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Molecular Characterization of Two *Triticum speltoides* Interstitial Translocations Carrying Leaf Rust and Greenbug Resistance Genes

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ABSTRACT

Resistance genes for leaf rust (*Puccinia recondita* Rob. ex Desm.) and greenbug (*Schizaphis graminum* Rondani) were transferred from chromosome 7S of *Triticum speltoides* (Tausch) Gren. to chromosome 7A of hexaploid wheat (*Triticum aestivum* L.) by means of the *ph1b* mutation that promotes homeologous recombination. The chromosome segments from *T. speltoides* were characterized by C-banding and restriction fragment length polymorphisms (RFLP). Since the segments of *T. speltoides* chromosome 7S do not recombine with wheat chromosome 7A in the presence of the wild-type *Ph1* locus only one molecular marker per chromosome segment is required to monitor the introgressed genes in marker assisted selection programs. The new leaf rust resistance gene, designated *Lr47*, and the greenbug resistance gene *Gb5* were located on interstitial chromosome segments from *T. speltoides* translocated to wheat chromosome arms 7AS and 7AL, respectively. Physically, both were located in the distal one third of the arms, but genetically the *Lr47* segment was 2 to 10 centimorgans (cM) from the centromere and was 20 to 30 cM long; the *Gb5* segment was 18 to 22 cM from the centromere and was 40 to 50 cM long.

SINCE THE PER-ACRE VALUE OF WHEAT is lower than that of many alternative crops, wheat must be grown efficiently with minimum applications of pesticides. The use of disease resistance genes is the method of choice for controlling diseases in this crop and has been proven repeatedly to be an effective and environmentally sound method of controlling serious yield-reducing pathogens. Unfortunately, the gene pool of cultivated wheat for resistance to pests and pathogens is inadequate to respond to the evolution of different pathogen populations. Replacement of highly variable land races by higher yielding, pure-line varieties in many parts of the world has further reduced the wheat gene pool. In this context, it is important to import alternative genes from other sources.

Diploid species *T. monococcum* L., *T. speltoides* (Taush) Gren., and *T. tauschii* (Cosson) Schmalh., with genomes closely related to the A, B, and D genomes of bread wheat, offer a pool of genes for resistance that can contribute to crop genetic diversity. Genes from these species have been incorporated into bread wheat conferring resistance against leaf rust (*Puccinia recondita* Rob. ex Desm.), stem rust (*Puccinia graminis* Pers.:Pers.), Hessian fly [*Mayetiola destructor* (Say)], Russian wheat aphid [*Diuraphis noxia* Mordvilko], powdery mildew [*Blumeria graminis* (DC.) E.O. Speer (syn. *Erysiphe graminis* DC.)], greenbug, and root knot nematode [*Meloidogyne incognita* (Kofoid & White) Chitwood] (reviewed by [McIntosh, 1991; Friebe et al., 1996]).

In most experiments aiming at such interspecific transfers, recombination is induced by the *ph1b* mutation and primary recombinant chromosomes are recovered. Most often, these primary recombinants are single breakpoint translocations (Lukaszewski, 1995; Dubcovsky et al., 1996a) carrying large segments of alien chromosomes. Linkage between the targeted genes and undesirable genes on the alien segment usually result in yield and/or quality penalties and in a limited use of such alien transfers in practical breeding (Friebe et al., 1996). Consequently, to be deployed in agriculture the alien chromosome segments must be as short as possible.In this paper, we report the development of two interstitial translocations of *T. speltoides* chromosome 7S in common wheat. These translocations carrying leaf rust and greenbug resistance genes are characterized by C-banding and RFLP markers.

