

Molecular markers for leaf rust resistance genes in wheat

Jerzy CHEŁKOWSKI, Łukasz STĘPIEŃ

Institute of Plant Genetics, Polish Academy of Sciences, Poznań, Poland

Abstract. Over 100 genes of resistance to rust fungi: *Puccinia recondita* f. sp. *tritici*, (47 Lr – leaf rust genes), *P. striiformis* (18 Yr – yellow rust genes) and *P. graminis* f. sp. *tritici* (41 Sr – stripe rust genes) have been identified in wheat (*Triticum aestivum* L.) and its wild relatives according to recent papers. Sixteen Lr resistance genes have been mapped using restriction fragments length polymorphism (RFLP) markers on wheat chromosomes. More than ten Lr genes can be identified in breeding materials by sequence tagged site (STS) specific markers. Gene Lrk 10, closely linked to gene Lr 10, has been cloned and its function recognized. Available markers are presented in this review. The STS, cleaved amplified polymorphic sequence (CAPS) and sequence characterized amplified regions (SCAR) markers found in the literature should be verified using *Triticum* spp. with different genetic background. Simple sequence repeats (SSR) markers for Lr resistance genes are now also available.

Key words: brown rust, yellow rust, stem rust, RAPD, RFLP, STS, SCAR, resistance genes, wheat.

Introduction

Common wheat, including spring and winter cultivars, is the most important cereal crop both in Poland and in Europe. The biotrophic species *Puccinia recondita* f. sp. *tritici* (synonym *Puccinia tritici*) is in some regions the principal pathogen of wheat. The result of infection is leaf rust – an important disease worldwide, causing in some regions significant losses to cereal growers (McINTOSH 1998). Epidemics of wheat leaf rust were observed in southern regions of Poland in 2000 and are frequently recorded there. The pathogen developed a high number of races oc-

Received: October 2000. Accepted: February 2001.

Correspondence: J. CHEŁKOWSKI, Institute of Plant Genetics, Polish Academy of Sciences, ul. Strzeszyńska 34, 60-479 Poznań, Poland, e-mail: jche@igr.poznan.pl

curing worldwide (ROELFS et al. 1992). Virulences of Lr 9, 19 and 24 have not been detected in Hungary, Czech Republic, Poland, Germany and Russia so far (LIMPERT et al. 1996, CSOSZ et al. 2000, GULTYAEVA et al. 2000, MANNINGER 2000).

The number of named and later mapped Lr resistance genes in wheat increased significantly during the last decade (McINTOSH et al. 1998). However, the wheat genome (17.3 pg per cell) belongs to the largest among crop species and contains nearly 17,000 Mbp per haploid nucleus (ARUMUGANATHAN, EARLE 1991). The size of this genome as well as the high percentage (over 90%) of non-coding sequences and three genomes A, B and D with 7 homoeologous chromosomes cause molecular identification and cloning of wheat resistance genes to be difficult. Each of 42 hexaploid wheat chromosomes has the average size of about 800 Mbp. Physical distance between crossing-overs (=1 cM) varies from 0.3 to 3 Mbp (FEUILLET et al. 1995). Wild relative species of wheat usually have one genome in common with wheat, which makes them very helpful for searching and mapping new resistance genes. Because various wheat-related species carry different genomes (*Triticum* sp., genome B; *Aegilops speltoides*, genome S, similar to B; *Triticum boeoticum*, genome A; and *Aegilops squarrosa*, genome D), they have been and still are used as sources of resistance genes in breeding. A frequent way to transfer the resistance genes is using wheat lines with translocation of a chromosome fragment carrying the gene from a wild species. This was done in the case of genes Lr 19, Lr 24 and Lr 29 derived from *Agropyron elongatum* (PROCUNIER et al. 1995, SCHACHERMAYR et al. 1995, PRINS et al. 1996). The development of new DNA-based assays has led to their application for designing direct and tightly linked markers – restriction fragments length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), cleaved amplified polymorphic sequence (CAPS), sequence characterized amplified regions (SCAR) and sequence tagged sites (STS) to identify individual resistance genes in wheat accessions. In a previous paper markers available for identifying resistance genes to powdery mildew of wheat were reviewed (CHEN, CHEŁKOWSKI 1999). The aim of this paper is to review the current knowledge on the mentioned markers for Lr resistance genes.

