RESEARCH

Wheat–Rye T2BS·2BL–2RL Recombinants with Resistance to Hessian Fly (*H21*)

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ABSTRACT

Hessian fly, *Mayetiola destructor* (Say), is a destructive insect pest of common wheat (*Triticum aestivum* L.) and durum wheat (*T. turgidum* L.) worldwide. Although 32 genes conferring resistance to Hessian fly have been identified, only a few genes are still effective in North America. A highly effective gene is *H21,* transferred to wheat from Chaupon rye via a whole-arm wheat-rye translocation T2BS·2R#2L. This translocation also carries a gene for field resistance to powdery mildew. To broaden the use of T2BS·2R#2L in wheat improvement, we attempted to reduce the length of the rye segment by recombination with another wheat-rye translocation T2BS·2BL-2R#2L. Recombination data indicated that the *H21* locus was linked to the telomere; the powdery mildew locus was closely linked to the translocation breakpoint in T2BS·2BL-2R#2L. Recovered short-segment rye translocation chromosomes confer resistance to Hessian fly; however, no crossover event in the desirable configuration was recovered to produce a short-segment wheat-rye translocation with both *H21* and the powdery mildew resistance gene. The T2BS·2BL-2R#2L recombinant chromosome was transferred to adapted winter and spring wheat cultivars.

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Abbreviations: GISH, genomic in situ hybridization; MI, metaphase I.

Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), is a destructive insect pest of common wheat (*Triticum aestivum* L.) and durum wheat (*T. turgidum* L.) worldwide. Average annual yield losses caused by Hessian fly range from 5 to 10% (Ratcliffe and Hatchett, 1997; Buntin, 1999), but losses up to 35% have been reported in Morocco (Amri et al., 1992). The use of host-plant resistance is the most efficient means of controlling the damage caused by this pest. To date, 32 genes conferring resistance to Hessian fly have been identified and named (McIntosh et al., 2008). In a recent virulence analysis of Hessian fly populations from Texas, Oklahoma, and Kansas, Chen et al. (2009) reported that resistance genes *H13*, *H21*, *H25*, *H26*, and *Hdic* were highly effective against all Hessian fly populations tested. Two of these genes, *H21* and *H25*, were derived from rye (*Secale cereale* L.). *H21* originated from 'Chaupon' rye and was transferred to wheat in the form of a Robertsonian wheat-rye T2BS·2R#2L translocation present in the germplasm 'Hamlet' (KS89WGRC8, TA5018) (Friebe et al., 1990; Sears et al., 1992; Hatchett et al., 1993). *H25* was derived from 'Balbo' rye

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and transferred to wheat in the form of terminal wheat-rye translocations T6BS·6BL-6R#2L (KS92WGRC17, TA5030) and T4BS·4BL-6R#2L (KS92WGRC18, KSWGRC19, TA5031, TA5032) and an intercalary wheat-rye translocation Ti4AS·4AL-6R#2L-4AL (KS92WGRC20, TA5033) (Friebe et al., 1991; Mukai et al., 1993; Sebesta et al., 1997). T2BS·2R#2L and Ti4AS·4AL-6R#2L-4AL were transferred to durum wheat (Friebe et al., 1999). In addition to *H21*, the rye chromosome arm in Hamlet has a powdery mildew resistance gene that offers a good level of field resistance against pathotypes common in the Southeastern United States. The allele present in Hamlet has not been identified or named.

As is usually the case with alien introgressions in wheat, especially when the segments are large, the T2BS·2RL Hamlet translocation has some negative effects. While there is no measurable effect on milling and baking qualities (Knackstedt et al., 1994), it delays maturity and reduces grain weight (Fritz and Sears, 1991). Perhaps for this reason, it has not been widely used in wheat breeding. This study was undertaken to reduce the amount of rye chromatin present in the Hamlet chromosome. The standard approach in such manipulations is to induce a round of homeologous recombination between the alien segment and one of its wheat homeologues and recover desirable recombinants, always a complicated effort. Instead, we are testing here a simpler approach, by using homologous recombination in two rye segments, both of the same chromosome: the entire rye arm 2RL in Hamlet and a relatively short segment of 2RL in a recombinant chromosome T2BS2BL-2R#2L produced in a different study (Lukaszewski et al., 2004). Recovered short-segment rye translocation chromosomes still confer resistance to Hessian fly, but no crossover event in the desirable configuration was recovered to produce a short-segment wheat-rye translocation with both *H21* and the powdery mildew resistance gene.

