J. Appl. Genet. 44(3), 2003, pp. 291-309

Review article

Resistance genes in barley (*Hordeum vulgare* L.) and their identification with molecular markers

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Abstract. Current information on barley resistance genes available from scientific papers and on-line databases is summarised. The recent literature contains information on 107 major resistance genes (R genes) against fungal pathogens (excluding powdery mildew), pathogenic viruses and aphids identified in *Hordeum vulgare* accessions. The highest number of resistance genes was identified against *Puccinia hordei*, *Rhynchosporium secalis*, and the viruses BaYMV and BaMMV, with 17, 14 and 13 genes respectively. There is still a lot of confusion regarding symbols for R genes against powdery mildew. Among the 23 loci described to date, two regions *Mla* and *Mlo* comprise approximately 31 and 25 alleles. Over 50 R genes have already been localised and over 30 mapped on 7 barley chromosomes. Four barley R genes have been cloned recently: *Mlo*, *Rpg1*, *Mla1* and *Mla6*, and their structures (sequences) are available. The paper presents a catalogue of barley resistance gene symbols, their chromosomal location and the list of available DNA markers useful in characterising cultivars and breeding accessions.

Key words: barley, DNA markers, PCR, resistance genes, RAPD, RFLP, STS.

Introduction

Besides wheat, rice and maize, barley (*Hordeum vulgare L.*) is one of the most economically important crops around the world. Cultivars grown in Poland and other European countries are characterised by high yield (8t/ha) and good grain quality. However, diseases caused by fungi and viruses reduce yield, and

Received: January 21, 2003. Accepted: March 10, 2003.
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the quality of both spring and winter cultivars depend on seasonal conditions. Barley has recently been studied extensively in relation to the mapping of major resistance genes (R genes) and partial disease resistance genes as well as QTL linked to resistance reaction (CHEN et al. 1994, BACKES et al. 1995, THOMAS et al. 1995, ATTARI et al. 1998, KICHERER et al. 2000, SCHEURER et al 2001).

The barley genome (HH, 2n = 2x = 14) is among the largest genomes of cultivated plants, with the size of 4873 Mbp per haploid nucleus (ARUMUGANATHAN, EARLE 1991). Comparative studies of wheat, rye and barley genetic maps show that apart from a number of gross chromosome rearrangements (such as the position of nucleolus organiser regions), the order of loci in these crop species is very similar, reflecting a general evolutionary conservation of linkage group structure. Information on the comparative mapping of cereals can be found at the Gramene HomePage (http://www.gramene.org/)(index.html). Recent data on genes identified in barley, their symbols and mapping on chromosomes are reviewed every year. Updates are available in the on-line database: http://wheat.pw.usda.gov/ggpages/bgn/.

Some disease resistance genes (R genes) contain conserved sequence motifs, like the nucleotide-binding site (NBS) and leucine-rich repeats (LRR). An interesting feature of this class of R genes is that they are involved in gene-for-gene resistance towards either fungal, viral, bacterial or nematode disease resistance. The conservation between different NBS-LRR resistance genes opens the possibility for the use of polymerase chain reaction (PCR)-based strategies for isolating and cloning other R gene family members or analogs using degenerate or specific primers for these conserved regions (see review of BENT et al. 1994, WHITHAM et al. 1994, GRANT et al. 1995, LAWRENCE et al. 1995, BAKER et al. 1997, LAGUDAH et al. 1997, YU et al. 2000). Specific primer sequences derived from a previously isolated NBS-LRR sequence at the *Cre3* locus, which confers resistance to the cereal cyst nematode (CCN) in wheat (*Triticum aestvum* L.), were used to isolate a family of resistance gene analogs (RGAs) through a polymerase chain reaction (PCR) cloning approach. This class of R gene belongs to a superfamily that is present in both dicotyledons and monocotyledons, as suggested from sequence comparisons of those that have been isolated. Such analyses have revealed several highly conserved functional amino acid motifs, notably the NBS sequences (P-loop and Kinase-2a) and others of unknown function between the NBS and LRR region (SEAH et al. 1998).

