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Molecular identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L.)

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Abstract RFLP markers for the wheat powdery mildew resistance genes *Pm1* and *Pm2* were tagged by means of near-isogenic lines. The probe Whs178 is located 3 cM from the *Pm1* gene. For the powdery mildew resistance gene *Pm2*, two markers were identified. The linkage between the *Pm2* resistance locus and one of these two probes was estimated to be 3 cM with a F_2 population. Both markers can be used to detect the presence of the corresponding resistance gene in commercial cultivars. „Bulked segregant analysis" was applied to identify linkage disequillibrium between the resistance gene *Pm18* and the abovementioned marker, which was linked to this locus at a distance of 4 cM. Furthermore, the RAPD marker OPH-11_{1900} (5′-CTTCCGCAGT-3′) was selected with pools created from a population segregating for the resistance of 'Trigo BR 34'. The RAPD marker was mapped about 13 cM from this resistance locus.

Key words Mildew resistance · *Triticum aestivum* Near-isogenic lines · Bulked segregant analysis RFLP RAPD

Introduction

In central Europe, one aim of wheat breeding is to increase resistance to powdery mildew caused by *Erysiphe graminis* DC f.sp. *tritici*. To accelerate breeding programs in anticipation of rapid changes in pathogen populations (Limpert and Fischbeck 1991), a set of molecular markers linked to resistance genes are required. Furthermore, in wheat the identification of resistance genes with the help of host-pathogen interactions described by Flor (1955) is limited by an increasing number of major resistance genes and gene combinations. Closely linked molecular markers are needed to identify powdery mildew resistance genes in a complex genetic background and to facilitate the selection towards pyramiding resistance genes.

In cereals, several strategies have been employed to map genes for resistance. Doubled-haploid (DH) mapping populations were used to localize the resistance gene *ym4* against Barley Yellow Mosaic Virus (Graner and Bauer 1993). The most common way to map resistance genes is to screen near-isogenic lines (NILs). This has been done in barley to identify RFLP markers linked to the *Mla* locus conferring powdery mildew resistance (Schüller et al. 1992) and in oat to isolate a cosegregating random amplified polymorphic DNA (RAPD) marker linked to the *Pg3* resistance gene against *Puccinia graminis* f. *avenae* (Penner et al. 1993a).

The use of pooled DNA samples, designated as "bulked segregant analysis" by Michelmore et al. (1991), offers an alternative to NILs for the detection of linkage disequillibrium (Arnheim et al. 1985). With this method polymorphic restriction fragment length polymorphisms (RFLP) and RAPD markers can be directly identified using pools (bulks) that are selected from a segregating population scored for the trait of interest. In cereals, Penner et al. (1993b) used homozygous pools from F_3 families to find a cosegregating RAPD marker linked to a crown rust resistance gene in oat.

In wheat, many resistance genes have been assigned to particular chromosomes or chromosome arms (McIntosh 1993), but only a few of them have been localized at the molecular level. Ma et al. (1993) identified RFLP markers associated with two Hessian fly resistance genes *H23* on chromosome 6D and *H24* on chromosome 3DL. With the help of NILs the *Pm3* locus for resistance to powdery mildew on chromosome 1A was tagged by means of an RFLP marker closely linked to the resistance locus. This marker also differentiated the alleles at this locus (Hartl et al. 1993). Similarly, Schachermayr et al. (1994) found RFLP and RAPD markers that cosegregated with the *Lr9* leaf rust resistance gene derived from *Aegilops umbellulata*.

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In the investigation presented here, RFLP and RAPD markers linked to the powdery mildew resistance genes, *Pm1*, *Pm2*, *Pm18*, and an unknown resistance gene in a wheat cultivar from Brazil were identified using different strategies. The "bulked segregant analysis" for recently discovered resistance genes was used if NILs were not available. In order to investigate the applicability of the linked markers for the identification of the resistance genes *Pm1* and *Pm2*, several wheat cultivars and lines with known powdery mildew resistance genes or gene combinations were included in the present study.

