Theor Appl Genet (1991) 81:381–389

© Springer-Verlag 1991

Identification of alien chromatin specifying resistance to wheat streak mosaic and greenbug in wheat germ plasm by C-banding and in situ hybridization*

B. Friebe[1], **Y. Mukai**[2], **H.S. Dhaliwal**[3], **T.J. Martin**[4] **and B.S. Gill**[5,**]

[1] Institute of Plant Breeding, Technical University of Munich-Weihenstephan, Munich, Germany
[2] Department of Biology, Osaka Kyoiku University, Ikeda, Osaka, Japan
[3] P.A.U. Regional Research Station, Gurdaspur, Punjab, India
[4] Hays Experiment Station, Hays, KS 67601, USA
[5] Department of Plant Pathology, Throckmorton Hall, Kansas State University, Manhattan, KS 66506-5502, USA

Received May 10, 1990; Accepted August 7, 1990
Communicated by J.W. Snape

Summary. The chromosome constitutions of eight wheat streak mosaic virus (WSMV)-resistant lines, three of which are also greenbug resistant, derived from wheat/*Agropyron intermedium*/*Aegilops speltoides* crosses were analyzed by C-banding and in situ hybridization. All lines could be traced back to CI15092 in which chromosome *4A* is substituted for by an *Ag. intermedium* chromosome designated *4Ai-2*, and the derived lines carry either *4Ai-2* or a part of it. Two (CI17881, CI17886) were *4Ai-2* addition lines. CI17882 and CI17885 were *4Ai-2(4D)* substitution lines. CI17883 was a translocation substitution line with a pair of *6AL.4Ai-2S* and a pair of *6AS.4Ai-2L* chromosomes substituting for chromosome pairs *4D* and *6A* of wheat. CI17884 carried a *4DL.4Ai-2S* translocation which substituted for chromosome *4D*. CI17766 carried a *4AL.4Ai-2S* translocation substituting for chromosome *4A*. The results show that the *4Ai-2* chromosome is related to homoeologous group 4 and that the resistance gene(s) against WSMV is located on the short arm of *4Ai-2*. In addition, CI17882, CI17884, and CI17885 contained *Ae. speltoides* chromosome *7S* substituting for chromosome *7A* of wheat. The greenbug resistance gene *Gb5* was located on chromosome 7S.

Key words: Wheat curl mite – Alien addition line – Alien translocation line – *Agropyron intermedium* – *Aegilops speltoides*

Introduction

Wheat streak mosaic (WSM) is a serious virus disease of wheat in the United States, Canada, and other countries of the world. Estimated losses due to WSM in Kansas from 1976–1987 ranged from very low to 13% with an average of 2.5% (Sim et al. 1988). Wheat curl mite (*Aceria tulipae* Keifer) is the virus vector of WSM (Slykhuis 1955). No wheat cultivar is immune to WSM. In earlier as well as recent studies, among the Triticeae, only the perennial genera (*Secale cereale* [rye], *Agropyron elongatum, Ag. intermedium*, and other *Agropyron* species) have been found resistant to either the virus, vector, or both (McKinney and Sando 1951; Somsen and Sill 1970; Martin et al. 1976; Sharma et al. 1984; Stoddard et al. 1987a, b).

Wheat streak mosaic virus (WSMV)-resistant germ plasm has been derived from wheat × *Ag. intermedium* (Lay et al. 1971; Wells et al. 1973; Wang et al. 1977; Liang et al. 1979; Wells et al. 1982) and wheat × *Ag. elongatum* hybrids (Sebesta and Bellingham 1963; Larson and Atkinson 1970; Sebesta et al. 1972). The chromosomal constitution of some of the wheat-*Agropyron* germ plasm has been partially analyzed (Larson and Atkinson 1970; Wang and Liang 1977). However, all released germ plasm has been found to possess one or more undesirable agronomic traits and has not led to the development of new cultivars. Therefore, the development of an agronomically superior germ plasm with good levels of resistance against WSMV remains an important objective.

Greenbug [*Schizaphis graminum* (Rondani)] has been a serious pest of wheat since 1882 and of *Sorghum bicolor* (L.) Moench since 1968. Resistance to greenbug has been reported in *Aegilops* species and rye (Arriaga 1954; Wood et al. 1974; Harvey et al. 1980; Gill et al. 1985, 1986; Tyler et al. 1988; Joppa et al. 1980). Tyler et al. (1985,

---

* Contribution No. 90-515-J from the Kansas Agricultural Experiment Station, Kansas State University, Manhattan, Kan., USA

** To whom offprint requests should be addressed.

1986) reported that some WSMV-resistant lines were also resistant to greenbug biotype E and that both resistance genes showed independent segregation. They also suggested that *Ae. speltoides* was most probably the donor of the greenbug resistance.

Giemsa C-banding, which allows the identification of all chromosomes and most chromosome arms of hexaploid wheat, *Triticum aestivum* L. em Thell. (Gill 1987), was used to identify the *Ag. intermedium* and *Ae. speltoides* chromosomes or chromosome segments in lines with resistance to both WSMV and greenbug or WSMV alone. In situ hybridization (ISH) using biotin-labeled DNA probes (Rayburn and Gill 1985 a) was used to further verify the identification of *Ag. intermedium* and *Ae. speltoides* chromosomes. This information will be crucial in chromosome engineering experiments aimed at producing agronomically desirable WSMV-resistant and greenbug-resistant germ plasm.

