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Identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L). II. French cultivars

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Summary — Major genes for resistance to the wheat powdery mildew pathogen, *Erysiphe graminis* f sp *tritici*, were analysed in 35 French wheat cultivars and in part in their parents. Cultivars were tested with a set of differential pathogen isolates which had specific interactions for each host line. The results were supplemented by cytological investigations and by consideration of pedigrees. Eighteen cultivars showed susceptible reactions. The remainder formed 9 groups with 1 or 2 resistance genes. Of the 5 known resistance genes present, *Pm2* was the most common (in 5 cultivars), followed by *Pm4b* and *Pm6* (each present in 4 cultivars), *Pm5* (3 cultivars) and *Pm8* (2 cultivars). In addition, an unknown resistance, tentatively designated *Mlar*, was identified in 3 cultivars.

***Triticum aestivum* = common wheat / *Erysiphe graminis* f sp *tritici* = wheat powdery mildew / resistance genes**

Résumé — Identification des gènes de résistance à l'oïdium chez le blé tendre *(Triticum aestivum* L*). II. Cultivars français. *Des gènes majeurs de résistance à l'agent de l'oïdium du blé* Erysiphe graminis *f sp* tritici *ont été recherchés chez 35 cultivars français de blé, et quelques-uns de leurs parents. Les cultivars ont été testés avec un ensemble d'isolats différentiels présentant des interactions spécifiques sur chaque lignée hôte. Les résultats ont été complétés par des observations cytologiques et par une analyse des généalogies. Dix huit cultivars ont montré des réactions de sensibilité. Les autres forment 9 groupes possédant 1 ou 2 gènes de résistance. Des 5 gènes de résistance connus présents chez les cultivars étudiés,* Pm2 *apparaît le plus fréquemment (chez 5 cultivars) suivi de* Pm4b *et* Pm6 *(chacun présent chez 4 cultivars),* Pm5 *(3 cultivars) et* Pm8 *(2 cultivars). De plus, un gène de résistance inconnu a été identifié chez 3 cultivars, nommé provisoirement* Mlar.

Triticum aestivum = *blé* / Erysiphe graminis *f sp* tritici = *oïdium / gènes de résistance*

INTRODUCTION

Powdery mildew occurs annually throughout the common wheat growing regions in France and many other countries. This disease is known to reduce yield significantly. Prior knowledge on the distribution and efficiency of resistance genes in current wheat cultivars is necessary, in order to introduce new genes or to substitute and supplement those which are no longer effective. The present study deals with the characterization and identification of mildew resistance in common wheat cultivars grown in France.

One of the first common wheat cultivars in Europe that showed resistance against powdery mildew caused by *Erysiphe graminis* f sp *tritici* was the French cultivar Normandie. This cultivar had excellent resistance to individual mildew races in the greenhouse and in field trial (Schlichting, 1938; von Rosenstiel, 1938; Roemer, 1941; Nover, 1941). However, it appears that none of the resistance genes in Normandie was directly transferred into French wheat cultivars which are currently in agricultural use. Another cultivar used in French breeding programmes was Lontoï from Finland. This cultivar had a dominant resistance gene as de-

scribed by Goujon (1965). However, it is notable that with the exception of cultivar Foison the Finnish cultivar Lontoï is not mentioned in the pedigrees of currently grown cultivars in France.

Furthermore, several French breeding stations have been using wheat material of foreign origin carrying resistance to powdery mildew for decades. In particular, the British wheat cultivar Maris Huntsman which has a very high level of mildew resistance conferred by genes from the tetraploid wheat species *Triticum timopheevii* and the Dutch cultivar Clement, whose mildew resistance can be traced to the alien variation derived from rye chromosome 1R, are prominent examples. In addition, the French wheat strain VPM1, first described by Maia (1967) and known to carry the major resistance gene *Pm4b* (Doussinault, personal communication) was extensively used in French resistance breeding of common wheat. No systematic inventory of mildew specific resistance genes has been made in French wheat cultivars. This paper reports on the resistance phenotype of 35 recently registered accessions, as well as of their progenitors and mildew resistance sources.