The number of named and mapped resistance genes in barley increased significantly in the last decade (Table 1). At present a catalogue of gene symbols for barley is not available. There is a "Catalogue of gene symbols for wheat", which has been published and is also updated on-line, initiated about 32 years ago (MCINTOSH et al. 1998). Knowledge of the effectiveness of barley resistance genes and linked DNA markers, along with detailed characteristics of genetic stocks, can improve breeding strategies. The aim of this work was to collect infor-

Table 1. Symbols of identified major resistance genes (R) against 15 fungal pathogens, four viruses and two pests in barley. (Complete list of barley diseases can be found at www.apsnet.org/online/common/names/barley.asp)

Gene symbol	Pathogen/pest (and caused disease)	Number of genes
Rph	*Puccinia hordei* (leaf rust)	17
Rpg	*Puccinia graminis* (stem rust)	4
Rps	*Puccinia striiformis* f. sp. *hordei* (stripe rust)	4
Ml (Reg)	*Erysiphe graminis* f. sp. *hordei* (powdery mildew)	23
Rcs	*Cochliobolus sativus* (spot blotch)	5
Rpt	*Pyrenophora teres* (net blotch)	6
Rdg (Rhg)	*Pyrenophora graminea* (barley stripe)	3
Rrs (Rh)	*Rhynchosporium secalis* (scald)	14
Run (un)	*Ustilago nuda* (loose smut)	8
Ung	*Ustilago nigra* (semiloose smut)	1
Ruh	*Ustilago hordei* (covered smut)	4
Rsp	*Septoria passerini* (leaf blotch)	3
Rti	*Typhula incarnata* (gray snow mold)	1
fb	*Fusarium* spp. (scab)	1
Ryd	BYDV (barley yellow dwarf virus)	2
Rym (ym)	BaYMV (barley yellow mosaic virus) BaMMV (barley mild mosaic virus)	13
Rsm (sm)	BSMV (barley stripe mosaic virus)	5
Rsg	*Schizaphis graminum* (green bug-aphid)	3
Rha	*Heterodera avenae* (cereal cyst nematode)	3

Reg – several symbols are used in the literature for resistance genes against *Erysiphe graminis*, like *Mlo, Mla, MILa* and *Reg*

mation on barley resistance genes, their mapping and DNA markers available for marker-assisted selection (MAS).

Resistance genes identified in barley

Marker technology is moving from hybridization-based RFLP markers to PCR-based markers, as the latter are more economical and enable high sample throughput and simultaneous analysis of multiple loci. Sequence-tagged sites (STSs) (OLSON et al. 1989) and random amplified polymorphic DNAs (RAPDs) (WILLIAMS et al. 1991) are the most common PCR markers used to date in gene identification in plants. However, the mapping of resistance genes has utilised