Table 1. Reaction to wheat streak mosaic infection in wheat-*Agropyron intermedium* derivatives

Germ plasm	Visual symptoms	Bioassay	
		Corn	Wheat
CI15092	–	–	–
CI17881	–	–	–
CI17882	–	–	+ (2/10)
CI17883	–	–	–
CI17884	–	–	–
CI17885	–	–	–
CI17886	–	–	+ (2/10)
CI17766[a]	–	Not done	–
Infected control 'Wichita'	+	+	+
Healthy control 'Wichita'	–	–	–

+, infected; –, immune response

[a] Data from Stoddard et al. (1987). Out of 15 plants 1 showed symptoms 14 days postinoculation

Materials and methods

The material analyzed in the present investigation comprised eight lines of wheat with WSMV resistance derived from *Ag. intermedium.* The history, genetic background, and chromosomal constitution of these lines are as follows:

CI15092 (SD447-4) is a spring wheat immune to WSMV. This line was selected from a cross between 'TA25' and 'Lathrop' spring wheat. 'TA25', an octoploid *Agrotricum*, was developed at the Max Planck Institute in Germany from the cross 'Carstens V'/*Ag. intermedium* (Wells et al. 1973). Plants from irradiated F_1 seeds of 'TA25' × 'Lathrop' were backcrossed to wheat. From the self of BC_3, a 42-chromosome line immune to WSMV involving either a wheat-*Agropyron* chromosome substitution or translocation was derived (Lay et al. 1971). This line was identified as being a substitution line in which chromosome pair *4A* of wheat (formerly *4B*) has been replaced by its homoeologue from *Ag. intermedium.* The major gene conditioning resistance against WSMV may be located on the short arm of the *Ag. intermedium* chromosome (Wang and Liang 1977). The line is resistant to WSMV but not its vector, the wheat curl mite (Martin et al. 1976).

CI15092 was used to produce a number of derivative lines from CI17881 to CI17886. A disomic substitution line from a cross CI10592/*Ae. speltoides*/'Fletcher' was crossed to 'Centurk', and 300 of the F_1 seeds were irradiated with fast neutrons. After four backcrosses to 'Centurk', five translocation lines and a number of disomic substitution lines resistant to WSMV were released (Kota 1980; Wells et al. 1982). Lines CI17881, CI17882, CI17883, CI17884, and CI17886 have been described as translocation lines, except for line CI17885, which was described as a substitution line. However, neither the *Ag. intermedium* chromosome substituting for chromosome *4A* in line CI15092 has been identified by describing its C-banding pattern, nor has the identity of the wheat-*Agropyron* translocations present in lines CI17881 to CI17885 been established.

Line CI17766 (Sel. no. B-6-37-1) was selected by Liang et al. (1979) in the progeny of the cross, 'Chinese Spring' monosomic 5B × CI15092, and the F_1 was then crossed with a ph mutant line. Line CI17766 is resistant against all known strains of WSMV and was described as a translocation line (Liang et al. 1979). Furthermore, it was assumed that the wheat-*Ag. intermedium* chromosome translocation was produced by ph-induced homoeologous meiotic pairing.

Tyler et al. (1985) determined that CI17882, CI17884, and CI17885 were also resistant to greenbug biotype E. KS90H445 and KS90H450 were derived from CI17884 following two random matings with many wheat parents in a recurrent breeding program. KS90H445 is resistant to both WSMV and greenbug, whereas KS90H450 is resistant to WSMV, but susceptible to greenbug.

All lines were screened for their resistance against WSMV to confirm the presence of *Agropyron* chromosomes or chromosome segments. One WSMV culture isolated from a greenhouse-infected wheat plant, and maintained on a maize inbred (Uyemoto and Ferguson 1980), was used for the resistance screening (Martin 1978).

The C-banding was performed using the technique of Giraldez et al. (1979). The in situ hybridization protocol followed that of Rayburn and Gill (1985a).

Photographs were taken either with an Olympus NC SPlanAPo 60 (oil) objective, using Kodak technical Pan film 2415 for in situ hybridization, or with a Zeiss Photomicroscope III using a Kodak Image Capture AHU microfilm 5460 for C-banded chromosomes.

Results

WSMV resistance evaluation

The results of the resistance analysis are summarized in Table 1. All seven wheat × *Agropyron* derivatives were resistant to WSMV under greenhouse conditions whereas the control cv 'Wichita' gave a susceptible reaction. The line CI17881 which was found to be susceptible to WSMV by Stoddard et al. (1987b) gave a resistant reaction in the present analysis. However, a few susceptible plants (2/8) were observed in CI17882 and CI17886, which could be due to cytological instability of the lines.