Materials and methods

Plant material

Wheat NILs for several powdery mildew resistance genes were used to test for polymorphic RFLP markers linked to resistance genes. A set of NILs was developed by Briggle (1969) after seven backcross generations with 'Chancellor' (Cc) as recurrent parent and 'Axminster' (*Pm1*), 'Ulka' (*Pm2*), 'Asosan' (*Pm3a*), 'Chul' (*Pm3b*), 'Sonora' (*Pm3c*), and 'Khapli' (*Pm4a*) as donor lines (supplied by R.A. McIntosh, Cubbitty, Australia). An additional set of NILs with the genetic background of 'Prins' were used, 'CI12559/8*Prins' (*Pm6*), 'Halle 8810–47/7*Prins' (*Pm2*), 'Hope/9*Prins' (*pm5*), which was provided by J. MacKey, Uppsala, Sweden. For the bulked segregant analysis, leaves of 10–20 plants from F_2 generations which were clearly resistant or susceptible to powdery mildew were pooled to extract DNA. The F_2 generations originated from crosses between 'Chinese Spring' and 'Weihenstephan M1N' (*Pm18*) (Zeller et al. 1993a) or 'Chinese Spring' and the Brazilian cultivar 'Trigo BR 34', provided by A. Zanatta, Passo Fundo, Brazil. The probes were assigned to chromosomes by a set of nulli-tetrasomic lines developed by Sears (1966). The F_2 generation of the cross between the German wheat cultivar 'Ralle' and the synthetic wheat line 'XX85' (*T. dicoccoides* × *Ae. squarrosa*=ABD-11), provided by Dr. Ohta, Kyoto, Japan, was used to map the RFLP probes.

The genetic distance between powdery mildew resistance genes *Pm1*, *Pm2* and the polymorphic markers was measured with the F_2 generation of the cross between 'Axminster/8*Cc' (*Pm1*) and 'Ulka/8*Cc' (*Pm2*). The determination of linkage to *Pm18* was conducted on the cross between 'Khapli/8*Cc' (*Pm4a*) and 'Weihenstephan M1N' (*Pm18*). For the localization of the resistance gene in 'Trigo BR 34', the same F_2 generation was used as for pool formation. A total of 35 wheat cultivars or lines which had already been scored by Heun and Fischbeck (1987), Schneider et al. (1991), and Zeller et al. (1993c) for their powdery mildew resistance genes in our laboratory were employed to assess the applicability of the markers for identification of resistance genes (Table 1).

Table 1 Wheat cultivars and lines with known powdery mildew resistance genes and hybridization pattern of selected markers. Shadowed cells indicate cultivars not fitting the association (178 *Xwhs178-Eco*RI 9.4 kb; 295 Whs295-*Eco*RV 3.2 kb, 350 Whs350-*Eco*RV 6.5 kb)

Cultivars or lines	*Pm1*	178	*Pm2*	295	350
Chinese Spring	–	–	–	–	+
BGRC 44514	+	+	–	–	+
Halle 13471	–	–	+	+	–
Normandie	+	+	+	–	+
Maris Dove	–	–	+	+	–
Axona	–	[b]	+	+	–
Lichtis früh	–	–	–	–	+
Maris Huntsman	–	–	+	+	–
Sappo	+	+	+	–	+
Herold	–	+	–	–	+
Turbo	–	–	–	–	+
Planet	+	+	+	+	–
Timmo[a]	+	+	[b]	+	–
Syros	–	+	–	–	+
Attis	+	+	+	+	–
Troll	+	+	+	+	–
Nandu	–	–	+	+	–
Sokrates	–	–	–	–	+
Star	–	+	–	–	+
Kolibri	–	–	–	–	+
Urban	–	–	–	–	+
Kanzler	–	–	–	–	+
Ares	–	[b]	–	–	+
Boheme	–	–	–	–	+
Greif	–	–	–	–	+
Disponent	–	–	–	–	+
Kronjuwel	–	–	–	–	+
Clan	–	–	–	–	+
Zorba	–	–	–	–	+
Kontra	–	–	+	+	–
Rektor	–	–	–	–	+
Herzog	–	–	–	–	+
Knirps	–	[b]	+	+	–
Kormoran	–	+	–	–	+
Club	–	–	–	–	+

[a] Containing *Lr 20* closely linked to *Pm1* (The and McIntosh 1975)
[b] Missing data

Southern analysis

The preparation of the wheat genomic library, DNA extraction, restriction digestion, Southern blotting, and hybridization have been described by Hartl et al. (1993).

