Theor Appl Genet (1991) 83:33–40

THEORETICAL AND APPLIED GENETICS

Transfer of Hessian fly resistance from rye to wheat via radiation-induced terminal and intercalary chromosomal translocations *

B. Friebe [1,], J.H. Hatchett [2], B.S. Gill [1], Y. Mukai [1,***] and E.E. Sebesta [3,†]**

[1] Department of Plant Pathology, [2] USDA-ARS, Department of Entomology, Kansas State University, Manhattan, KS 66506, USA
[3] USDA-ARS, Department of Agronomy, Oklahoma State University, Stillwater, OK, USA

Received October 25, 1990; Accepted March 25, 1991
Communicated by J.W. Snape

Summary. A new Hessian fly (*Mayetiola destructor*) resistance gene derived from 'Balbo' rye and its transfer to hexaploid wheat via radiation-induced terminal and intercalary chromosomal translocations are described. Crosses between resistant 'Balbo' rye and susceptible 'Suwon 92' wheat and between the F_1 amphidiploids and susceptible 'TAM 106' and 'Amigo' wheats produced resistant BC_2F_3 lines that were identified by C-banding analysis as being 6RL telocentric addition lines. Comparative chromosomal analyses and resistance tests revealed that the resistance gene is located on the 6RL telocentric chromosome. X-irradiated pollen of 6RL addition plants was used to fertilize plants of susceptible wheats 'TAM 106,' 'TAM 101,' and 'Vona.' After several generations of selection for resistance, new sublines were obtained that were homogeneous for resistance. Thirteen of these lines were analyzed by C-banding, and three different wheat-6RL chromosomal translocations (T) were identified. Wheat chromosomes involved in the translocations were 6B, 4B, and 4A. Almost the complete 6RL arm is present in T6BS·6BL-6RL. Only the distal half of 6RL is present in T4BS·4BL-6RL, which locates the resistance gene in the distal half of 6RL. Only a very small segment (ca 1.0 μm) of the distal region of 6RL is present in an intercalary translocation (Ti) Ti4AS·4AL-6RL-4AL. The 6RL segment is inserted in the intercalary region between the centromere of chromosome 4A and the large proximal C-band of 4AL. The break-points of the translocations are outside the region of the centromere, indicating that they were induced by the X-ray treatment. All three translocations are cytologically stable and can be used directly in wheat breeding programs.

Key words: Hessian fly resistance – Insect antibiosis – Wheat-rye hybrids – C banding

Introduction

Cultivated rye, *Secale cereale* L., is an important resource for improving the genetic variability of hexaploid wheat, *Triticum aestivum* L. (for reviews, Riley and Macer 1966; Zeller and Hsam 1983). Rye is known to carry genes for resistance to the wheat pathogens stripe rust (*Puccinia striiformis* West), leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*), stem rust (*Puccinia graminis* Pers. f. sp. *tritici* Eriks. & Henn.) (McIntosh 1988, for compilation), powdery mildew (*Erysiphe graminis* DC. f. sp. *tritici* Eriks. & Henn.) (Riley and Macer 1966; Heun and Friebe 1990; Heun et al. 1990), Karnal bunt [*Neovossia indica* (Mitra) Mundkur] (Sethi et al. 1988), and to the insects greenbug [*Schizaphis graminum* (Rondani)] (Sebesta and Wood 1978) and Hessian fly [*Mayetiola destructor* (Say)] (Painter 1951). However, so far, only the short arm of rye chromosome 1R has been intensively used in breeding programs and incorporated in tetraploid and hexaploid wheats, in the form of either T1BL·1RS or T1AL·1RS wheat-rye chromosomal translocations (Zeller and Fuchs 1983; Friebe et al. 1989).