MATERIAL AND METHODS

A chromosome of *T. speltoides* was found in some stocks of wheat originating from Kansas State University (Lukaszewski, 1995). The origin of the material, identical C-banding patterns and the presence of a gene conferring resistance to biotypes C and E of greenbug, *Schizaphis graminum* Rondani, suggest that this may be chromosome 7S#1 described by Friebe et al. (1991). This chromosome was originally transferred from *T. speltoides* to bread wheat by irradiating hybrid seed (CI15092 / *T. speltoides* // 'Fletcher' / 3 / 5*'Centruk') with fast neutrons (Wells et al., 1982). The dominant greenbug resistance gene present in the derived translocation lines (CI17882, CI17884, and CI17885) was designated *Gb5* (Tyler et al., 1987) and was later transferred to line KS90H450 from Kansas State University (Friebe et al., 1991). Tests at University of California, Riverside, showed that this chromosome also carried a gene for resistance to leaf rust and, possibly, to blackpoint. The causal agent of black point was identified as *Fusarium proliferatum* (T. Matsushima) Nirenberg (syn.

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Abbreviations: cM, centimorgans; Gb, greenbug resistance gene; Lr, leaf rust resistance gene *Ph1* (gene controlling homeologous pairing); RFLP, restriction fragment length polymorphisms.

Table 1. 'Pavon' and T7AS-7S 1S-7AS-7AL response to eight races of leaf rust and virulence (V)/avirulence (av) patterns of each race on near isogenic *Lr* lines with their respective Prt code†.

Race id.	Host response: Pavon	Host response: Pavon T7AS-7S#1S-7AS-7AL	Virulence/avirulence pattern: Lr 1	Lr 2a	Lr 2b	Lr 2c	Lr 3a	Lr 3ka	Lr 3bg	Lr 9	Lr 10	Lr 11	Lr 14a	Lr 14b	Lr 16	Lr 17	Lr 19	Lr 20	Lr 23	Lr 24	Lr 25	Lr 26	Lr 30	Lr 33	Prt code†
1888	MR-MS‡	R	V§	V	V	V	V	V	V	av	V	V	V	av	av	V	av	V	av	av	av	av	V	av	TBT
3298	S	R	V	av	V	V	av	av	av	av	V	av	V	V	av	av	av	V	av	av	av	av	av	av	NBB
3956	MS-S	R	V	av	av	av	V	V	av	av	V	V	V	V	av	av	av	av	V	av	av	av	V	av	MBR
4206	MS-S	R	V	av	av	av	av	av	av	av	V	V	V	V	av	av	av	av	V	av	av	V	av	av	LCG
4483	MR-MS	R-MR	V	V	V	V	av	av	av	av	V	V	V	V	av	V	av	V	av	V	av	av	av	av	SDJ
4689	S	R	V	av	av	av	V	av	V	av	V	V	V	V	av	av	av	av	V	av	av	av	av	av	MBG
4703	S	R	V	av	av	V	av	av	av	av	V	av	V	V	av	av	av	V	av	V	av	av	av	av	NDB
5560	S	R	V	av	av	av	V	av	V	av	V	V	V	V	av	av	av	av	V	av	av	V	av	av	MCG
5810	S	R	V	V	V	V	V	av	V	av	V	av	V	V	av	V	av	V	V	V	av	av	av	av	TDD

† Long and Kolmer (1989).
‡ Host response: R = resistant, MR = moderately resistant, MS = moderately susceptible, S = susceptible.
§ Pathogen phenotype: V = virulent, av = avirulent, – = not tested.

Cephalosporium proliferatum T. Matsushima) (R. Conner, 1996, personal communication).

The short arm of chromosome 7S#1 paired with telocentric 7AS of 'Chinese Spring' in 97% of pollen mother cells indicating the presence of a terminal segment of chromosome 7A. C-banding pattern suggests that the translocation point between 7S#1 and 7A must be located in the distal 15% of the short arm (Lukaszewski, 1995). This translocation was labeled by Friebe et al. (1996) as T7AS-7S#1S·7S#1L ("-" = interstitial breakpoint, "·" = centromeric breakpoint, "#" = different translocations, "S" = short arm, "L" = long arm). Here, this original translocated chromosome will be referred to as 7S-7A.

Recombinant chromosome 7S-7A was transferred to Pavon through backcrosses and combined with the *ph1b* mutation to produce plants with the chromosome constitution 19″ + *5Bph1b′* + (7S-7A + 7A)″. These plants were backcrossed as male to Pavon, and the resulting progeny were screened by C-banding to identify recombinants (Lukaszewski, 1995). Primary recombinant chromosomes were selected by C-banding and tested for resistance to leaf rust and greenbug.