PCR analysis

On the basis of a protocol described by Williams et al. (1990), the amplification reaction (25 µl) contained 5 ng template DNA, 1 Unit *Taq*-DNA-polymerase (Pharmacia), 1PCR buffer (50 m*M* KCl, 1.5 m*M* $MgCl_2$, 10 m*M* TRIS-HCl pH 9.0), 2.0 m*M* $MgCl_2$, 100 µ*M* each of dATP, dTTP, dGTP, dCTP, as well as 200 n*M* primer. In order to prevent evaporation the samples were overlaid with mineral oil. The PCR reaction mixture was prepared at room temperature. The samples were subjected to 45 cycles in a Perkin-Elmer Cetus DNA Thermal Cycler under the following conditions: 4 min at 94 °C before the cycles start; 1 min at 94 °C, 1 min at 35 °C, 1 h and 30 min with a prolongation of 2 s at each cycle at 72 °C; and at the end of the reaction, 5 min at 72 °C. The PCR products were stored at 4 °C. The 10-mer random primers were obtained from Operon Technologies, Alameda, Calif. Amplified products were analyzed by electrophoresis on a 1.5% agarose gel containing ethidium bromide. The notation of the RAPD primer designates the source of the primer, the used set, and the molecular size of marker fragment.

Data analysis

The estimation of recombination percentages was based on the method of maximum likelihood and was conducted with the computer program Linkage-1 (Suiter et al. 1983). The recombination fraction was transformed to centiMorgan (cM) according to Kosambi (1944).

Powdery mildew test

Powdery mildew tests were conducted at the seedling stage using detached leaves that had been placed on agar containing 50 mg/l benz-

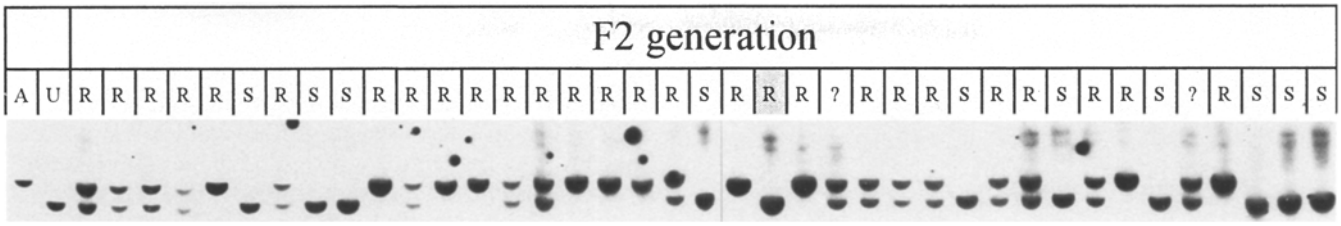

Fig. 1 Segregation of the RFLP marker Whs178 on the F_2 generation of the cross 'Axminster/8*Cc' (*Pm1*,A, 7.2 kb) × 'Ulka/8*Cc' (*Pm2*, U, 5.8 kb). *Shadowed* cell indicates the recombinant line. *S* Susceptible, *R* resistant

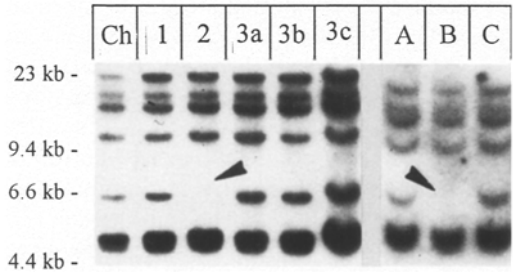

Fig. 2 Southern blot analysis of NILs digested with *Eco*RV and hybridized to probe WHS350. *Ch* recurrent parent 'Chanellor' (Cc), *1* 'Axminster/8*Cc' (*Pm1*), *2* 'Ulka/8*Cc' (*Pm2*), *3a* 'Asosan/8*Cc' (*Pm3a*), *3b* 'Chul/8*Cc' (*Pm3b*), 'Sonora/8*Cc' (*Pm3c*), *A* 'CI12559/8*Prins' (*Pm6*), *B* 'Halle8810-47/7*Prins' (*Pm2*), *C* 'Hope/9*Prins' (*pm5*)

imidazol and 50 g/ml ampicillin. Seedlings were raised in a growth chamber in order to prevent contamination. Powdery mildew infections were carried out according to the method described by Aslam and Schwarzbach (1980). The powdery mildew isolates used in this study originate from a collection of single-spore progenies that differ in virulence. After inoculation, the agar plates were kept under controlled conditions for 9 days until disease readings were scored as described by Lutz et al. (1992).

