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Powdery mildew resistance genes in wheat: verification of STS markers

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Abstract. Five accessions of *Aegilops speltoides* and 67 European wheat cultivars (winter and spring) originating from the Czech Republic, Germany, Poland, Russia, Slovakia, United Kingdom, and 4 non-European wheat cultivars from Brazil and the USA were examined with molecular Sequence Tagged Site (STS) markers for resistance genes to powdery mildew: *Pm 1*, *Pm 2*, *Pm 3* and *Pm 13*. All markers gave clear, repeatable results, although three of them (*Pm 1*, *Pm 2* and *Pm 3*) appeared as not specific for resistance genes. Comparison of STS analysis results with *Pm* genes, postulated as the reaction type after inoculation with differential isolates of *Erysiphe graminis* f.sp. *tritici* (*Blumeria graminis*), revealed a high number of disparities. The marker for *Pm 13* was not detected in any examined cultivar but was present in five accessions of *Aegilops speltoides*.

Key words: powdery mildew, resistance genes, STS markers, wheat.

Introduction

Randomly Amplified Polymorphic DNA (RAPD), Sequence Tagged Site (STS) and Sequence Characterized Amplified Regions (SCAR) markers have been recently developed to identify the presence of resistance genes in cereal cultivars, lines, breeding materials and gene bank accessions. Concerning the wheat resistance genes to *Erysiphe graminis* f.sp. *tritici,* which causes powdery mildew, resulting in important economic losses in agriculture worldwide, 25 *Pm* genes have been identified using genetic methods, and localized on wheat chromosomes (see for review: CHEN, CHEŁKOWSKI 1999, SZUNICS, SZUNICS 1999). However, none of *Pm* resistance genes has been cloned. STS markers have been designed for four

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Pm genes: *Pm 1*, *Pm 2*, *Pm 3* and *Pm 13* (MOHLER, JAHOOR 1996, HU et al. 1997, CENCI et al. 1999). Resistance gene *Pm 2* is present in numerous cultivars grown in Europe, but its resistance has been broken for a long time. Resistance gene *Pm 13* is of particular interest to breeders, because it confers complete resistance to all known virulences of the pathogen *E. graminis* f.sp. *tritici* (DONINI et al. 1995, CEOLONI et al. 1996). Recently HARTL et al. (1999) has described Amplified Fragment Length Polymorphism (AFLP) markers closely linked to *Pm 1c* and *Pm 4a* resistance genes, and HUANG et al. (2000) found an AFLP marker for the *Pm 24* gene. Genes of resistance to powdery mildew have been identified in wheat cultivars as the type of plant reaction to the pathogen isolate used for inoculation (HANUŠOVA, BARTOŠ 1998, KOWALCZYK et al. 1998, 2000). The following resistance *Pm* genes were found in Polish cultivars of wheat by KOWALCZYK et al. (1998): *Pm 2* in combination with *Pm 6*, *Pm 3d*, *Pm 4b*, *Pm 5*, *Pm 8* and *Pm 9*.

Information on resistance genes present in material used in the breeding process is very useful, and PCR assay using STS markers is a very promising method to identify these genes. It is important to verify the reliability of molecular PCR markers and reproducibility in various laboratories. JONES et al. (1997) after interlaboratory analyses of DNA markers in the European network found that SSR (Simple Sequence Repeats) and AFLP markers are more reproducible than RAPD markers. The aim of this study was to verify STS markers available in the literature in Polish and other European cultivars and accessions. Also a simple and low-cost DNA extraction and purification procedure was chosen, making the method suitable for use in breeding laboratories. Results of marker identification were compared with data on the reactions of the same accessions after inoculation with *Erysiphe graminis* virulences, available in the literature (KOWALCZYK et al. 1998).

Material and methods

Seeds of 3 American, 1 Brazilian, 3 British, 15 Czech, 13 German, 25 Polish, 7 Russian and 4 Slovak (in total 71) cultivars were used to examine the presence of *Pm 1*, *Pm 2*, *Pm 3* and *Pm 13* resistance gene markers. Forty-five of the examined cultivars were earlier analysed for reaction to powdery mildew inoculation and thus *Pm* resistance genes were postulated (KOWALCZYK et al. 1998). Other cultivars used in this work were not examined by inoculation tests. Additionally, five accessions of *Aegilops speltoides* were tested for the presence of the *Pm 13* marker.