The Hessian fly is a destructive pest of wheat throughout most of the production areas of the world. In

* Cooperative investigations of the Kansas Agricultural Experiment Station, Departments of Entomology and Plant Pathology, the Wheat Genetics Resource Center, Kansas State University, and the US Department of Agriculture, Agricultural Research Service. Contribution No. 91-117-J

** Present address: Plant Breeding Institute, Technical University of Munich, D-8050 Freising-Weihenstephan, Germany
*** Present address: Department of Biology, Osaka Kyoiku University, Ikeda, Osaka, Japan
† Deceased

the USA, genetic resistance has been used for many years to protect wheat (*T. aestivum* L.) cultivars from damage caused by the insect. More than 20 resistance genes have been identified in *Triticum* species for use in breeding resistant cultivars (Gallun 1977, for review; Amri et al. 1990). However, the identification of new resistance genes is essential because deployed genes are periodically overcome by new virulent biotypes of the insect (Hatchett and Gallun 1968; Sosa 1981). Thus, germ plasm of wheat and its relatives is being searched continually for diverse sources of resistance to Hessian fly.

Among the genetic resources available, cultivated rye offers great potential as a source of resistance to Hessian fly. Although this resistance has been known for many years, only in the last decade have efforts been made to introgress resistance genes of rye into the wheat genome. Friebe et al. (1990) reported the first transfer of Hessian fly resistance from rye to hexaploid wheat via either a spontaneous or tissue culture-induced T2BS · 2RL wheat-rye chromosomal translocation.

In 1978, two of us (E.E.S. and J.H.H.) began studies using pollen irradiation techniques, in an attempt to produce translocations between wheat chromosomes and rye chromosomes carrying resistance to Hessian fly. The basis for the studies was the transfer of greenbug resistance from rye to wheat by an apparent radiation-produced chromosomal translocation (Sebesta and Wood 1978). Ionizing radiation as a method for recombining alien genetic material with that of wheat was first used by Sears (1956), who transferred a gene for leaf rust resistance from *Aegilops umbellulata* to hexaploid wheat. Since then, irradiation has been used widely for transferring desirable alien genes to wheat. However, relatively few agronomically important traits have been successfully transferred (Knott 1971, for review).

In this paper, we describe the transfer of a Hessian fly resistance gene or gene complex from 'Balbo' rye chromosome 6RL to the A- and B-genomes of hexaploid wheat via radiation-induced terminal and intercalary chromosomal translocations.

Materials and methods

Production of rye addition lines and irradiated wheat-rye lines

Hexaploid wheats cultivars 'Suwon 92,' 'TAM 106,', and 'Amigo' and diploid rye cv 'Balbo' were used as parents to produce amphiploid stocks and rye addition lines. All of the wheat parents are susceptible and 'Balbo' is resistant to Hessian fly. With the exception of 'Amigo' ('Chinese Spring 'X' Insave F.A.' rye), which carries T1AL·1RS (Zeller and Fuchs 1983; Lapitan et al. 1986), none of the wheat parents is known to carry rye chromatin.

The following procedure was used for the production of resistant rye addition lines. 'Suwon 92' was crossed with 'Balbo,' and the F_1 hybrids were colchicine treated to obtain amphidiploids. Amphidiploid plants were crossed as females with 'TAM 106,' and the resulting species-backcross plants were selfed and selected for vigor and fertility. Selfed progeny (BC_1F_2 plants) of first backcross plants were screened for Hessian fly resistance, and the resistant plants were crossed as females with 'Amigo.' Selfed progeny of BC_2F_1 plants were screened and resistant plants were identified.

Resistant BC_2F_2 putative rye addition plants were selfed and/or used as pollen donors for the production of irradiated wheat-rye lines. Young spikes were X-rayed in the premeiotic stage with a total dose of 750 R and crossed to susceptible wheat cultivars 'TAM 106,' 'TAM 101,' and 'Vona.' Progeny of X_1 plants of each cross were screened for resistance, and the resistant plants were selfed to produce X_3 lines. Subsequent derived lines were screened for resistance, and resistant plants were identified at each generation through the X_6, X_7, or X_8 generation, depending on when the original cross was made. The number of derived lines propagated at each generation varied, but at least ten resistant plants were selected to propagate each line. A total of 14, 33, and 26 derived lines from crosses between resistant rye addition plants and TAM 106, TAM 101, and Vona, respectively, were selected for screening in the final generation. All plant breeding operations used in the development of the lines were performed in a greenhouse at Oklahoma State University. Testing of the lines for Hessian fly resistance and selection of resistant plants was carried out in a greenhouse at Kansas State University.