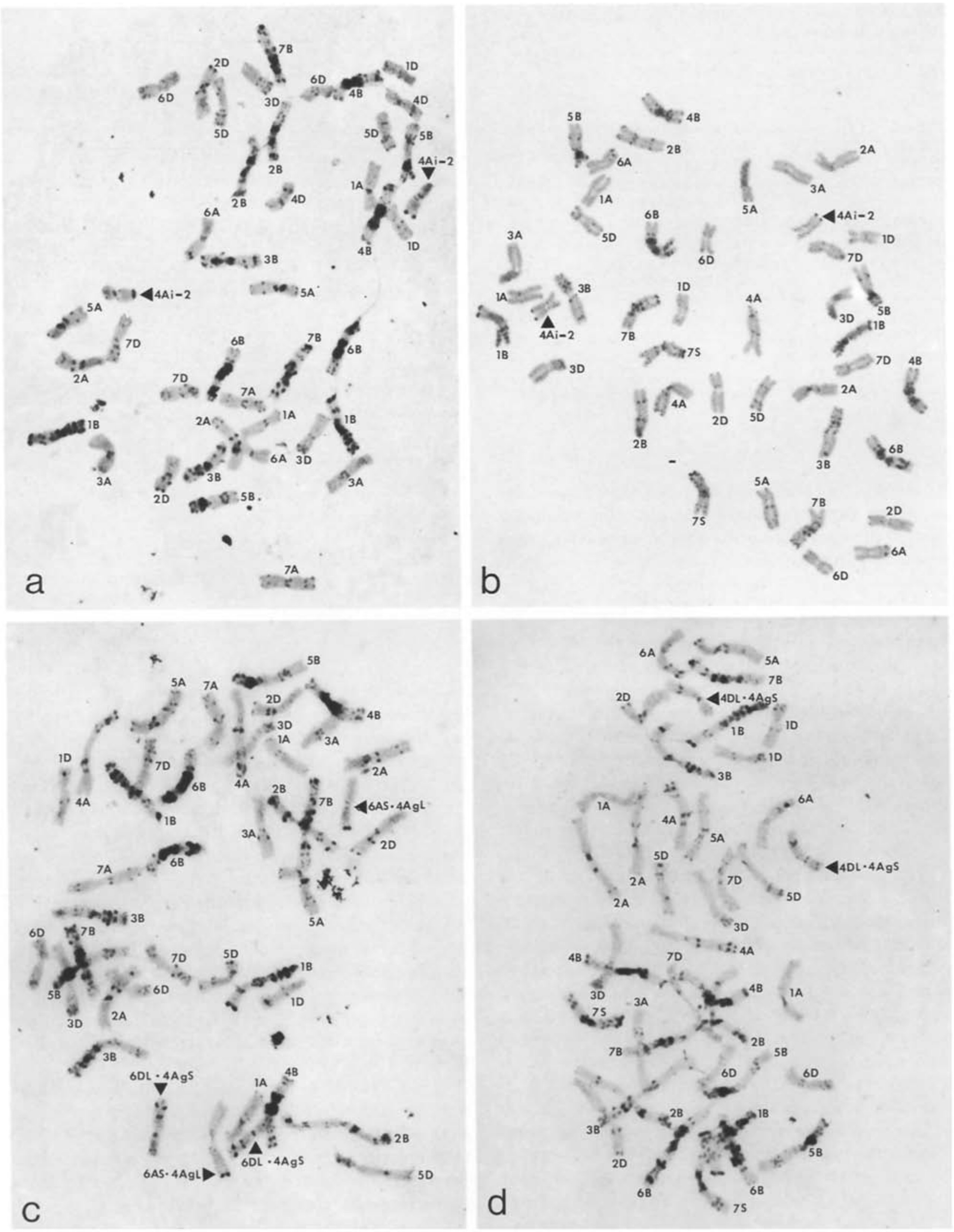

Fig. 1a–d. C-banded mitotic metaphases of WSMV-resistant lines: **a** CI15092 (2n = 42), *4Ai-2(4A)* substitution line; **b** CI17882 (2n = 42), *4Ai-2(4D)* substitution line; **c** CI17883, (2n = 42, homozygous for a *6AL.4Ai-2S* and *6AS.4Ai-2L* translocation substituting for chromosomes *6A* and *4D*; **d** CI17884 (2n = 42), *4DL.4Ai-2S* translocation line. In lines CI17882 and CI17884 chromosome *7A* of wheat is missing and replaced by a chromosome pair from *Aegilops speltoides* designated *7S*. (*Ag. intermedium* chromosomes or chromosome arms are marked with *triangles*)

Table 2. Chromosome constitution of wheat germ plasm resistant to wheat streak mosaic virus

Line	Previous results[c]	Present results[d]
CI15092	S	42, S *4Ai-2(4A)*
CI17881	T	44, A *4Ai-2*
CI17882[a]	T	42, S *4Ai-2(4D), 7S(7A)*
CI17883	T	42, T *6AL.4Ai-2S+6AS.4Ai-2L (6A+4D)*
CI17884[a]	T	42, T *4DL.Ai-2S, S 7S (7A)*
CI17885[a]	S	42, S *4Ai-2(4D), 7S(7A)*
CI17886	T	44, A *4Ai-2*
CI17766[b]	T	42, T *4AL.4Ai-2S*

[a] Tyler et al. (1985) found these lines to be greenbug resistant also. All contain chromosome *7S* from *Aegilops speltoides* substituting for chromosome *7A* of wheat

[b] Liang et al. (1979)

[c] Wells et al. (1982); S = substitution, T = translocation

[d] A = addition

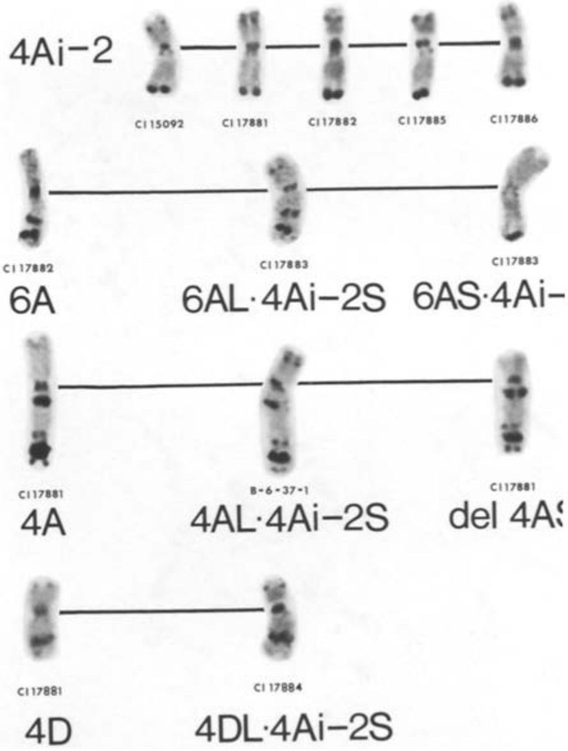

Fig. 2. C-banding pattern of the critical chromosomes or chromosome arms present in the WSMV-resistant germ plasm. Note B-6-37-1 is CI17766

The results of a bioassay on the maize inbred and 'Chinese Spring' for the presence of the virus in the inoculated plants of the wheat-*Agropyron* derivatives without symptoms were also negative.