MATERIALS AND METHODS

The plant material consisted of the germplasm Hamlet (PI 549276) with a wheat-rye whole arm T2BS·2R#2L translocation that carries *H21* and a powdery mildew (caused by *Blumeria graminis* DC f. sp. *tritici*) resistance gene located in undetermined locations on the 2RL arm and the Hessian fly and powdery mildew–susceptible wheat-rye recombinant stock Pavon 2B(L)+20 (Lukaszewski et al., 2004) having a recombinant wheat-rye chromosome represented by T2BS·2BL-2R#5L. This chromosome is essentially wheat 2B with a terminal approximately 20% of the long arm derived from 'Blanco' rye. This translocation was produced by homeologous recombination in the absence of the *Ph1* locus (Lukaszewski et al., 2004). Additionally, winter wheat cultivars 'Karl 92' (PI 564245), 'Jagger' (PI593688), 'Culver' (PI606726), and a spring cultivar 'Pavon 76' (PI 519847) were used. For convenience the presumed single powdery mildew resistance locus present in the Hamlet translocation (originating from Chaupon rye) was designated as Pm_{chau}.

The two wheat-rye translocations are readily distinguished cytologically by the presence and size of diagnostic C-bands (Fig. 1). The Hamlet chromosome (centric translocation) has a very large terminal C-band on the long arm that otherwise is devoid of intercalary bands (with the exception of a very small band adjacent to the centromere). The 2B(L)+20 stock has a very small terminal C-band on the rye segment and a series of intercalary C-bands diagnostic for 2BL (Fig. 1). To produce homologous recombinants in the rye segment shared by the two translocations, Hamlet and Pavon 2B(L)+20 stocks were intercrossed and the resulting F_1 plants were backcrossed to cultivars Karl 92, Jagger, Culver, and Pavon 76. The resulting BC_1 plants were screened by C-banding to identify putative recombinant chromosomes T2BS·2BL-2R#2L. Plants with recombined chromosomes were grown, self pollinated, and again backcrossed to Pavon 76, Jagger, and Culver. The BC_1F_2 plants were evaluated for reaction to Hessian fly and powdery mildew. Resistant plants were saved and screened by genomic in situ hybridization (GISH) to identify homozygotes for the T2BS·2BL-2R#2L recombinant chromosomes. C-banding and chromosome identification was according to Lukaszewski and Gustafson (1983) and Gill et al. (1991), and GISH was according to Zhang et al. (2001).

Hessian fly reaction was determined using the Kansas Hessian fly population, which consists predominantly of biotype GP (Chen et al., 2009). Testing was undertaken at the seedling stage in a greenhouse according to Hatchett et al. (1981). Adult flies were allowed to oviposit for 8 h on plants at the one-leaf stage, and reactions were evaluated 15 d postinfestation. Susceptible plants were dark green, stunted, and had live larvae, whereas resistant plants were light green, grew normally, and had dead larvae.

For tests of powdery mildew reaction, progenies of plants with recombinant chromosomes were grown in a controlled environment of 15°C for 12 hr then 13°C for 12 hr, a 15-hr photoperiod, and 70% relative humidity. Seedlings were inoculated at Feekes' growth stage 1.3 to 2 (Large, 1954) by shaking conidia from infected plants onto the leaves. The source of inoculum was originally a field-grown plant of cv. Coker 9663 at the University of Georgia Research Center, Griffin, GA. Disease was assessed on the upper two leaves 21 d after inoculation. The presence of resistant plants in segregating progenies was taken as indicative that the parent plant had a recombinant chromosome with the Pm_{chau} gene.