Hessian fly resistance tests and chromosomal analyses

All plant materials were tested in the seedling stage for reaction to biotype L Hessian fly. Biotype L is the most virulent biotype now found in the field (Sosa 1981); larvae can infest wheats carrying resistance genes *H1* through *H8*, *H11*, and *H15*. The wheat and rye parents, putative rye addition lines, and irradiated wheat-rye lines were tested in separate experiments. The testing procedures, including methods of infestation and of determining resistance or susceptibility of individual seedlings, were reported in detail previously (Friebe et al. 1990). Susceptible plants were stunted and dark blue-green in color. Resistant plants were not stunted and retained their light-green color. Resistant plants were examined under a stereoscopic microscope (20×) for presence of larvae at the base of the second leaf sheath. When no larvae were found, the plant was considered to be an escape and was discarded.

The plant materials selected for chromosomal analyses were 'Balbo' rye, five BC_2F_3 lines derived from resistant BC_2F_2 rye addition plants described previously, and 13 irradiated lines derived from crosses between irradiated resistant rye addition plants and 'TAM 106,' 'TAM 101,' and 'Vona.' In some experiments, both chromosomal analyses and resistance tests were performed on the same plants to test agreement between the resistance genotype of the plant and its chromosome constitution.

The Giemsa C-banding technique described by Giraldez et al. (1979) was used for identification of chromosomes and detection of rye chromatin. C-banded polymorphic karyotypes of a series of 'Balbo' chromosomes and a karyotype of a resistant rye addition line were established and used as standards for detection of wheat-rye chromosomal translocations.

Results and discussion

Resistance and chromosomal analyses of 'Balbo' rye and rye addition lines

'Balbo' was homogeneously resistant to biotype L Hessian fly (Table 1). Plants were highly antibiotic to first

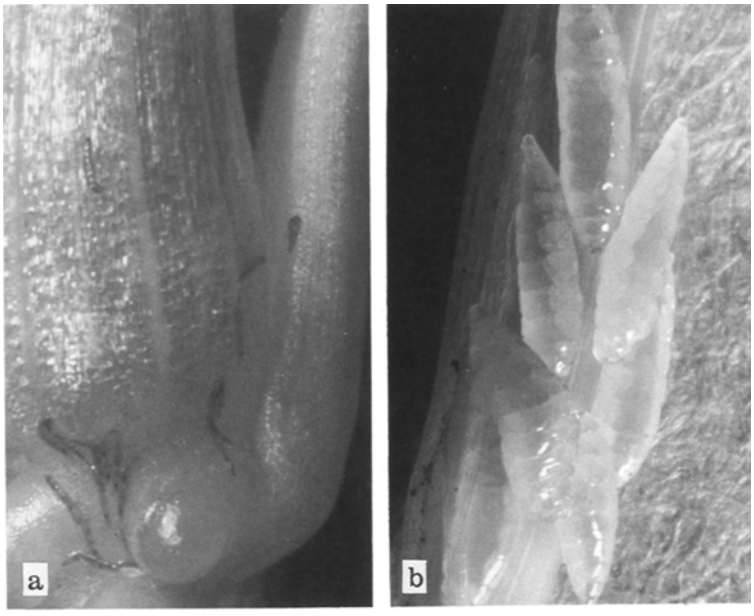

Fig. 1 a and b. Hessian fly larvae on resistant and susceptible plants showing **a** dead first-instar larvae on 'Balbo' rye, **b** live second-instar larvae on 'TAM 196' wheat. First leaf sheaths have been removed to expose larvae at the base of seedlings

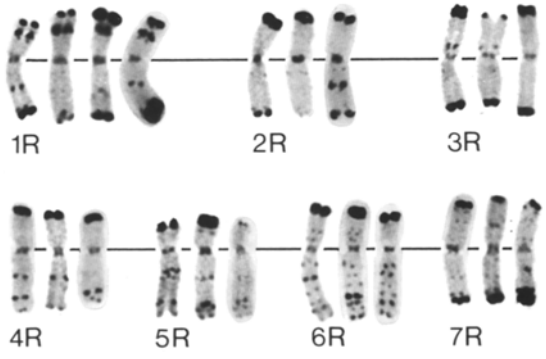

Fig. 2. C-banding pattern and polymorphisms observed in chromosomes of 'Balbo' rye

