Theor. Appl. Genet. 61, 27–33 (1982)

Investigation of a Preferentially Transmitted *Aegilops sharonensis* Chromosome in Wheat

T. E. Miller, J. Hutchinson, and V. Chapman
Plant Breeding Institute, Cambridge (England)

Summary. An attempt to produce a set of addition lines of *Aegilops sharonensis* to the wheat variety 'Chinese Spring' produced only one addition line. This was due to preferential transmission of one chromosome from *Ae. sharonensis.* This chromosome was studied in detail by established cytological methods of chromosome observation and by the newer techniques of C-banding and in situ hybridization of a cloned DNA sequence. The chromosome was found to be partially homologous to an *Ae. sharonensis* chromosome of similar behaviour in another wheat addition line. The incomplete homology of the two *Ae. sharonensis* chromosomes was due to the presence of a translocated segment of a wheat chromosome. – Substitution lines of the *Ae. sharonensis* chromosome for wheat homoeologous group 4 were produced and the *Ae. sharonensis* chromosome thereby designated $4\,S^l$.

Key words: Preferential transmission – In situ hybridization – C-banding – *Aegilops sharonensis* – Wheat – Addition – Substitution

Introduction

Ever since O'Mara (1950) published a technique for adding alien chromosomes to bread wheat, *Triticum aestivum,* addition lines have been generally accepted as a valuable means of studying individual chromosomes of related species in the wheat genotype. The substitution of these chromosomes in place of wheat chromosomes enables them to be assigned homoeology relative to the chromosomes of hexaploid wheat (Riley et al. 1966; Sears 1968). Alien additions and substitutions provide a suitable starting point for the introduction of desirable alien characters into wheat by techniques utilising the manipulation of the genetic control of homoeologous chromosome pairing (Riley et al. 1968; Sears 1973).

During the systematic attempt to produce a set of addition and substitution lines to wheat of *Aegilops sharonensis,* it was found that one chromosome of *Ae. sharonensis* was transmitted preferentially. This chromosome was examined in detail by established methods and also by the newer techniques of C-banding and in situ hybridization.

Materials and Methods

1 Plant Stocks

The following plant stocks were used in the investigations: *T. aestivum* cv. 'Chinese Spring' ($2n=6x=42$) and its appropriate aneuploids; *Ae. sharonensis* acc. A ($2n=2x=14$) from the collection of the Plant Breeding Institute; a *T. aestivum* cv. 'Chinese Spring' × *Ae. sharonensis* amphiploid ($2n=8x=56$) and a *T. aestivum* cv. 'Selkirk' – *Ae. sharonensis* addition line ($2n=6x=44$). The latter was produced and kindly supplied by Professor S. S. Maan of North Dakota State University, USA

2 Production of Addition and Substitution Lines

Disomic addition lines ($2n=6x=44$) were produced by self pollination of monosomic addition lines ($2n=6x=43$) extracted either from the second or third backcross progenies of the 'Chinese Spring' × *sharonensis* A amphiploid or direct from the progenies of selfed 44 and 45-chromosome plants resulting from the second backcross.

The substitution lines for chromosomes 4A and 4D were extracted from the F_2 monosomic progenies of the crosses between 'Chinese Spring' monosomic 4A and 4D respectively with the 'Chinese Spring' – *sharonensis* A addition. The 4B substitution line was isolated from a plant with $20''2'$ in the backcross progeny of a 43-chromosome plant extracted with the 43-chromosome monosomic additions.

3 Cytology

Both somatic chromosome number determinations in root tips pretreated with 1-bromonaphthalene and meiotic pairing

0040-5752/82/0061/0027/$ 1.40

studies in pollen mother cells (PMC's) were made on squash preparations stained by the Feulgen procedure.

Material for mitotic chromosome examination by C-banding and in situ hybridization was pre-treated with 1-bromonaphthalene and then fixed in 1:3 acetic alcohol. The meristematic regions were then dissected out in 45% acetic acid as described by Appels et al., (1978). The meiotic chromosomes of PMC's were prepared as described by Hutchinson et al., (1980).