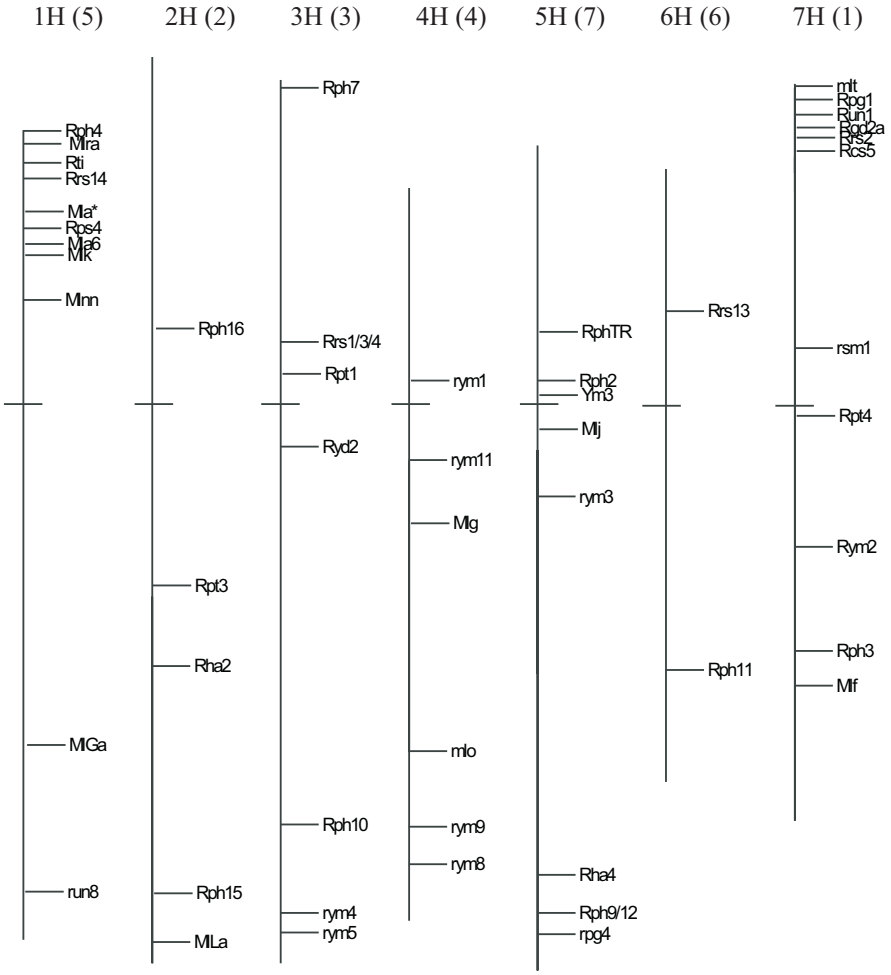

Figure 1. Consensus map of identified resistance genes (* complex locus)

AFLP (amplified fragment length polymorphism), SSR (simple sequence repeat) and RGAP (resistance gene analog polymorphism) techniques.

There are two nomenclature systems for barley chromosomes. Our merging of previous maps published by FRANCKOWIAK (1997), JENSEN (2002) and KLEINHOFS (2002), and the map available on the Barley Genomics page of Washington State University (http://barleygenomics.wsu.eu/arnis/linkage_maps/ maps-svg.html) resulted in a consensus map of barley disease resistance genes (Figure 1). This map was supplemented with resistance genes *Rgd2a*, *Rrs2*, *Rpt4* and *Rpt3* (WILLIAMS et al. 1999, MOLNAR et al. 2000, SCHWEIZER et al. 2000, TACCONI et al. 2001).

Table 2. DNA markers developed for resistance genes in barley (*Hordeum* spp.)