DNA extraction

DNA was extracted from 7-day-old seedling leaves by a modified CTAB method (according to DOOHAN et al. 1998). In short, 0.1 g of fresh leaves (containing ap-

proximately 2-5 µg of DNA) of each cultivar were harvested to an Eppendorff tube, frozen at –70°C and then freeze-dried. After grinding the material with the pestle, 1 ml of CTAB buffer with 0.4% 2-mercaptoethanol was added, followed by adding 100 µl of chloroform-octanol (24 : 1/vol.) mixture. Then samples were incubated at 65°C for 25 minutes. Subsequently, after addition of 400 µl of chloroform-octanol mixture, samples were vigorously shaken and left at room temperature for 10 minutes.

After centrifugation (10 minutes at 11,000 rpm) the water upper phase was transferred to a new Eppendorff tube. Then 1/10 vol. of sodium acetate (50 µl) was added and DNA was precipitated with 800 µl of ice-cold ethanol (96%) and left in the refrigerator for 2 h. The precipitate was centrifuged at 14,000 rpm for 20 minutes, the supernatant was removed and DNA was washed carefully with 1 ml of cold ethanol (75%) and resolved with 200 µl of TE buffer pH 8.0. The extracts were stored at –20°C until used.

PCR amplification and gel electrophoresis

Each sample contained 0.75 U of Taq DNA polymerase (Finnzymes), 2.5 µl of PCR buffer, 12.5 pmol of forward/reverse primers (Table 1), 2.5 mM of each dNTP and about 50 ng of plant DNA. PCR conditions (Perkin Elmer DNA Thermal Cycler) for all primer sets are listed in Table 2. Amplification products were

Table 1. Primer sequences, original markers and references for *Pm* gene markers

Gene	STS marker set	Original marker	Sequence of primers 5'-3'	Reference
Pm 1	C320-1	RAPD	fwd: CCG GCA TAG ATC GAG AAT AG	HU et al. 1997
	C320-2	UBC 320	rev: CCG GCA TAG AAC TTT AAG CG	
Pm 2	Whs 350-1	RFLP	fwd: AGC TGT TTG GGT ACA AGG TG	MOHLER, JAHOOR 1996
	Whs 350-2	Whs 350	rev: TCC CCT GTG CTA CTA CTT CTC	
Pm 3	N/A	RFLP	fwd: AGC AAG ACT ACA TGG CAT GG	MOHLER (pers. comm.)
			rev: AGG GCA GCA GTG AGA ATT AG	
Pm 13	UTV 14F	RAPD	fwd: CGC CAG CCA ATT ATC TCC ATG A	CENCI et al. 1999
	UTV 14R	OPX 12_{570}	rev: AGC CAT GCG CGG TGT CAT GTG AA	

Table 2. PCR amplification programmes for different primer combinations used

Marker	PCR programme
Pm 1	94°C - 4 min., 35 cycles (94°C - 1 min., 60°C - 1 min.30 sec., 72°C - 2 min.), 72°C - 5 min.
Pm2	94°C - 4 min., 35 cycles (92°C - 1 min., 60°C - 2 min., 72°C - 1 min.), 72°C - 5 min.
Pm 3	94°C - 4 min., 35 cycles (92°C - 1 min., 60°C - 1 min., 72°C - 2 min.), 72°C - 5 min.
Pm 13	94°C - 3 min., 35 cycles (94°C - 1 min., 60°C - 1 min., 72°C - 2 min.), 72°C - 5 min.

electrophoresed at 5 V/cm for about 3 h in 1.5% agarose gel (Amersham Biotech) stained with ethidium bromide, visualised under UV light and photographed (Syngen UV visualiser).

Results and discussion

Amplification products of 420, 598 and 610 bp in size were found in DNA extracts of most cultivars examined, corresponding to markers for genes *Pm 1*, *Pm 2* and *Pm 3*, respectively, as presented in Table 3. The bands of all markers gave clear and strong fluorescence after separation (Figures 1-4). The marker for *Pm 13* (517 bp) was not identified in any of the examined cultivars, but it was identified in five accessions of *Aegilops speltoides* (Figure 4).