Identification of resistance genes and their localization on chromosomes

Results concerning identification of Lr, Yr and Sr resistance genes in wheat using inoculation procedures have been comprehensively described by ROELFS et al. (1992), and some resistance problems by McINTOSH (1998). Wheat near-isogenic lines with known leaf rust resistance genes and collections of isolates of rust fungi have been used to identify the presence of resistance genes in cultivars and sources of resistance genes (ROELFS et al. 1992). Total of 47 Lr resistance genes are given in the literature (ROELFS et al. 1992, SINGH et al. 1998, SEYFARTH et al. 1999,

HELGUERA et al. 2000). Besides new resistance genes identified in common wheat (like the slow-rusting gene Lr 46, SINGH et al. 1998), there are genes transferred from other species (like the Lr 24 gene from *Agropyron elongatum* and Lr 47 from *Aegilops speltoides* [= *Triticum speltoides*], HELGUERA et al. 2000).

A promising procedure to identify resistance genes seems to be identification of genes by markers for detection of sequences encoding proteins of nucleotide-binding sites and leucine-rich repeats (NBS/LRR). The mentioned sequences are present in numerous resistance genes, identified in various crop species (tomato, potato, wheat, rice, flax) as well as in model plant species: *Arabidopsis* and *Nicotiana* (LEHMANN 1997, SPIELMEYER et al. 1998, LEISTER et al. 1999, SALAMINI 1999, SALMAN et al. 2000). SPIELMEYER et al. (1998), using RFLP probes from *Aegilops squarrosa* (*Triticum tauschii*) having resistance genes to cereal cyst nematode, identified 29 loci suggested to be homological to the resistance gene analogs (RGAs). The mentioned loci showed 30-70% amino-acid identity to the sequence of the cre locus for cereal cyst nematode from *T. tauschii*. The loci were mapped in genomes A, B and D of wheat; 3 in all genomes (A, B and D) and 6 in two genomes only (A and B, or B and D). LEISTER et al. (1999) deduced peptide sequences of 25 resistance gene homologues from rice and barley. SALMAN et al. (2000) used RAPD and primers corresponding to NBS/LRR sequences for identification of resistance gene candidates in near-isogenic lines. It was possible to amplify bands and prove the presence of possible resistance gene candidates in the examined accessions.

Table 1. Number of identified wheat genes of resistance to rust fungi

Pathogen	Gene symbol	No. of identified resistance genes
<i>Puccinia recondita</i> f. sp. <i>tritici</i>	Lr	47* (42)
<i>Puccinia striiformis</i>	Yr	18
<i>Puccinia graminis</i>	Sr	41

* the last described Lr gene is Lr 47, but some earlier identified genes appeared to be alleles, so the number of Lr genes is lower. Lr 4, Lr 5, Lr 6, Lr 7 and Lr 8 are not available as separate gene lines (McINTOSH et al. 1998).

A significant number of Lr resistance genes originate from *Triticum aestivum* cultivars, but some resistance genes were originally introgressed into common wheat cultivars from wild species accessions: *Aegilops umbellulata* – Lr 9, *Aegilops squarrosa* – Lr 21, Lr 22, Lr 32, Lr 39, Lr 40, Lr 41, Lr 42, Lr 43, *Agropyron elongatum* – Lr 19, Lr 24, Lr 29, *Aegilops speltoides* – Lr 28, Lr 35, Lr 36, Lr 47, or *Aegilops ventricosa* – Lr 37. The following Lr genes have been recently identified in Polish wheat cultivars: Lr 1, Lr 3, Lr 11, Lr 14, Lr 16 and Lr 26. Unfortunately, these genes, when present as single genes, do not prevent significant infection of wheat cultivars. Gene Lr 26 is present in cultivars Aleta,

Jubilatka, Lama, Lanca, Olma, Turnia and Wilga, carrying translocation T1BL/1RS from rye genome (KOWALCZYK et al. 2000). Gene Pm 8, conferring the resistance to *Erysiphe graminis*, is present in above-mentioned cultivars, as it has been introduced by the same translocation.

Identification and mapping of Lr resistance genes using DNA markers and their tagging

Leaf rust resistance genes, namely Lr 1, Lr 9, Lr 10, Lr 13, Lr 19, Lr 23, Lr 24, Lr 25, Lr 27, Lr 28, Lr 29, Lr 31, Lr 34, Lr 35, Lr 37 and Lr 47 have been mapped on chromosomes, usually by RFLP molecular markers (Table 2).

