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NBS-LRR sequence family is associated with leaf and stripe rust resistance on the end of homoeologous chromosome group 1S of wheat

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Abstract A detailed RFLP map was constructed of the distal end of the short arm of chromosome 1D of *Aegilops tauschii* and wheat. At least two unrelated resistance-gene analogs (RGAs) mapped close to known leaf rust resistance genes (*Lr21* and *Lr40*) located distal to seed storage protein genes on chromosome 1DS. One of the two RGA clones, which was previously shown to be part of a candidate gene for stripe rust resistance (*Yr10*) located within the homoeologous region on 1BS, identified at least three gene family members on chromosome 1DS of *Ae. tauschii*. One of the gene members cosegregated with the leaf rust resistance genes, *Lr21* and *Lr40*, in *Ae. tauschii* and wheat segregating families. Hence, a RGA clone derived from a candidate gene for stripe rust resistance located on chromosome 1BS detected candidate genes for leaf rust resistance located in the corresponding region on 1DS of wheat.

Key words Wheat · Rust resistance · RGA markers · *Ae. tauschii*

Introduction

Several resistance genes effective against rust pathogens, *Puccinia* sp., are located on the short arms of the group-1 chromosomes of wheat (McIntosh et al. 1998). Most of these rust resistance genes have been mapped within a genetic interval of approximately 15 cM flanking the seed storage protein genes (*Gli-1*/*Glu-3*) located near the end of the chromosome arms 1AS, 1BS and 1DS. This region on chromosome 1BS contains *Yr10*, a gene that confers resistance to *Puccinia striiformis*. A recently described stripe rust resistance gene transferred from *Triticum vavilovi* also showed tight linkage to the *Gli-B1* locus (Bariana et al. 1999). The *T. vavilovi*-derived gene and *Yr10* appear to have the same pathogenic specificity and it remains to be shown whether these stripe rust genes are identical. The short arm of chromosome 1D contains at least two genes that confer resistance to *Puccinia recondita* (*Lr21*, *Lr40*) as well as genes effective against races of *Puccinia graminis* (*Sr45*, *Sr33*). Leaf rust resistance genes *Lr21* and *Lr40* were positioned approximately 5 cM distal, and stem rust resistance genes *Sr33* and *Sr45* were located 3–10-cM proximal to the storage protein genes (Huang et al. 1998; Jones et al. 1990, 1991). Crosses between parental lines that carried *Lr40* and a gene assumed to be an allele of *Lr21* did not yield susceptible progeny (Cox et al. 1994). However, in the absence of intercrosses between lines that were confirmed to carry *Lr21* and *Lr40*, the allelic relationship of these genes remains unclear, although both could be distinguished on the basis of their infection type to North American rust isolates (Huang 1998).

Plant resistance genes have been isolated from a wide range of species (Staskawicz et al. 1995) including at least one cereal rust resistance gene isolated from maize (Collins et al. 1999). To-date no resistance genes have been isolated from wheat, although candidate genes encoding resistance to cereal cyst nematode (Lagudah et al. 1997), stripe rust (Frick et al. 1998) and leaf rust (Feuillet et al. 1997) were identified. Subsequent analysis showed that a receptor-like kinase gene reported to be at the *Lr10* leaf rust resistance locus recombined with leaf rust resistance (Feuillet, personal communication). Leaf rust genes, *Lr21* and *Lr40*, and stem rust genes, *Sr33* and *Sr45*, were originally described in *Aegilops*

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tauschii, the D-genome donor, from where they were transferred into hexaploid wheat. To assist with the task of isolating candidate genes from chromosome 1DS, we are using *Ae. tauschii* and wheat transfer lines for the detailed molecular analysis of that region (Gill et al. 1991; Lagudah et al. 1991b).