Chromosome constitution of WSMV-resistant germ plasm

The chromosomal constitutions of the eight WSMV-resistant lines analyzed in the present study are summarized in Table 2. A C-banded mitotic metaphase from a plant of line CI15092 is shown in Fig. 1 a. With the exception of chromosome *4A*, which is missing in this line, all the other *A*-, *B*-, and *D*-genome chromosomes of wheat show a similar C-banding pattern to that described for other cultivars of wheat (Gill 1987). This line carries a small submetacentric chromosome pair derived from the *Ag. intermedium* parent that differs in C-banding pattern from all chromosomes of cultivated wheat. A small but distinct subterminal C-band is present in the short arm, whereas the long arm of this chromosome shows a small band adjacent to the centromere and a prominent C-band at the telomere (see Fig. 2). Since the *Ag. intermedium* chromosome pair compensates for the loss of chromosome pair *4A* of wheat, this indicates that it belongs to homoeologous group 4 of the *Triticinae* and was designated *4Ai-2* accordingly. The genomic constitution of *Ag. intermedium* is *E1E1E2E2XX* (Dewey 1984), and three different pairs of chromosomes comprise the group 4 set. Because one group 4 chromosome has already been reported that should be *4Ai-1* (Cauderon et al. 1973; Forster et al. 1987), the present chromosome is designated *4Ai-2*. The *Ai* designation is preferable because of precedence, and also because genomic origin is unknown.

Wang and Liang (1977) reported that in line CI15092 chromosome pair *4A* of wheat (formerly *4B*) was missing and replaced by a chromosome pair from *Ag. intermedium*, but evidence in support of their conclusion was missing. However, Shepherd and Islam (1988) indicated that this determination was made by Larson (entry no. 563, p 1386, Proc 7th Int. Wheat Genet Symp., Cambridge, England). Our results not only confirm the presence of a *4Ai-2(4A)* chromosome substitution in this line but furthermore, we were able to identify the *4Ai-2* by its characteristic C-banding pattern.

CI17881 and CI17886, although being described as wheat-*Agropyron* translocation lines (Wells et al. 1982), have a chromosome number of 2n = 44, indicating that they are in fact chromosome addition lines and carry the *4Ai-2* chromosome pair in addition to the normal chromosome complement of wheat. CI17881 was heterozygous for a deletion of the distal part of wheat chromosome arm *4AS* (see Fig. 2).

Lines CI17882 to 17885 and CI17766 showed a chromosome number of 2n = 42. In line CI17882, chromosome pair *4D* is replaced by a chromosome pair of *4Ai-2* (Fig. 1 b). In addition, this line carries a chromosome pair designated *7S* from the *Ae. speltoides* parent substituting for wheat chromosome pair *7A* (Fig. 3).

In CI17883, chromosome pair *4D* of wheat is missing, and chromosome *4Ai-2* is involved in a reciprocal translocation with chromosome *6A* of wheat with breakpoints in the centromeric region (Fig. 1c). All analyzed plants of this germ plasm were homozygous for the *6AL.4Ai-2S* and *6AS.4Ai-2L* translocation chromosomes (Fig. 2).

Our results confirm earlier reports (Wells et al. 1982) that line CI17883 carries a wheat-*Agropyron* translocation. However, both arms of chromosome *4Ai-2* are still present in this line. CI17883 can be best described as a *4Ai-2(4D)* chromosome substitution line, carrying a chromosome pair *4Ai-2* in the form of *6AL.4Ai-2S* and *6AS.4Ai-2L*.

In line CI17884, the short arm of chromosome *4Ai-2* is translocated to the long arm of *4D* to form *4DL.4Ai-2S*, and the breakpoints of this translocation are within the centromeric region (Figs. 1d, 2). In addition, CI17884 also carries chromosome *7S* substituting for chromosome *7A*.

Our data confirm an earlier report (Wells et al. 1982) that CI17884 is a translocation line. Since CI17884 lacks the *4Ai-2L* arm but still shows resistance against WSMV (Table 1), our results further confirm that the gene or gene complex conditioning resistance against WSMV is located on the short arm of *4Ai-2* (Wang and Liang 1977).

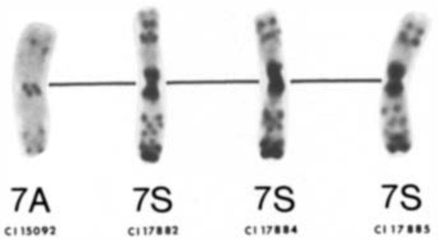

Fig. 3. C-banding pattern of *7S* chromosomes substituting for *7A* chromosomes in wheat germ plasm

In line CI17885, chromosome pair *4D* is missing and replaced by *4Ai-2* pair (Fig. 2). In addition, CI17885 has a *7S(7A)* substitution (Fig. 3).

In CI17766, the short arm of *4Ai-2* is translocated to the long arm of wheat chromosome *4A*, resulting in a *4AL.4Ai-2S* translocation substituting for *4A*; the breakpoints of this translocation are within the centromeric region (Figs. 2, 4). This result again confirms that *4Ai-2S* arm carries gene(s) for WSMV resistance.

Chromosome constitution of greenbug-resistant germ plasm

Tyler et al. (1985) analyzed the reaction of the parental CI15092 line and derived lines CI17881 to CI17886 to infestation with greenbug (*Schizaphis graminum*) biotype E. CI17882, CI17884, and CI17885 were resistant, while the remaining lines including CI15092 were susceptible. These results indicated that greenbug resistance was not due to *4Ai-2*, since the parental line CI15092 was susceptible. In addition, F_2 analysis indicated that resistance to WSMV and greenbug showed independent assortment (Tyler et al. 1986). Since all lines derived from CI15092 included *Ae. speltoides* in their pedigree, which is known to harbor resistance to greenbug (Gill et al. 1985), Tyler et al. (1985) concluded that greenbug resistance in CI17882, CI17884, and CI17885 was derived from *Ae. speltoides*.