Results

RFLP analysis of *Pm1* and *Pm2* resistance genes

Out of 250 screened genomic wheat DNA probes, only one probe Whs178 showed polymorphism between the near-isogenic line 'Axminster/8*Cc' (*Pm1*) and the recurrent parent. The genetic distance to the resistance locus *Pm1* was estimated from the cross between 'Axminster/8*Cc' (*Pm1*) and 'Ulka/8*Cc' (*Pm2*). The segregation of the F_2 population was tested with three powdery mildew isolates, one avirulent against *Pm1* and virulent against *Pm2*, and two avirulent against *Pm2* and virulent against *Pm1* resistance gene. The observed ratio was consistent with a 3:1 segregation as expected for a dominant resistance gene. After the hybridization of Southern blots to DNA from 39 F_2 plants (Fig. 1), the marker locus *Xwhs178* mapped at a distance of 2.8±2.7 cM to the *Pm1* locus. In agreement with cytological data on the resistance gene *Pm1* (Sears and Briggle 1969), this probe was assigned to chromosome 7A using nulli-tetrasomic lines. After restriction with the enzyme *Eco*RI the RFLP band (9.4 kb) was observed in all lines containing the resistance gene *Pm1*. However, one exception was found in 4 out of 25 lines without the *Pm1* mildew resistance gene (Table 1).

With regard to the *Pm2* powdery mildew resistance locus, the probes Whs295 and Whs350 revealed polymorphisms between the NIL 'Ulka/8*Cc' and the recurrent parent. On the basis of the F_2 analysis of the cross between the near-isogenic lines for *Pm1* and *Pm2* the genetic distance between the marker locus *Xwhs295* and the resistance gene was 2.7±2.6 cM. In the mapping population 'Ralle × XX85', this marker mapped within the linkage group of chromosome 5D, where the *Pm2* resistance gene is located (McIntosh and Baker 1970). In addition, after digestion with *Eco*RV the marker Whs350 revealed a deletion of the 6.5-kb band compared to the recurrent parents in the NILs, 'Ulka/8*Cc' and 'Halle 8810–47/7*Prins', both with *Pm2* resistance and originating from two different backcross programs (Fig. 2). With nulli-tetrasomic lines the marker locus *Xwhs350*-6.5 kb-*Eco*RV was assigned to chromosome 5D. The marker Whs350 was not mapped in a segregating population.

To verify the *Pm2* specific pattern of these markers, a set of wheat cultivars and lines with known powdery mildew resistance genes were examined (Table 1). RFLP patterns, which were revealed with the markers Whs295 and Whs350 in 22 lines without the *Pm2* resistance gene, were identical with those of the recurrent parents of the NILs. Ten cultivars and lines with the *Pm2* gene showed restriction fragments typical for the resistance gene locus *Pm2*. Only the cultivars 'Normandie' and 'Sappo', which are known to contain *Pm2*, showed a pattern identical to that of the susceptible recurrent parent.

Bulked segregant analysis for identification of *Pm18* and the resistance gene in 'Trigo BR 34'

The RFLP probe Whs178 revealed polymorphism between the pools for resistant and susceptible plants classified by two races avirulent against the *Pm18* powdery mildew resistance gene. The Southern blot analysis of the susceptible pools displayed a single band similar to that shown by the susceptible parent 'Chinese Spring'. In the resistant pool a heterozygous pattern was obtained for both parents

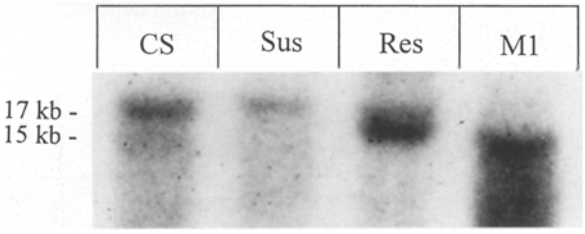

Fig. 3 Southern blot of susceptible (*Sus*) and resistant (*Res*) pools and parents. *CS* 'Chinese Spring', *M1* 'Weihenstephan M1N' (*Pm18*)