Gene symbol	Chromosome localisation	Origin	Marker type	Reference
Rph2	7HS	*H. vulgare*	RAPD, STS, RFLP	BOROVKOVA et al. (1997)
Rph7		*H. vulgare*	CAPS	GRANER et al. (2000)
			RFLP, STS-ASA	BRUNNER ET al. (2000)
Rph9, 12	5HL	*H. vulgare*	STS	BOROVKOVA et al. (1998)
Rph16		*H. vulgare* ssp. *spontaneum*	STS, CAPS	IVANDIC et al. (1998)
Rpg1	1H	*H. vulgare*	RFLP	JIN et al. (1993)
Mla	1H	*H. vulgare*	RFLP	KINTZIOS et al. (1995)
Mlg	4HS	*H. vulgare*	RFLP	GÖRG et al. (1993) KURTH et al. (2001)
MlLa	2HL	*H. laevigatum*	RFLP, STS	GIESE et al. (1993)
Mlo	4HL	*H. vulgare*	RFLP AFLP	HINZE et al. (1991) SIMONS et al. (1997)
Ml-a	5H	*H. vulgare* ssp. *spontaneum*	RFLP	JAHOOR, FISCHBECK (1993)
rcs	6H	*H. vulgare*	RAPD	KUTCHER, BAILEY (1994)
Rpt1			RFLP	GRANER et al. (1996)
Rpt3	2H	*H. vulgare*	RAPD	MOLNAR et al. (2000)
Rpt4	7HL	*H. vulgare*	RFLP	WILLIAMS et al. (1999)
Rgd2a	7HS	*H. vulgare*	STS, CAPS	TACCONI et al. (2001)
Rrs1	3H	*H. vulgare*	RFLP, RAPD	BARUA et al. (1993)
			AFLP	WILLIAMS et al. (2001)
Rrs2	7HS	*H. vulgare*	RFLP, RAPD	SCHWEIZER et al. (1995, 2000)
Rrs13	6HS	*H. vulgare* ssp. *spontaneum*	RFLP	ABBOTT et al. (1995)
Rrs14	1HS	*H. vulgare* ssp. *spontaneum*	RFLP, STS	GARVIN et al. (2000)
run8	1H	*H. vulgare*	SSR STS-ASA	LI et al. (2000) ECKSTEIN et al. (2002)
Ruh		*H. vulgare*	RAPD, SCAR	ARDIEL et al. (2002)
Ryd2		*H. vulgare*	AFLP	PALTRIDGE et al. (1998)
rym4	3HL	*H. vulgare*	RFLP	GRANER, BAUER (1993), TUVESSON et al. (1998)
			RAPD, SSR	ORDON et al. (1994)
rym5		*H. vulgare*	CAPS, SSR	GRANER et al. (1999)
rym8		*H. vulgare*	RAPD	BAUER et al. (1997)
rym9		*H. vulgare*	STS, SSR	WERNER et al. (2000)
rym11		*H. vulgare*	RAPD, SSR	BAUER et al. (1997)
rym13		*H. vulgare*	SSR	ORDON et al. (2003)

Table 3. Catalogue of resistance gene symbols for barley

Locus symbol[a]	Synonyms	Chromosome location	Parental cultivar (source)	Gene reference[b]
1	2	3	4	5
Reaction to *Puccinia hordei*				
Rph1	*Pa*	2H	Oderbrucker	BGN 26:107
Rph2b,j,k,l,m,n, q,r,s,t,u,y,	*Pa2*	5HS		BGN 26:126 FRANCKOWIAK et al. (1996)
Rph3c,w,aa	*Pa3*	7HL	Estate	BGN 26:156 FRANCKOWIAK et al. (1996)
Rph4	*Pa4*	1HS	Gull	BGN 26:217
Rph5	*Pa5*	3HS	Magnif 102	BGN 26:157
Rph6	*Pa6*	3HS	Bolivia	BGN 26:501
Rph7g,ac	*Pa7*	3HS	Cebada Capa	BGN 26:173 FRANCKOWIAK et al. (1996)
Rph8	*Pa8*		Egypt 4	BGN 26:502
Rph9	*Pa9, Rph12*	5HL	HOR 2596	BOROVKOVA et al. (1998)
Rph10		3HL	Clipper C8	BGN 26:174
Rph11		6HL	Clipper C67	BGN 26:247
Rph12	*Rph9*		Triumph	BOROVKOVA et al. (1998
Rph13			PI 531849	BGN 28:31
Rph14			PI 584760	BGN 28:32
Rph15		2HL	PI 355447	BGN 28:29 BGN 28:33
Rph16		2HS	*H. vulgare* ssp. *spontaneum* HS078, HS084	IVANDIC et al. (1998)
RphTR		5HS	TR306	STEFFENSON (BG-WSU)
Rph19			Reka 1	PARK, KARAKOUSIS (2002)
Reaction to *Puccinia graminis*				
*Rpg1**	*T*	7HS	Chevron	BGN 26:437
Rpg2	*T2*		Hietpas 5	BGN 26:439
Rpg3			PI 382313	JEDEL (1991)
rpg4		5HL	Q21861	BGN 26:267
Reaction to *Puccinia striiformis*				
rps1.a,b,c	*yr1*		BBA 2890, Bigo, Mazurka	CHEN, LINE (2001)
rps2	*yr2*		Abed Binder 12	
rps3	*yr3*		I 5	NOVER, SCHOLZ (1969)
Rps4	*Yr4*	1H	Cambrinus	
rpsHF			Heils Franken	
rpsEm1			Emir	
rpsEm2			Emir	
rpsAst			Astrix	CHEN, LINE (2001)
rpsHi1			Hiproly	
rpsHi2			Hiproly	
rpsVa1			Varunda	