Sears' (1981) strategy to reduce the length of alien chromosome segments was followed. Briefly, reciprocal primary recombinants with the breakpoints flanking the locus of interest were intercrossed and allowed to recombine in the presence of the wild-type *Ph1* locus that permits only homologous recombination. Secondary recombinant chromosomes with interstitial inserts of alien chromatin into wheat chromosomes were then selected. The translocated chromosomes were designated according to the rules described in Friebe et al. (1996). Centric translocations were designated T7AS·7S#1L and T7AS-7S#1S·7AL respectively. Leaf rust resistance testing of the plants with the primary recombinant chromosomes was done by injection of a water suspension of spores of races PRTUS 06 and 17 (kindly supplied by Dr. B.S. Gill, Kansas State University, Manhattan, KS) into the coleoptiles of small seedlings. The line carrying a recombinant chromosome conferring resistance to leaf rust was further screened with nine races of *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* from Argentina (Table 1), selected because of their known avirulence/virulence formulae and their virulence on *Lr10* and *Lr1*, two leaf rust resistance genes known to be present in Pavon. The selected races are a part of the collection of the Genetic Institute "Edwald A. Favret" and their avirulence-virulence characteristics were established by means of near-isogenic international reference stocks (McIntosh et al., 1995). Seedlings were grown in a greenhouse and inoculated by dusting dry spores with talc when the third leaf was expanded. A qualitative assessment of the seedling response was done about 2 wk after inoculation, following McIntosh et al. (1995). A race was considered virulent (V) when the resulting host response corresponded to infection types 3, 4, X+, and Y+. Lower infection types qualified a race as avirulent (av).

Screening for greenbug resistance was performed at the USDA-ARS laboratory at Stillwater, OK. The substitution of the 7S-7A chromosome for 7A in Pavon wheat was tested by a range of greenbug biotypes. The resistance offered by this chromosome (resistant to biotypes C and E; susceptible to biotype B) was determined to be similar to that of 'Largo' wheat reported by Tyler et al. (1987). All subsequent tests on the lines of Pavon with recombinant chromosomes were performed with greenbug biotype C.

RFLP markers previously mapped on chromosome $7A^m$ of *T. monococcum* (Dubcovsky et al., 1996b) were tested in DNA from the two selected lines with interstitial translocations, the line of Pavon with the original 7S.7A chromosome and the normal variety Pavon, digested with restriction enzymes *Bam*HI, *Dra*I, *Eco*RI, *Hin*dIII, and *Xba*I. The presence of common polymorphisms on chromosome 7S-7A and the chromosomes with the interstitial translocations was used as a criterion to establish the boundaries of the *T. speltoides* segments in the secondary recombinant chromosomes. The distance between RFLP markers present on chromosome $7A^m$ was used to infer the length and the position of the *T. speltoides* chromosome segments.

RESULTS

Twenty-five recombinant chromosomes, and two chromosomes which appeared to be centric translocations, were identified among 165 BC_1 (Fig. 1 and 2). Twelve lines showed recombination between chromosome 7A of Pavon and the *T. speltoides* segment of the short arm of chromosome 7S-7A. All these recombinants had interstitial 7S#1S insertions because of the short terminal segment of 7A present in the original chromosome 7S-7A. All 13 chromosomes showing exchanges in the long arm resulted from single recombination events. The distribution of the translocation breakpoints along the chromosome arms was discussed before (Lukaszewski, 1995).