The first molecular STS marker was developed by SCHACHERMAYR et al. (1994) for the Lr 9 gene derived from *Aegilops umbellulata*, and soon results on the identification of several markers for other Lr resistance genes were published (Table 2).

RFLP markers are reliable but expensive and labour-intensive, and need DNA of high purity, so are not suitable for marker-assisted selection. For the reason of more practical usage, RFLP markers that are completely linked with the given resistance gene, are converted into specific PCR markers – STS or CAPS markers and RAPD markers can be converted into SCAR markers.

So far STS or SCAR and CAPS markers for genes Lr 1, Lr 9, Lr 10, Lr 24, Lr 28, Lr 35, Lr 37 and Lr 47 have been described in the literature (Table 2). Enzymatic marker (endopeptidase Ep-D1c) for Lr 19 has also been developed and used (WINZELER et al. 1995). Moreover, microsatellite markers (simple sequence repeats – SSR) for resistance genes Lr 3bg and Lr 18 have been recently developed (PURNHAUSER et al. 2000).

Gene Lrk 10, close to gene Lr10, has been cloned and sequenced (FEUILLET et al. 1997). By screening a set of near-isogenic lines carrying different leaf rust resistance genes with a wheat probe encoding a serine/threonine protein kinase, those researchers detected a polymorphic DNA fragment in the line with Lr 10 resistance gene. This fragment was mapped to the Lr 10 disease resistance locus. The Lrk 10 is not resistance gene encodes a receptor-like protein called kinase LRK 10. The LRK 10 enzyme contains a new type of extracellular domain, not found in any other known plant or animal receptor kinases. Molecular description of this gene in wheat provides a unique biological system to study the molecular basis of specificity of wheat-pathogen interaction. Probably this will also allow the transformation of wheat and manipulation of wheat resistance genes to increase the resistance durability. Moreover, pyramiding of different resistance genes in classical breeding process to achieve durable resistance will be facilitated by molecular markers. Durable resistance may be achieved by combination of several

Table 2. DNA markers for wheat leaf rust resistance gene identification

Gene	Localization	Origin	Marker type	Reference
Lr 1	5DL	<i>Triticum aestivum</i>	RFLP, STS	FEUILLET et al. 1995
Lr 9	6BL	<i>Aegilops umbellulata</i>	RFLP cMW 684, STS, RAPD, RFLP PSR 546	SCHACHERMAYR et al. 1994
Lr 10	1AS	<i>Triticum aestivum</i>	RFLP, STS	SCHACHERMAYR et al. 1997
Lr 13	2BS	<i>Triticum aestivum</i>	RFLP	SEYFARTH et al. 1999
Lr 19	7DL	<i>Agropyron elongatum</i>	RFLP, RAPD	NAIK et al. 1998
Lr 23	2BS	<i>Triticum aestivum</i>	RFLP	NELSON et al. 1997
Lr 24	3DL	<i>Agropyron elongatum</i>	RFLP PSR 1205, PSR 1203, PSR 388, PSR 904, PSR 931, PSR 1067 RAPD OPJ-09 STS; J09/1 i J09/2	SCHACHERMAYR et al. 1995
Lr 24	3DL	<i>Agropyron elongatum</i>	SCAR	DEDRYVER et al. 1996
Lr 25	4AL/2RS	<i>Secale cereale</i>	RAPD, DGGE	PROCUNIER et al. 1995
Lr 27	1BL/1RS	<i>Triticum aestivum</i>	RFLP	NELSON et al. 1997
Lr 28	4AL	<i>Aegilops speltoides</i>	RAPD OPJ-01, STS	NAIK et al. 1998
Lr 29	7DS/Ae#1S	<i>Agropyron elongatum</i>	RAPD, DGGE	PROCUNIER et al. 1995
Lr 31	4BS	<i>Triticum aestivum</i>	RFLP	NELSON et al. 1997
Lr 34	7DS	<i>Triticum aestivum</i>	RFLP	NELSON et al. 1997
Lr 35	2B	<i>Triticum speltoides</i>	RFLP, STS	SEYFARTH et al. 1999
Lr 37	2A	<i>Aegilops ventricosa</i>	RAPD, SCAR	ROBERT et al. 1999
Lr 47	7AS	<i>Triticum speltoides</i>	CAPS	HELGUERA et al. 2000

genes encoding partial resistance in one cultivar, rather than by a single resistance gene.