The C-banding was carried out as described by Seal and Bennett (1981) with the exception that the whole procedure, including the hydrolysis step, was carried out after the dissection of the meristems. The chromosomes were finally stained in 20% Wright's stain (Seal and Bennett, in preparation).

In situ hybridization of both mitotic and meiotic chromosomes followed the method of Hutchinson et al. (1980). The probe was tritium labelled cRNA transcribed by *E. coli* RNA polymerase from the plasmid pCS(1)C40, which is abbreviated to C40 in the text. This chimaeric plasmid consists of a complex 1.7 K b. sequence from wheat in the vector plasmid pACYC 184 (Lonsdale and Hutchinson, in preparation). 100,000 cpm were applied per slide, and the autoradiographs exposed for one month.

Results

1 The Extraction of the Disomic Addition Lines

Monosomic addition plants were obtained after crossing the amphiploid either two or three times with 'Chinese Spring'. It was necessary to carry out a third cross since few 43-chromosome plants were produced after the secondcross. This contrasts with the typical progeny obtained from the second backcross of other similar amphiploids, for example *T. aestivum* cv. 'Chinese Spring' × *Secale cereale* cv. 'King II' (Table 1) (Miller, unpublished).

The third cross using double (44-chromosome) and triple monosomic (45-chromosome) additions as female parents did yield a large number of 43-chromosome plants. However, 44-chromosome disomic addition plants (21″ wheat, 1″ *sharonensis)* were common in the progenies of the selfed double and triple monosomic additions, and 13 of the 18 disomic lines established were from this source.

All of the monosomic additions resembled each other phenotypically. The 18 disomic addition lines also appeared to be morphologically identical. All were about 15 cm shorter than 'Chinese Spring' with stiff dark straw and lax tapering ears with round glumes (Fig. 1). Fertility was low because of partial pistillody. On intercrossing, all 18 lines were found to make 22 bivalents at meiosis, proving that they were all disomic additions of the same chromosome.

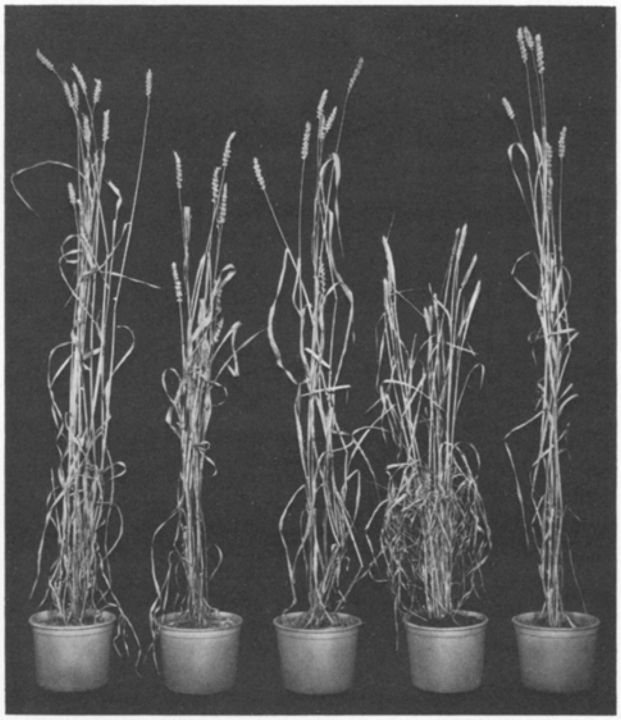

Fig. 1. From left to right. *T. aestivum* cv. 'Chinese Spring' euploid; *T. aestivum* 'Chinese Spring' – *Ae. sharonensis* $4S^l$ addition and the *T. aestivum* 'Chinese Spring' (4A) $4S^l$, (4B) $4S^l$ substitutions

Table 2 shows the chromosome numbers of plants in the progenies of different alien monosomic additions. The 'Chinese Spring' – 'King II' addition shows a typical segregation whereas the 'Chinese Spring' – *sharonensis* A addition shows the atypical segregation comprising almost entirely disomic additions. It is clear that there must be preferential transmission of the alien chromosome. A similar situation has been reported by Maan (1975) in an addition of an *Ae. sharonensis* chromosome to *T. aestivum* cv. 'Selkirk.'