Short Arm Recombinants

The tests of leaf rust resistance performed on the backcross progenies with the two centric translocations indicated that the resistance locus was located on the

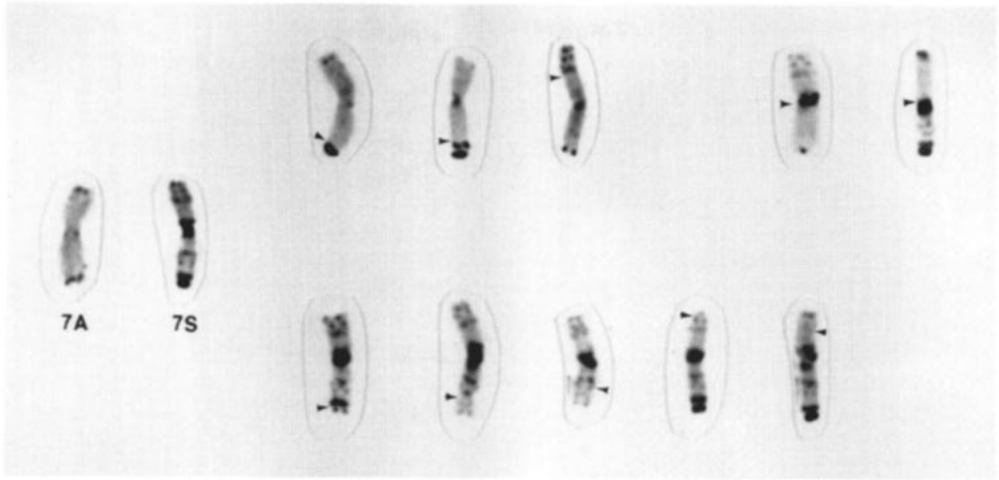

Fig. 1. Primary recombinant chromosomes obtained from the *ph1b*-induced recombination between chromosome 7A of wheat and 7S#1 of *T. speltoides*. Upper row: recombinant chromosomes with 7A centromere. From left to right, two long arm recombinants and one short arm recombinant (T7AS-7S#1S-7AS·7AL). Far right, centric translocations (T7AS-7S#1S·7AL and T7AS·7S#1L). Bottom row: chromosomes with 7S#1 centromeres and terminal segments of 7A. From left to right, three long arm recombinants and two short arm recombinants. Arrowheads point to the location of translocation breakpoint.

short arm of 7S-7A. All seven short-arm recombinants with 7S#1 centromeres were resistant suggesting that the translocation breakpoints in this group of recombinants were distal to the *Lr* locus. Among the five reciprocal short-arm recombinants with 7A centromeres only one, labeled T7AS-7S#1S-7AS·7AL (Fig. 1, upper row, third from right) conferred resistance to leaf rust. This chromosome had the most proximal translocation breakpoint among all short arm recombinants. Additional three backcrosses of recombinant chromosome T7AS-7S#1S-7AS·7AL to Pavon wheat were performed and plants homozygous for the interstitial translocation were selected by C-banding. Homozygous T7AS-7S#1S-7AS·7AL line showed resistant response to leaf rust races PRTUS 06 and 17 used in the original screening of the 7S-7A substitution line and the primary recombinants, as well as to nine leaf rust races from Argentina with simultaneous virulence on *Lr1* and *Lr10* genes (Table 1). The *Lr* resistance gene present in the T7AS-7S#1S-7AS·7AL line is designated *Lr47*.

The position and length of the interstitial *T. speltoides* chromosome segment present in homozygous line T7AS-7S#1S-7AS·7AL, was characterized with 14 RFLP clones previously mapped in the short arm of chromosome 7A^{m}S (Dubcovsky et al., 1996 b). Loci *Xcdo57* and *Xabc455*, located close to the centromere, showed an additional restriction fragment (from *T. speltoides* 7SS) and an absent fragment (presumably from the replaced *T. aestivum* 7AS) in substitution line 7S-7A. These RFLPs were not detected in line T7AS-7S#1S-7AS·7AL indicating that this line originated by a recombination event that occurred between loci *Xcdo57* and *Xabc465*, 2 to 9 cM from the centromere (Fig. 3). Physically, the *T. speltoides* segment in chromosome T7AS-7S#1S-7AS·7AL is located in the distal third of the arm. The distal 7AS-7S#1S breakpoint is at FL (fractional length) 0.85 (Friebe et al., 1996).