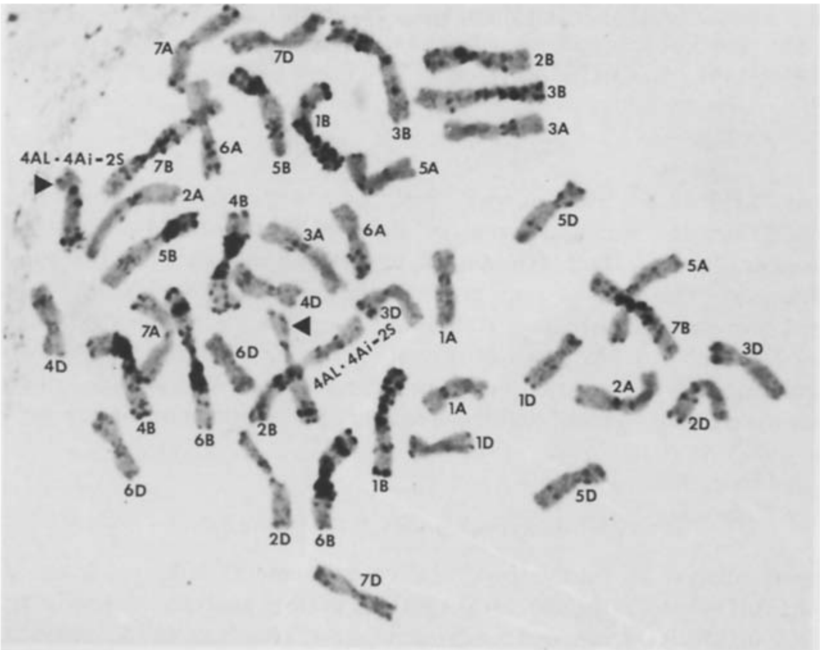

Fig. 4. C-banded mitotic metaphase of CI17766 carrying a *4AL.4Ai-2S* translocation

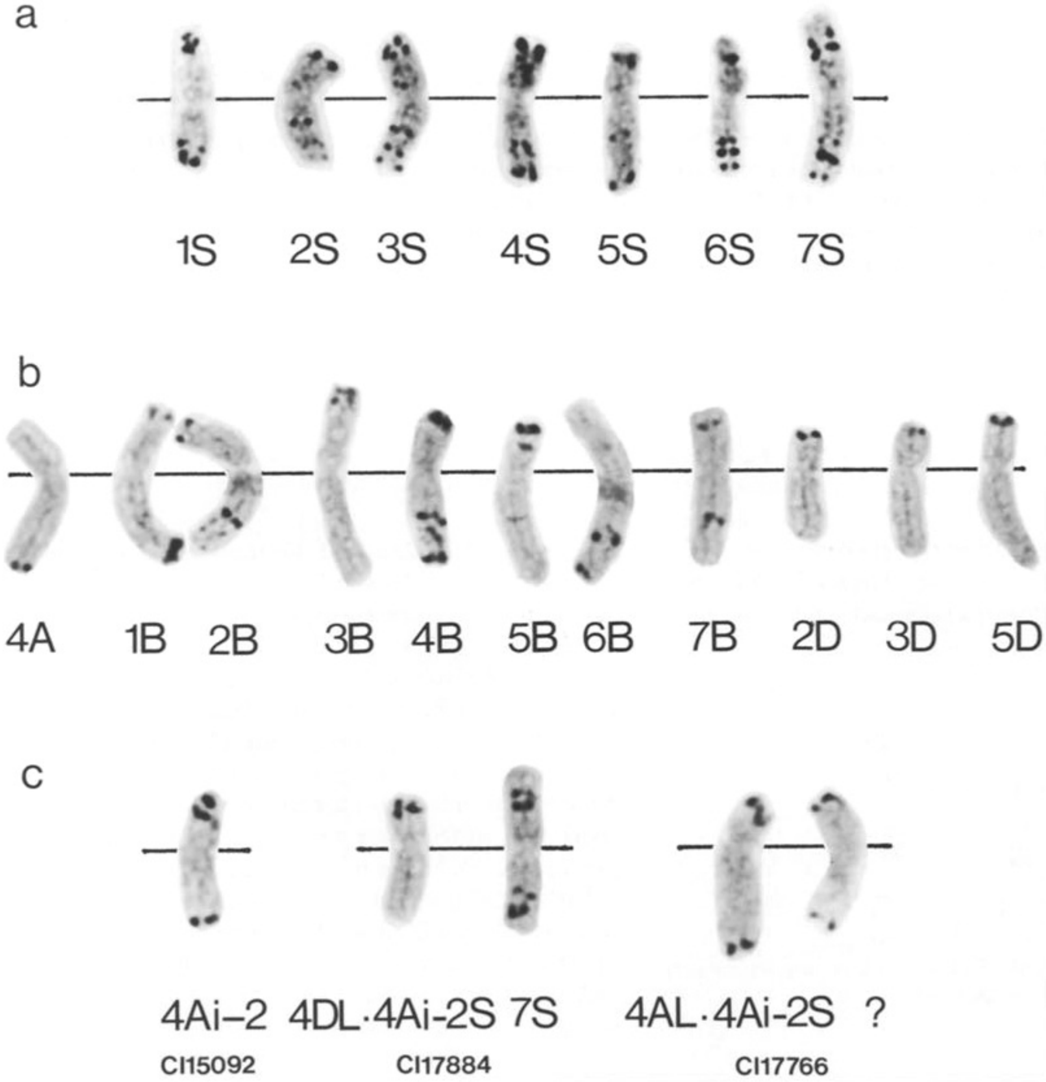

Fig. 5a–c. ISH karyotypes using pSc119 probe. **a** *Aegilops speltoides* (TA1783) ISH karyotype. **b** ISH-labeled wheat chromosomes in WSMV-resistant lines. **c** CI15092 had *4Ai-2* with three ISH sites substituting for chromosome *4A*. CI17884 had chromosomes *4DL.4Ai-2S* and *7S* substituting for chromosomes *4D* and *7A*. CI17766 had *4AL.4Ai-2S* substituting for *4A* and an unidentified chromosome with a terminal ISH site in each arm

Our C-banding results indicate that CI17882, CI17884, and CI17885 contain chromosome *7S* from *Ae. speltoides* substituting for missing chromosome *7A* of wheat (Fig. 3). All greenbug-susceptible lines carry the normal chromosome *7A* of wheat. Therefore, our results indicate that the chromosome *7S* of *Ae. speltoides* carries the greenbug resistance gene. Thus, the greenbug-resistance gene, which was designated *Gb5*, is located on chromosome *7S* of *Ae. speltoides* (Tyler et al. 1987). It is interesting to note that *Gb3*, which originated from *Ae. squarrosa*, was mapped on *7D*, also a group 7 chromosome (Hollenhorst and Joppa 1983).