Table 1. Chromosome numbers of plants in progenies of the first backcross (49-chromosome $F_1 \times CS$) of octoploid amphiploids

	Total	Chromosome numbers							
		42	43	44	45	46	47	48	49
'Chinese Spring' × *S. cereale* King II	25	3	7	9	3	2	1	–	–
'Chinese Spring' × *Ae. sharonensis* A	23	–	2	6	12	1	–	2	–

Table 2. Chromosome number of plants in progenies of selfed monosomic additions

		Chromosome numbers				
		41	42	43	44	Others
'Chinese Spring' – 'King II' (sum of three lines)	97	6	65	21	4	1 (21′ haploid)
'Chineses Spring' – *sharonensis* A	32	–	–	1	31	1 (21′ 1″)
'James Fife' – *caudata*[a]	44	–	1	2	41	–
'James Fife' – *cylindrica*[b]	20	–	–	–	20	–

[a] Data from Endo and Katayama 1978; [b] Data from Endo 1979

To check whether the chromosome added here was homologous to that added to 'Selkirk', two investigations were carried out. Firstly, the morophology of the *Ae. sharonensis* A chromosomes was examined in detail, utilising the techniques of C-banding and in situ hybridization. Secondly, the two addition lines were crossed together and the pairing behaviour of the F_1 hybrid was examined.

2 The Morphology of Ae. sharonensis A Chromosomes

The chromosomes of *Ae. sharonensis* A all have submedian centromeres, of which two pairs are distinguished by satellites (Riley et al. 1958; Chennaveeraiah 1960). In size, the *Ae. sharonensis* A chromosomes are very similar to the B genome chromosomes of wheat and cannot be easily distinguished from them in normal mitotic feulgen stained squashes.

Examination of the C-banding pattern of *Ae. sharonensis* A at mitosis showed that all chromosomes possess heterochromatic bands located predominantly near the centromeres (Fig. 2a). Previous C-banding and N-banding studies have established that this banding pattern is characteristic of the B genome chromosomes of hexaploid wheat (Gill and Kimber 1974; Iordansky et al. 1978; Gerlach 1977). Therefore, as illustrated in Fig. 2b, it is very difficult to distinguish added *Ae. sharonensis* chromosomes from those of wheat in the wheat – *sharonensis* addition lines by means of C-banding.

However, *Ae. sharonensis* and B genome chromosomes can also be distinguished by the technique of in situ hybridization. Figure 2c shows the pattern of labelling shown when the tritium labelled cRNA probe C40 is hybridized in situ to the mitotic chromosomes of *Ae. sharonensis* A. This C40 probe consists of a complex 1.7 Kb repetitive sequence isolated from wheat, cv. 'Chinese Spring', by cloning in the vector plasmid pACYC184. It hybridizes predominantly to one or both of the telomeres of all *Ae. sharonensis* chromosomes. In situ hybridizations of C40 to the chromosomes of wheat have shown eight pairs of chromosomes to be labelled, of which only one pair of chromosomes shows labelling on both telomeres. This chromosome also has two interstitial sites on one arm (Hutchinson, in preparation). When the 'Chinese Spring' – *sharonensis* A addition line is probed with C40, it is possible to distinguish not only these eight pairs of labelled chromosomes, but also one additional pair of chromosomes with very heavy labelling on both telomeres (Fig. 2d). This therefore provides a method of easily identifying the *Ae. sharonensis* A chromosomes within the wheat background. The method was, therefore, used to examine the morphology, at mitosis, of the 'Selkirk' – *sharonensis* addition line produced by Maan. Fig. 3 shows that in contrast to the addition line chromosome described here, the *Ae. sharonensis* chromosome of the 'Selkirk' addition line is heavily labelled only on the telomere of the short arm, while a small interstitial band occurs on the long arm.

