Theor Appl Genet (2003) 106:1420–1424
DOI 10.1007/s00122-002-1187-7

Ch. Singrün · S. L. K. Hsam · L. Hartl · F. J. Zeller · V. Mohler

Powdery mildew resistance gene *Pm22* in cultivar Virest is a member of the complex *Pm1* locus in common wheat (*Triticum aestivum* L. em Thell.)

Received: 24 July 2002 / Accepted: 25 September 2002 / Published online: 13 February 2003

Abstract The powdery mildew resistance gene *Pm22*, identified in the Italian wheat cultivar Virest and originally assigned to wheat chromosome 1D, was mapped to chromosome 7A with the aid of molecular markers. Mapping of common AFLP and SSR markers in two wheat crosses segregating for *Pm22* and *Pm1c*, respectively, indicated that *Pm22* is a member of the complex *Pm1* locus. *Pm22* also showed a pattern of resistance reaction to a differential set of *Blumeria graminis* f. sp. *tritici* isolates that was distinguishable from those from other *Pm1* alleles in lines Axminster/8*Cc (*Pm1a*), MocZlatka (*Pm1b*), Weihenstephan Stamm M1N (*Pm1c*) and *Triticum spelta* var. *duhamelianum* TRI 2258 (*Pm1d*). Based on these results, the gene symbol *Pm1e* is proposed for the powdery mildew resistance gene in cv. Virest.

Keywords Wheat · Powdery mildew resistance · *Pm22* · *Pm1* · AFLP

Introduction

Powdery mildew, caused by *Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal DC, is a destructive foliar disease of common wheat in areas with cool or maritime climates. The deployment of resistant cultivars is the most economical and environmentally safe method for reducing the use of fungicides to control this disease. Thirty gene loci determining qualitative resistance to this disease (*Pm1–Pm30*) have been reported so far (McIntosh et al. 2002). Most of these loci have been located on individual wheat chromosomes by means of monosomic analyses. Following assignment to chromosomes harbouring already known *Pm* genes, allelism tests were made to establish linkage relationships among the genes. This procedure has led to the discovery of several alleles at *Pm1* (Hsam et al. 1998), *Pm3* (Zeller et al. 1993; Zeller and Hsam 1998), *Pm4* (The et al. 1979), *Pm5* (Huang et al. 2000a; Hsam et al. 2001) and *Pm8*/*Pm17* (Hsam and Zeller 1997) loci.

Molecular markers have not only been successfully employed in determining the location of *Triticum aestivum*- and *T. dicoccoides*-derived powdery mildew resistance loci at the subchromosomal level (Hartl et al. 1995, 1999; Huang et al. 2000b; Rong et al. 2000; Tao et al. 2000; Liu et al. 2002; Neu et al. 2002), but they have also been instrumental in the genetical delimitation of alien translocation fragments harbouring powdery mildew resistance determinants: *Pm13* from *Aegilops longissima* was mapped to a translocated3S^{l}S segment distal to *Xcdo460-3B* (Cenci et al. 1999), and *Pm27* from *T. timopheevii* was pinpointed to a fragment with breakpoints between the marker loci *Xpsr8*/*Xpsr964* on 6BS and *Xpsr154*/*Xpsr546* on 6BL (Järve et al. 2000).

The present study describes the relocation of wheat powdery mildew resistance gene *Pm22*, originally allocated to chromosome 1D (Peusha et al. 1996), to chromosome 7AL, and its relationship to the complex *Pm1* locus by means of molecular markers.