The majority of resistance genes isolated belong to the class encoding nucleotide binding sites-leucine rich repeat proteins (NBS-LRR) (see review in Martin 1999). Short peptide sequences adjacent to the NBS are well-conserved among gene members of this class and have been used to design primers to amplify resistance gene analogs (RGAs) from many plant genomes (Kanazin et al. 1996; Leister et al. 1996; Yu et al. 1996; Collins et al. 1998; Seah et al. 1998). Several RGA markers were previously mapped to the short arm of the homoeologous group 1 of wheat (Spielmeyer et al. 1998). In this study we report the detailed mapping in *Ae. tauschii* of gene family members belonging to two NBS-LRR classes and assess the linkage of these markers to leaf rust resistance genes *Lr21* and *Lr40* located on chromosome 1DS and a stripe rust resistance gene from *T. vavilovi* located on chromosome 1BS.

Materials and methods

Plant materials and mapping families

An F_2 family of 116 individuals was derived from a cross between *Ae. tauschii* var. *meyeri* accession AUS 18911, carrying leaf rust resistance gene *Lr21* and stem rust resistance gene *Sr45*, and accession CPI 110799, carrying stem rust resistance gene *Sr33*. This F_2 family therefore segregated for *Lr21*, *Sr45* and *Sr33*, and F_3 progeny were scored for *Lr21* and *Sr33* phenotypes according to Bariana et al. (1993). A wheat F_2 family of 165 individuals was developed from a cross between cv Wichita and WGRC7 which carried the leaf rust resistance gene *Lr40* and F_3 progeny were scored using the North American rust isolate PRTUS6 (Huang 1998). Upon infection with the rust isolate PRTUS6, wheat lines carrying *Lr40* displayed infection type IT 1–2, whereas lines carrying *Lr21* showed a higher infection type, IT 3. The *Lr40* gene was originally derived from *Ae. tauschii* accession TA1649 (Huang1998). An additional wheat-mapping family of 95 lines which segregated for *Lr21* was used to confirm the association of RGA markers with this resistance phenotype. This mapping family was derived from a derivative of 'Chinese Spring' (DSTt5406) containing a substituted 1D chromosome from the *Ae. tauschii* donor line of *Lr21* (RL 5289) and the recurrent parent 'Chinese Spring' (Jones et al. 1990).

To determine the linkage of RGA markers to a stripe rust resistance gene derived from *T. vavilovi* and located on chromosome 1BS, we examined 40 F_3 lines from a cross between a *T. vavilovi* derivative and a susceptible cv, Avocet.

RFLP clones

RFLP clones previously mapped to chromosome 1SS were kindly supplied by A. Graner, Gatersleben (Mwg938, Mwg60, Mwg2083, Mwg2021), M. Sorrells, Cornell University (Cdo388, Bcd1434), A. Kleinhoff, Washington State University (Abc156), G. Wricke, University of Hannover (Iag95), C. Feuillet, University of Zurich (LrK10, Mwg2245), and V. Mohler, TU Munich (Whs179). A member of the gamma-gliadin gene family was provided by O. Anderson, USDA Albany, to map the *Gli-D1* locus.

RGA clones

The clone Rga5.2 was isolated by PCR from a *Ae. tauschii* BAC clone assigned to the region of interest and designated A6 (Spielmeyer et al. 2000) using degenerate primers for conserved motifs (kinase-2 and GLPLAL domains) found within or adjacent to the NBS region (Collins et al. 1998). Rga5.2 clone (350 bp) is 70% identical at the nucleotide level to other previously identified RGA sequences tightly linked to the *Cre3* cereal cyst resistance gene of wheat (Spielmeyer et al. 1998). PCR amplification conditions and cloning of PCR products were carried out according to Collins et al. (1998). RgaYr10 is a cDNA clone (400 bp) containing the kinase-2, kinase-3 and GLPLAL motifs showing less than 50% DNA sequence homology to Rga5.2. This cDNA sequence, a sub-clone of an ORF encoding a NBS-LRR gene, detected a marker co-segregating with the stripe rust resistance gene *Yr10* located distal to the storage protein genes on chromosome 1BS and is considered a candidate gene for *Yr10* (Frick et al. 1998). Additional RGA clones were mapped which were previously isolated from *Ae. tauschii* (Ttrga1) (Lagudah, unpublished), barley (b6) and maize (pic 18) and mapped to the orthologous region in barley (Leister et al. 1999).