RESULTS AND DISCUSSION

The long arm of the rye chromosome in the original Hamlet translocation T2BS·2RL has a small C-band adjacent to the centromere and a large C-band at the telomere. The long arm in TBS·2BL-2R#5L stock [recombinant 2B(L)+20] has a long, proximal segment of 2BL with all its diagnostic intercalary C-bands and a small, telomeric C-band typical of Blanco rye chromosome arm 2RL (Fig. 1). The only segment of homology shared by the two long arms of these two translocation chromosomes is the rye segment stretching from the translocation breakpoint in 2B(L)+20 to the telomere. Because both the telomere and the breakpoint were

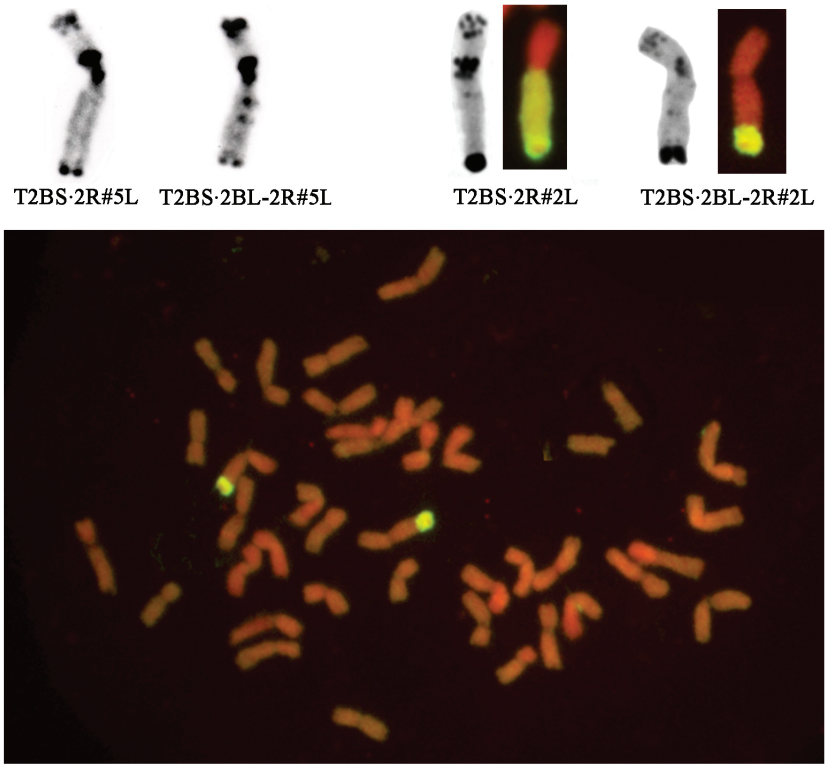

Fig. 1. C-banding pattern of T2BS·2RL#5L and recombinant T2BS·2BL-2R#5L chromosome (top left); C-banding and genomic in situ hybridization patterns of Robertsonian wheat-rye T2BS·2RL#2L and recombinant T2BS·2BL-2R#2L chromosomes (top right); genomic in situ hybridization pattern of a partial mitotic metaphase of a homozygous T2BS·2BL-2R#2L recombinant stock (bottom, rye chromatin visualized by yellow-green fluorescein fluorescence; wheat chromosomes were counterstained with rhodamine and fluoresce red).

identifiable cytologically, odd-numbered crossover events involving the homologous rye chromosome region were cytologically detectable. If *H21* and Pm_{chau} were located in the region of the Hamlet translocation shared with the 2B(L)+20 stock, homologous recombination within the rye segments would transfer the loci to the shorter rye segment of 2B(L)+20. Location of both or any of the two loci proximal to the translocation breakpoint in T2BS·2BL-2R#5L would make the transfer impossible.

As the shared segment of rye homology appeared long enough to cover the area of the first crossover in the arm (Lukaszewski et al., 2004) and both segments were terminal, a high recombination rate was expected. Hence, the pools of backcross seed produced were relatively small with the expectation that each one of them would produce the desired recombinants. Surprisingly, recombination frequency in the rye segment was low, and all 463 BC_1 plants were screened. Thirty-six recombinant chromosomes were found, an overall recombination frequency for the entire rye segment of 7.8%. Hessian fly and powdery mildew testing of all recombinants indicated that the *H21* locus was located in the vicinity of the telomere: 34 recombinants involved crossovers between the 2B(L)+20 translocation breakpoint and *H21*, and only 2 were between *H21* and the telomere. The Pm_{chau} locus was located at the proximal end of the rye segment, close to the breakpoint in 2B(L)+20; only one confirmed crossover between Pm_{chau} and the breakpoint was identified, and unfortunately, it was in the wrong configuration, being a chromosome in the Hamlet configuration (the entire 2RL present) and susceptible to both powdery mildew and Hessian fly. The point of exchange in one recombinant was in doubt and could not be reliably assigned to a specific interval.