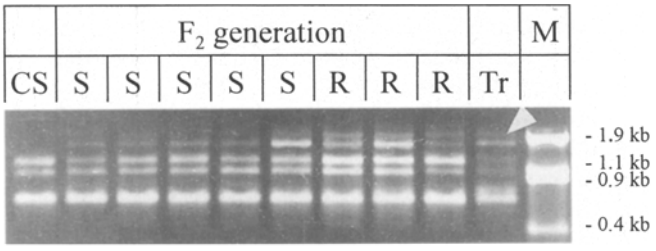

Fig. 4 Segregation of the RAPD marker OPH-11_{1900} (*arrowhead*) in the F_2 generation of the cross 'Chinese Spring' (*CS*) × 'Trigo B 34' (*Tr*). *M* pBR322 × BstNI, *S* susceptible, *R* resistant

that was characteristic of a dominant gene (Fig. 3). The segregation analysis of 34 F_2 plants of the cross between 'M1N' (*Pm18*) and 'Khapli/8*Cc' (*Pm4a*) showed a close linkage of *Pm18* and the marker locus *Xwhs178*, estimated at a distance of 4.4±3.6 cM.

In addition to the RFLP screening, RAPDs were also applied to the "bulked segregant analysis". Because of the intermediate reaction type of the resistance gene from the cv 'Trigo BR 34', only the extreme phenotypes were included in the pools. Twenty-decamer primers were evaluated, resulting in an average of 6 products per primer. The reproducibility of the RAPD experiments was checked with other pools from crosses of 'Chinese Spring' and several powdery mildew resistant lines. Artifacts could be easily identified by repetitions within and between the experiments.

The primer OPH-11 (5′-CTTCCGCAGT-3′) generated a 1.9-kb product in the resistant parent and in the resistant pool of the cross 'Chinese Spring' × 'Trigo BR 34' only. F_2 analysis suggested a linkage between this marker and the resistance gene (Fig. 4). For the linkage analysis, we had to score the F_3 segregation to verify exactly the genotypes of the F_2 plants. Linkage was estimated to be 13±16 cM in the F_2 population. Because of the absence of the marker fragment in 'Chinese Spring', the chromosomal location with nulli-tetrasomic lines could not be determined. Furthermore, the amplified marker fragment was used as RFLP probe, but in this hybridization experiment only a repetitive pattern was observed.

Discussion

In the large genome of wheat in particular the screening of NILs is an effective way to isolate molecular markers linked to powdery mildew resistance genes. With the use of NILs, the *Pm3* locus conferring powdery mildew resistance was marked with the RFLP probe Whs179 (Hartl et al. 1993). In the present study, markers for *Pm1* and *Pm2* resistance genes were identified. Although the use of NILs is well-established, the development of NILs for recently identified resistance genes is time-consuming and labor-intensive.

For the resistance gene *Pm18* and the resistance gene in 'Trigo BR 34', the "bulked segregant analysis" offers a strategy to screen markers immediately after the discovery of these genes. Only the segregating population is required, which is used to study the mode of inheritance by means of host-pathogen interactions. Even if the expression of the resistance phenotype is not complete or if it is influenced by minor genes – as was the case in the cross between 'Chinese Spring' and 'Trigo BR 34' – it is no longer essential to divide all of the F_2 plants into susceptible and resistant pools as long as 10–20 plants can be scored unequivocally (Williams et al. 1993). The attempt to use the amplified marker fragment OPH-11_{1900} as a RFLP probe is likely to have failed because it is probable that the amplified fragments derived from repetitive DNA sequences of the wheat genome (Devos and Gale 1992).

To screen markers linked to single traits within NILs or bulks, RAPD markers provide a useful alternative to RFLP analysis. A large number of loci can be detected in a single run on a thermal cycler. Although the RAPD marker OPH-11_{1900} is sensitive to minor changes of conditions, the sequence of the 1.9 kb fragment could be determined, and a specific primer pair for this region could be generated to tag specific regions reliably (Olson 1989; Paran and Michelmore 1993).