1	2	3	4	5
rpsVa2			Varunda	
rpsTr1			Trumpf	
rpsTr2			Trumpf	
rpsBBA809			BBA 809	
rpsPI548708-1			PI 548708	
rpsPI548708-2			PI 548708	
rpsPI548734			PI548734	
rpsPI548747-1			PI548747	CHEN, LINE (2001)
rpsPI548747-2			PI548747	
rpsA14-1			Abyssinian 14	
RpsA14-2			Abyssinian 14	
rpsGZ			Grannelose Zweizeilige	
rpsI5			I 5	
rpsSO-1			Stauffers Obersulzer	
rpsSO-2			Stauffers Obersulzer	
Reaction *to Blumeria (Erysiphe) graminis* f. sp. *hordei*				
**Mla1*	*Reg1*	1H	C.I. 16,137	MOSEMAN (1972)
**Mla6*	*Reg1*	1H	*H. spontaneum*	DESCENZO, WISE (1996)
Mla12	*Reg1*	1H	Arabische	HEUN (BG-WSU)
Mla13	*Reg1*	1H	Rupee	DESCENZO, WISE (1996)
Mla14	*Reg1*	1H	*H. spontaneum*	DESCENZO, WISE (1996)
Mlat		1H		
MlBo		4H		JØRGENSEN (1994)
mldb				
Ml(CP)a		4H		
Mle			*H. spontaneum*	SCHÖNFELD el al. (1994)
Mlf		7H	*H. spontaneum*	SCHÖNFELD el al. (1994)
Mlg	*Reg2*	4H		STEFFENSON (BG-WSU)
MlGa		1H		JØRGENSEN (1994)
Mlh		6H		JØRGENSEN (1994)
Mlhb			*H. bulbosum*	KASHA et al. (1996)
Mlj		5H	*H. spontaneum*	SCHÖNFELD el al. (1994)
Mlk		1H		JØRGENSEN (1994)
MlLa		2H	*H. laevigatum*	GIESE (BG-WSU)
Mlnn		1H		
**mlo*	*reg6*	4H		JØRGENSEN (1994)
Mlpb				
Mlra		1H		
mlt		7H		SCHÖNFELD el al. (1994)
Reaction to *Cochliobolus sativus*				
Rcs1	*Hl*	2H		
rcs2	*hl2*	1H		
rcs3	*hl3*	5H		STEFFEON et al. (1996)ns
rcs4	*hl4*			
Rcs5	*Sbl*	7HS		

1	2	3	4	5
Reaction to *Pyrenophora teres*				
Rpt1	*Pt, Rpt,a*	3H		GRANER (BG-WSU)
Rpt2	*Pt2*	1H		JØRGENSEN (1994)
Rpt3	*Pt3*	2H		JØRGENSEN (1994)
Rpt4		7HL	Galleon	WILLIAMS et al. (1999)
Pt d		6HS		JØRGENSEN (1994)
Rpt?			CIho 9819	MANNINEN et al. (2000)
Reaction to *Pyrenophora graminea* (*Drechslera graminea*)				
Rdg1	*Hg, Rhg1*		Vada	THOMSEN et al. (1997)
Rdg2	*Hg2* Rhg2			JØRGENSEN (1994)
Rdg3	*Hg3* *Rhg3*			JØRGENSEN (1994)
Reaction to *Rhynchosporium secalis*				
Rrs1	*Rh, Rha*	3HS		JØRGENSEN (1994)
Rrs2	*Rh2*	7HS		SCHWEIZER et al. (1995)
Rrs3	*Rh3*	3HS		
Rrs4	*Rh4*	3HS		
Rrs5	*Rh5*			
rrs6	*rh6*	4H		
rrs7	*rh7*			JØRGENSEN (1994)
rrs8	*rh8*			
Rrs9	*Rh9*	4H		
Rrs10	*Rh10*			
rrs11	*rh11*			
Rrs12				
Rrs13		6H	*H. vulgare* ssp. *spontaneum*	BROWN (BG-WSU)
Rrs14		1H	*H. vulgare* ssp. *spontaneum* 208	GARVIN et al. (1997)
Reaction to *Ustilago nuda*				
Run1	*Un*	7HS	Trebi	BGN 26:67
Run2				
Run3				
Run4				JØRGENSEN (1994)
Run5				
Run6				
run7				
run8		1HL		LI et al. (2000)
Reaction to *Ustilago nigra*				
Ung				JØRGENSEN (1994)
Reaction to *Ustilago hordei*				
Ruh1				JØRGENSEN (1994)
Ruh2				
ruh3				
ruh4				