Communicated by Möllers

C. Singrün · S. L. K. Hsam · F. J. Zeller · V. Mohler (✉)
Lehrstuhl für Pflanzenbau und Pflanzenzüchtung,
Department Pflanzenwissenschaften, Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt,
Technische Universität München, Alte Akademie 12,
85350 Freising-Weihenstephan, Germany,
e-mail: mohler@wzw.tum.de

L. Hartl
Bayerische Landesanstalt für Bodenkultur und Pflanzenbau,
Am Gereuth 2, 85354 Freising-Weihenstephan, Germany,

Materials and methods

Plant materials

A total of 78 F_3 families, derived from a cross between powdery mildew-susceptible wheat cultivar Chinese Spring and resistant cultivar Virest, was used for analysis of linkage between molecular markers and *Pm22*. Wheat cultivar Virest was derived from the cross of Est 39-12 × Virgilio (Zeven and Zeven-Hissink 1976). Resistant and susceptible bulked segregants from *Pm1c* mapping population Khapli/8*Chancellor × Weihenstephan Stamm M1N

consisting of 92 F_4 families (Hartl et al. 1999) were used for evaluating molecular markers across genotypes. Lines Axminster/8*Cc (*Pm1a*), MocZlatka (*Pm1b*), Weihenstephan Stamm M1N (*Pm1c*) and *Triticum spelta* var. *duhamelianum* TRI 2258 (*Pm1d*) were used to compare resistance reactions in relation to cv. Virest.

Evaluation of resistance reactions

The *Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* (Bgt) isolates used for the differentiation of documented major resistance genes were collected from different parts of Europe and selected from single-spore progeny (Felsenstein et al. 1991). The Bgt isolates are classified under Weihenstephan accession numbers and maintained at the Chair of Agronomy and Plant Breeding, Technical University Munich. Powdery mildew resistance reactions were surveyed on agar-detached primary leaf segments. The methods of inoculation, conditions of incubation and disease assessment were according to Hsam and Zeller (1997). Three main classes of host reactions were distinguished: r = resistant (0–20% infection relative to cv. Kanzler), i = intermediate (30–50% infection), s = susceptible (>50% infection).

Molecular marker and mapping techniques

Wheat primary leaf tissue was used for DNA extraction following essentially the procedure of Huang et al. (2000c). For AFLP (amplified fragment length polymorphism), SSR (simple sequence repeat) and RFLP (restriction fragment length polymorphism) screening, two DNA bulks (Michelmore et al. 1991) were assembled by using equal amounts of DNA from ten susceptible and ten homozygous resistant segregants of the F_3 mapping population, respectively. *Eco*RI + ANN/*Mse*I + CNN AFLPs were generated according to Schwarz et al. (2000). Protocols for amplification of wheat SSR loci *Xgwm33c-1DS, Xgwm106-1DS, Xgwm458-1DL, Xgwm642-1DL, Xgwm-232-1DL, Xgwm350-7AS, Xgwm573-7AS, Xgwm260-7AS, Xgwm63-7AL, Xgwm282-7AL, Xgwm332-7AL and Xgwm344-7AL* were as described in Röder et al. (1998). *Xgwm344* was allocated to 7AL in *Triticum dicoccoides* by Peng et al. (2000). Both molecular marker types were detected on an ABI PRISM 377 platform (Applied Biosystems). Fragment size-calling was performed with GeneScan analysis software version 3.0 (Applied Biosystems). *Sse*8387I + NN/*Mse*I + NN AFLPs were produced and detected according to Hartl et al. (1999). RFLP analysis followed standard methods. DNA was digested with restriction endonucleases *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, and *Xba*I. Partial linkage maps were constructed with the computer programme JOINMAP 3.0 (Stam 1993). Map distances were calculated using the Kosambi function (Kosambi 1944). Charts of genetic linkage maps were drawn with the computer programme MAPCHART 2.1 (Voorrips 2002).

Marker nomenclature

AFLP markers were designated according to the standard list for AFLP primer nomenclature made available at the GrainGenes database (http://wheat.pw.usda.gov/) by the Keygene company. Detected loci in wheat were marked with an 'X', the basic symbol for molecular marker loci of unknown function in wheat. AFLP markers from the partial 7AL map based on *Pm1c* mapping population Khapli/8*Chancellor × Weihenstephan Stamm M1N (Hartl et al. 1999) were renamed, with the former designations given in brackets: S14M20-137/138 (M1), S11M20-134 (M2), S11M23-139 (M3), S13M26-116 (M5), S19M18-280 (M6), S19M22-325/200 (M7), S22M25-200 (M8), S19M20-134 (M9). AFLPs M1 and M7 are codominant markers: M1 displays fragments with 137 bp in M1N and 138 bp in Khapli/8*Chancellor, M7 with 325 bp in M1N and 200 bp in Khapli/8*Chancellor.

