i	d	e	c

* The numbers underlined indicate different arrangement of chromosomes among authors

ent from those other authors (Zurabishvili et al. 1978; Hutchinson and Miller 1982; Chen and Gill 1983; Dvorak 1983; Badaeva et al. 1986). This indicates that chromosome classification in the tetraploid Timopheevi group is not yet finalized. Gill and Kimber (1974) have reported the banding patterns of two accessions (G367 and G435) of *T. monococcum* by a different Giemsa C-banding technique. They seem to be very similar to the patterns of some accessions of *T. monococcum* (G1483, G3302, and PI306543) banded by our HKG banding procedure.

Analysis based on heterochromatin banding patterns and Giemsa staining intensity indicates that it is easy to distinguish between A genome chromosomes of diploids and polyploids, particularly chromosomes 4 and 7. Evidence from often repeated DNA sequence analysis also distinguishes them (Appels et al. 1980; Gerlach and Peacock 1980; Peacock et al. 1981). Obviously, these data

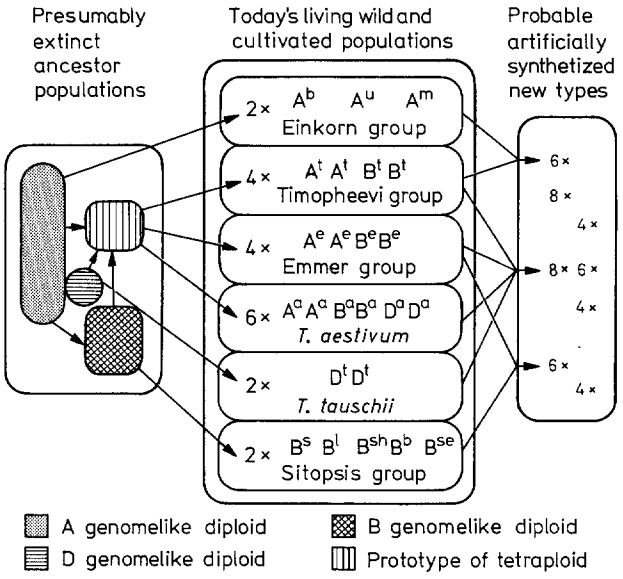

Fig. 7. A schematic representation of *Triticum* evolution; superscripts to the genome symbols are used to indicated related genomes carried by different populations

suggest that the genomes of today's living diploid species could not be the direct donor of either the A or B genomes of polyploid wheats; the similarity among the genomes of diploid and polyploid species only indicates that they are close relatives. Therefore, efforts made to identify and to search for the exact donor or ancestral genomes of polyploid wheats from extant diploid wheat taxa could be fruitless and arguments could also be endless, especially for the B genomes (Gill and Kimber 1974; Johnson 1975; Dvorak 1976; Chapman et al. 1976; Peacock et al. 1981; Dhaliwal and Johnson 1982; Konarev, 1983; Furuta et al. 1986). The data from Dvorak (1983), Rayburn and Gill (1985), and Wazuddin and Driscoll (1986) on chromosomes 4A and 4B or $4B_1$ and $4B_2$ redesignations in the genomes of polyploid wheats also indicate that chromosome 4 of extant diploid and polyploid wheats do not represent donor and recipient relationships. However, these polyploid wheats probably have a common origin.

Phylogenetic relationships in *Triticum* species are proposed in Fig. 7. Comparing this scheme with those of Johnson (1975), Konarev (1983), and Kimber and Feldman (1987), there are four special points to consider: (1) all of today's genomes of *Triticum* species could share a common, extinct A genome: (2) tetraploid wheats, including the Timopheevi and Emmer groups, and hexaploid *T. aestivum* could share a common extinct 4× prototype; (3) all of the extant wild and cultivated species are close relatives; and (4) artificially synthesized polyploids from today's living diploid and tetraploid wheat taxa have already revealed the major mechanisms of the origin of the extant wild and cultivated polyploid wheats. We believe that this scheme will also be supported by other well-documented data.

It has been supposed that heterochromatinization or increase in the amount of heterochromatin primarily in the B genome is one of the major wheat genome evolutionary pathways (Dvorak and Appels 1982; Endo and Gill 1984; Badaeva et al. 1986). However, our data suggest that heterochromatinization independently occurred within the A genomes of polyploid wheats. Heterochromatinization occurred in chromosome $4A^t$ and $7A^t$ but is almost lacking in chromosome $2A^t$, $3A^t$, $5A^t$, and $6A^t$ within the A^t genome of the Timopheevi group. Differential rates of heterochromatinization have occurred within the A^e genome of the Emmer group (Fig. 3a–m). Seal (1982) seems to have ignored the A genome heterochromatin diversity among cultivars of hexaploids, but Iordansky et al. (1978) suggested that the amount of heterochromatin decreased from primitive genomes of Chinese Spring to advanced genomes of other cultivars. However, our data indicate that heterochromatin differentiation has occurred also within the A^a genome, i.e., heterochromatinization and deheterochromatinization could occur in chromosome $4A^a$ and $7A^a$ among various hexaploid cultivars (Fig. 5a–g).

It is important to note that heterochromatin increase or decrease and site rearrangement could influence active gene loci and spatially change the intrinsinc chromosome environment. Such a spatial or positional effect could be responsible for new patterns of recombination, new linkage groups, and new gene frequencies (Hutchinson et al. 1982; Macgregor 1984; Lange et al. 1987; Vega et al. 1987).

Acknowledgements. This work was supported by grants from Texas Advanced Technology Research Program and the National Science Foundation (BSR-8552915).