3 The Pairing Behaviour at Meiosis in the F_1 Hybrid Between the two Wheat – sharonensis Addition Lines

Examination of the meiosis in feulgen squashes of PMC's of the F_1 hybrid between the 'Chinese Spring' – *sharonensis* A addition line and the 'Selkirk' addition line showed a mean pairing of 1.27′, 20.53″, 0.33‴ and 0.17^{IV} instead of the 22 bivalents expected if the two chromosomes were homologous. The alien chromosomes were easily recognisable when unpaired and it was clear that one frequently paired in a trivalent while the other remained unpaired (Table 3). However, cells with 22 bivalents, in which the alien chromosomes paired together were also observed. In an attempt to try to identify which of the two *sharonensis* chromosomes was paired in the trivalent, meiotic preparations were hybridised in situ with the probe C40. As shown in Fig. 4, it was quite easy to distinguish the two types of *sharonensis* chromosome when they occurred as uni-

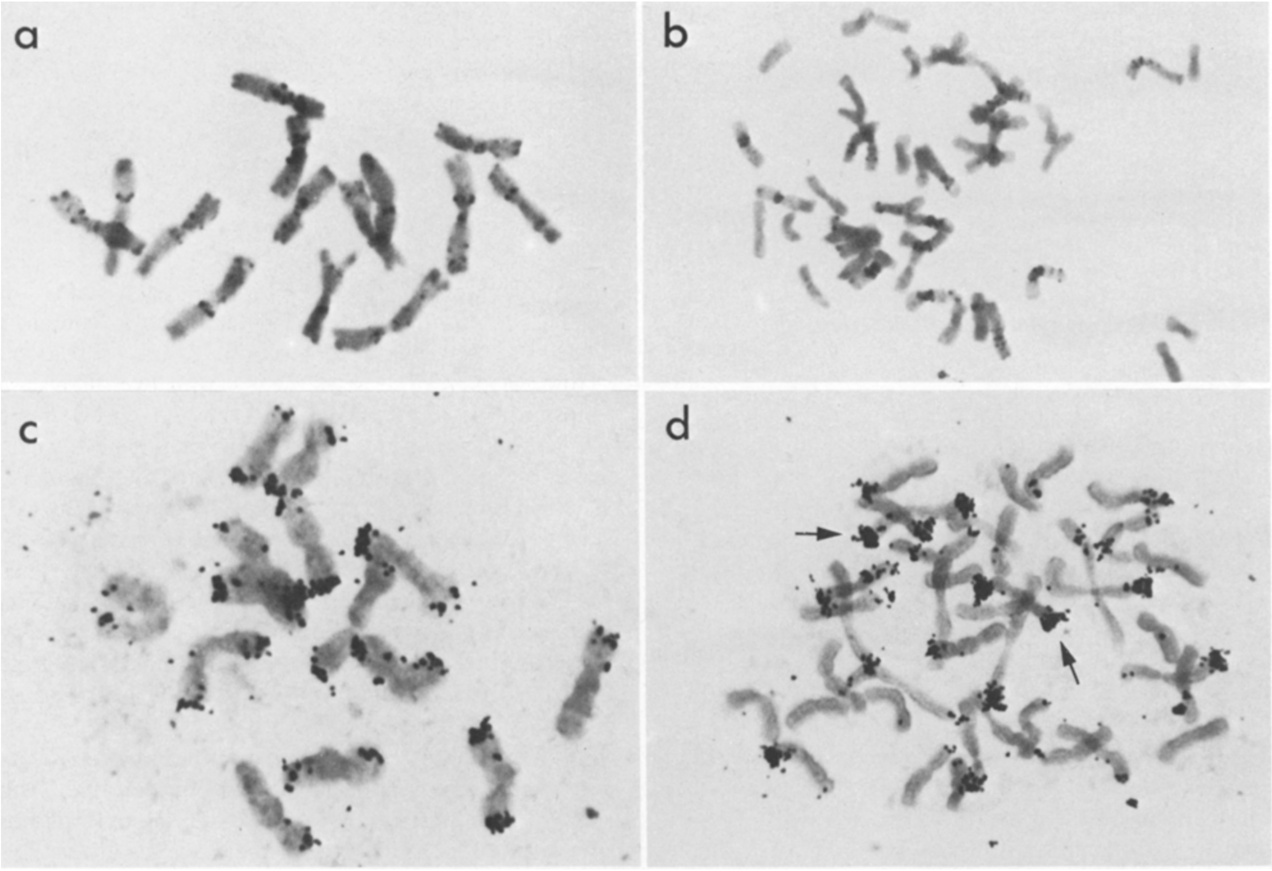

Fig. 2a–d. **a** C-banding pattern of somatic metaphase chromosomes of *Aegilops sharonensis* A.; **b** C-banding of the *T. aestivum* Selkirk – *Ae. sharonensis* addition line; **c** in situ hybridization of the triticum labelled cRNA probe C40 on mitotic chromosomes of *Ae. sharonensis* A.; **d** pattern of labelling shown by the *T. aestivum* 'Chinese Spring' – *Ae. sharonensis* A addition line with probe C40. The *Ae. sharonensis* chromosomes, which are heavily labelled on both telomeres, are arrowed

valents. Examination of 30 cells with univalents showed that in 17 of these cells only one univalent occurred. In all cases, this univalent was of the *sharonensis* A type not the 'Selkirk' addition *sharonensis* type. Following in situ hybridization of meiotic preparations, chromosome morphology may not be very clear, especially where chromosomes are close together or overlapping, but in some cells the 'Selkirk' addition *sharonensis* chromosome was seen to pair with wheat chromosomes. This observation, together with that of cells in which all chromosomes were paired (Table 3), leads to the conclusion that the two added *sharonensis* chromosomes are at least partially homologous, and that there is a translocation of part of a wheat chromosome to the long arm of the Selkirk addition *sharonensis* chromosome.