The actual genetic map locations of the two loci can be corrected for low pairing of the two chromosomes. Such correction would be a factor of 6.4*x*. Given the distal distribution of crossing over in wheat and rye (Lukaszewski, 1992; Werner et al., 1992; Gill et al., 1993), the physical length of the segment of homology in the two translocations should have permitted normal metaphase I (MI) pairing and 50% recombination. If this were the case, genetic distances in the segment corrected for normal pairing would be: breakpoint – Pm_{chau}, 1.4 cM; Pm_{chau} – *H21*, 44.3 cM; *H21* – telomere, 2.8 cM. No mapping functions need to be applied, as it can be safely assumed that all crossovers were single. All recombinants were selected for odd numbers of crossovers and, given the overall low recombination rate of the entire segment, triple exchanges were unlikely.

Severe pairing reduction in the segment was presumably brought about by polymorphism for the very large telomeric C-band. In rye, polymorphism for terminal C-bands affects synapsis, especially in distal regions of the arms, and restricts chiasmate pairing (Gillies and

Lukaszewski, 1989). In Hamlet, the telomeric C-band is very large and probably equal in length to the entire euchromatic rye segment in 2B(L)+20, producing a misalignment at the start of synapsis in the order of 50% of the entire stretch of homology. In a similar manner large misalignments in deficiency heterozygotes in wheat almost completely eliminated MI pairing (Curtis et al., 1991).

BC_1 plants with recombinant chromosomes were grown and self-pollinated, and samples of the resulting BC_1F_2 populations were again evaluated for reaction to Hessian fly. These populations segregated and resistant plants were self-pollinated; progenies from one plant in each of the three backgrounds were evaluated again for resistance to Hessian fly and screened by GISH to verify the presence of wheat-rye recombinant chromosomes in the expected configuration and to select translocation homozygotes. No additional tests for powdery mildew resistance were conducted.

The Pavon 76 BC_2F_3 family segregated 53 Hessian fly–resistant and 16 susceptible plants (Table 1). Genomic in situ hybridization was performed on 12 resistant and 9 susceptible plants. All resistant plants were either heterozygous or homozygous for the wheat-rye recombinant chromosome T2BS·2BL-2R#2L, consisting of the complete short arm of wheat chromosome 2B, the proximal 80% of 2BL, and about the distal 20% of this arm derived from 2RL of rye (Fig. 1). Eight susceptible plants had no detectable rye chromatin, and one plant was heterozygous for the T2BS·2BL-2R#2L chromosome.

The Jagger BC_2F_3 family segregated 11 Hessian fly–resistant and 2 susceptible plants. Five of the resistant plants had one or two copies of the T2BS·2BL-2R#2 L recombinant chromosomes, whereas both susceptible plants had no detectable rye chromatin (Table 1). Similarly, the Culver BC_2F_3 family segregated 30 Hessian fly–resistant and 12 susceptible plants. Among the 18 plants tested by GISH, 10 resistant plants had one or two copies of T2BS·2BL-2R#2L, whereas 5 of the susceptible plants had no GISH signal and 3 had one copy of T2BS·2BL-2R#2L (Table 1). These results show that the resistance to Hessian fly in these families co-segregated with the T2BS·2BL-2R#2L recombinant chromosome. However, 3 of 19 susceptible plants had one copy of T2BS·2BL-2R#2L, whereas the remaining 16 plants, as expected, had no rye chromatin. Although the susceptible plants with one copy of the wheat-rye recombinant chromosome looked stunted, we did not assess them for the presence of dead larvae, and likely, their reactions were misclassified.

Plants homozygous for T2BS·2BL-2R#2L were recovered in three partially reconstituted genetic backgrounds and were designated as TA5084 (Jagger), TA5085 (Culver), and TA5086 (Pavon). Together with the appropriate control wheat cultivars, progenies of these lines were evaluated again for reaction to Hessian fly. Whereas all plants of the homozygous recombinant stocks and of Hamlet were resistant, all plants of the wheat cultivars Culver, Karl92, and Jagger were susceptible. Resistant plants had dead, red, first-instar larvae, whereas the susceptible wheat cultivars had late second instars that were translucent, white, and alive. Thus we had successfully transferred the Hessian fly resistance gene *H21* from the Robertsonian translocation T2BS·2R#2L to the T2BS·2BL-2R#2L recombinant chromosome, reducing the amount of rye chromatin present by approximately 80%. Only about the distal 20% of the 2BL-2R#2L arm is now derived from rye, which hopefully will improve the agronomic performance and allow for a broader use of this transfer in wheat improvement.