Results

Selection of molecular markers linked to *Pm22*

The Italian cultivar Virest harbours the dominant powdery mildew resistance gene *Pm22* (Peusha et al. 1996). A subset of 80 F_2 plants from the cross Chinese Spring × Virest used in the present study was randomly chosen and selfed. The disease reactions of 78 F_3 families (20–25 progeny of individual F_2 plants) were assessed separately on detached primary leaves following inoculation with Bgt isolates nos. 2, 6 and 10, respectively. The segregation for resistance to powdery mildew within this random sample deviated from the expected 3:1 ratio (48 resistant:30 susceptible, $\chi^2 = 7.54$; $P = 0.006$). For gene mapping, this skewed segregation is not expected to affect the recombination values estimated between loci (Kjær et al. 1995).

Pm22 was found to be located on chromosome 1D by means of monosomic analysis (Peusha et al. 1996) and showed no allelism to *Pm24*, located near the centromere on 1DS (Huang et al. 2000b). Due to these observations, SSRs distributed along chromosome 1DL and from the distal segment of 1DS were assayed on the DNAs from susceptible and resistant bulked segregants from *Pm22* mapping population Chinese Spring × Virest. No polymorphic markers were revealed between the bulks, although the parental lines did display polymorphism for all of the SSR markers tested. Therefore, a total of 75 *Eco*RI + ANN/*Mse*I + CNN AFLP primer combinations was added for a marker search. Out of 7,725 amplified marker loci, assuming each AFLP fragment to be one genetic locus and neglecting possible allelism between fragments, five AFLPs, namely *XE34M53-439, XE35M54-184, XE35M59-360, XE39M58-77* and *XE42M55-206*, were polymorphic between both the phenotypic bulks and the parental lines and, therefore, putatively linked to *Pm22*. Since the bulks were compiled from F_3 families, the screening procedure also allowed the detection of AFLP markers in *trans*, thereby increasing the number of scorable polymorphic fragments by 50%. *XE35M54-184* was linked to *Pm22* in coupling, while the remaining four AFLPs provided markers in repulsion. 'De-bulking analysis' – the DNA from individual plants of each bulk was used to confirm the polymorphism of putative markers – revealed that all five AFLP fragments displayed complete linkage to *Pm22* within individuals from each pool. The assignment of repulsion markers *XE34M53-439, XE35M59-360* and *XE39M58-77*, originating from the genome of Chinese Spring, to wheat chromosome 7A was simply achieved by using data collected from AFLP analysis of nulli-tetrasomics from cv. Chinese Spring (Huang et al. 2000c). An inspection of seven SSR markers that were evenly distributed along wheat chromosome 7A, revealed polymorphic fragments between both the bulks and the parental lines for *Xgwm282-7AL, Xgwm332-7AL* and *Xgwm344-7AL* (exhibiting a null allele in cv. Virest and an allele with 131 bp in Khapli/8*Chancellor) and, hence, these latter three