DNA isolation and RFLP mapping

Genomic DNA preparation from leaves and DNA-blot analysis was carried out according to Lagudah et al.(1991a, b). RFLP markers were mapped using progeny from the above mapping families after probes were screened for DNA polymorphism between parental lines which had been digested with a set of restriction enzymes (*Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Nsi*I and *Xba*I). The marker order and genetic distances were determined using the MAPMAKER program (Lander et al. 1987).

Results

Detailed RFLP map of the distal region of chromosome 1DS

To assess the map locations of agronomically important genes in the distal region of chromosome 1DS, a detailed RFLP linkage map was constructed using a F_2 family of 116 *Ae. tauschii* lines (Fig. 1). The linkage map contains RFLP markers identified by DNA probes derived from three sources: DNA sequences previously assigned to this region (Whs179, Mwg938, Iag95, LrK10, Mwg2245, Bcd1434, Mwg2021, Mwg60, Mwg2083, Cdo388, Abc156 and KsuG9), RGA probes Rga5.2, RgaYr10, Ttrga1, b6 and pic18 derived from NBS-LRR sequences, and a DNA sequence corresponding to the gamma-gliadins (*Gli-1*) (Van Deynze et al. 1995). The genomic clone KsuD14, which was previously located to this region (Van Deynze et al. 1995), contained significant sequence homology to Rga5.2; therefore this clone cross-hybridised and detected the same loci as Rga5.2.

Both RGA clones, Rga5.2 and RgaYr10, identified duplicated loci in the region distal to the *Gli-D1* locus (Fig. 1). These clones were not expected to cross-hybridise because both sequences contained insufficient DNA homology (less than 50%). Hybridisation of Rga5.2 to *Eco*RI digested genomic DNA of *Ae. tauschii* produced three major bands which mapped to two separate loci within the target interval (Fig. 1). RgaYr10 also detected

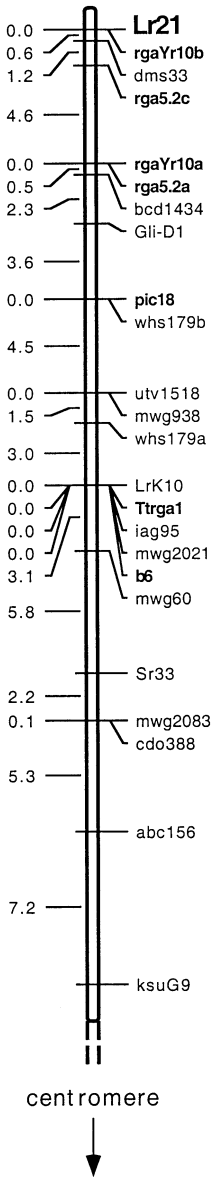

Fig. 1 RFLP map of the distal end of chromosome 1DS. The map was constructed with 116 F_2 individuals derived from a cross between *Ae. tauschii* lines AUS 18911 (*Lr21*) and CPI 110799 (*Sr33*).The most distal RGA marker, *rgaYr10b*, co-segregated with leaf rust resistance. Duplicated loci were identified with clones RgaYr10, Rga5.2 and Whs179. Genetic distances (cM) are denoted by *numbers* on the left