Table 1. Reactions of 'Balbo' rye and 'Suwon 92,' 'TAM 106,' and 'Amigo' wheat and five BC_2F_3 putative rye addition lines derived from the cross [(Suwon 92 × Balbo) × TAM 106] × Amigo to biotype L Hessian fly

Parent or line	No. of plants	
	Resistant	Susceptible
'Balbo'	27	0
'Suwon 92'	0	21
'TAM 106'	0	24
'Amigo'	0	16
87HF634	11	3
87HF635	18	1
87HF636	16	0
87HF637	15	2
87HF639	10	1

instars and contained large numbers of dead larvae (Fig. 1 a). Dead larvae retained the normal red body color of 1- to 3-day-old first instars and were approx. 0.5 mm long. Wheat cultivars 'Suwon 92,' 'TAM 106,' and 'Amigo' were uniformly susceptible, and plants contained only live second instars that were translucent white and ca. 3.0 mm long (Fig. 1 b).

Chromosomal analyses performed on 30 'Balbo' plants identified all seven chromosomes by their characteristic C-band patterns, which are similar to those described for other rye cultivars (Sybenga 1983). However, a large amount of C-band polymorphism was expressed between the two homologues of a given chromosome. Figure 2 shows the range of polymorphism for C-heterochromatin in a series of homologous chromosomes taken from 'Balbo' plants. The polymorphisms between homologues, which were expressed for both C-band size and position, did not prevent identification of chromosomes. The large amount of C-band polymorphism expressed in 'Balbo' is not atypical; similar amounts of variation have been observed for other rye cultivars (B. Friebe, unpublished results).

The BC_2F_3 putative rye addition lines were homogeneous or heterogeneous for resistance to larval feeding (Table 1). Like 'Balbo' resistant plants, they exhibited a high level of antibiosis and contained dead first instars, indicating the presence of the critical chromosome for resistance. Also, none of the resistant plants developed chlorotic lesions at larval feeding sites, a reaction characteristic of Hessian fly resistance derived from 2RL of 'Chaupon' rye (Friebe et al. 1990). This indicates that the larval antibiosis expressed in 'Balbo' and 'Chaupon' is not the same.

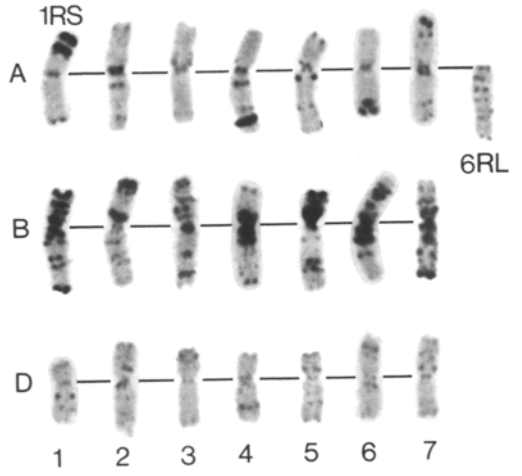

Fig. 3. C-banded karyotype of the Hessian fly resistant 6RL addition line 87HF636

C-banding analyses confirmed the presence of rye chromatin in the putative rye addition lines. A detailed C-banded karyotype of resistant line 87HF636 is shown in Fig. 3. All 21 pairs of wheat chromosomes were identified by their characteristic C-banding patterns as described previously (Gill 1987). In addition, line 87HF636 carries two rye chromosome segments that were readily identified by their C-banding patterns. One segment shows a large terminal and a subterminal C-band, characteristic of the short arm of chromosome 1R, and was present in the form of the T1AL·1RS chromosomal translocation. This translocation is identical to the T1AL·1RS described previously in 'Amigo' (Zeller and Fuchs 1983; Heun et al. 1990). The second rye segment occurs as a pair of telocentric chromosomes, which were identified as the long arms of chromosome 6R. These 6RL telocentrics show five distinct intercalary C-bands, in addition to C-bands at the centromere and at the telomere. The two proximal C-bands are slightly larger than the three distal C-bands. This banding pattern is similar to that of the long arm of rye chromosome 6R (Fig. 2). The fact that 'Amigo,' which contains T1AL·1RS, is susceptible to Hessian fly indicates that the resistance of this line is conditioned by the 6RL telocentric chromosome and not by 1RS.