Recently BARTOŠ et al. (2000) used an STS marker for the Lr 10 gene to identify this resistance gene in Czech cultivars Alka and Siria. The presence of this gene was examined by SCHACHERMAYR et al. (1997) in 62 wheat accessions from European breeding programmes with various genetic backgrounds. The Lr 10 marker has been found to be highly specific for the Lr 10 resistance gene and present in 12 accessions.

The development of PCR-based allele-specific markers in polyploid species is more complex than in diploid species because PCR can result in the amplification

of multiple fragments of similar size from more than one genome (HELGUERA et al. 2000). For this reason markers described in published papers, designed for cultivars and lines used in the first experimental work, may give false-positive answers concerning the presence of the marker in different lines and cultivars with different genetic backgrounds (not used yet in experiments). Published markers should be verified before they will be recommended for their application in genetic and breeding programmes.

Partial resistance genes

Partial resistance (PR) in cereal plants is getting recently more attention, also in research on biotrophic pathogens. QTLs of partial resistance to *Puccinia hordei* have been found in barley (NIKS et al. 2000). A high number of quantitative trait loci (to date 13 QTLs of partial resistance) contributing to the resistance of barley to *Puccinia hordei* have been mapped by QI et al. (2000). The mentioned authors, using AFLP markers (amplified fragments length polymorphism), constructed linkage map of barley, derived from a cross of the susceptible line L 94 and the partially resistant line 11b-5 or cv. Vada (NIKS et al. 2000).

FARIS et al. (1999) identified 50 loci conferring defence response (DR) genes, corresponding to QTLs in wheat. The highest effect on adult plant resistance of wheat to brown rust was exhibited by gene clusters on chromosome 7BL, coding catalase, chitinase, thaumatins and ion channel regulators, and on chromosome 4AL, coding oxalate oxidase. Several RFLP markers allow to select desirable QTLs.

Partial resistance to brown rust in wheat cultivars was identified by ITTU (2000) in three cultivars out of 86 examined in Romania. So far it has been possible to identify PR in wheat accessions by inoculation procedure or growing them under epidemic conditions. It is suggested that genes causing "slow rusting", like gene Lr 34 or Lr 46, are involved in this type of resistance. Contribution of other minor genes is also likely.

Quantitative resistance has also been proved by BAI et al. (1999) in their studies on wheat *Fusarium* scab. The authors identified a major quantitative locus controlling scab resistance in wheat on chromosome 7A (Figure 1), and also several loci of smaller significance, controlling both resistance to infection and to accumulation of a fungal toxin, deoxynivalenol.

Irrespective of the identification of a high number of resistance genes in wild wheat-related species, some of them being successfully transferred to cultivated wheat, the genetic mechanism of partial resistance can operate also in common wheat and its wild relatives.

The strategy of pyramiding of partial resistance loci to derive resistant cultivars (horizontal resistance) is actually suggested, with possible contribution to durable resistance.