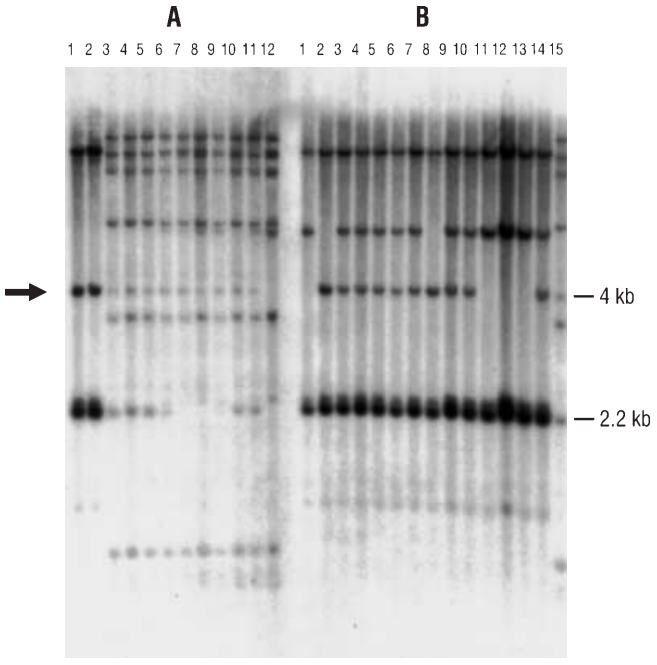

Fig. 2 DNA hybridisation of RgaYr10 probe to *Eco*RV-digested genomic DNA detected a co-segregating marker for leaf rust resistance *Lr21* and *Lr40* in F_2 segregating families of *Ae. tauschii* and wheat. **A** *Lane 1=Ae. tauschii* line AUS 18911 (*Lr21*), lane 2=*Ae. tauschii* line TA1649 (*Lr40*), lane 3=resistant wheat line WGRC7 (*Lr40*), *lanes 4 to 11*=subset of F_2 progeny derived from a cross between WGRC7 and cv Wichita (susceptible), *lane 12*=cv Wichita. The 4-kb DNA fragment (see *arrow*) co-segregated with *Lr40* resistance in 165 F_2 wheat lines. **B** *Lane 1=Ae. tauschii* parental line CPI 110799 (*Sr33*), *lane 2=Ae. tauschii* parental line AUS 18911 (*Lr21*), *lanes 3* to *14*=subset of F_2 progeny from cross between CPI 110799 and AUS 18911, *lane 15*=wheat line carrying *Lr40* (WGRC7). A DNA fragment of approximately the same size (4 kb, see arrow) was present in both *Lr21* and *Lr40 Ae. tauschii* donor lines AUS 18911 and TA1649 which co-segregated with *Lr21* in 116 F_2 lines

three major *Eco*RI RFLP fragments, two of which mapped to *rgaYr10a* and *rgaYr10b*, while a remaining monomorphic fragment was not mapped. The observed multiple loci suggested that gene-duplication events have occurred within the distal end of chromosome 1DS.

Association of RGA markers with rust resistance

At least two leaf rust resistance genes, *Lr21* and *Lr40*, have been mapped previously within the region distal to the *Gli-1* genes on chromosome 1DS (Jones et al. 1990; Huang 1998). Both of these rust resistance genes were introgressed from different *Ae. tauschii* lines into hexaploid wheat. On the basis of infection type, *Lr21* and *Lr40* appear to be different (Huang, unpublished), although they may constitute different alleles of the same locus. Cox et al. (1994) reported no susceptible segregants amongst 213 F_2 progeny obtained from a cross between wheat lines WGRC7 (*Lr40*) and U1866 postulated to carry an allele of *Lr21*. Further work is required involving a wheat parent that carries *Lr21* to determine whether *Lr21* and *Lr40* are located at separate, but linked, loci. To shed light on the respective map locations of *Lr21* and *Lr40* and determine their linkage to RGA markers, we studied their segregation in diploid and hexaploid F_2/F_3 families.

In an *Ae. tauschii* family (AUS 18911×CPI 110799) of 116 F_2 lines the most distal marker, *rgaYr10b*, co-segregated with leaf rust resistance conferring *Lr21* specificity (Fig. 2). The same RGA clone also detected a co-segregating marker for *Lr21* resistance in 95 wheat lines derived from a cross between a ‘Chinese Spring’ substitution line (DSTt5406) and ‘Chinese Spring’ (Jones et al. 1990). The lack of recombination between the RGA marker and resistance in two independent segregating families confirmed the tight linkage of *rgaYr10b* and *Lr21* and may indicate that RgaYr10 hybridised to a candidate gene which conferred *Lr21* speci-