1	2	3	4	5
Reaction to *Septoria passerinii* (*Leptsphaeria avenaria* f. sp. *triticea*)				
Rsp1	*Sep1*		CIho 14300	BGN 26:441
Rsp2	*Sep2*		PI 70837	BGN 26:442
Rsp3	*Sep3*		CIho 10644	BGN 26:443
Reaction to *Typhula incarnata*				
Rti		1H	Franka	GRANER (BG-WSU)
Reaction to *Fusarium* spp.				
fb	*sc*			JØRGENSEN (1994)
Reaction to BYDV				
ryd1	*yd*			JØRGENSEN (1994)
Ryd2	*Yd2*	3HL	CIho 2376	BGN 26:158
Reaction to BaYMV and BaMMV				
rym1	*Ym*	4HL	Mokusekko 3	BGN 32:96
Rym2	*Ym2*	7HL	Mihori Hadaka 3	BGN 26:66
rym3	*ym3*	5HS	Chikurin Ibaraki	BGN 32:105
rym4	*ym4, rmm1*	3HL	Franka	KONISHI (2000)
rym5	*ym5*	3HL	Mokusekko 3	BGN 32:90
rym6			*Hordeum distichum*	IIDA et al. (1999)
rym7	*rmm2*		HOR3365	
rym8	*rmm3*	4HL	10247	
rym9	*rmm4*	4HL	Bulgarian 347	KONISHI (2000)
rym10	*rmm5*		Hiberna	
rym11	*ym11, rmm6*	4HS	Russia 57	
rym12		4HL	Muju covered 2	GÖTH, FRIEDT (1993)
rym13		4HL	Taihoku A	GÖTH, FRIEDT (1993)
Reaction to BSMV				
rsm1(rms1)	*sm*	7HS	Modjo 1	BGN 26:84
rsm2	*sm2*		Modjo 1	NILAN (1964)
rsm3	*sm3*			VASQUEZ et al. (1974)
Rsm4	*Sm4*			JØRGENSEN (1994)
rsm5	*sm5*			VASQUEZ et al. (1974)
Reaction to *Schizaphis graminum*				
Rsg1	*Grb*	7H	Omugi	BGN 26:68
Rsg2	*Grb2*		PI 426756	BGN 26:503
Rsg3	*Grb3*			JØRGENSEN (1994)
Reaction to *Heterodera aveanae* Woll.				
Rha1	*Ha1*			ANDERSEN (1972) JØRGENSEN (1994)
Rha2	*Ha2, Ha*	2H	191	JØRGENSEN (1994) KRETSCHMER (BG-WSU)
Rha4			Galleon	BARR et al. (1998)

[a] genes of known sequence are marked with *

[b] BGN and BG-WSU indicate internet resources: http://wheat.pw.usda.gov/ ggpages/bgn/ and http:// barleygenomics.wsu.eu/

The number of putative resistance genes increased during the last five years. DNA markers developed to identify barley resistance genes are listed in Table 2.