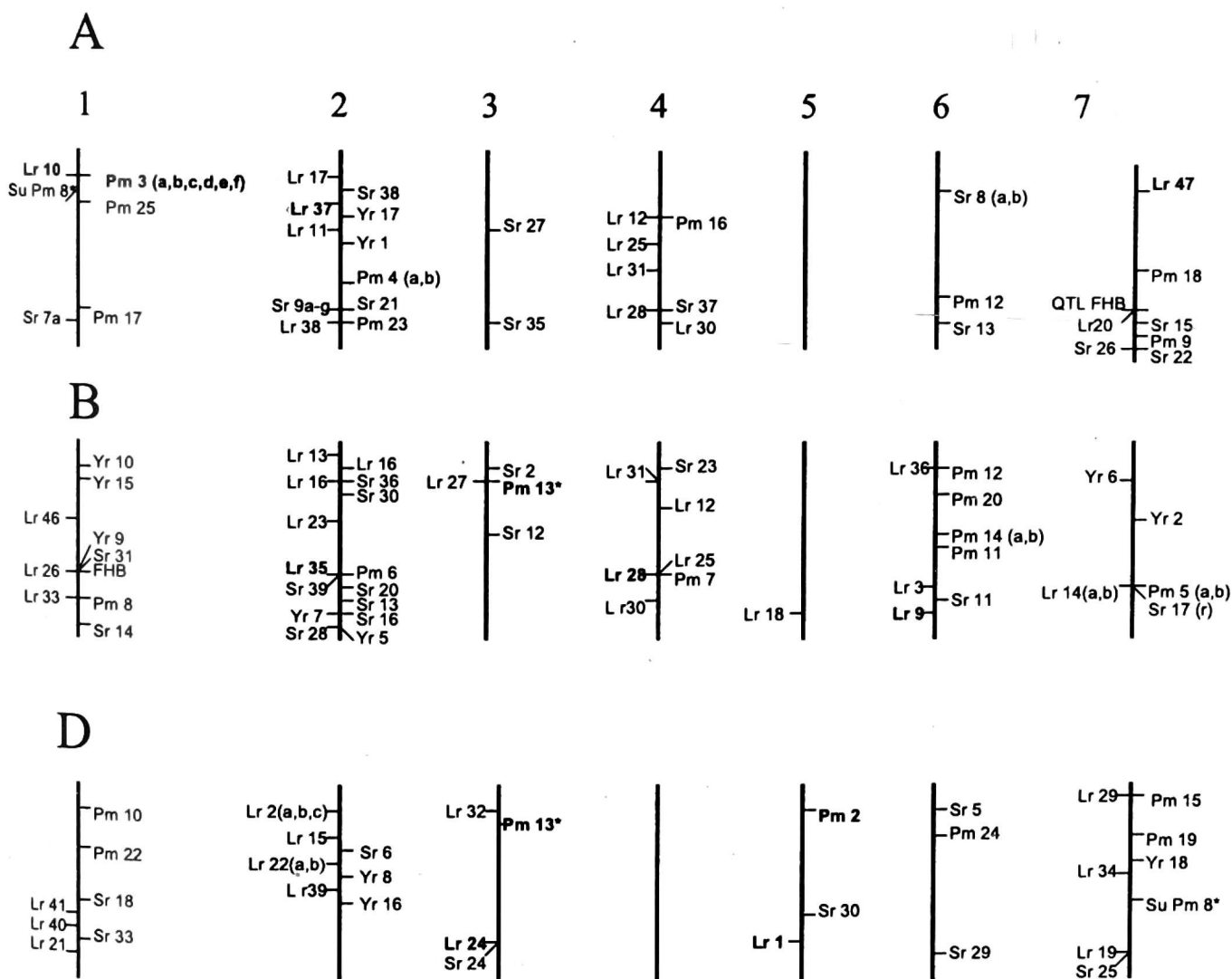


Figure 1. Schematic location of identified Lr (leaf rust), Yr (yellow rust), Sr (stripe rust) and Pm (powdery mildew) resistance genes in genomes of hexaploid wheat and its wild relatives (according to McINTOSH et al. 1998)

* Pm 13 and SuPm 8 gene location depends on wheat line; Pm and Lr resistance genes with available STS markers are bolded

Conclusions

The use of a reliable STS marker may help in resistance breeding of wheat and resistance gene pyramiding, providing durable resistance. However, the resistance gene that is actually present in the material may be inactive or inefficient. Available markers should be verified with a possibly wide selection of wheat lines and, if possible, combined with studies of field resistance to rust fungi.

REFERENCES

- ARUMUGANATHAN K., EARLE E.D. (1991). Nuclear DNA content of some important plant species. *Plant Mol. Biol. Reporter*. 9: 208-218.