On the basis of host-pathogen interactions it is difficult to identify and differentiate more than the 20 powdery mildew resistance genes so far characterized and localized in the wheat genome (Zeller et al. 1993a). Due to the lack of sufficient differential isolates, combinations of highly effective resistance genes could not be detected phenotypically. The incomplete cosegregation of the marker Whs178 with the *Pm1* resistance gene in the F_2 generation (Fig. 1) indicates that recombinations between the marker locus and the resistance gene are the most likely reason for the exceptions observed in the cultivars (Table 1). The markers Whs295 and Whs350 appear to be closely linked to the *Pm2* locus, since we found only 1 recombination between marker Whs295 and the *Pm2* locus and a close association with both markers to the resistance composition in the cultivars and lines. The probes Whs295 and WHS350 should faciliate determination of *Pm2* resistance in different genetic backgrounds. Combinations with the *Pm2* gene have been used in several European cultivars (Heun and Fischbeck 1987; Lutz et al. 1992; Zeller et al. 1993b). However, cultivars 'Normandie' and 'Sappo', which were re-

ported by Schneider et al. (1991) to possess *Pm2*, did not show specific RFLP patterns for this gene with either probe. The present finding is consistent with the results of Hovmøller (1989) who also concluded that 'Sappo' lacks *Pm2*. On the basis of allelism tests between 'Normandie' and 'Ulka' (*Pm2*), Carter (1954) suggested that 'Normandie' contains *Pm2*. However, further cytogenetic studies are required to clarify the identity of mildew resistance genes in 'Normandie'.

The resistance gene of 'Trigo BR 34' and the resistance gene *Pm18* in 'M1N' seem to be highly effective against all existing races of the pathogen in Europe. That is why these genes would provide the complete control of powdery mildew disease (Zeller and Stephan unpublished). The strategy of marker-assisted selection (Paterson et al. 1991) accelerates breeding for pyramiding resistance genes and for optimizing the durability of genes through the combining of resistance factors. The codominant makers for the resistance genes *Pm1*, *Pm2* and *Pm18* are linked at a distance less than 5 cM, which is sufficient for marker assisted selection in breeding programs. For a rapid screening approach, specific primers should be developed from the RAPD and the RFLP markers to facilitate selection using the advantages of the PCR technique.

Apart from applying these markers in a marker-assisted breeding program, molecular markers offer a great opportunity for understanding the relationship between resistance genes, and the origin and mechanism of resistance. Zeller et al. (1993a) located the *Pm18* powdery mildew resistance gene on chromosme 7A. On the basis of the close genetic linkage of marker locus *Xwhs178* to both resistance genes *Pm1* and *Pm18*, several arrangements of the powdery mildew resistance genes on chromosome 7A are possible. Both resistance genes *Pm1* and *Pm18* are suggested to be closely linked or to be located at a distance of about 7 cM (2.8 cM+4.4 cM) from each other, with marker Whs178 placed in between. Moreover, Schneider et al. (1991) estimated the distance between the *Pm1* and *Pm9* powdery mildew resistance genes to be 8.5 cM. However, it has been repeatedly observed that disease resistance genes are often located in a complex region containing different race specifities (Sudupak et al. 1993; Jahoor and Fischbeck 1993). Therefore, it could be assumed that a complex region for mildew resistance exists on chromosome 7A. On the basis of these data, relations between the resistance genes *Pm1*, *Pm9*, and *Pm18* should be determined by means of tests at the phenotypic level or by the use of more molecular markers in this region.

Since homoeologous relationships within the genomes of wheat and within the tribe *Triticeae* have been clearly elucidated during the past decades, both by various means of cytogenetic methods (Sears 1968; Islam and Shepherd 1981) as well as by molecular markers (Devos et al. 1993; Wang et al. 1992; Chao et al. 1989), it may be anticipated that these relationships exist among disease resistance loci in the *Triticeae*. Analogous structures of the multi-allelic regions around the powdery mildew resistance locus *Pm3* in wheat (Briggle and Sears 1966; Zeller et al. 1993c) and around the *Mla* locus in barley (Jensen et al. 1980) have been reported. Moreover, in wheat, *Pm1*, *Pm9*, and *Pm18* are located on the long arm of chromosome 7A and *pm5* on 7BL, and in barley the mildew resistance gene *Mlf* is assigned to 7HL (Schönfeld and Jahoor unpublished). These facts support the existence of homoeo-allelism between the species of the tribe Triticeae for these regions.