References

Appels R, Gerlach WL, Dennis ES, Swift H, Peacock WJ (1980) Molecular and chromosomal organization of DNA sequences coding for the ribosomal RNAs of cereals. Chromosoma 78:293–311

Asins MJ, Carbonell EA (1986) A comparative study on variability and phylogeny of *Triticum* species. 2. Interspecific relationships. Theor Appl Genet 72:559–568

Badaeva ED, Shkutina FM, Bogdevich IN, Badaev NS (1986) Comparative study of *Triticum aestivum* and *T. timopheevi* genomes using C-banding technique. Pl Syst Evol 154: 183–194

Bennet MD, Smith JB (1976) Nuclear DNA amounts in angiosperms. Philos Trans R Soc London Ser B 274:228–274

Chapman V, Miller TE, Riley R (1976) Equivalence of the A genome of bread wheat and that of *Triticum urartu*. Genetic Res 27:69–76

Chen PD, Gill BS (1983) The origin of chromosome 4A, and genomes B and G of tetraploid wheats. Proc 6th Int Wheat Genet Symp Jpn 1983:39–48

Dennis ES, Gerlach WL, Peacock WJ (1980) Identical polypyrimidine-polypurine satellite DNAs in wheat and barley. Heredity 44:349–366

Dhaliwal HS, Johnson BL (1982) Diploidization and chromosomal pairing affinities in the tetraploid wheats and their putative amphiploid progenitor. Theor Appl Genet 61: 117–123

Dvorak J (1976) The relationship between the genome of *Triticum urartu* and the A and B genomes of *Triticum aestivum* species. Theor Appl Genet 63:349–360

Dvorak J (1983) The origin of wheat chromosomes 4A and 4B and their genome reallocation. Can J Genet Cytol 25: 210–214

Dvorak J, Appels R (1982) Chromosome and nucleotide sequence differentiation in genomes of polyploid *Triticum* species. Theor Appl Genet 63:349–360

Endo TR, Gill BS (1984) Somatic karyotype, heterochromatin distribution, and nature of chromosome differentiation in common wheat *T. aestivum* L. em Thell. Chromosoma 89: 361–369

Furuta Y, Nishikawa K, Yamaguchi S (1986) Nuclear DNA content in diploid wheat and its relatives in relation to the phylogeny of tetraploid wheat. Jpn J Genet 61:97–105

Gerlach WL (1977) N-banded karyotypes of wheat species. Chromosoma 62:49–56

Gerlach WL, Peacock WJ (1980) Chromosomal location of highly repeated DNA sequences in wheat. Heredity 44: 269–276

Gill BS, Kimber G (1974) Giemsa C-banding and the evolution of wheat. Proc Natl Acad Sci USA 71:4086–4090

Hutchinson J, Miller TE, Jahier J, Shepherd KW (1982) Comparison of the chromosomes of *Triticum timopheevi* which related wheats using the techniques of C-banding and in situ hybridization. Theor Appl Genet 64:31–40

Iordansky AB, Zurabishvili TB, Badaev NS (1978) Linear differentiation of cereal chromosomes. 1. Common wheat and its supposed ancestors. Theor Appl Genet 51:145–152

Johnson BL (1975) Identification of the apparent B-genome donor of wheat. Can J Genet Cytol 17:21–39

Kimber G, Feldman M (1987) Wild wheat: An introduction. Spec Rpt 353, College of Agric, Univ of Missouri, Columbia

Konarev VG (1983) The nature and origin of wheat genomes on the data of grain protein immunochemistry and electrophoresis. Proc 6th Int Wheat Genet Symp, Kyoto, Japan, pp 65–75

Lange W, Laursen IL, Ljunberg A, Ellerstrom S (1987) Cytogenetic analysis of structural rearrangements in three varieties of common wheat *Triticum aestivum*. Theor Appl Genet 73:635–645

Macgregor HC (1984) The evolutionary consequence of major genomic changes in *Amphibia*. Chromosomes Today 8: 256–267

Morris R, Sears ER (1967) The cytogenetics of wheat and its relatives. In: Quisenberry KS, Reitz LP (eds) Wheat and wheat improvement. Am Soc Agron, pp 19–88

Peacock WJ, Gerlach WL, Dennis ES (1981) Molecular aspects of wheat evolution: Repeated DNA sequences. In: Evans LT, Peacock WJ (eds) Wheat science – today and tomorrow. Cambridge Univ Press, Cambridge, pp 41–60

Rayburn AL, Gill BC (1985) Molecular evidence for the evolution of chromosome 4A in polyploid wheats. Can J Genet Cytol 27:246–250

Seal AG (1982) C-banded wheat chromosomes in wheat and triticale. Theor Appl Genet 63:39–47

Sears ER (1974) The wheats and their relatives. In: King RC (ed) Handbook of genetics, vol 2. Plenum Press, New York, pp 59–91

Sharma HC, Waines GL (1981) The relationship between male and female fertility and among taxa in diploid wheats. Am J Bot 68:449–451

Vega C, Fominaya A, Ferrer E (1987) Influence of chromosome structure on the degree of meiotic pairing of intercultivar wheat hybrids (*Triticum aestivum* L.). Heredity 58:357–363

Wagenaar EB (1966) Studies on the genome constitution of *T. timopheevi*. II. The timopheevi complex and its origin. Evolution 20:150–164

Waines JG, Payne PI (1987) Electrophoretic analysis of the high-molecular weight glutenin subunits of *Triticum monococcum*, *T. urartu*, and the A genome of bread wheat (*T. aestivum*). Theor Appl Genet 74:71–76

Wazuddin M, Driscoll CJ (1986) Chromosome constitution of polyploid wheats: introduction of diploid wheat chromosome 4. Proc Natl Acad Sci USA 83:3870–3874

Zurabishvili TG, Iordensky AB, Badaev NS (1978) Linear differentation of cereal chromosomes. 2. Polyploid wheats. Theor Appl Genet 51:201–210