CI17884 was used in a random mating population to obtain lines KS90H445 and KS90H450. KS90H445 is resistant to both WSMV and greenbug. KS90H450 is resistant to WSMV, but is susceptible to greenbug. C-banding analysis indicated that KS90H445 contained both *4DL.4Ai-2S* and *7S* chromosomes and that these must respectively condition resistance to WSMV and greenbug. KS90H450 contained chromosome *4DL.4Ai-2S* but was missing *7S* chromosome and was WSMV resistant but greenbug susceptible. This provided direct proof that the greenbug gene is located on chromosome *7S*.

In situ hybridization (ISH) analysis

Further proof that chromosome *7S* is derived from *Ae. speltoides* was obtained by ISH analysis. As previously reported for chromosome *4S* (Rayburn and Gill 1985 b), *Ae. speltoides* gave distinct patterns of hybridization with rye probe pSc119. A complete ISH karyotpye of *Ae. speltoides* using pSc119 probe is shown in Fig. 5. All individual chromosomes can be classified in terms of homoeology as deduced from the similarity of their ISH karyotype to the ISH karyotype of wheat (Rayburn and Gill 1985a). The ISH sites observed on *7S* in CI17884 were similar to *7S* of *Ae. speltoides* with one minor exception: the long arm of *7S* in the latter showed three ISH sites compared to two found in *7S* in CI17884. This could be due to a translocation of *7S* with an unidentified chromosome of wheat or ISH polymorphism as the original *Ae. speltoides* accession used in the breeding of CI17884 was not available for analysis.

ISH analysis with pSc119 also revealed two ISH sites in the short arm and one terminal ISH site in the long arm of chromosome *4Ai-2* in CI15092, thereby providing a distinct fingerprint of this chromosome (Fig. 5). In CI17884, a chromosome was observed with the short arm fingerprint of *4Ai-2S* translocated to a long arm devoid of an ISH site (Fig. 5). This confirmed the results obtained by C-banding that CI17884 contains the short arm of chromosome *4Ai-2*. The *4DL* arm of wheat is known to be devoid of pSc119-generated ISH sites (Rayburn and Gill 1985a). No ISH sites were observed on the *4DL* arm in the *4DL.4Ai-2S* translocation chromosome (Fig. 5).

ISH analysis of CI17766 with pSc119 showed the short arm fingerprint of *4Ai-2S* translocated to chromosome arm *4AL* of wheat. The *4AL* arm can be identified because of its terminal ISH site (Fig. 5). These results confirmed the identification from C-banding analysis. However, another unidentified chromosome with terminal ISH sites in each arm was observed in CI17766. This chromosome could not have originated from *4Ai-2L* as an isochromosome because of its unequal arm ratio. Moreover, C-banding analysis clearly revealed that except for the *4AL-4Ai-2S* translocation in CI17766, the remaining chromosomes are typical of wheat. At present, the origin of the terminally labeled chromosome remains obscure.

Discussion

With the exception of CI17766 all the other WSMV-resistant lines analyzed in this study were produced after mutagenic irradiation treatment. C-banding analysis shows that the chromosome translocations found in lines CI17883 and CI17884 involved complete chromosome arms and could have originated by the common centromeric-breakage-fusion mechanism (Lukaszewski and Gustafson 1983; Friebe and Larter 1988; also see next paragraph). This result again indicates that interstitial chromosome translocations are rare following mutagenic irradiation treatment (Driscoll and Sears 1965; Driscoll and Bielig 1968; Sebesta and Wood 1978; Heun and Friebe, in press).

It has been assumed that the translocation in CI17766 was produced by ph-induced homoeologous pairing (Liang et al. 1979). Our data show that the breakpoint of this translocation is within the centromeric region. Similar centromeric-breakage-fusion products have been frequently observed in wheat-rye hybrids between chromosomes, which are seen as univalents at meiotic metaphase I (Lukaszewski and Gustafson 1983; Friebe and Larter 1988). These univalents can misdivide at the centromere, and the resulting telocentric chromosomes have a tendency to fuse again. If this fusion occurs between telocentrics of different chromosomes, the resulting translocation consists of complete arms of two different chromosomes. CI17766 was produced by crossing 'Chinese Spring' monosomic for chromosome *5B* to the *4Ai-2(4A)* wheat-*Ag. intermedium* substitution line CI15092. In the F_1-hybrid chromosomes *5B, 4A*, and *4Ai-2* were univalents and had a chance to undergo centromeric-breakage-fusion. Thus, the *4AL.4Ai-2S* translocation might have been produced by this mechanism.

Although the S genome of *Ae. speltoides* is closely related to the B genome of wheat, it is interesting to note that the chromosome *7S* spontaneously substituted for chromosome *7A* rather than *7B*. However, this was not unexpected since the *7B* chromosome is known to be involved in a cyclical translocation with chromosomes *4A* and *5A* (Naranjo et al. 1987) to form translocation chromosomes *4A/7B, 5A/4B*, and *7B/5A*. Therefore, the genetic content of chromosome *7S* is closer to *7A* rather than to the structurally modified (*7B*) chromosome.