In early studies, most resistance genes were identified by using RFLP makers. Of the 28 markers developed, 22 are PCR-based. STS markers have been developed mainly to identify leaf rust resistance genes in barley accessions (BOROVKOVA et al. 1997, 1998, IVANDIC et al. 1998, BRUNNER et al. 2000). RFLP markers for the resistance genes *MlLa*, *Mlo*, *Mla*, *Mlg*, *Rrs1*, *Rrs2*, *Rrs13*, *Rrs14*, *Rph2, Rph7*, *Rpt4*, *Rpg1*, *rym4* have also been described in the literature (Table 2).

PCR-based strategies provide a means of comparative mapping of genetic regions in different species. Comparisons of the barley genetic map with those of other cereals have indicated that the order of genes on barley chromosomes is similar to that on chromosomes of wheat, rice and maize. The wheat leaf rust resistance gene *Lrk10* located on 1AS chromosome arm corresponds to the tip of 3HS barley chromosome, whereas locus *Lr1* in wheat on chromosome 5D corresponds to a locus on 5H in barley (GALLEGO et al. 1998). Mapping of sequences related to *rp1* (a maize gene that confers race-specific resistance to the rust fungus *Puccinia sorgi*) in barley enabled the identification of three loci on chromosomes 1HL, 3HL and 7HS. The three rust resistance genes that have been cloned to date (*Lrk*, *Rpg1*, *rp1d*) are members of a plant disease resistance gene class that encodes proteins containing an ATP or GTP nucleotide-binding site (NBS) and C-terminal leucine-rich repeat region (LRR) (CHEN et al. 1998, AYLIFFE et al. 2000).

PECCHIONI et al. (1999) mapped the pathogen-related (PR) genes *Tha* (thaumatin-like locus) and *Chi1* (chitinase 1) to chromosome 1 (7H), *Prx7* (peroxidase 7) to chromosome 2 (2H), *Glb32* (b-(1-3)-glucanase isoform 32) to chromosome 3 (3H), *Ftt* (a fourteen three three (14-3-3) protein analog produced in response to powdery mildew infection) to chromosome 4 (4H), *Chs3* (chalcone synthase) to chromosome 5 (1H), and *Rip1* (ribosome inactivating protein 1) to chromosome 7 (5H).

Gene symbols available for barley resistance genes are given in Table 1. JØRGENSEN (1994) listed 14 different loci with 110 different alleles responsible for reaction to powdery mildew, located on chromosomes 1H, 2H, 4H and 6H, using Ml based symbols. Additionally, the gene *mlt* was found on chromosome 7H, and *Mlj*, *Mle* and *Mlf* were found in *H. vulgare* ssp. *spontaneum* (SCHÖNFELD et al. 1994, 1996) and *Mlhb* in *H. bulbosum* (KASHA et al. 1996). The mildew resistance genes: *Mlo*, *Mla* and *MlLa* have high numbers of alleles, with most allelic variation found in the *Mla* and *Mlo* regions – at least 29 and 25 alleles, respectively (JØRGENSEN 1994). A map of the *Mla* region with closely linked markers and resistance gene analog families was reported by WEI et al. (1999). At least seven of the 11 nucleotide-binding site/leucine-rich repeat (NSB-LRR) resistance homologues co-segregated with *Mla*. The complexity of the *Mla* locus for resistance to powdery mildew on chromosome 1H of the barley genome is demon-

strated by the 29 alleles that have already been assigned to this locus (KINTZIOS et al. 1995). Table 3 reviews information on resistance genes against 20 pathogens and pests. Recent works by FRANCKOWIAK et al. (1996) and CHEN, LINE (2001) summarise data on *Rph* and *Rps* genes, respectively.