Although partially homologous, the two *sharonensis* chromosomes remain unpaired in 40% of the cells (Table 3). This may be the result of the wheat segment preventing normal synapsis of the two chromosomes or it may be pairing failure of the type reported by Chang

Table 3 Chromosome pairing at meiosis in the 'Chinese Spring' – *sharonensis* A addition × 'Selkirk' – *sharonensis* addition hybrid

	sharonensis chromosomes unpaired		*sharonensis* chromosomes paired		
			With wheat		Together
Configurations	20″ 4′	21″ 2′	20″ 1‴ 1′	$20''\ 1^{\mathrm{iv}}$	22″
No. of cells	1	11	10	5	3
Total	12		15	8	

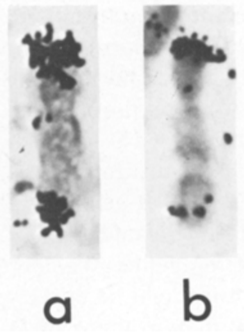

Fig. 3a and b. Pattern of labelling shown by the probe of plasmid C40 on the mitotic *Aegilops sharonensis* chromosomes of the two addition lines. **a** The *Ae. sharonensis* chromosome from the *T. aestivum* 'Chinese Spring' – *Ae. sharonensis* A addition line. **b** The *Ae. sharonensis* chromosome from the *T. aestivum* 'Selkirk' – *Ae. sharonensis* line

et al. (1973) between added homologous chromosomes from different accessions of *Secale cereale.* Similarly, pairing failure of alien homologues has been found in hybrids between amphiploids of wheat with different accessions of the same alien species (Miller 1981). In spite of the translocated chromosome being mainly *sharonensis,* it paired more frequently with a wheat chromosome (50% of the cells), than with the other *sharonensis* chromosome (26.7% of cells). In 16.7% of the cells it was paired with both a wheat and the other *sharonensis* chromosome.

4 The Production of Substitution lines

To determine the homoeology of the added chromosome, the seven D genome monosomics of 'Chinese Spring' were pollinated with the disomic addition. 42-chromosome plants, monosomic for a wheat and the alien chromosome (20″,2′), were selected with a view to extracting the substitution from the F_2 progeny of the matching wheat homoeologue. Table 4 shows the chromosome numbers of plants in the seven F_2 progenies. The progeny of the 4D cross clearly shows the highest frequency of 42-chromosome plants.