Molecular confirmation of the presence of *Pm 1*, *Pm 2* and *Pm 3* gene markers was in full agreement with postulated *Pm* genes only in 6 cultivars out of the 45 examined (Agra, Iris, Planet, Korweta, Lama, Sakwa: Table 3). The *Pm 1* gene marker was identified in 5 cultivars examined by inoculation test (Planet, Helia, Hezja, Jawa and Omega: KOWALCZYK et al. 1998) and in all five cultivars that was confirmed by STS analysis. However, positive results of the *Pm 1* marker identification were obtained in 33 cultivars which are not supposed to have the *Pm 1* gene (Table 3). The presence of the *Pm 2* gene was proved as a reaction type to powdery mildew isolates in 21 cultivars. Amplicon of 598 bp, corresponding to the *Pm 2* gene marker, was present in 39 out of 45 cultivars, including 20 cultivars for which the *Pm 2* gene was not detected on the basis of reaction type examination (Table 3). The *Pm 2* gene was not detected in cultivars Jawa and Maltanka by the STS marker, although it was found in both cultivars in the inoculation test (KOWALCZYK et al. 1998). The presence of the *Pm 3* gene in 5 cultivars: Borenos, Alkora, Hezja, Maltanka, Omega (KOWALCZYK et al. 1998) was confirmed by the STS marker; however, the marker was identified also in 17 other cultivars (Table 3).

Molecular analysis was performed also for cultivars that were not examined by inoculation tests. The STS marker of *Pm 1* was present in 24 cultivars, the marker of *Pm 2* in 18 cultivars and the marker of *Pm 3* in 14 cultivars (Table 4).

There are several reasons why the results of the identification with STS markers are so different from the results of reaction type analysis. This difference can be explained by suppression of resistance genes, or gene markers are not tightly linked with the resistance gene in wheat cultivars of various genetic background used in this work. Suppression of resistance genes *Pm 8* and *Pm 17* was found in some European cultivars and *Pm 17* proved to be an allele of *Pm 8* (HANUŠOVA et al. 1996, 1997, ZELLER, HSAM 1996). REN et al. (1997) found that gene *Pm 8*, present in wheat accessions with translocation 1BL*1RS, was suppressed in wheats from Mexico and China, due to the presence of a dominant suppressor