- BAI G., KOLB F.L., SHANER G., DOMIER L.L. (1999). Amplified Fragment Length Polymorphism markers linked to a major quantitative trait locus controlling scab resistance in wheat. *Phytopathology* 89: 343-348.
- BARTOŠ P., HANZALOVA A., BLAŽKOVA V. (2000). Leaf rust resistance of winter wheat cultivars registered in the Czech Republic. *Acta Phytopathol. Entomol. Hung.* 35(1-4): 149-151.
- CHEN YU, CHEŁKOWSKI J. (1999). Genes for resistance to wheat powdery mildew. *J. Appl. Genet.* 40: 317-334.
- CSOSZ M., MESTERHAZY A., SZUNICS L. VIDA GY., MANNINGER K. (2000). Leaf rust resistance of the wheat Lr near-isogenic lines in adult stage in Hungary, 1995-1999. *Acta Phytopathol. Entomol. Hung.* 35(1-4): 177-185.
- DEDRYVER F., JUBIER M.-F., THOUVERIN J., GOYEAU H. (1996). Molecular markers linked to the leaf rust resistance gene Lr 24 in different wheat cultivars. *Genome* 39: 830-835.
- FARIS J.D., LI W.L., LIU D.J., CHEN P.D., GILL B.S. (1999). Candidate gene analysis of quantitative disease resistance in wheat. *Theor. Appl. Genet.* 98: 219-225.
- FEUILLET C., MESSMER M., SCHACHERMAYR G., KELLER B. (1995). Genetical and physical characterization of the Lr 1 leaf rust resistance locus in wheat (*Triticum aestivum* L.). *Mol. Gen. Genet.* 248: 553-562.
- FEUILLET C., SCHACHERMAYR G., KELLER B. (1997). Molecular cloning of a new receptor-like kinase gene encoded at the Lr 10 disease resistance locus of wheat. *The Plant Journal* 11(1): 45-52.
- GULTYAEVA E., WALTHER D., KOPAHNKE D., MIKACHAILOVA L. (2000). Virulence of *Puccinia recondita* Rob. × *Desm. f. sp. tritici* in Germany and European part of Russia in 1996-1999. *Acta Phytopathol. Entomol. Hung.* 35(1-4): 409-412.
- HELGUERA M., KHAN I.A., DUBCOVSKY J. (2000). Development of PCR markers for the wheat leaf rust resistance gene Lr 47. *Theor. Appl. Genet.* 100: 1137-1143.
- ITTU M. (2000). Components of partial resistance to leaf rust in wheat. *Acta Phytopathol. Entomol. Hung.* 35(1-4): 161-168.
- KOWALCZYK K., HSAM S.L.K., ZELLER F.J. (2000). Preliminary results of leaf rust resistance genes in Polish common wheat cultivars. *Proc. Xth Conf. Microscopic Fungi*, March 23rd, 2000, Poznań, Poland: 46-49.
- LEHMANN P. (1997). Molekularne podstawy odporności roślin na choroby; Struktura i funkcja roślinnych genów odporności [Molecular basis of plant resistance to diseases: structure and function of plant resistance genes]. *Postępy biologii komórki* 24(2): 99-125.
- LEISTER D., KURTH J., LAURIE D.A., YANO M., SASAKI T., GRANER A., SCHULZE-LEFERT P. (1999). RFLP and physical mapping of resistance gene homologues in rice (*O. sativa*) and barley (*H. vulgare*). *Theor. Appl. Genet.* 98: 509-520.
- LIMPERT E., FINCKH M.R., WOLFE M.S. (1996). Population studies of airborne pathogens on cereals as a means of improving strategies for disease control – integrated control of cereal mildews and rusts: towards coordination of research across Europe. *Eur 16884-COST 817*, Official publications of European Communities. Luxembourg.
- MANNINGER K. (2000). Virulence survey of wheat leaf rust in Hungary: Races/pathotypes in 1999. *Acta Phytopathol. Entomol. Hung.* 35(1-4): 421-428.