The seven loci tested for the chromosome segment including *Xabc465* and *Xwg834* were polymorphic between Pavon and the substitution line 7S-7A (Fig. 3). Each of these loci showed a polymorphic *T. speltoides* fragment present in substitution line 7S-7A and in recombinant line T7AS-7S#1S-7AS·7AL that was absent in Pavon and in the recombinant line for the long arm T7AS·7AL-7S#1L-7AL (Fig. 4). On the basis of the distances between these markers in *T. monococcum* (Dubcovsky et al., 1996b), it was inferred that the length of this *T. speltoides* segment was between 27 cM (*Xabc465* to *Xwg834* in 7A^m) and 43 cM (*Xcdo57* to *Xbcd93* in 7A^m).

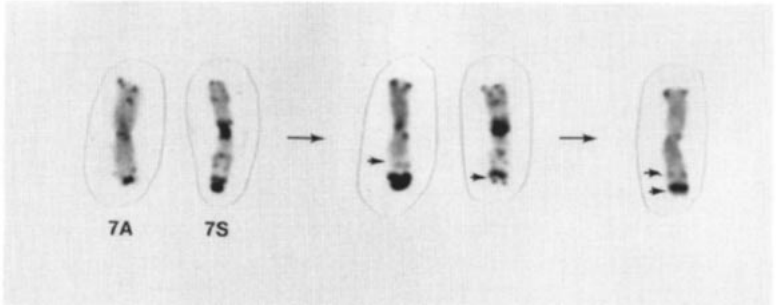

Fig. 2. Transfer of the *Gb5* locus from chromosome 7S#1 of *T. speltoides* to 7A of wheat. From left to right: original chromosomes 7A and 7S-7A; two reciprocal recombinants T7AS·7AL-7S#1L and T7AS-7S#1S·7S#1L-7AL both of which carry *Gb5*; crossing over within the segment of 7S#1 common to the two primary recombinants results in chromosome T7AS·7AL-7S#1L-7AL with an interstitial insert of 7S#1. Arrowheads point to the translocation breakpoints.