C-banding analyses and resistance tests performed on the same plants provided further evidence that the 6RL telocentric chromosome conditions resistance in the rye addition lines. A total of 79 plants from the rye addition lines was analyzed and tested for resistance. All plants were homozygous for the T1AL·1RS, but segregation was observed for the presence or absence of the 6RL telocentric chromosome. However, presence or absence of 6RL matched, without exception, the plants' reaction to larval feeding. A total of 57 plants, all of which were resistant and contained dead larvae, was either monosomic or disomic for 6RL. In 22 plants, all of which were susceptible, the 6RL telocentric was absent. Because all susceptible plants carried T1AL·1RS, the gene or gene complex conditioning resistance is located on the long arm of chromosome 6R.

Table 2. Reaction to biotype L Hessian fly and chromosomal constitution of 13 irradiated wheat-rye lines derived from crosses between three susceptible wheat cultivars and a radiated rye addition line carrying resistance on 6RL derived from 'Balbo' rye

Pedigree generation line	Reaction and no. plants		Chromosome number	Chromosome constitution
	Resistant	Susceptible		
TAM 106 × {[(Suwon 92 × Balbo) × TAM 106] × Amigo}				
X_6				
88HF16	28	0	42	T6BS · 6BL-6RL
88HF20	24	0	44	T6BS · 6BL-6RL, T6BL-6RL · 6RS
88HF25	26	0	44	T6BS · 6BL-6RL, T6BL-6RL · 6RS
Vona × {[(Suwon 92 × Balbo) × TAM 106] × Amigo}				
X_8				
88HF79	25	0	42	T4BS · 4BL-6RL
88HF80	22	0	42	T4BS · 4BL-6RL
88HF81	24	0	42	T4BS · 4BL-6RL
88HF117	24	0	42	T4BS · 4BL-6RL, T1AL · 1RS
TAM 101 × {[(Suwon 92 × Balbo) × TAM 106] × Amigo}				
X_8				
89HF17	24	0	42	Ti4AS·4AL-6RL-4AL
89HF18	23	0	42	Ti4AS·4AL-6RL-4AL
89HF25	26	0	42	Ti4AS·4AL-6RL-4AL
X_7				
88HF32	30	0	42	Ti4AS·4AL-6RL-4AL
88HF51	28	0	42	Ti4AS·4AL-6RL-4AL
88HF89	30	0	42	Ti4AS·4AL-6RL-4AL

Resistance and chromosomal analyses of irradiated wheat-rye lines

All 13 X_6- to X_8-derived lines were homogeneous for resistance to biotype L Hessian fly (Table 2). Plants contained only dead first instars. The reaction type was similar to that of 6RL addition plants: larvae died at the base of the second leaf sheath. This indicates that the lines carry the resistance gene from the rye telocentric chromosome 6RL.

None of the lines carried 6RL as a telocentric chromosome. However, all lines carried segments of 6RL in the form of wheat-rye chromosomal translocations. Three different types of 6RL translocations associated with wheat chromosomes 6B, 4B, and 4A were identified: two terminal translocations, designated T6BS·6BL-6RL

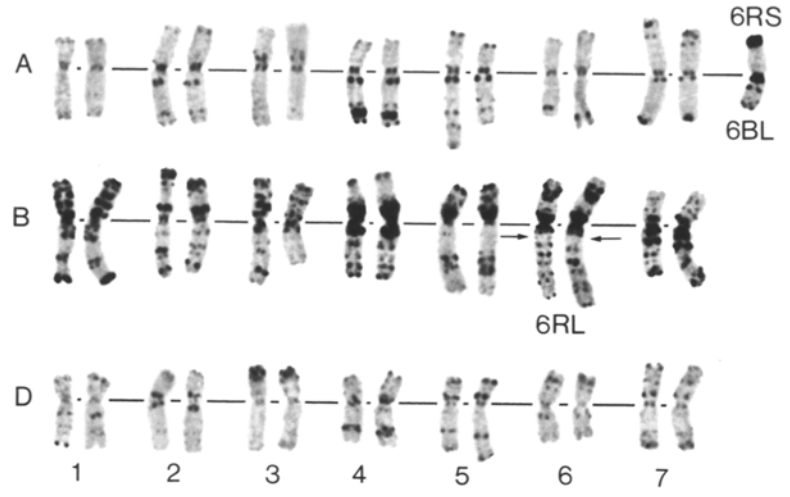

Fig. 4. C-banded karyotypes of T6BS · 6BL-6RL lines 89HF16 (chromosomes shown on the *right*) and 88HF25 (chromosomes shown on the *left*) (*arrows* point to break-points of the translocations)