Sequencing of resistance gene clusters is an objective of projects recently funded by the National Science Foundation Plant Genome Program (http://www.nsf.gov/bio/pubs/awards/genome02.htm). Four resistance genes of barley have been cloned and sequenced recently: *Mlo*, *Rpg1, Mla1* and *Mla6*. The barley stem rust resistance gene *Rpg1*, since implementation of this gene in 1942 in barley cultivars in US and Canada, had provided resistance against stem rust losses till late 1980's. *Rpg1* has a novel structure and encodes a receptor kinase-like protein, with two tandem protein kinase domains (BRUEGGEMAN et al. 2002). *Mla1* encodes a 108-kDa protein containing an N-terminal coiled-coil structure, a central NB domain and a C-terminal LRR region (SCHULZE-LEFERT, VOGEL 2000, ZHOU et al. 2001). The deduced protein sequence encoded by the *Mla6* open reading frame contains 956 amino acids with an estimated molecular mass of 107.8 kDa. MLA6 belongs to the coiled-coil subset of NBS-LRR resistance proteins and contains the five conserved motifs indicative of a nucleotide-binding site (HALTERMAN et al. 2001). The *Mlo* resistance locus encodes a 60-kDa protein and confers a broad spectrum resistance to almost all isolates of *Blumeria graminis* f. sp. *hordei* (BÜSCHGES et al. 1997). *Mlo* resistance has been identified in only 18% of Polish barley cultivars. This gene is highly valuable due to lack of known virulence for this gene and selected cultivars are proposed to be good sources for breeding for durable powdery mildew resistance (CZEMBOR, CZEMBOR 1998).

Recently in Europe, many major genes for resistance have been overcome by the process of adaptation of the pathogens. This includes the leaf resistance genes *Rph3* and *Rph12*, which were considered to be the most effective and were common in barley breeding programmes. Genes *Rph13* and *Rph14*, recently found in 5 accessions of *H. vulgare* ssp. *spontaneum*, might partly solve this problem (MANISTERSKI, ANIKSTER 1994). However, the loss of major resistance sources against barley leaf rust has increased the importance of quantitative resistance in - breeding programmes. TOOJINDA et al. (1998) showed the effectiveness of quantitative trait loci (QTL) analysis in the process of introgression into unrelated genetic background with one cycle of marker-assisted backcrossing. WENZEL et al. (2001) hypothesised that both QTL and qualitative loci may form tightly linked clusters that act as functional units. Data on identified QTL markers are available in the online database: http://www.css.orst.edu/barley/nabgmp/QTLsum42401.xls

While the genomic positions of QTL are presumably constant, the effects of QTL alleles may vary with environment. This becomes especially important in the study of disease resistance, because different pathotypes in different environments may affect resistance mechanisms, stressing the importance of studying

QTL effects in more than one environment (SPANER et al. 1998). TOOJINDA et al. (2000) used RFLP, SSR, AFLP and RGAPs to map genes contributing to resistance to leaf rust, stripe rust and the serotypes MAV and PAV of barley yellow dwarf virus of barley in five environments.

The expression of resistance genes depends on genetic and environmental factors. Many *Mla* resistance genes require the presence of genes *Rar1* and *Rar2* to function, and some appear to have different signalling requirements (JØRGENSEN 1996). It has been demonstrated that the number and chromosomal location of loci controlling net blotch and spot blotch resistance in barley depends on plant developmental stage. In seedlings, resistance to *Pyrenophora teres* f. *teres* is controlled by loci on chromosomes 4H and 6H, whereas adult plant resistance is controlled primarily by loci on chromosomes 2H, 3H and 7H. A similar situation is observed in response to *Cochliobolus sativus*, where seedling resistance is governed by a locus on chromosome 1H and adult plant resistance primarily by a locus on chromosome 5H (STEFFENSON et al. 1996). When water-stress is relieved, powdery mildew infection increases on both *Mlo*-susceptible and *mlo*-resistant spring barley cultivars (BAKER et al. 2000). Both plant development and environmental stress are strictly connected with DNA methylation. However, there is no data on the role of methylation process in expression of resistance genes.

Conclusions

Collected data show that the growing number of available PCR markers of barley resistance genes can be used to accelerate the breeding process. National and international efforts on SNP development coupled with adaptation of available R gene markers can lead to acceleration of genes pyramiding in cultivars.

Acknowledgements. This study was supported by the State Committee for Scientific Research, Poland, project No. PBZ/KBN/029/P06/2000.

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