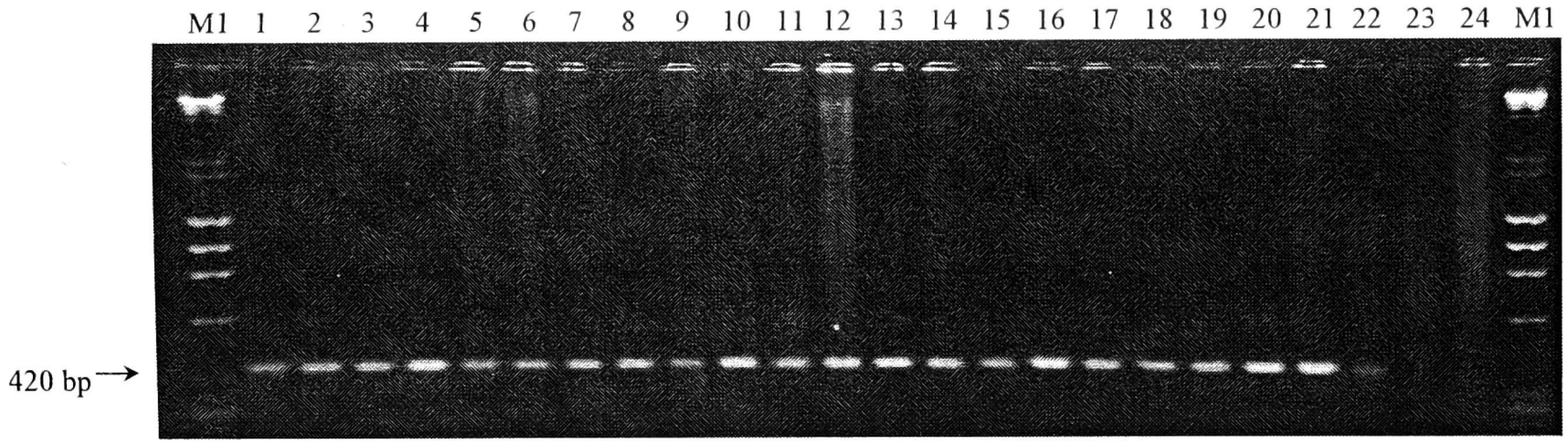

Figure 1. Amplification products of PCR with primers specific to *Pm 1* gene marker. Lanes 1-23=cultivars, lane 24=control, M1=λDNA Hind III and ΦX174 DNA Hae III (Finnzymes).

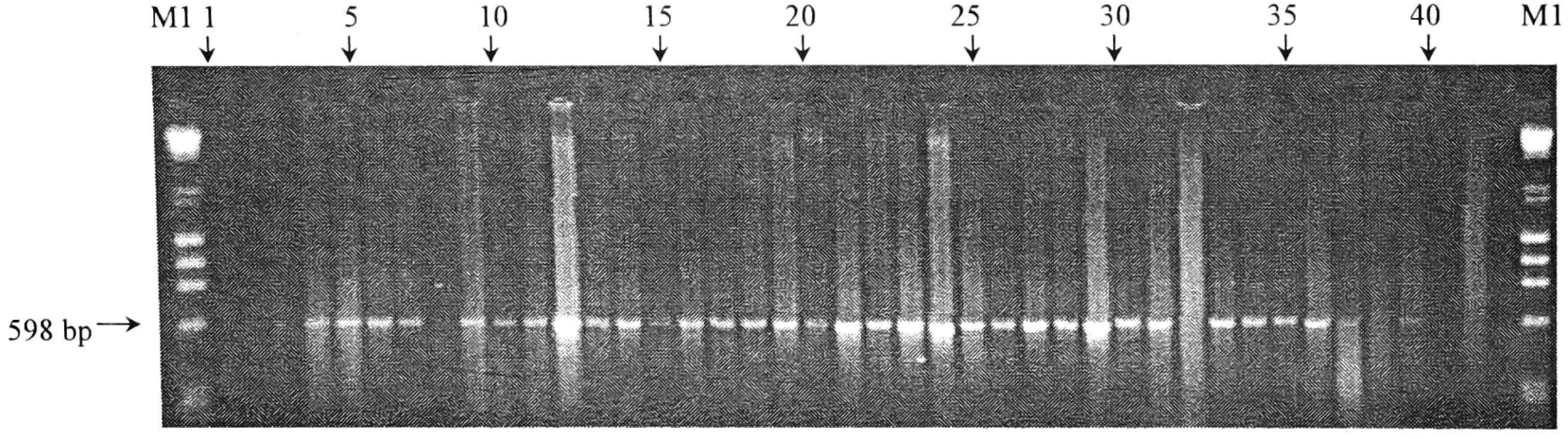

Figure 2. Amplification products of PCR with primers specific to *Pm 2* gene marker. Lanes 1-41=cultivars, lane 42=control. M1=λDNA Hind III and ΦX174 DNA Hae III (Finnzymes).