The *4Ai-2S* arm has been shown to contain one subterminal C-band and two ISH sites as revealed by clone pSc119 (one terminal and one subterminal). Furthermore we have identified one RFLP probe that marks this arm (unpublished results). These cytological and molecular markers will be useful in further recombinational analysis of the *4Ai-2S* arm.

The *Ag. intermedium* chromosome pair *4Ai-2* substituted for the loss of wheat chromosome pair *4A* in line CI15092 and chromosome pair *4D* in lines CI17882, CI17883, and CI17885. These results indicate that *4Ai-2* belongs to the homoeologous group four of *Triticinae*. In lines CI17884 and CI17766, the short arm of *4Ai-2* is translocated either to the long arm of wheat chromosome *4D* (CI17884) or to the long arm of wheat chromosome *4A* (CI17766). In this case the translocation has occurred between chromosomes of the same homoeologous group, and the loss of the short arm of wheat chromosomes *4A* and *4D* is compensated by the presence of the *4Ai-2S* arm. Since these lines also show resistance against WSMV, the resistance gene(s) are located on the short arm of the *4Ai-2* chromosome.

It is known that the *4DL* and *4BL* arms share homoeology with the *4AS* arm of wheat and vice versa (Hart 1973). In this sense *4Ai-2S.4AL* in CI17886 may not be a truly compensating type of translocation. Thus, CI17766 is nullisomic for part of the chromatin homoeologous to group 4 long arms and is tetrasomic for part of the group 4 short arms. On the other hand, CI17884 contains translocation chromosome *4DL.4Ai-2S* in which the *4DS* arm is substituted by the *4Ai-2S* arm. Because these arms are homoeologous, CI17884 may be agronomically more desirable.

Unfortunately, line CI17884 was also crossed with *Ae. speltoides* and carries chromosome pair *7S* of *Ae. speltoides*, which replaces chromosome pair *7A* of wheat. By crossing CI17884 with a number of wheat parents, it was possible to select a new WSMV-resistant line that only possesses the *4DL.4Ai-2S* translocation, but does not carry the *7S* chromosome pair of *Ae. speltoides.* KS90H450 hopefully will perform better than the presently available WSMV-resistant germ plasm. However, if KS90H450 is also found to be agronomically undesirable, then further chromosome manipulation of the *4Ai-2S* arm will be required to break the linkage between deleterious traits and resistance to WSMV.

By the same crosses it should be possible to isolate greenbug-resistant lines carrying chromosome *7S* but lacking chromosome *4Ai-2*. This will permit evaluation of the agronomic performance of greenbug-resistant germ plasm and further cytogenetic manipulation of chromosome *7S* to produce superior greenbug-resistant germ plasm.

Acknowledgements. We thank Duane Wilson for expert technical assistance. This research was supported in part by a USDA-CSRS special research grant "Wheat Genetics Resource Center at Kansas State University" and in part by a grant from the "Kansas Wheat Commission-worldwide promoters of wheat on behalf of 50,000 Kansas wheat producers". This work was completed while Drs. Dhaliwal, Friebe, and Mukai were visiting scientists at Kansas State University under the auspices of the Wheat Genetics Resource Center. Dr. Friebe further acknowledges his support from the Deutsche Forschungsgemeinschaft.

References

Arriaga HO (1954) Resistencia a la toxemia de *Schizaphis graminum* (Rond) en cereales finos. Univ Nac de Eva Peron, Rev Fac Agron (Terecera Epoca) 30:65–101

Cauderon Y, Saigne B, Dange M (1973) The resistance of wheat rusts of *Agropyron intermedium* and its use in wheat improvement. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Missouri, Columbia, Mo. pp 401–407

Dewey DR (1984) The genomic system of classification as a guide to intergeneric hybridization with the perennial *Triticeae.* In: Gustafson JP (ed) Gene manipulation in plant improvement. Plenum Publ, New York, pp 209–280

Driscoll CJ, Bielig LM (1968) Mapping of the Transec wheat-rye translocation. Can J Genet Cytol 10:421–425

Driscoll CJ, Sears ER (1965) Mapping of a wheat-rye translocation. Genetics 51:439–443

Forster BP, Reeder SM, Forsyth SA, Koebner RMD, Miller TE, Gale MD, Cauderon Y (1987) An assessment of the homoeology of six *Agropyron intermedium* chromosomes added to wheat. Genet Res Camb 50:91–97

Friebe B, Larter EN (1988) Identification of a complete set of isogenic wheat/rye D-genome substitution lines by means of Giemsa C-banding. Theor Appl Genet 76:474–479

Gill BS (1987) Chromosome banding methods, standard chromosome band nomenclature, and applications in cytogenetic analysis. In: Heyne EG (ed) Wheat and wheat improvement, 2nd edn. ASA Monograph, Madison, Wisconsin, pp 243–254

Gill BS, Sharma HC, Raupp WJ, Browder LE, Hatchett JH, Harvey TL, Moseman JG, Waines JG (1985) Evaluation of *Aegilops* species for resistance to wheat powdery mildew, wheat leaf rust, Hessian fly, and greenbug. Plant Dis 69:314–316

Gill BS, Raupp WJ, Sharma HC, Browder LE, Hatchett JH, Harvey TL, Waines JG (1986) Resistance in *Aegilops squarrosa* to wheat leaf rust, wheat powdery mildew, greenbug, and Hessian fly. Plant Dis 70:553–556

Giraldez R, Cermeno MC, Oreleana J (1979) Comparison of C-banding pattern in the chromosomes of inbred lines and open pollinated varieties of rye, *Secale cereale* L. Z Pflanzenzuecht 83:40–48

Hart GE (1973) Homoeologous gene evolution in hexaploid wheat. In: Sears ER and Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Missouri, Columbia, Mo., pp 805–810

Harvey TL, Martin TJ, Livers RW (1980) Resistance to biotype C greenbug in synthetic hexaploid wheats derived from *Triticum tauschii.* J Econ Entomol 73:387–389