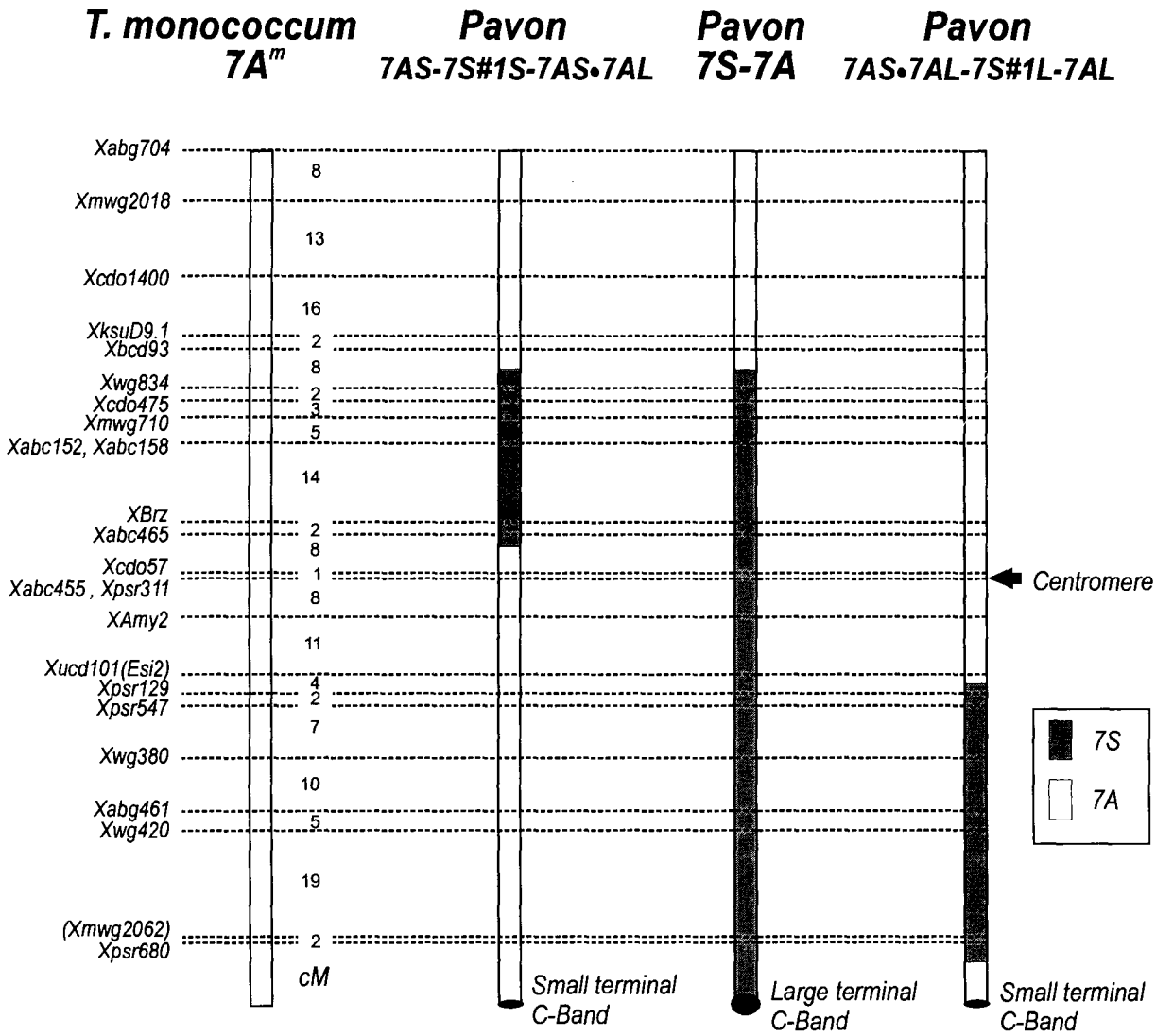

Fig. 3. RFLP of chromosome 7A^m of *T. monococcum* and inferred location of the *T. speltoides* chromosome segments (in gray) on the basis of RFLPs in substitution line 7S-7A, and recombinant lines T7AS-7S#1S-7AS-7AL and T7AS-7AL-7S#1L-7AL. Distances are in centimorgans and the arrowhead points to the centromere. Locus *Xabc455* is in the short arm and locus *Xpsr311* is in the long arm.

The five loci distal to *Xwg834* (*Xbcd93* to *abg704*, Fig. 3) showed no polymorphisms present simultaneously in substitution line 7S-7A and T7AS-7S#1S-7AS·7AL. This contrasts with the high level of polymorphism observed for the rest of chromosome 7S-7A and suggests that these markers are included in the 7A region of chromosome 7S-7A. A low level of polymorphisms in this region was expected, because the distal 7A segment present in the original 7S-7A had numerous opportunities for recombination with chromosome 7A from Pavon during the backcrossing process.

Long Arm Recombinants

Screening of the 7S-7A-substitution line of Pavon showed that chromosome 7S#1 conferred resistance to greenbug biotype C. Centric translocation T7AS-7S#1S·7AL was susceptible indicating that the resistance gene was located on the long arm. To confirm this result, backcross progenies with all 25 recombinant chromosomes were screened for greenbug resistance with biotype C. Since the screened progenies segregated for normal chromosomes 7A and the primary recombinants, segregation for resistance to biotype C was taken as a sign that the given recombinant carried the *Gb5* locus. Uniform susceptible progenies indicated lack of the locus.

The resistant response of all recombinants with complete 7S#1L arms and the susceptible response of all recombinants with complete 7AL arms confirmed the long arm location of *Gb5*. Among the long arm recombinants with the centromere of 7A, only one chromosome, T7AS·7AL-7S#1L, conferred resistance. This recombinant had the most proximal translocation breakpoint and encompasses the three distal C-bands of 7S#1L (Fig. 2). Among the plants with reciprocal recombinant chromosomes with the 7S#1 centromere one was susceptible and the remaining ones were resistant. Chromosome T7AS-7S#1S·7S#1L-7AL was selected among the long arm recombinants with 7S#1 centromeres and *Gb5* for the production of the interstitial segment of 7S#1L on the long arm of chromosome 7A.