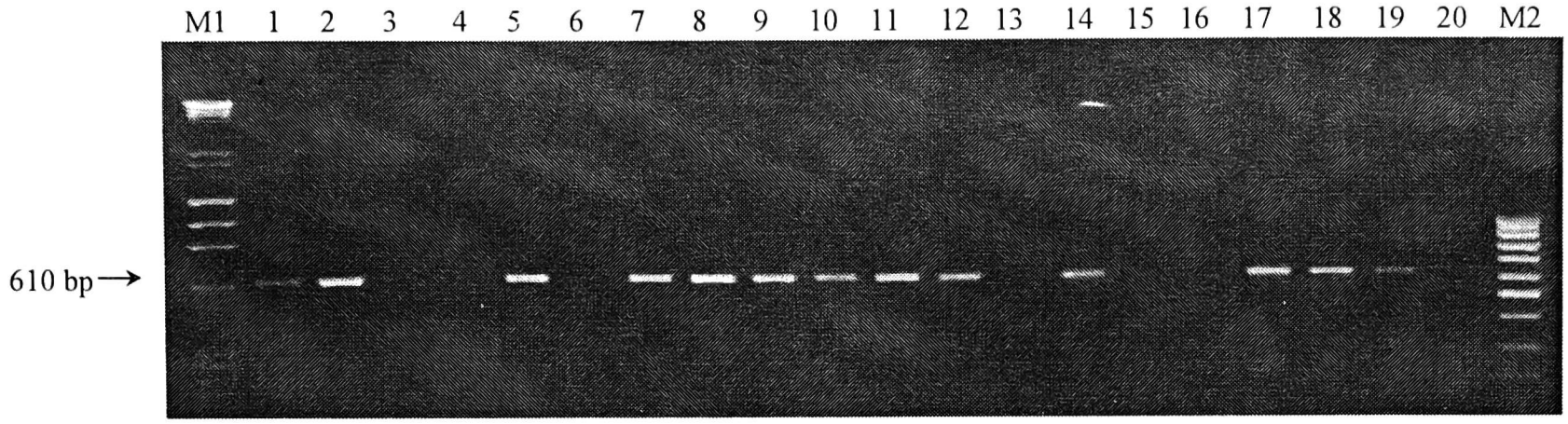

Figure 3. Amplification products of PCR with primers specific to *Pm 3* gene marker. Lanes 1-19 = cultivars, lane 20 = control. M1 = λDNA Hind III and ΦX174 DNA Hae III (Finnzymes), M2 = 100 bp ladder (TIB MolBiol).

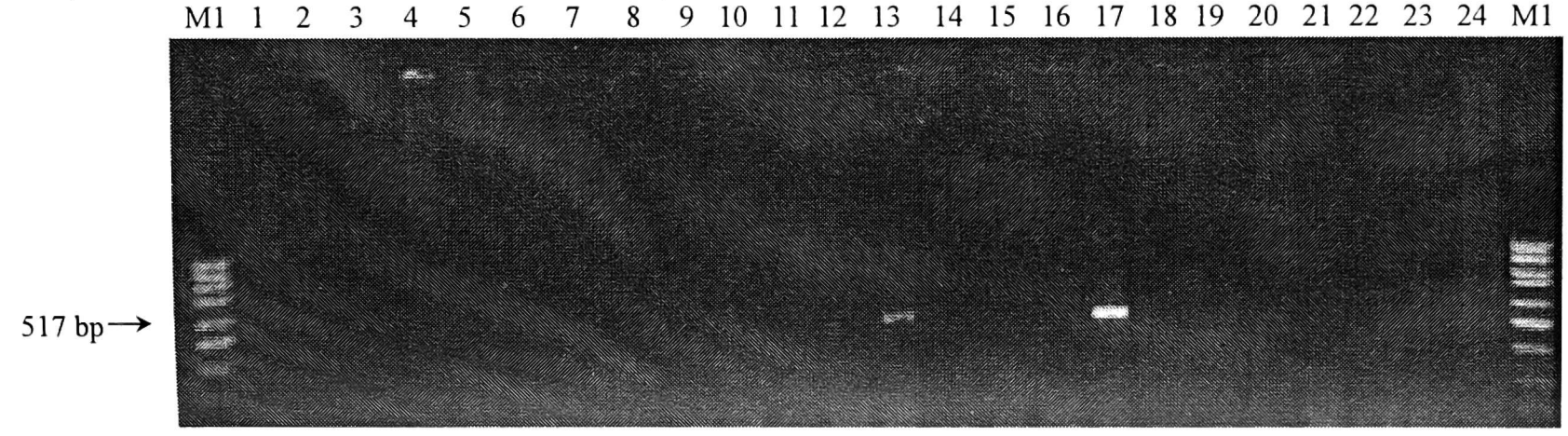

Figure 4. Amplification products of PCR with primers specific to *Pm 13* gene marker. Lanes 1-23 = cultivars (lane 13 = *Ae. speltoides* 2056, lane 17 = *Ae. speltoides* 2067), lane 24 = ontrol, M1 = 100 bp ladder (TIB MolBiol).

gene (or genes) in wheat genome. Translocation T1BL*1RS (or T1AL*1RS) is the most successful wheat-alien translocation used worldwide for hexaploid wheat improvement, as containing resistance genes *Pm 8*, *Lr 26*, *Sr 31* and *Yr 9*. About 40% of international wheat nursery material had this translocation (LUKASZEWSKI 1990). However, gene *Pm 8* is not expressed in all backgrounds (FRIEBE et al. 1996). Suppression of resistance genes *Pm 1*, *Pm 2* and *Pm 3* has not been reported in the literature yet.