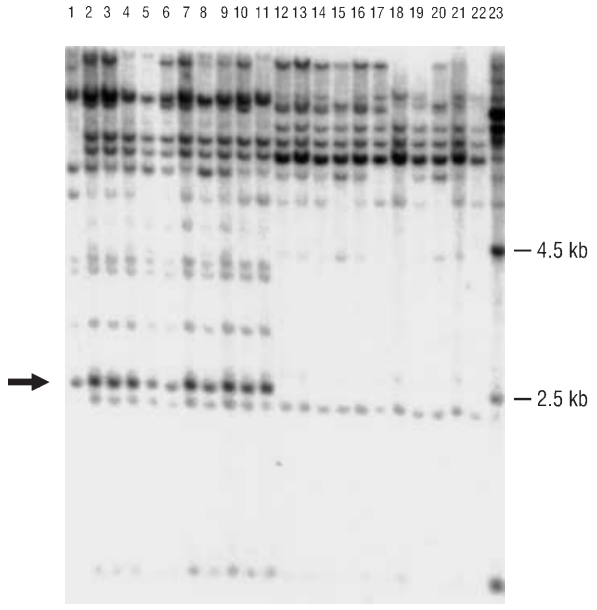

Fig. 3 DNA hybridisation of the RgaYr10 probe to *Xba*I-digested genomic DNA of wheat lines segregating for stripe rust resistance derived from *T. vavilovi*. *Lane 1*=resistant wheat *T. vavilovi*, *lanes 2* to *11*=homozygous resistant F_3 lines from a cross between *T. vavilovi* and cv Avocet, *lanes 12* to *21*=homozygous susceptible F_3 lines from the above cross, lane 22=cv Avocet, *lane 23*=near-isogenic line of Avocet carrying *Yr10* from cv Moro. RgaYr10 detected at least four RFLPs which were linked to stripe rust resistance, of which one fragment was common in size (2.5 kb, see *arrow*) to the DNA fragments detected in the *Yr10* NIL

ficity. In the same *Ae. tauschii* mapping family both Rga5.2 loci recombined with leaf rust resistance. However, in the wheat segregating family a Rga5.2 marker co-segregated with resistance to *Lr21* (data not shown).

Markers detected by RGA clones, RgaYr10 and Rga5.2, were also mapped in a wheat F_2 family segregating for resistance to *Lr40*. The RgaYr10 probe detected restriction fragments of similar size (approximately 4 kb) in both the *Lr40* (TA1649) and the *Lr21* (AUS18911) donor lines, where this marker was shown to co-segregate with resistance to *Lr21*. This 4-kb DNA fragment was one of two fragments transferred from TA1649 into the resistant hexaploid wheat line WGRC7 carrying *Lr40* and co-segregated with the resistance in a wheat segregating family of 165 F_2 lines (Fig. 2). A second DNA fragment (approximately 2.5 kb) which was transferred from TA1649 into WGRC7 was linked, but recombined with leaf rust resistance. It is likely that this RgaYr10 gene member corresponded to the proximal *rgaYr10a* locus identified on the *Ae. tauschii* linkage map (Fig. 1). The Rga5.2 probe identified a tightly linked marker that recombined with *Lr40* resistance in 2 out of 165 F_2 lines. In a separate F_2/F_3 mapping family involving a cross between a wheat line 'WGRC2' that carried a *Lr* gene tightly linked or allelic to *Lr40* and the susceptible cv 'Wichita', one recombinant line was identified between the diagnostic *rgaYr10b* marker and resistance to leaf rust (Huang, unpublished). In the absence of specific intercrosses between wheat lines 'WGRC2', 'WGRC7' (*Lr40*) and a line carrying *Lr21* the relationship of these resistance genes located within the distal region of chromosome 1DS remains unresolved.