Heun M, Friebe B, Introgression of powdery mildew resistance from rye into wheat. Phytopathology (in press)

Hollenhorst MM, Joppa LR (1983) Chromosomal location of genes for resistance to greenbug in 'Largo' and 'Amigo' wheats. Crop Sci 23:91–95

Joppa LR, Timian RG, Williams ND (1980) Inheritance to greenbug toxicity in an amphiploid of *Triticum turgidum*/*T. tauschii.* Crop Sci 20:343–344

Kota RS (1980) A cytogenetic and agronomic study of induced translocation lines of common wheat (*Triticum aestivum* L. em Thell) immune from wheat streak mosaic virus. MSc thesis. South Dakota State University, S.D., USA

Larson RI, Atkinson TG (1970) Identity of the wheat chromosomes replaced by *Agropyron* chromosomes in a triple alien chromosome substitution line immune to wheat streak mosaic. Can J Genet Cytol 12:145–150

Lay CL, Wells DG, Gardner WAS (1971) Immunity from wheat streak mosaic virus in irradiated *Agrotricum* progenies. Crop Sci 11:431–432

Liang GH, Wang RC, Niblett CL, Heyne EG (1979) Registration of B-6-37-1 wheat germ plasm. Crop Sci 19:421

Lukaszewski AS, Gustafson JP (1983) Translocations and modifications of chromosomes in Triticale × wheat hybrids. Theor Appl Genet 64:239–284

Martin TJ (1978) Procedures for evaluating wheat streak mosaic virus resistance. Plant Dis Rep 62:1062–1066

Martin TJ, Harvey TL, Livers RW (1976) Resistance to wheat streak mosaic virus and its vector, *Aceria tulipae.* Phytopathology 66:346–349

McKinney HH, Sando WJ (1951) Susceptibility and resistance to the wheat streak mosaic virus in the genera *Triticum, Agropyron, Secale*, and certain hybrids. Plant Dis Rep 35:476–478

Naranjo T, Roca A, Goicoechea PG, GIraldez R (1987) Arm homoeology of wheat and rye chromosomes. Genome 29:873–882

Rayburn AL, Gill BS (1985a) Use of biotin-labeled probes to map specific DNA sequences on wheat chromosomes. J Hered 76:78–81

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

Sebesta EE, Bellingham RC (1963) Wheat viruses and their genetic control. In: Proc 2nd Int Wheat Genet Symp. Lund, Sweden. Hereditas [Suppl] 2:184–201

Sebesta EE, Wood EA Jr (1978) Transfer of greenbug resistance from rye to wheat with X-rays. Agron Abstr 61–62

Sebesta EE, Young HC, Wood EA (1972) Wheat streak mosaic virus resistance. Annu Wheat Newsl 18:136

Sharma HC, Gill BS, Uyemoto JK (1984) High level of reistance in *Agropyron* species to barley yellow dwarf and wheat streak mosaic virus. Phytopathol Z 110:143–147

Shepherd KW, Islam AKMR (1988) Fourth compendium of wheat-alien chromosome lines. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp. Cambridge, England, pp 1373–1398

Sim IV T, Willis WG, Eversmeyer MG (1988) Kansas plant disease survey. Plant Dis 72:832–836

Slykhuis JT (1955) *Aceria tulipae* Kiefer (*Acarina eriophyidae*) in relation to spread of wheat streak mosaic. Phytopathology 45:116–128

Somsen HW, Sill Jr WH (1970) The wheat curl mite, *Aceria tulipae* Keifer, in relation to epidemiology and control of wheat streak mosaic. Kans State Univ Agric Exp Sta Res Publ 162

Stoddard SL, Gill BS, Lommel SA (1987a) Genetic expression of wheat streak mosaic virus resistance in two wheat-wheatgrass hybrids. Crop Sci 27:514–519

Stoddard SL, Lommel SA, Gill BS (1987b) Evaluation of wheat germ plasm for resistance to wheat streak mosaic virus by symptomatology, ELISA, and slot-blot hybridization. Plant Dis 71:714–719

Tyler JM, Webster JA, Smith EL (1985) Biotype E greenbug resistance in wheat streak mosaic virus-resistant wheat germ plasm lines. Crop Sci 25:686–688

Tyler JM, Webster JA, Sebesta EE, Smith EL (1986) Inheritance of biotype E greenbug resistance in bread wheat CI17882 and its relationship with wheat streak mosaic virus resistance. Euphytica 35:615–620

Tyler JM, Webster JA, Merkle OG (1987) Designation of genes in wheat germplasm conferring greenbug resistance. Crop Sci 27:526–527

Tyler JM, Webster JA, Merkle OG (1988) Identification of rye genotypes resistant to biotypes B, C, E, and F of the greenbug. Euphytica 37:65–68

Uyemoto JK, Ferguson MW (1980) Wheat streak mosaic virus: Increased yields of purified virus from corn. Plant Dis 64:460–462

Wang RC, Liang GH (1977) Cytogenetic location of genes for resistance to wheat streak mosaic in an *Agropyron* substitution line. J Hered 68:375–378

Wang RC, Liang GH, Heyne EG (1977) Effectiveness of *ph* gene in inducing homoeologous chromosome pairing in *Agrotricum*. Theor Appl Genet 51:139–142

Wells DG, Wong R, Sze-Chung, Lay CL, Gardner WAS, Buchenau GW (1973) Registration of C.I. 15092 and C.I. 15093 wheat germ plasm. Crop Sci 13:776

Wells DG, Kota RS, Sandhu HS, Gardner WAS, Finney KF (1982) Registration of one disomic substitution line and five translocation lines of winter wheat germ plasm resistant to wheat streak mosaic virus. Crop Sci 22:1277–1278

Wood EA Jr, Sebesta EE, Starks KJ (1974) Resistance of 'Gaucho' triticale to *Schizaphis graminum*. Environ Entomol 3:720–721