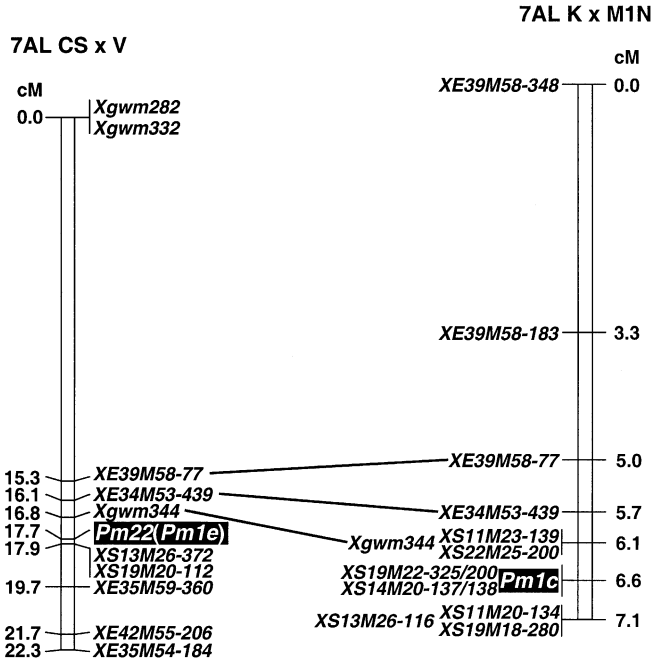

Fig. 1 Genetic maps of wheat chromosome arm 7AL surrounding the wheat powdery mildew resistance alleles *Pm22* (*Pm1e*) and *Pm1c*. Lines connect common AFLP and SSR marker loci between maps from Chinese Spring × Virest (CS × V) and Khapli/8*Chancellor × Weihenstephan Stamm M1N (K × M1N)

markers were applicable for integration in the genetic map around the *Pm22* locus.

Linkage mapping of *Pm22*

Mapping of the selected molecular markers in 78 F_3 families showed that *Xgwm344-7AL* was the closest marker to *Pm22*, with a map distance of 0.9 cM (Fig. 1). Proximal to the gene, *XE34M53-439* mapped at 1.6 cM, *XE39M58-77* at 2.4 cM, while SSR loci *Xgwm282-7AL* and *Xgwm332-7AL* linked at a distance of 17.7 cM. Distal to *Pm22*, the nearest marker locus was *XE35M59-360* with 2.0 cM, followed by *XE42M55-206* and *XE35M54-184* with 4.0 and 4.6 cM, respectively.

Cross-referencing with common AFLP and SSR markers revealed *Pm22* to be a member of the *Pm1* locus

Like *Pm22*, the complex *Pm1* locus is located on the long arm of chromosome 7A. In order to investigate the relationship of genes *Pm22* and*Pm1c*, we used AFLPs retrieved from screening of bulked segregants from *Pm1c* mapping population Khapli/8*Chancellor × Weihenstephan Stamm M1N (Hartl et al. 1999) to survey resistant and susceptible bulks from the *Pm22* mapping population. Of seven *Sse*8387I + NN/*Mse*I + NN AFLPs, not one was common across genotypes. However, primer combinations S13M26 and S19M20 displayed new polymorphic fragments among the phenotypic pools with molecular weights of 372 bp and 112 bp, respectively, with both fragments amplified from resistant cultivar Virest. Segregation analysis across the population revealed these coupling phase markers to map 0.2 cM distant from *Pm22* (Fig. 1). Vice versa, primer pairs for markers found in this study were used to amplify bulked segregants from the *Pm1c* mapping population. Of five *Eco*RI + ANN/*Mse*I + CNN AFLP markers, *XE39M58-77* and *XE34M53-439* differentiated the bulked segregants from the *Pm1c* mapping population, with the amplified fragments derived from the non-*Pm1c* wheat Khapli/8*Chancellor. These common AFLP markers showed comparable map distances between *Pm22* and *Pm1c* mapping populations (Fig. 1), suggesting that gene *Pm22* in cv. Virest belongs to the complex *Pm1* locus. Furthermore, new AFLPs E39M58-183 and E39M58-348 linked in coupling phase were detected that had map distances to *Pm1c* of 3.3 and 6.6 cM, respectively. Likewise, SSR marker locus *Xgwm344-7AL* was shown to be polymorphic in both mapping populations. An allelic variant of *Xgwm344-7AL* with 117 bp was present in bulked segregants carrying *Pm1c*. Susceptible bulked segregants carried a marker allele with 131 bp. Mapping of *Xgwm344-7AL* showed tight linkage with the *Pm1c* resistance gene (Fig. 1). An analysis of RFLP marker *Xwhs178*, known to be closely linked to the *Pm1* locus (Hartl et al. 1995, 1999), failed to detect polymorphism between the parental lines of the *Pm22* mapping population. Thus, this marker locus was not available for cross-referencing.