This study illustrates a nonstandard approach to alien transfers and chromosome engineering in wheat. In the standard approach, a donor alien chromosome is identified, placed in an appropriate genetic background, combined with the *ph1b* mutation or a system suppressing the *Ph1* locus, and recombinant wheat-alien chromosomes are recovered (Sears, 1981). These can be further engineered to generate small intercalary alien inserts in wheat chromosomes. Depending on the level of affinity between the donor alien and the recipient wheat chromosome, populations needed to generate and identify the primary wheat-alien chromosome recombinants can be very large (Lukaszewski, 2000) and any structural difference between the donor and recipient chromosomes may make the entire project unfeasible (Lukaszewski et al., 2001). In this study, we show that once sets of wheat-alien recombinant chromosomes are available, and we propose to designate them "stock recombinants," even if originating from donor chromosomes that do not carry the locus or loci of interest, they can be used to transfer onto their alien segments any desired locus or loci from any other sources within the same species. In other words, the sets of

Table 1. Reactions of BC_2F_2 plants to Hessian fly [*Mayetiola destructor* (Say)] biotype GP and their chromosome constitutions determined by genomic in situ hybridization (GISH). R, resistant; S, susceptible.

BC_2F_2 composition	No. of plants resistant, susceptible	GISH on R plants	GISH on S plants
Pavon family TA5086	53 16	9 plants: 1 × T2BS·2BL-2R#2L 3 plants: 2 × T2BS·2BL-2R#2L	8 plants: no rye chromatin 1 plant: 1 × T2BS·2BL-2R#2L
Jagger family TA5084	11 2	1 plant: 1 × T2BS·2BL-2R#2L 4 plants: 2 × T2BS·2BL-2R#2L	2 plants: no rye chromatin
Culver family TA5085	30 12	5 plants: 1 × T2BS·2BL-2R#2L 5 plants: 2 × T2BS·2BL-2R#2L	5 plants: no rye chromatin 3 plants: 1 × T2BS·2BL-2R#2L

alien-wheat recombinants have to be generated only once, saving a considerable amount of time and labor. A similar approach was used previously to transfer the powdery mildew resistance gene *Pm20* from chromosome 6R of 'Prolific' rye via homologous recombination to a Robertsonian wheat-rye translocation chromosome T6BS·6RL (Friebe et al., 1994). More recently, Ayala-Navarrete et al. (2007) recombined two introgressions of *Thinopyrum* in wheat to combine two highly desirable resistance genes in one alien segment, but this effort required manipulation of the *Ph1* locus of wheat.

The major issue in this approach to alien transfer is the choice of the most appropriate starting stock recombinant chromosome. An ideal transfer has as little alien chromatin as possible. Therefore, the translocation breakpoint in the selected stock recombinant chromosome should be proximal but as close as possible to the locus of interest. In this study, with no prior knowledge of the *H21* or Pm_{chau} locations, the worst-case scenario was assumed: that at least one locus was very proximal. The chosen stock recombinant chromosome, 2B(L)+20, had one of the most proximal translocation breakpoints available among an entire set of available 2BL-2RL recombinants (Lukaszewski et al., 2004). As it turned out, this approach was justified: the Pm_{chau} locus was very close to the translocation breakpoint. In fact, so close that no recombinant in the desired configuration was recovered. On the other hand, *H21* mapped very close to the telomere, hence the length of the rye segment in the final *H21* transfer can be reduced further, both by eliminating the large telomeric heterochromatic and most of the proximal euchromatin. Suitable stock recombinants are available for this purpose. To reduce the segment containing *H21*, the entire experiment can be repeated with a far more distal breakpoint recombinant stock, or the chromosomes produced here can be recombined with selected recombinant stocks with suitably distal breakpoints. If the Pm_{chau} is to be included, either additional homologous recombinants would have to be produced to generate one large rye segment with both resistance loci, or chromosome 2B with two separate rye inserts could be produced.

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