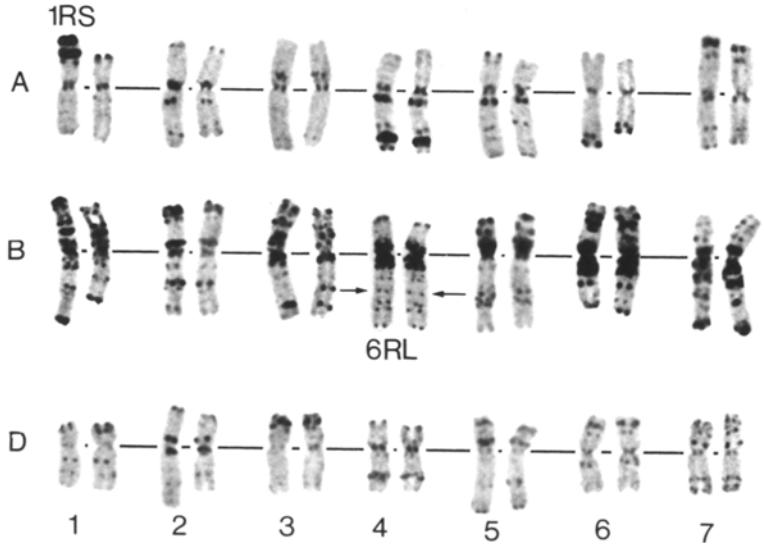

Fig. 5. C-banded karyotypes of T4BS · 4BL-6RL lines 88HF789 (chromosomes shown on the *right*) and 88HF117 (chromosomes shown on the *left*) (*arrows* point to the break-points of translocations)

and T4BS·4BL-6RL (Figs. 4 and 5), and an intercalary translocation, designated Ti4AS·4AL-6RL-4AL (Fig. 6). The chromosome constitutions and C-banding pattern of the critical chromosomes of the lines are summarized in Table 2 and Fig. 8, respectively.

T6BS·6BL-6RL translocation. Three lines – 88HF16, 88HF20, and 88HF25 – carried almost the complete arm of 6RL translocated to the long arm of 6B. Line 88HF16 showed a chromosome number of 2n = 42 (Table 2) and carried only T6BS·6BL-6RL (Fig. 4). Lines 88HF20 and 88HF25 showed a chromosome number of 2n = 44 (Table 2) and carried, in addition to T6BS·6BL-6RL, a second wheat-rye chromosomal translocation identified as T6BL-6RL·6RS (Fig. 4).

The C-banding pattern showed that the break-point in T6BS·6BL-6RL is not within the centromeric region (Fig. 8), but between the two proximal C-bands present in 6BL and close to the centromere of 6RL. With the exception of the centromeric band, the C-banding pattern of 6RL in T6BS·6BL-6RL is identical to that of the 6RL telocentric chromosome of the rye addition line 87HF636 (Fig. 3). Only occasionally were two faint dots observed close to the proximal C-band, which represents the remaining part of the centromeric heterochromatin of the rye telocentric 6RL (Fig. 4).

T6BL-6RL·6RS present in lines 88HF20 and 88HF25 is the fusion product of the remaining region of 6BL, a small part of 6RL, the centromere, and the short arm of rye chromosome 6R. As shown in Fig. 8, 6RS has a large telomeric and a faint proximal C-band, a pattern similar but not identical to that of 6RS of 'Balbo' (Fig. 2). In 'Balbo,' polymorphic variation was observed for intensity of proximal and intercalary C-bands in the