The clone RgaYr10 was isolated from the wheat cultivar 'Moro' carrying the *Yr10* gene for stripe rust resistance, which was mapped distal to the gamma-gliadins on the end of chromosome 1BS (McIntosh et al. 1998). This clone detected a marker which co-segregated with *Yr10* resistance in more than 500 segregating wheat lines and was shown to be part of a candidate gene for *Yr10* (Frick et al. 1998). A recently described stripe rust resistance gene from *Triticum vavilovi* was also located in this region distal to the seed storage protein genes on chromosome 1BS (Bariana et al. 1999). To investigate whether RgaYr10 also detected a marker linked to the *T. vavilovi*-derived stripe rust gene, we examined a random subset of 40 F_3 lines from a cross between resistant *T. vavilovi* derivative and a susceptible wheat cv 'Avocet.' Their respective DNA hybridisation profiles were compared to the near-isogenic line (NIL) of 'Avocet' carrying *Yr10* from cv 'Moro' (Wellings, personal communication). The RgaYr10 probe hybridised to at least four restriction fragments of *Xba*I-digested genomic DNA from *T. vavilovi* that were linked to stripe rust resistance (Fig. 3). One of these hybridising bands corresponded in size to a fragment (approximately 2 kb) present in the Avocet-*Yr10* NIL. Apart from this relatively minor 2-kb band, the Avocet-*Yr10* NIL contained at least four additional strongly hybridising bands which were absent in 'Avocet' and *T. vavilovi*, indicating that only a subset of RgaYr10-hybridising fragments were present in *T. vavilovi* as compared to a wheat line carrying *Yr10* (Fig. 3).

Discussion

To develop a detailed genetic linkage map of the end of chromosome 1DS we used the diploid species *Ae. tauschii* as a model system. Because of the lower ploidy level and less-complex DNA hybridisation patterns, a greater number of co-dominant markers with a higher degree of confidence were mapped in *Ae. tauschii* than would have been possible to map in wheat. Gene-duplication events have probably generated multiple loci detected by three DNA probes mapped within this region. Two non-crosshybridising RGA clones (Ttrga1 and b6) and a clone encoding a receptor-like kinase gene (LrK10) detected co-segregating markers on the genetic linkage map (Fig. 1). To our knowledge no resistance phenotype has been mapped to this genetic position on chromosome 1DS. Tight linkage of markers detected by divergent RGA clones has been previously reported in cereals (Spielmeyer et al. 1998; Leister et al. 1999). Also close physical association between *LrK10* and a

NBS-LRR gene has been previously reported in wheat, where both genes were physically located within a 14 kb fragment (Feuillet and Keller 1999).

Two RGA clones, Rga5.2 and RgaYr10, which belong to unrelated NBS-LRR gene families, detected markers tightly linked to leaf and stripe rust resistance genes located at the end of chromosome 1S of wheat. Previous work showed that RgaYr10 detected a cosegregating marker for *Yr10*, a stripe rust resistance gene located approximately 5 cM distal to the *Gli-B1* locus on chromosome 1BS (Frick et al. 1998). Within the same chromosomal region on 1BS an additional stripe rust resistance gene was mapped which had been introgressed from *T. vavilovi* (Bariana et al. 1999). The relationship of the *T. vavilovi*-derived gene and *Yr10* remains unclear, although these genes appear to have the same pathogenic specificity to Australian rust isolates. RgaYr10 also hybridised to markers linked to the *T. vavilovi*-derived gene, but resulting in a different DNA hybridisation pattern to the profile generated with the same restriction enzyme of a near-isogenic line carrying *Yr10*. The same clone identified *rgaYr10b*, a marker cosegregating with *Lr21* and *Lr40*, two leaf rust genes located within the homoeologous region on chromosome 1DS. There was no recombination detected between this marker and leaf rust resistance in *Ae. tauschii* and wheat segregating families. These results confirm that both leaf rust resistance genes are either tightly linked or constitute different alleles of the same locus. Given that the majority of plant disease resistance genes isolated so far encode NBS-LRR proteins, including rust resistance genes isolated from flax (Lawrence et al. 1995) and maize (Collins et al. 1999), it is likely that leaf and stripe rust resistance genes in wheat may also belong to this class of NBS-LRR genes. We have shown that RgaYr10 which identified a candidate gene for stripe rust resistance also detected candidate genes for leaf rust resistance genes located within homoeologous regions. Future work will focus on the isolation of candidate genes for *Lr21* and *Lr40* from *Ae. tauschii* using RgaYr10 as a probe and the induction and analysis of mutants involving these rust specificities in both *Ae. tauschii* and hexaploid wheat lines.

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