Table 1 Differential reactions of five wheat cultivars/lines carrying different powdery mildew resistance alleles at the *Pm1* locus after inoculation with 14 isolates of *Blumeria graminis* f. sp. *tritici*

Line/cultivar	*Blumeria graminis* f. sp. *tritici* isolate no.														*Pm* gene
	2	5	6	8	9	10	12	13	14	15	16	17	94	96	
Axminster/8*Cc[a]	r[c]	i	r	s	s	s	s	s	s	r	s	s	s	s	*Pm1a*
MocZlatka	r	r	r	r	r	i	i	r	r	r	s	s	r	i	*Pm1b*
Weihenstephan M1N	r	r	r	r	r	r	r	r	r	r	r	r	s	r	*Pm1c*
Tsd[b] TRI 2258	r	r	r	r	r	r	r	r	r	r	r	r	r	r	*Pm1d*
Virest	r	r	r	r	i	s	s	s	s	r	s	s	r	s	*Pm1e* (*Pm22*)

[a] seven times backcrossed to Chancellor
[b] *T. spelta* var. *duhamelianum*
[c] r, Resistant; s, susceptible; i, intermediate

Molecular analysis of wheats possessing already known members of the *Pm1* locus with comigrating AFLPs *XE39M58-77* and *XE34M53-439* showed that both markers were absent in all *Pm1* genotypes, irrespective of allele configuration at this gene locus (data not shown).

Disease responses of wheats carrying different alleles at the *Pm1* locus

In addition to the 11 Bgt isolates of the standard set, three further isolates from the Weihenstephan powdery mildew isolates collection were used to classify the disease response pattern of cv. Virest in comparison with cultivars/lines previously reported to carry different powdery mildew resistance alleles at the *Pm1* locus. All cultivars/lines were shown to exhibit patterns of disease response different one from another (Table 1). Based on this result, gene symbol *Pm1e* is proposed for powdery mildew resistance gene in cv. Virest.

Discussion

The investigation reported here identified powdery mildew resistance gene *Pm22* in the Italian cultivar Virest to be a member of the complex *Pm1* locus by cross-referencing with comigrating AFLP markers *XE39M58-77* and *XE34M53-439*, and SSR marker locus *Xgwm344-7AL*, which are all tightly linked to the *Pm1* locus. Allele-specificity of comigrating AFLP markers has been used in potato (Rouppe van der Voort 1997), barley (Waugh et al. 1997) and oat (Groh et al. 2001; Portyanko et al. 2001) to align genetic maps from different genotypes. In addition, since disease response studies using a differential set of 14 Bgt isolates clearly attributed a unique reaction pattern to the *Pm* resistance gene in cv. Virest, this gene is considered to be a new allele at the *Pm1* locus.

The allelic relationships of genes are conventionally determined in crosses with tester lines. In crosses between two powdery mildew resistant lines, a lack of appearance of susceptible plants in the offspring would indicate that the two lines being tested are carrying resistance genes that are either allelic or very closely linked. Analysis in the F_3 generation is then repeated with Bgt isolates possessing different virulences but simultaneously showing avirulence to both parents of the cross to clarify if the resistance genes, assumed to be at the same locus, share or produce a different disease resistance spectrum. In winter wheat, this effort takes at least 3 years. Molecular markers that can specifically detect disease resistance loci would help to speed up the process of allelism tests remarkably. The AFLP marker *XE34M53-439* closely linked to the *Pm1* locus would fulfill the qualifications, if it were linked in coupling phase. A great number of molecular markers are now available for the *Pm1* locus (Hu et al. 1997; Hartl et al. 1999; Neu et al. 2002; this study). This collection should facilitate the selection of marker alleles that are common for all as well as specific for individual *Pm1* alleles in order to register and categorize lines with potential members of the *Pm1* locus.