MATERIAL AND METHODS

The near-isogenic lines of Chancellor with known powdery mildew resistance genes (Briggle, 1969) and line TP 114/2*Starke possessing gene *Pm6* (Jørgensen and Jensen, 1972) were kindly provided by RA McIntosh, Australia. The remaining differential cultivars, available French registered cultivars and parent lines were provided by plant breeders and the genebank of INRA, Clermont-Ferrand, France. Differential mildew isolates of the pathogen used were collected from different parts of Europe (Felsenstein *et al*, 1991). Mildew tests were performed on primary leaf segments kept on benzimidazole agar as described by Lutz *et al* (1992). Inoculum of the individual isolates was produced on leaf segments of the highly susceptible German wheat cultivar Nimbus (table I). By using a settling tower a homogenous spore deposition onto the plant material was guaranteed (inoculation densities ≈ 400–500 spores/cm^2). Ten d after inoculation (incubation conditions: 17 °C; continuous light, 10 μE m^{-2} s^{-1}) disease reactions were assessed on the base of colony number and size. Three main classes of host reactions were distinguished: r = resistant (0–20% infection in relation to Nimbus), i = intermediate (30–50% infection), s = susceptible (> 50% infection). In some cases, due to larger variation of disease reactions the creation of combined classes (r, i; i, s) was necessary. The results obtained are based on at least 3 experiments.

All cultivars that showed a response pattern indicative of the presence of the resistance gene *Pm8* were cytologically scored with respect to satellited chromosome number in root tip mitoses. As the nucleolus organizer regions of rye are suppressed in the wheat background it was expected that plants homozygous for the normal 1B and 6B wheat chromosomes would contain 4 major satellited chromosomes, whereas plants homozygous for the translocated chromosome pair 1BL/1RS would have only 2 (6B) satellited chromosomes (Zeller, 1973).

Table I. Reactions of 13 wheat cultivars/lines possessing known powdery mildew resistance genes or alleles after inoculation with 12 differential isolates of *E graminis tritici* (r = resistant, i = intermediate, s = susceptible reaction).

Cultivar/ line	*Major resistance gene(s)*	E graminis tritici *isolates*											
		2	*5*	*6*	*9*	*10*	*12*	*13*	*14*	*15*	*16*	*17*	*19*
Nimbus	–	s	s	s	s	s	s	s	s	s	s	s	s
Axminster/8CCa	*Pm1*	r	s	r	i,s	r	s	s	s	r	s	s	i,s
Ulka/8CC	*Pm2*	s	r	r	s	r	s	s	s	r	s	s	s
Asosan/8CC	*Pm3a*	r	s	r	r	r	s	r	r	s	s	i	r
Chul/8CC	*Pm3b*	r	s	s	r	r	r	r	r	s	r	i,s	r
Sonora/8CC	*Pm3c*	r	s	s	i	r	s	r	i,s	s	s	s	i
Khapli/8CC	*Pm4a*	s	r	s	r	i	r	s	s	i	s	i	r
Armada	*Pm4b*	s	r	s	r	r	r	s	s	r	s	s	r
Hope, Kormoran	*Pm5* (=Mli)	s	s	s	s	r	s	s	r	s	s	s	s
TP114/2 Starke b	*Pm6*	s	i	r,i	r	r,i	s	r,i	r,i	r,i	r,i	s	s
Disponent	*Pm8*	r	s	s	r	s	r	s	s	s	s	r	s
Normandie	*Pm9,2,1*	r	r	r	r	r	s	s	s	r	s	s	r
M Huntsman	*Pm2,6*	s	r	r	r	r	s	r,i	r	r	r,i	s	s
Kolibri	*Mlk*	s	s	s	r	s	r	s	r	r	s	r	r,i

[a] 8 times backcrossed to Chancellor; [b] twice backcrossed to Starke.

RESULTS

Twelve differential isolates of the pathogen (Lutz *et al,* 1992) were used which were able to distinguish between host lines/cultivars with known genes for resistance (table I). Table II shows the response patterns of 35 French wheat cultivars. In addition to a group of susceptible cultivars, 9 groups of mildew resistance could be recognized.

Table II. Reactions of 35 French wheat cultivars after inoculation with 12 differential isolates of *E graminis tritici* (*r* = resistant, *i* = intermediate, *s* = susceptible, / = segregating plants, – not tested).