The two primary recombinants, T7AS·7AL-7S#1L and T7AS-7S#1S·7S#1L-7AL, with breakpoints flanking

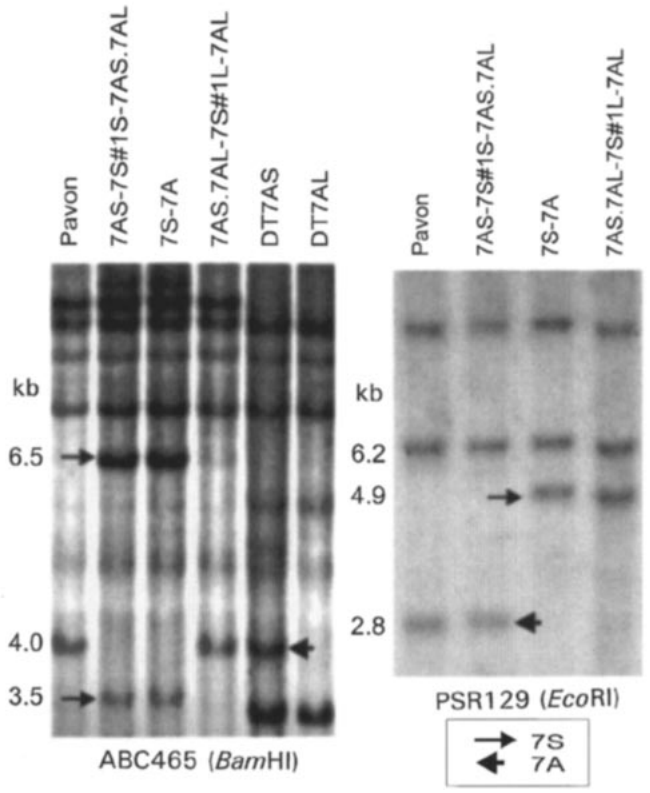

Fig. 4. Southern blot hybridization of the ABC465 and PSR129 clones with *Bam*HI- and *Eco*RI-digested DNAs of bread wheat variety Pavon, short arm recombinant line T7AS-7S#1S-7AS·7AL, original 7S-7A substitution line in Pavon, long arm recombinant line T7AS·7AL-7S#1L-7AL, Chinese Spring short arm ditelocentric 7AS, and Chinese Spring long arm ditelocentric 7AL. Lengths of the polymorphic fragment are in kilobase pairs (kb) and were calculated from *Hind*III-digested bacteriophage λ. Arrowheads indicate 7A restriction fragments and arrows indicate 7S#1 restriction fragments.

the *Gb5* locus, were intercrossed and allowed to recombine in the presence of the wild-type *Ph1* locus. Among 59 progeny from the double heterozygote (20" + T7AS·7AL-7S#1L + T7AS-7S#1S·7S#1L-7AL) screened by C-banding, 23 products of recombination within the *T. speltoides* segment were observed. Of these, 11 were secondary recombinants 7A-7S (Fig. 2) and 12 were reconstituted 7A-7S chromosomes. This population of recombinant chromosomes gives a crossover frequency of the two chromosomes of 19.5%, suggesting considerable genetic length of the *T. speltoides* overlapping segment between T7AS·7AL-7S#1L and T7AS-7S#1S·7S#1L-7AL.

A homozygous greenbug resistant line with a secondary recombinant chromosome designated T7AS·7AL-7S#1L-7AL, was further characterized using 10 RFLP clones previously mapped in the long arm of chromosome $7A^m$ (Dubcovsky et al., 1996b). The three loci located in the chromosome segment adjacent to the centromere, *Xpsr311*, *XAmy2*, and *Xucd101(Esi2)* showed polymorphisms between Pavon and substitution line 7S-7A. Absence of these polymorphisms in T7AS·7AL-7S#1L-7AL indicated that this region correspond to the 7A segment in T7AS·7AL-7S#1L-7AL and that the primary recombinant T7AS·7AL-7S#1L was originated by a recombination event that occurred between loci *Xpsr129* and *Xucd101(Esi2)*, 19 to 23 cM from the centromere (Fig. 3).