In order to avoid false chromosomal location by using monosomics, as has occurred for the *Pm* gene in cv. Virest (Peusha et al. 1996), we propose the concurrent molecular analysis of the progeny obtained from crossing the line having the new resistance gene with disomic Chinese Spring – if segregation of a single gene is expected. The use of experimental crosses involving Chinese Spring in bulked segregant analysis will normally provide repulsion phase markers to unequivocally anchor unknown linkage groups to wheat chromosomes by means of Chinese Spring aneuploid stocks. Thus, this procedure will serve as a validation of results from monosomic analysis and vice versa. However, monosomic analysis is the most appropriate tool to date when the test line harbours more than one qualitatively inherited resistance to a single pathogen.

Acknowledgements The authors gratefully acknowledge Amalie Fiedler for excellent technical assistance.

References

Cenci A, D'Ovidio R, Tanzarella OA, Ceoloni C, Porceddu E (1999) Identification of molecular markers linked to *Pm13*, an *Aegilops longissima* gene conferring resistance to powdery mildew in wheat. Theor Appl Genet 98:448–454

Felsenstein FG, Limpert E, Fischbeck G (1991) Wheat mildew populations in the FRG and neighbouring regions – some aspects of their change. In: Jørgensen H (ed) Integrated control of cereal mildews: virulence patterns and their change, Risø National Laboratory, Roskilde, Denmark, pp 1–7

Groh S, Zacharias A, Kianian SF, Penner GA, Chong J, Rines HW, Phillips RL (2001) Comparative AFLP mapping in two hexaploid oat populations. Theor Appl Genet 102:876–884

Hartl L, Weiss H, Stephan U, Zeller FJ, Jahoor A (1995) Molecular identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L.). Theor Appl Genet 90:601–606

Hartl L, Mohler V, Zeller FJ, Hsam SLK, Schweizer G (1999) Identification of AFLP markers closely linked to the powdery mildew resistance genes *Pm1c* and *Pm4a* in common wheat (*Triticum aestivum* L.). Genome 42:322–329

Hsam SLK, Zeller FJ (1997) Evidence of allelism between genes *Pm8* and *Pm17* and chromosomal location of powdery mildew and leaf rust resistance genes in the common wheat cultivar Amigo. Plant Breed 116:110–122

Hsam SLK, Huang XQ, Ernst F, Hartl L, Zeller FJ (1998) Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 5. Alleles at the *Pm1* locus. Theor Appl Genet 96:1129–1134

Hsam SLK, Huang XQ, Zeller FJ (2001) Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 6. Alleles at the *Pm5* locus. Theor Appl Genet 101:127–133

Hu XY, Ohm HW, Dweikat I (1997) Identification of RAPD markers linked to the gene *PM*1 for resistance to powdery mildew in wheat. Theor Appl Genet 94:832–840

Huang XQ, Hsam SLK, Zeller FJ (2000a) Chromosomal location of powdery mildew resistance genes in Chinese wheat landraces Xiobaidong and Fuzhhuang 30. J Genet Breed 54:311–317

Huang XQ, Hsam SLK, Zeller FJ, Wenzel G, Mohler V (2000b) Molecular mapping of the wheat powdery mildew resistance gene *Pm24* and marker validation for molecular breeding. Theor Appl Genet 101:407–414

Huang XQ, Zeller FJ, Hsam SLK, Wenzel G, Mohler V (2000c) Chromosomal location of AFLP markers in common wheat utilizing nulli-tetrasomic stocks. Genome 43:298–305

Järve K, Peusha HO, Tsymbalova J, Tamm S, Devos KM, Enno TM (2000) Chromosome location of a *T. timopheevii*-derived powdery mildew resistance gene transformed to common wheat. Genome 43:377–381