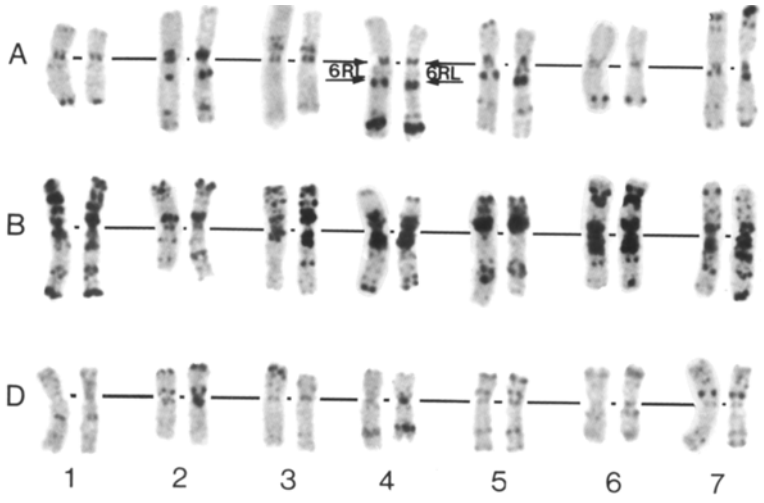

Fig. 6. C-banded karyotypes of the Ti4AS · 4AL-6RL-4AL lines 88HF89 (chromosomes shown on the *left*) and 89HF18 (chromosomes shown on the *right*) (*arrows* point to the break-points of translocations)

short arms of 6R. The presence of T6BL-6RL · 6RS indicates that the original rye addition plant that was irradiated and crossed to 'TAM 106' was not a 6RL addition but carried a complete rye chromosome 6R. Thus, the 6RL addition lines may have originated at later stages in the progeny of plants that were monosomic for rye chromosome 6R.

T4BS · 4BL-6RL translocation. All four lines – 88HF79, 88HF80, 88HF81, and 88HF117 – showed a chromosome number of 2n = 42 (Table 2) and carried only a part of the rye segment 6RL as a T4BS · 4BL-6RL (Fig. 5). However, in line 88HF117, chromosome 1A of wheat was replaced by T1AL · 1RS (Fig. 5). This was the only irradiated line in which T1AL · 1RS from 'Amigo' was maintained.

T4BS · 4BL-6RL carries about half of the long arm of chromosome 4B, including the two large proximal C-bands and the following two fainter C-bands (Fig. 8). The distal half of the long arm of T4BS · 4BL-6RL, including the telomere and the three distal C-bands, is derived from 6RL. The C-bands of this region are identical to those in the distal half of the 6RL telocentrics (see Fig. 3). The break-point of this translocation must be close to the intercalary C-band of chromosome 4B (Fig. 8) and close to the medial C-band of rye chromosome arm 6RL. Because the intercalary C-band of 4BL is similar in size and position to the medial C-band in 6RL, the exact break-points cannot be determined. Thus, the C-band, marked with an arrow in T4BS · 4BL-6RL in Figs. 5 and 8, may have originated either from 4BL or 6RL. However, at least the following two distal C-bands and the region up to the telomere of T4BS · 4BL-6RL were derived from 6RL, which further locates the resistance gene or gene complex on the distal half of 6RL.

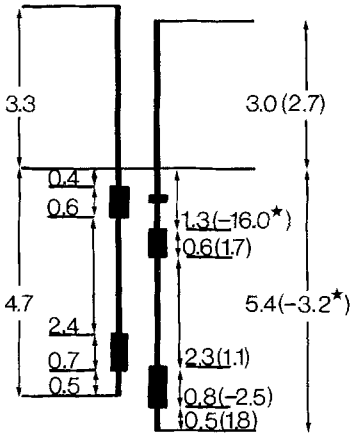

Fig. 7. Comparison of chromosome 4A of 'Suwon 92' (*left*) and chromosome Ti4AS · 4AL-6RL-4AL of line 88HF89 (*right*). Chromosome length data are given in micrometer and were analyzed by a student's *t*-test. Calculated *t* values are shown in parentheses with $P < 0.01$ and significance limits $t = \pm 2.7$, $df = 38$

Ti4AS · 4AL-6RL-4AL translocation. All six lines derived from the cross between the irradiated 6RL addition plant and 'TAM 101' showed a chromosome number of 2n = 42 (Table 2), but did not carry a large segment from the rye telocentric chromosome 6RL (Fig. 6). However, all plants were homozygous for a modified chromosome 4A, which differs from a normal chromosome 4A with respect to the proximal region of the long arm. In the modified chromosomes 4A, the region between the centromere and the large proximal C-band of the long arm is slightly longer and carries an additional C-band (Fig. 8). Because a similar modification has not been reported for any 4A chromosome of wheat, we hypothesize that the small additional C-band originated from the