The seven loci analyzed for the distal region of the long arm of chromosome 7 were polymorphic between Pavon and the substitution line 7S-7A (Fig. 3 and 4). These loci showed the same polymorphism between Pavon and recombinant line T7AS·7AL-7S#1L-7AL suggesting that the *T. speltoides* chromosome 7S#1L segment in this line was at least 45 cM long. No RFLP was found in the distal region of the long arm of chromosome 7 that was present in 7S-7A but absent in T7AS·7AL-7S#1L-7AL. However, a strong telomeric C-band present in the 7S-7A chromosome was absent in the secondary recombinant T7AS·7AL-7S#1L-7AL and was replaced by a small telomeric C-band characteristic of chromosome arm 7AL (Fig. 2 and 3). This indicates that the *T. speltoides* segment in T7AS·7AL-7S#1L-7AL is interstitial and that the crossing over that originated primary recombinant 7AS-7S#1S·7S#1L-7AL occurred between RFLP marker *Xpsr680* and the telomeric C-band. Comparison of Fig. 3 with deletion maps of homeologous group 7 (Hohman et al., 1995; B.S. Gill, 1995, personal communication) suggests that the *T. speltoides* segment starts approximately at FL 0.7.

DISCUSSION

Many wheat derivatives carrying resistance genes from alien species have had limited use in practical breeding because of cytological instability of alien chromosome segments incorporated in non-homeologous regions or because of the linkage of undesirable genes on the long alien segments (Friebe et al., 1996). Chromosome segments transferred by homeologous recombination are usually in the correct location in the genome, but the size of the alien segment may still be a problem.

The methodology to reduce the length of these segments was described many years ago (Sears, 1981). The precision of this approach depends on the number of primary recombinants recovered and the accuracy with which the location of the translocation breakpoints can be determined relative to the locus of interest. High numbers of primary recombinants increase the probability that two breakpoints very close to the locus of interest can be recovered. However, mapping of the translocation breakpoints by pairing frequencies with a tester chromosome (Sears, 1981) is tedious and slow. C-banding may be helpful in some situations but molecular markers provide a more precise way to characterize the primary recombinants for the production of the secondary recombinants.

In this study, by means of a combination of C-banding and molecular mapping, two recombinant wheat chromosomes with interstitial segments of *T. speltoides* were produced and characterized. Clearly, the original number of primary recombinants was too low and the final inserts in the secondary recombinants were of considerable length. Their fate in practical breeding will demonstrate if the amount of the introgressed alien chromosome is acceptable. Since chromosomes 7A and 7S#1 do not recombine in the presence of the *Ph1* gene, the presence of any marker from chromosome 7S#1 is

sufficient to indicate the simultaneous presence of the corresponding resistance gene.

Orthologous relationships between *Lr47* and leaf rust resistance genes *Lr29* and *Lr34* located in the short arm of homeologous group 7 (McIntosh et al., 1995) cannot be conclusively demonstrated with the available information. *Lr29* has a similar pattern of avirulence reactions to *Lr47* but its location within the short arm of homeologous group 7 is not known. The map position of *Lr34*, close to *Xwg834* on 7DS (Nelson et al., 1995), is within the limits of *T. speltoides* segment in T7AS-7S#1S-7AS·7AL. However, *Lr34* differs from *Lr47* in that is mainly an adult plant resistance gene (McIntosh et al., 1995).

There is only one additional greenbug resistance gene reported on homeologous group 7 (Hollenhorst and Joppa, 1983). This gene, labeled *Gb3*, is present in variety Largo chromosome 7D and confers resistance to greenbug biotypes C, E, H, I, and K but not to biotypes B, F, and G. *Gb3* differs from *Gb5* only in its resistance to biotype H (Porter et al., 1997). More precise mapping information of *Gb3* and *Gb5* is required to elucidate the relationship between these two genes.

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