The results of amplification of *Pm* gene markers may be caused by the limited specificity of markers, mainly due to the complex genetic structure of the hexaploid wheat genome. There is a strong possibility that amplified DNA fragments are not linked to the *Pm* gene, coming rather from homoeologous chromosome regions. To support this hypothesis, *Pm 1*, *Pm 2* and *Pm 3* markers were tested on a number of diploid wheat-related accessions of Triticeae. The marker for the *Pm 1* gene was present in all tested samples, and frequencies of positive results for *Pm 2* and *Pm 3* were similar to those for hexaploid wheat (our studies).

Gene *Pm 2* in European cultivars of wheat originate from cv. Maris Huntsman, which was used extensively in Poland as a source of resistance genes *Pm 2* + *Pm 6*, and both genes are present in numerous cultivars. *Pm 2* is located on chromosome 5DS and originates from *Aegilops tauschii* (HEUN, FISHBECK 1987, CHEN, CHEŁKOWSKI 1999). MOHLER and JAHOOR (1996) confirmed the presence of the *Pm 2* gene marker in Maris Huntsman and Planet, in agreement with results of this paper, and also in Ulka/8*Cc, Attis, Nandu, Troll, Mephisto, Maris Dove, Knirps, Sappo, Normandie and Axona. HU et al. (1997) identified two RAPD markers for the *Pm 1* gene in cultivars Axminster, Converse, Norka and Thew in agreement with the resistance to the isolate 94-6 of powdery mildew and revealed the absence of the marker in 15 other accessions.

Recently KELLER et al. (1999) has mapped and characterized quantitative trait loci (QTLs) for adult plant powdery mildew resistance in a segregating population of 226 recombinant inbred lines derived from a cross between *Triticum aestivum* cv. Forno and *Triticum spelta* cv. Oberkulmer. Those authors suggest that QTLs for resistance offer the possibility of simultaneous marker-assisted selection for major and minor genes. The attempt to control powdery mildew with major resistance genes (*Pm* genes) has not provided any durable resistance in cultivars available in Europe. The new strategy with QTL markers seems to be promising.

In general there is a limited number of results on marker usefulness in wheat. At the moment the STS marker for the *Pm 13* resistance gene seems to be rather specific, as we found the amplicon of the marker only in five *Aegilops* accessions. This gene was transferred from *Ae. longissima* (3S'1S) into common wheat chromosome arms 3BS and 3DS (FRIEBE et al. 1996). *Pm 13* conditions complete resistance to all known races of wheat powdery mildew (DONINI et al. 1995), and is

Table 3. Identification of powdery mildew resistance genes *Pm 1*, *Pm 2* and *Pm 3* in wheat cultivars from European countries: comparison of reaction type and STS marker results