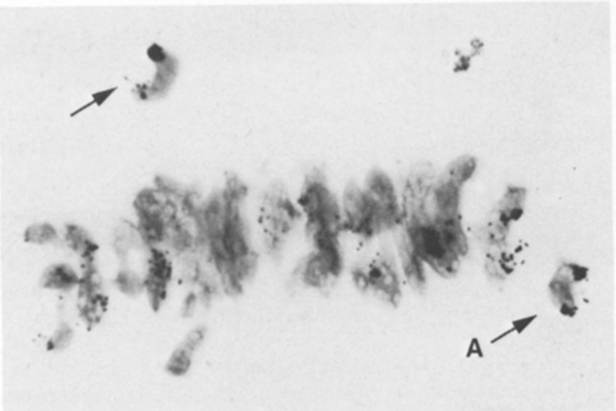

Fig. 4. In situ hybridization of the tritium labelled cRNA probe of plasmid C40 to meiotic chromosomes of the F_1 hybrid between the *T. aestivum* 'Chinese Spring' – *Ae. sharonensis* A addition line and the *T. aestivum* 'Selkirk' – *Ae. sharonensis* addition line. Both *Ae. sharonensis* chromosomes occur as univalents, the *Ae. sharonensis* A chromosome being labelled A

From the evidence of the transmission of the alien chromosome in the addition line, all plants in the F_2 monosomic progenies could be expected to contain at least two alien chromosomes, one from each gamete. However, 42-chromosome plants, with two alien chromosomes and lacking a pair of wheat chromosomes would only be expected to form vigorous well compensated plants if both the substituted and the deficient chromosomes were homoeologous. In fact only the 42-chromosome plants in the 4D deficient progeny were of similar vigour to the euploid 'Chinese Spring'. These plants had 21 bivalents at meiosis. In addition the meiosis of the F_1 hybrids of the cross with the 'Chinese Spring' double ditelocentric 4D stock made 20″ 1′ 2t′. This confirmed them as disomic substitutions for chromosome 4D.

The substitution for chromosome 4A was constructed by specifically crossing the disomic addition with the 'Chinese Spring' monosomic 4A. The disomic substitution was then extracted in the same was as for 4D.

Both the 4B substitution, which arose spontaneously during the development of the addition lines, and the 4A substitution also made 20″ 1′ 2t′ when crossed respectively with the 'Chinese Spring' 4B and 4A double ditelocentric lines.

The *sharonensis* A chromosome compensated well for the deficiency of chromosome 4A and 4D with both lines being phenotypically very like 'Chinese Spring'. This included complete compensation for the male sterility normally associated with the absence of chromosome 4A in 'Chinese Spring'. The compensation for chromosome 4B was, however, less satisfactory. The di-

Table 4. Chromosome numbers of F_2 progenies of 'Chinese Spring' D genome monosomics × 'Chinese Spring' – *sharonensis* A addition

'Chinese Spring' Monosomic	No. of plants	Chromosome numbers		
		42	43	44
1 D	2	–	–	2
2 D	2	1	1	–
3 D	16	1	10	5
4 D	18	11	7	–
5 D	2	–	–	2
6 D	3	1	1	1
7 D	3	–	3	–

somic substitution was 30 cm shorter than 'Chinese Spring' with a more bushy habit and very low fertility. The ears which were clavate and tip awned did not fully emerge from the sheaths at maturity (Fig. 1). The presence of tip awned ears results from the deficiency of the *Hd* gene carried by chromosome 4B which suppresses awning. As *Ae. sharonensis* is an awned species it would not be expected to carry an awn suppressor and could not therefore compensate for the missing suppressor.

Discussion

Selectively retained addition chromosomes have been reported for *Ae. caudata* (Endo and Katayama 1978), *Ae. cylindrica* (Endo 1979) and *Ae. triuncialis* (Endo and Tsunewaki 1975; Endo 1978) as well as for *Ae. sharonensis* (Maan 1975, 1976) (Table 2).