- McINTOSH R.A. (1998). Breeding wheat for resistance to biotic stress. *Euphytica* 100:19-34.
- McINTOSH R.A., HART G.E., DEVOS K.M., GALE M.D., ROGERS W.J. (1998). Catalogue of gene symbols for wheat. Proc. 9th Intern. Wheat Genet. Symp., Saskatchewan, Canada. V.5: 235.
- NAIK S., GILL K.S., PRAKASA R.V.S., GUPTA V.S., TAMHANKAR S.A., PUJAR S., GILL B.S., RANJEKAR P.K. (1998). Identification of a STS marker linked to the *Aegilops speltoides*-derived leaf rust resistance gene Lr 28 in wheat. *Theor. Appl. Genet.* 97: 535-540.
- NELSON J.C., SINGH R.P., AUTRIQUE J.E., SORRELLS M.E. (1997). Mapping genes conferring and suppressing leaf rust resistance in wheat. *Crop Sci.* 37: 1928-1935.
- NIKS R.E., FERNANDEZ E., VAN HAPEREN B., BEKELE ALEYE B., MARTINEZ F. (2000). Specificity of QTLs for partial and non-host resistance of barley to leaf rust fungi. *Acta Phytopathol. Entomol. Hung.* 35(1-4): 13-21.
- PRINS R., MARAIS G.F., JANSE B.J.H., PRETORIUS Z.A., MARAIS A.S. (1996). A physical map of the *Thinopyrum*-derived Lr 19 translocation. *Genome* 39: 1013-1019.
- PROCUNIER J.D., TOWNLEY-SMITH T.F., FOX S., PRASHAR S., GRAY M., KIM W.K., CZARNECKI E., DYCK P.L. (1995). PCR-based RAPD/DGGE markers linked to leaf rust resistance genes Lr 29 and Lr 25 in wheat (*Triticum aestivum* L.). *J. Genet. Breed.* 49: 87-92.
- PURNHAUSER L., GYULAI G., CSOSZ M., HESZKY L., MESTERHAZY A. (2000). Identification of leaf rust resistance genes in common wheat by molecular markers. *Acta Phytopathol. Entomol. Hung.* 35 (1-4): 31-36.
- QI X., FUFA F., SIJTSMA D., NIKS R.E., LINDHOUT P., STAM P. (2000). The evidence for abundance of QTLs for partial resistance to *Puccinia hordei* on the barley genome. *Mol. Breeding* 6: 1-9.
- ROBERT O., ABELARD Ch., DEDRYVER F. (1999). Identification of molecular markers for the detection of the yellow rust resistance gene Yr 17 in wheat. *Mol. Breeding* 5: 167-175.
- ROELFS A.P., SINGH R.P., SAARI E.E. (1992). *Rust Diseases of Wheat: Concepts and Methods of Disease Management*. CIMMYT, Mexico, D.F.
- SALAMINI F. (1999). Where do we go from this point? In: *Genetics and Breeding for Crop Quality and Resistance* (G.T.S. Mugnozza, E. Porcedolu, M.A. Pagnotta, eds.). Kluwer Acad. Publ. Amsterdam: 397-417.
- SALMAN S., ÖZGEN M., SAYAR M.T. (2000). Isolation of rust disease (*Puccinia* spp.) resistance markers from wheat near-isogenic lines using RAPD and NBS/LRR primers. *Acta Phytopathol. Entomol. Hung.* 35 (1-4): 81-90
- SCHACHERMAYR G., FEUILLET C., KELLER B. (1997). Molecular markers for the detection of the wheat leaf rust resistance gene Lr 10 in diverse genetic backgrounds. *Mol. Breeding* 3: 65-74.
- SCHACHERMAYR G., MESSMER M.M., FEUILLET C., WINZELER H., WINZELER M., KELLER B. (1995). Identification of molecular markers linked to the *Agropyron elongatum*-derived leaf rust resistance gene Lr 24 in wheat. *Theor. Appl. Genet.* 90: 982-990.

- SCHACHERMAYR G., SIEDLER H., GALE M.D., WINZELER H., WINZELER M., KELLER B. (1994). Identification and localization of molecular markers linked to the Lr 9 leaf rust resistance gene of wheat. *Theor. Appl. Genet.* 88: 110-115.
- SEYFARTH R., FEUILLET C., SCHACHERMAYR G., WINZELER M., KELLER B. (1999). Development of a molecular marker for the adult plant leaf rust resistance gene Lr 35 in wheat. *Theor. Appl. Genet.* 99: 554-560.
- SINGH R.P., MUJEEB-KAZI A., HUERTA-ESPINO J. (1998). Lr 46: A gene conferring slow-rusting resistance to leaf rust in wheat. *Phytopathology* 88: 890-894.
- SPIELMEYER W., ROBERTSON M., COLLINS N., LEISTER D., SCHULZE-LEFERT P., SEAH S., MOULLET O., LAGUDAH E.S. (1998). A superfamily of disease resistance gene analogs is located on all homoeologous chromosome groups of wheat (*Triticum aestivum*). *Genome* 41: 782-788.
- WINZELER M., WINZELER H., KELLER B. (1995). Endopeptidase polymorphism and linkage of the Ep-D1c null allele with the Lr 19 leaf rust resistance gene in hexaploid wheat. *Plant Breeding* 114: 24-28.