Cultivar	Country of origin	Reaction type (*Pm* genes present)	Identification of STS marker*			Comparison of reaction type and marker presence
			Pm 1	*Pm 2*	*Pm 3*	
1	2	3	4	5	6	7
Agra	Czech Republic	2, 8	–	+	–	FA
Branka	Czech Republic	4b, 8	+	+	–	D
Iris	Czech Republic	5, 8	–	–	–	FA
Regina	Czech Republic	5+SuPm8	+	+	–	D
Simona	Czech Republic	–	+	+	–	D
Sofia	Czech Republic	2+4b+8	+	+	+	PA
Sparta	Czech Republic	2+4b+8	+	+	–	PA
Vega	Czech Republic	–	+	+	–	D
Viginta	Czech Republic	–	+	+	–	D
Vlada	Czech Republic	5	+	+	+	D
Zdar	Czech Republic	4b, 5	+	+	+	D
Alidos	Germany	5	+	+	–	D
Aron	Germany	4b	+	–	+	D
Borenos	Germany	3c	+	+	+	PA
Bussard	Germany	2	+	+	+	PA
Glockner	Germany	4b+8	+	+	+	D
Planet	Germany	1+2+4b+9	+	+	–	FA
Rektor	Germany	5	+	–	–	D
Mikon	Germany	–	+	+	+	D
Alkora	Poland	3d	–	+	+	PA
Almari	Poland	2+6	+	+	–	PA
Emika	Poland	5	–	–	+	D
Helia	Poland	1+2+4b+9	+	+	+	PA
Hezja	Poland	1+3d+4b	+	+	+	PA
Jawa	Poland	1+2+U	+	–	+	PA
Juma	Poland	2+6	+	+	+	PA
Kamila	Poland	2+6	+	+	+	PA
Kobra	Poland	2	+	+	–	PA
Korweta	Poland	2+6	–	+	–	FA
Lama	Poland	2+6	–	+	–	FA
Maltanka	Poland	2+6	+	–	+	D
Mona	Poland	3d+4b	+	+	+	PA
Oda	Poland	2+6	+	+	–	PA

1	2	3	4	5	6	7
Olma	Poland	2+6	+	+	–	PA
Omega	Poland	1+3d+4b	+	+	+	PA
Roma	Poland	2+6	+	+	+	PA
Sakwa	Poland	2+6	–	+	–	FA
Zorza	Poland	2	+	+	–	PA
Granada	Russia	5+8	+	+	+	D
Mironowska	Russia	8	+	+	–	D
Blava	Slovakia	–	+	+	–	D
Ilona	Slovakia	5	+	+	+	D
Livia	Slovakia	8	+	+	–	D
Torysa	Slovakia	2+6	+	+	+	PA
Maris Huntsman	UK	2+6	+	+	–	PA

+/–: marker band present/absent
FA: full agreement between STS marker results and reaction type
PA: partial agreement between STS marker results and reaction type
D: disagreement between molecular analysis and reaction type
Pm 13 marker was not identified in any cultivar listed in this Table

Table 4. Results of molecular marker analysis for cultivars not used in inoculation tests

Gene	Cultivars with identified marker
Pm 1	Atlas 66 (USA), Borenos (D), Caribo (D), Castell (RUS), Charger (UK), Czerwnica odezka (RUS), Dahe (RUS), Danubia (CZ), Darumok (RUS), Frontana (BR), Hanseat (D), Hera (PL), Kornett (D), Mara (CZ), Mewa (PL), Mikon (D), Mironowska (RUS), Panda (PL), Redcoat (USA), Rysa (PL), Selekta (CZ), Senta (CZ), Sfera (RUS), Sturdy (USA), Thatcher (UK), Wanda (PL), Zentos (D)
Pm 2	Astron (D), Atlas 66 (USA), Borenos (D), Caribo (D), Charger (UK), Czerwnica odezka (RUS), Dahe (RUS), Darumok (RUS), Hanseat (D), Hera (PL), Kornett (D), Mara (CZ), Mewa (PL), Mikon (D), Mironowska (RUS), Panda (PL), Rysa (PL), Selekta (CZ), Sfera (RUS), Thatcher (UK), Wanda (PL)
Pm 3	Atlas 66 (USA), Borenos (D), Caribo (PL), Castell (RUS), Czerwnica odezka (RUS), Dahe (RUS), Darumok (RUS), Frontana (BR), Hanseat (D), Hera (PL), Kornett (D), Liryka (PL), Mikon (D), Rysa (PL), Sturdy (USA), Wanda (PL)
Pm 13	*Aegilops speltoides*: accessions 2056, 2067, d10, d42, d50

Abbreviations used (country of origin): CZ=Czech Republic, D=Germany, PL=Poland, RUS=Russia, BR=Brazil, UK=United Kingdom, USA=United States of America.

introduced to wheat lines with the developed STS marker (CEOLONI et al. 1996, CENCI et al. 1999). STS markers for *Pm 1*, *Pm 2* and *Pm 3* genes are not specific enough to detect these resistance genes. The reason of the high number of positive results remains unclear, but cloning and sequencing of amplification products could help in interpretation of those results.

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