It appears from the observed segregation that the alien chromosome ensures its continued presence in the wheat background by either conferring an overwhelming competitive advantage to gametes carrying it (meiotic drive), or in some way preventing gametes lacking it from functioning.

The unexpected ease of isolating disomic additions direct from the double and triple monosomic additions must be the result of this preferential transmission. If all effective gametes must carry at least one of these particular chromosomes then all 44-chromosome plants in the progenies of selfed multiple additions must be disomic for the preferred chromosome. By the same process, 43-chromosome plants produced by backcrossing would all carry at least one such chromosome. Therefore, it would appear to be impossible to isolate addition lines for the remaining chromosomes of a species with this type of chromosome by the usual procedures.

It is difficult to envisage why a chromosome would evolve a mechanism of the type observed here and by other workers; especially in a diploid species where it would be unnecessary due to their inability to tolerate chromosome deficiencies. This type of chromosome has been reported in two accessions of *Ae. sharonensis* (this paper; Maan 1975) and in one accession of *Ae. longissima* (Maan 1975, 1976, 1980). Also, in a previous attempt to produce addition lines of *Ae. longissima,* Riley et al. (1962) produced a number of identical lines. Since *Ae. sharonensis* and *Ae. longissima* are now thought to be the same species (Tanaka 1955; Miller 1981), this means that the phenomenon appears to be widespread within this species. However, at least one accession of *Ae. longissima* lacking this type of chromosome must exist since a series of wheat – *Ae. longissima* addition lines have been reported by Feldman (1978).

The allocation of the *Ae. sharonensis* A chromosome to homoeologous group 4 and its homology to the one isolated by Maan makes it probable that only one chromosome within the species is preferentially transmitted. Further support is provided by the substitution for chromosome 4A of a selectively retained chromosome of *Ae. longissima* (Maan 1976; 1980). It is proposed to designate this *Ae. sharonensis* chromosome $4S^l$.

The poor compensation of the 4B substitution was unexpected. If as generally accepted the B genome of wheat originated from a genome closely related to the S genomes of the Sitopsis section of the genus *Aegilops,* then the S^1 genome of *Ae. sharonensis* might be expected to have a closer affinity to the B than to the A or D genomes of wheat. Alternatively, chromosome 4B of hexaploid wheat may have become modified and no longer be a true fit for homoeologous group 4. This possibility is supported by the substitution of *Agropyron elongatum* chromosome 4E for the wheat group 4 chromosomes, where the compensation was poor for chromosome 4B (Dvorak 1979).

The presence of a selectively retained chromosome in a breeding programme might prove of value, if it carried desirable characters. The breeder would be able to concentrate on selecting other characters knowing that those on the retained chromosome would be maintained. Translocations of the $4S^l$ chromosome to wheat chromosomes are possible, on the evidence of the Selkirk-*sharonensis* addition line, chromosome. Maan (1976) also reported that the chromosome isolated from *Ae. longissima* was also seen to pair occassionally with a wheat chromosome. Therefore, it would appear possible to create selectively retained chromosomes with desired wheat characters.

The finding of selectively retained chromosomes in genomes of the Triticae may be of evolutionary significance. In situations where speciation occurred as a result of introgression (Zohary and Vardi 1967) selectively retained chromosomes, if present, would be included in the new species. This might explain the difficulty of finding the exact donor of some of the genomes of polyploid species.

Literature

Appels, R.; Driscoll, C.; Peacock, W.J. (1978): Heterochromatin and highly repeated DNA sequences in rye (*Secale cereale*). Chromosoma **70**, 67–89

Chang, T.D.; Kimber, G.; Sears, E.R. (1973): Genetic analysis of rye chromosomes added to wheat. Proc. 4th Int. Wheat Genet. Symp., pp. 151–153 Columbia, Mo. University of Missouri

Chennaveeraiah, M.S. (1960): Karyomorphologic and cytotaxanomic studies in *Aegilops.* Acta Horti-Gotoburgensis **23**, 85–178

Dvorak, J. (1980): Homoeology between *Agropyron elongatum* chromosomes and *Triticum aestivum* chromosomes. Can. J. Genet. Cytol. **22**, 237–259