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References

Arnheim N, Strange C, Erlich H (1985) Use of pooled DNA samples to detect linkage disequilibrium of polymorphic restriction fragments and human disease: Studies of the *HLA* class II loci. Proc Natl Acad Sci USA 82:6970–6974

Aslam M, Schwarzbach E (1980) An inoculation technique for quantitative studies of brown rust resistance in barley. Phytopathology Z 99:87–91

Briggle LW (1969) Near-isogenic lines of wheat with genes for resistance to *Erysiphe graminis* f. sp. *tritici*. Crop Sci 9:70–72

Briggle LW, Sears ER (1966) Linkage of resistance to *Erysiphe graminis* f. sp. *tritici* (*Pm3*) and hairy glume (*Hg*) on chromosome 1A of wheat. Crop Sci 6:559–561

Carter MV (1954) Additional genes in *Triticum vulgare* for resistance to *Erysiphe graminis tritici*. Aust J Biol Sci 7:411–414

Chao S, Sharp PJ, Worland AJ, Worham EJ, Koebner RMD, Gale MD (1989) RFLP-based genetic maps of wheat homoeologous group 7 chromosomes. Theor Appl Genet 78:495–504

Devos KM, Gale MD (1992) The use of random amplified polymporphic DNA markers in wheat. Theor Appl Genet 84:567–572

Devos KM, Miller T, Gale MD (1993) Comparative RFLP maps of the homoeologous group 2 chromosomes of wheat, rye and barley. Theor Appl Genet 85:784–792

Flor HH (1955) Host-parasite interaction in flax rust – its genetics and other implication. Phytopathology 45:680–685

Graner A, Bauer E (1993) RFLP mapping of the *ym 4* virus resistance gene in barley. Theor Appl Genet 86:689–693

Hartl L, Weiss H, Zeller FJ, Jahoor A (1993) Use of markers for the identification of the alleles of the *Pm3* locus conferring powdery mildew resistance in wheat (*Triticum aestivum* L.). Theor Appl Genet 86:959–963

Heun M, Fischbeck G (1987) Genes for powdery mildew resistance in cultivars for spring wheat. Plant Breed 99:282–288

Hovmøller MS (1989) Race specific powdery mildew resistance in 31 northwest European wheat cultivars. Plant Breed 103:228–234

Islam AKMR, Shepherd KW (1981) Wheat-barley addition lines: Their use in genetic and evolutionary studies of barley. In: Proc 4th Int Barley Genet Symp., Edingburgh, pp 729–739

Jahoor A, Fischbeck G (1993) Identification of new genes for mildew resistance of barley at the *Mla* locus in lines derived from *Hordeum spontaneum*. Plant Breed 110:116–122

Jensen J, Jørgensen JH, Jensen HP, Giese H, Doll H (1980) Linkage of the hordein loci *Hor1* and *Hor2* with the powdery mildew resistance loci *Ml-k* and *Ml-a* on barley chromosome 5. Theor Appl Genet 58:27–31

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Limpert E, Fischbeck G (1991) Wheat mildew populations in the FRG and neighbouring regions - some aspects of their change. In: Jørgensen JH (ed) Integrated control of cereal mildew: virulence patterns and their change. Risø National-Laboratory, Røskilde, Denmark, pp 1–17

Lutz J, Limpert E, Bartos P, Zeller FJ (1992) Identification of powdery mildew resistance genes in common wheat (*Triticum aestivum L.*). I. Czechoslowakian cultivars. Plant Breed 108:33–39

Ma ZQ, Gill BS, Sorrells ME, Tanksley SD (1993) RFLP markers linked to two Hessian fly-resistance genes in wheat (*Triticum aestivum L.*) from *Triticum tauschii* (Coss): Theor Appl Genet 85: 750–754

McIntosh RA (1993) Catalogue of symbols. In: Proc 8th Int Wheat Genet Symp., Beijing, China (in press)

McIntosh RA, Baker EP (1970) Cytogenetical studies in wheat. IV. Chromosome location and linkage studies involving the *Pm2* locus for powdery mildew resistance. Euphytica 19:71–77