Kjaor B, Jensen J, Giese H (1995) Quantitative trait loci for heading date and straw characters in barley. Genome 38:1098–1104

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

Liu Z, Sun Q, Ni Z, Nevo E, Yang T (2002) Molecular characterization of a novel powdery mildew resistance gene *Pm30* in wheat originating from wild emmer. Euphytica 123:21–29

McIntosh RA, Devos KM, Dubcovsky J, Rogers WJ (2002) Catalogue of gene symbols for wheat: 2002 Supplement. http://wheat.pw.usda.gov/ggpages/wgc/2002upd.htm

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 by using segregating populations. Proc Natl Acad Sci USA 88:9828–9832

Neu C, Stein N, Keller B (2002) Genetic mapping of the *Lr20-Pm1* resistance locus reveals suppressed recombination on chromosome arm 7AL in hexaploid wheat. Genome 45:737–44

Peng J, Korol AB, Fahima T, Röder MS, Ronin YI, Li YC, Nevo E (2000) Molecular genetic maps in wild Emmer wheat, *Triticum dicoccoides*: Genome-wide coverage, massive negative interference, and putative quasi-linkage. Genome Res 10:1509–1531

Peusha H, Hsam SLK, Zeller FJ (1996) Chromosomal location of powdery mildew resistance genes in common wheat (*Triticum aestivum* L. em Thell.). 3. Gene *Pm22* in cultivar Virest. Euphytica 91:149–152

Portyanko VA, Hoffman DL, Lee M, Holland JB (2001) A linkage map of hexaploid oat based on grass anchor DNA clones and its relationship to other oat maps. Genome 44:249–265

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier MH, Leroy P, Ganal MW (1998) A microsatellite map of wheat. Genetics 149:2007–2023

Rong JK, Millet E, Manisterski J, Feldman M (2000) A new powdery mildew resistance gene: introgression from wild emmer into common wheat and RFLP-based mapping. Euphytica 115:121–126

Rouppe van der Voort JNAM, van Zandvoort P, van Eck HJ, Folkertsma RT, Hutten RCB, Draaistra J, Gommers FJ, Jacobsen E, Helder J, Bakker J (1997) Use of allele specificity of comigrating AFLP markers to align genetic maps from different potato genotypes. Mol Gen Genet 255:438–447

Schwarz G, Herz M, Huang XQ, Michalek W, Jahoor A, Wenzel G, Mohler V (2000) Application of fluorescence-based semi-automated AFLP analysis in barley and wheat. Theor Appl Genet 100:545–551

Stam P (1993) Construction of integrated genetic linkage maps by means of a new computer package: JOINMAP. Plant J 3:739–744

Tao W, Liu D, Liu J, Feng Y, Chen P (2000) Genetic mapping of the powdery mildew resistance gene *Pm6* in wheat by RFLP analysis. Theor Appl Genet 100:564–568

The TT, McIntosh RA, Bennett FGA (1979) Cytogenetical studies in wheat. IX. Monosomic analysis, telocentric mapping and linkage relationships of genes *Sr21, Pm4* and *Mle*. Aust J Biol Sci 32:115–125

Voorrips RE (2002) MAPCHART: software for the graphical presentation of linkage maps and QTLs. J Hered 93:77–78

Waugh R, Bonar N, Baird E, Thomas B, Graner A, Hayes P, Powell W (1997) Homology of AFLP products in three mapping populations of barley. Mol Gen Genet 255:31–321

Zeller FJ, Hsam SLK (1998) Progress in breeding for resistance to powdery mildew in common wheat (*Triticum aestivum* L.). In: Slinkard AE (ed) Proc 9th Int Wheat Genet Symp, vol. 1. University Extension Press, Saskatoon, Sask., Canada, pp 178–180

Zeller FJ, Stephan U, Lutz J (1993) 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

Zeven AC, Zeven-Hissink NCh (1976) Genealogies of 14,000 wheat varieties. CIMMYT and The Netherlands Cereal Centre, Mexico, DF and Wageningen