Endo, T.R. (1978): On the *Aegilops* chromosomes having gametocidal action on common wheat. Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. Ind. Soc. of Genet. and Plant Breeding **1**, 306–314

Endo, T.R. (1979): Selective gametocidal action of a chromosome of *Aegilops cylindrica* in a cultivar of common wheat. Wheat Inf. Serv. **50**, 24–28

Endo, T.R.; Tsunewaki, K. (1975): Sterility of common wheat with *Aegilops triuncialis* cytoplasm. J. Hered. **66**, 13–18

Endo, T.R.; Katayama, Y. (1978): Finding of a selectively retained chromosome of *Aegilops caudata* L. in common wheat. Wheat Inf. Serv. **47–48**, 32–35

Feldman, M. (1978): Origin of the B genome. Proc. 5th Int. Wheat Genet. Symp., New Delhi, India. Ind. Soc. of Genet. and Plant Breeding **1**, 120–132

Gerlach, W.L. (1977): N-banded karyotypes of wheat species. Chromosoma **62**, 49–56

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

Hutchinson, J.; Chapman, V.; Miller, T.E. (1980): Chromosome pairing at meiosis in hybrids between *Aegilops* and *Secale* species: a study by in situ hybridisation using cloned DNA. Heredity **45**, 245–254

Iordansky, A.B.; Zurabishvili, T.B.; Badaev, N.S. (1978): Linear differentiation of cereal chromosomes I. Common wheat and its supposed ancestors. Theor. Appl. Genet. **51**, 145–152

Maan, S.S. (1975): Exclusive preferential transmission of an alien chromosome in common wheat. Crop Sci. **15**, 287–292

Maan, S.S. (1976): Alien chromosome controling sporophytic sterility in common wheat. Crop Sci. **16**, 580–583

Maan, S.S. (1980): Alteration of sporophytic sterility mechanism in wheat. J. Hered. **71**, 75–82

Miller, T.E. (1981): Chromosome pairing of intergeneric amphiploids as a means of assessing genome relationships in the Triticeae. Z. Pflanzenzücht. **87**, 69–78

O'Mara, J.G. (1950): Cytogenetic studies on Triticale I. A method for determining the effects of individual *Secale* chromosomes on *Triticum*. Genetics **25**, 401–408

Riley, R.; Chapman, V.; Johnson, R. (1968): The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synapsis. Genet. Res. **12**, 199–219

Riley, R.; Chapman, V.; Macer, R.C.F. (1966): The homoeology of an *Aegilops* chromosome causing stripe rust resistance. Can. J. Genet. Cytol. **8**, 616–630

Riley, R.; Kimber, G.; Law, C.N. (1962): Ann. Rep. Plant Breed. Inst., Cambridge, England 1961–62, 70

Riley, R.; Unrau, J.; Chapman, V. (1958): Evidence on the origin of the B genome of wheat. J. Hered. **49**, 91–99

Seal, A.G.; Bennett, M.D. (1981): The rye genome in winter hexaploid triticales. Can. J. Genet. Cytol. (in press)

Sears, E.R. (1968): Relationships of chromosomes 2A, 2B and 2D with their rye homoeologue. Proc. 3rd Int. Wheat Genetical Symp., pp. 53–61 Canberra: Aust. Acad. Sci.

Sears, E.R. (1973): *Agropyron* – wheat transfers induced by homoeologous pairing. Proc. 4th Int. Wheat. Genet. Symp., pp. 191–199. Columbia, Missouri: University of Missouri

Tanaka, M. (1955): Chromosome pairing in hybrids between *Aegilops sharonensis* and some species of *Aegilops* and *Triticum*. Wheat. Inf. Serv. **2**, 7–8

Zohary, D., Vardi, A. (1967: Introgression in wheat via triploid hybrids. Heredity **22**, 541–560

Received May 20, 1981
Communicated by R. Riley

Mr. T. E. Miller
Dr. J. Hutchinson
Mr. V. Chapman
Plant Breeding Institute
Maris Lane, Trumpington
Cambridge CB2 2LQ (England)