Michelmore RW, Paran I, Kesseli RV (1991) Identification of markers linked to disease resistance genes by bulked segregant analysis: a rapid method to detect markers in specific genomic regions using segregating populations. Proc Natl Acad Sci USA 88:9828–9832

Olson M, Hood L, Canto CH, Botstein D (1989) A common language for physical mapping of the human genome. Science 24: 1434–1435

Paran I, Michelmore RW (1993) Development of reliable PCR-based marker linked to downy mildew resistance genes in lettuce. Theor Appl Genet 85:985–993

Paterson AH, Tanksley SD, Sorrells ME (1991) DNA markers in plant improvement. Adv Agron 46:39–90

Penner GA, Chong J, Lévesque-Lemay M, Molnar SJ, Fedak G (1993a): Identification of a RAPD markers linked to the oat stem rust gene *Pg3*. Theor Appl Genet 85:702–705

Penner GA, Chong J, Wight CP, Molnar SJ, Fedak G (1993b) Identification of an RAPD marker for the crown rust resistance gene *Pc68* in oats. Genome 36:818–820

Pineda O, Bonierbale MW, Plaisted R, Brodie BB, Tanksley SD (1993) Identification of RFLP markers linked to the *H1* gene conferring resistance to the potato cyst nematode *Globodera rostochiensis*. Genome 36:152–156

Schachenmayr G, Siedler H, Gale MD, Winzeler H, Winzeler M, Keller B (1994) Identification and localization of molecular markers linked to the *Lr9* leaf rust resistance gene of wheat. Theor Appl Genet 88:110–115

Schneider DM, Heun M, Fischbeck G (1991) Inheritance of the powdery mildew resistance gene *Pm9* in relation to *Pm1* and *Pm2* of wheat. Plant Breed 107:161–164

Schüller C, Backes G, Fischbeck G, Jahoor A (1992) RFLP markers to identify the alleles on the *Mla* locus conferring powdery mildew resistance in barley. Theor Appl Genet 84: 330–338

Sears ER (1966) Nullisomic-tetrasomic combinations in hexaploid wheat. In: Riley R, Lewis KR (eds) Chromosome manipulation and plant genetics. pp 29–45

Sears ER (1968) Relationship of chromosomes 2A, 2B and 2D with their rye homeologue. In: Proc 3rd Int Wheat Genet Symp., Canberra, Australia, pp 185–195

Sears ER, Briggle LW (1969) Mapping of the gene *Pm1* for resistance to *Erysiphe graminis* f. sp. *tritici* on chromosome 7A of wheat. Crop Sci 9:96–97

Sudupak MA, Bennnetzen JL, Hulbert SH (1993) Unequal exchange and meiotic instability of disease-resistance genes in the *Rp1* region of maize. Genetics 133:119–125

Suiter KA, Wendel JF, Case JS (1983) Linkage-1: a Pascal computer program for the detection and analysis or genetic linkage. J Hered 74:203–204

The TT, McIntosh RA (1975) Cytogenetical studies in wheat. VIII. Telocentric mapping and linkage studies involving *Sr22* and other genes in chromosome 7AL. Aust J Biol Sci 28:531–538

Wang ML, Atkinson MD, Chinoy CN, Devos KM, Gale MD (1992) Comparative RFLP based maps of barley chromosome 5 (1H) and rye chromosome 1R. Theor Appl Genet 84:339–344

Williams JGK, Kubelik AR, Livak KJ, Rafalksi JA, Tingey SV (1990) DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucleic Acids Res 18: 6531 –6535

Williams JGK, Reiter RS, Young RM, Scolnik PA (1993) Genetic mapping of mutations using phenotypic pools and mapped RAPD markers. Nucleic Acids Res 21:2697–2702

Zeller FJ, Stephan U, Lutz J (1993a) Present status of wheat powdery mildew resistance genetics. In: Proc 8th Int Wheat Genet Symp., Beijing, China (in press)

Zeller FJ, Lutz J, Remlein EI, Limpert E, Koenig J (1993b) Identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L.). II. French cultivars. Agronomie 13: 201–207

Zeller FJ, Lutz J, Stephan U (1993c) Chromosome location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L.). 1. *Mlk* and other alleles at the *Pm3* locus. Euphytica 68:223–229