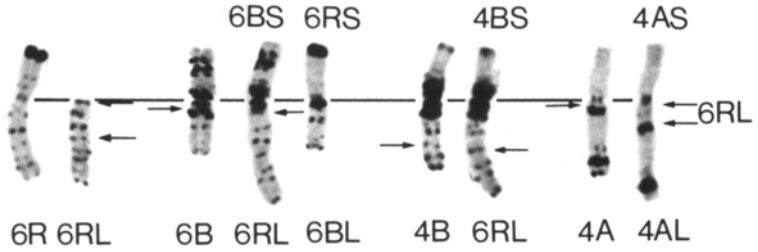

Fig. 8. C-banding patterns of the critical wheat chromosomes and wheat-rye chromosomal translocations observed in irradiated Hessian-fly resistant lines (*arrows* point to the break-points of translocations)

rye chromosome 6RL, and identifies an intercalary translocation in which a short segment of 6RL is inserted in the long arm of chromosome 4A.

Because the putative 6RL segment in the modified 4A chromosome (designated Ti4AS·4AL-6RL-4AL) is very small, chromosome measurements were carried out on 20 C-banded 4A chromosomes of 'Suwon 92' and 20 C-banded Ti4AS·4AL-6RL-4AL chromosomes of line 88HF89 (Fig. 7). Chromosome 4A of 'Suwon 92' shows a total chromosome length of 8.0 μm and an arm ratio (L/S) of 1.4, whereas Ti4AS·4AL-6RL-4AL has a total chromosome length of 8.4 μm and an arm ratio of 1.8. Comparative measurements of the two chromosomes using a student's *t*-test indicated that only the total lengths of the long arms and the lengths between the centromere and the large proximal C-band of the long arms were significantly different ($P > 0.01$, $df = 38$). The putative rye segment is about 1.0 μm long, which would place the break-point in 4AL between the centromere and the large proximal C-band, the site where the small segment of 6RL was inserted.

To confirm the presence of the Hessian fly resistance gene in Ti4AS·4AL-6RL-4AL, a heterozygous plant carrying one normal 4A chromosome and one Ti4AS·4AL-6RL-4AL chromosome was crossed with 'Chinese Spring,' which was nullisomic for chromosome 4A and tetrasomic for chromosome 4D. C-banding analyses and resistance tests were performed on 34 F_1 plants. These plants segregated 1:1 for resistance and susceptibility. Sixteen plants, all of which were resistant and contained dead larvae, were monosomic for Ti4AS·4AL-6RL-4AL, whereas 18 plants were monosomic for a normal 4A chromosome and were susceptible. These genetic data and the chromosome measurement data are strong evidence that Ti4AS·4AL-6RL-4AL carries the Hessian fly resistance gene derived from a segment of 6RL, and that the segment is inserted in an intercalary region between the centromere and the large proximal C-band of the long arm of chromosome 4A. The specific part of 6RL that is inserted in Ti4AS·4AL-6RL-4AL could not be determined. Further analysis by in situ hybridization using total rye DNA as a probe has confirmed the insertion of rye chromatin in the 4AL arm (Mukai et al. 1991).

Polymorphic variation. Several wheat chromosomes were polymorphic in C-banding patterns. Variations in 5A terminal C-band (Figs. 5 and 6), 3B, and 6A long arm C-bands (Figs. 3–6) were caused by polymorphic differences among the various wheat parents used in the production of irradiated lines. Other C-banding differences in chromosomes 2B, 3D, and 7B (Fig. 6) probably originated during the X-ray treatment.

Different lines segregated for many of the C-banding variants described above. However, segregation was not observed for Ti4AS·4AL-6RL-4AL, T4BS·4BL-6RL, and T6BS·6BL-6RL. These wheat-6RL chromosomal translocations appear to be cytologically stable and can be used directly in breeding programs. This transfer to hexaploid wheat of another gene for Hessian fly resistance from rye further demonstrates the importance of rye as a genetic resource for such resistance.

Acknowledgements. B.F. was partly supported by the Deutsche Forschungsgemeinschaft.

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