Cultivar	*Postulated major resistance gene(s)*	E graminis tritici *isolates*												*Growth habit*
		2	*5*	*6*	*9*	*10*	*12*	*13*	*14*	*15*	*16*	*17*	*19*	
Beauchamp	None	s	s	s	s	s	s	s	s	s	s	s	s	W
Camp-Remy	"	s	s	s	s	s	s	s	s	s	s	s	s	W
Capitole	"	s	s	s	i,s	s	s	s	i,s	s	s	s	s	W
Champlein	"	s	s	i,s	i	s	s	s	s	s	s	i	i	A
Darius	"	s	i	s	s	i	s	i,s	i,s	s	s	s	i	S
Festin	"	s	s	s	s	s	s	s	s	s	s	s	s	S
Festival	"	s	s	s	s	i,s	s	i	s	s	s	s	i	A
Fidel	"	s	s	s	s	s	s	s	s	s	s	s	i	S
Frandoc	"	s	s	s	i,s	s	s	s	i,s	s	s	s	i,s	S
Goelent	"	s	s	s	s	s	s	s	s	s	s	s	s	S
Iena	"	s	s	s	s	s	s	s	s	s	s	s	s	A
Milpain	"	s	s	s	s	s	s	s	s	s	s	s	s	W
Moisson	"	s	s	s	i	s	s	s	s	s	s	i,s	–	W
Petrel	"	s	s	s	s	s	s	s	s	s	s	s	s	A
Prometin	"	i,s	s	s	s	s	s	s	s	s	s	s	s	W
Recital	"	s	s	s	s	s	s	s	s	s	s	s	s	W
Rescler	"	s	s	s	i,s	s	s	s	s	s	s	s	i,s	A
Scipion	"	s	s	s	s	s	s	s	s	s	s	s	s	A
Austerliz	*Pm2*	s	r	r	s	r	s	s	s	r	s	s	s	W
Berlioz	*Pm2*	s	r	r	s	r	s	s	s	r	s	s	s	W
Gerbier	*Pm4b*	s	r	s	r	r	r	s	s	r	s	s	r	A
Pernel	*Pm4b*	s	r	s	r	r	r	s	s	r	s	s	r	W
Roazon	*Pm4b*	s	r	s	r	r	r	s	s	r	s	s	–	W
Talent	*Pm5+?*	i	i,s	i,s	s	r	s	i,s	r	i	s	s	s	A
Tarasque	*Pm5*	s	s	s	s	r	s	s	r	s	s	s	s	S
Thesée	*Pm6*	s	i	r,i	r	r,i	s	r,i	r,i	r,i	r,i	s	–	A
Voyage*	*Pm8*	r	s	s	r	s	r	s	s	s	s	r	–	W
Champtal	*Pm2,6*	s	r	r	r,i	r	s	r,i	i	r	i	s	s	S
Friedland	*Pm2,6*	s	r	r	r	r	s	r	r	r	r	s	s	A
Nougat	*Pm2,6*	s	r	r	r	r	s	r	r	r	r	s	s	S
Damier*	*Pm2,8*	r	r	r	r	r	r	s	s	r	s	r	s	W
Divio	*Pm4b,5 Pm4b*	s	r	s	r	r	r	i,s	r/s	r	s	s	r	W
Abo	*Mlar*	r	s	s	s	s	s	s	s	s	s	s	i,s	W
Aristide	*Mlar*	r	s	s	s	s	s	s	s	s	s	s	i,s	W
Courtot	*Mlar*	r	s	s	s	s	s	s	s	s	s	s	s	S

* Only one pair of satellited chromosomes instead of 2 pairs in root tip mitosis cells; W = winter type, needing a long vernalization period; A = alternative type; S = spring type, needing no or a very short vernalization period.

Eighteen cultivars: Beauchamp, Camp-Remy, Capitole, Champlein, Darius, Festin, Festival, Fidel, Frandoc, Goelent, Iena, Milpain, Moisson, Petrel, Promentin, Recital, Rescler and Scipion were highly susceptible to most or all of the mildew isolates used in this study, indicating that none of the *Pm* genes of table I was present.

Two cultivars, Austerlitz and Berlioz were found to carry the resistance gene *Pm2*, as their reaction corresponded well with the pattern displayed by line Ulka/8*CC (table I). Three cultivars, Gerbier, Pernel and Roazon showed a response pattern indicative of the presence of gene *Pm4b*. Another group of 2 cultivars (Talent and Tarasque, table II) appeared to possess the same response pattern as Hope and Kormoran (table I) which are known to carry *Pm5* (Heun and Fischbeck, 1987a,b; Lutz *et al,* 1992). The response pattern of Thesée seemed to correspond with gene *Pm6* of line TP114/2* Starke (table I). The pattern of cultivar Voyage, identical to that of the differential Disponent, is indicative of the presence of resistance gene *Pm8* (table I). This was confirmed by the presence of only 2 satellited chromosomes instead of 4 in mitotic root tip cells of Voyage.

A group of 3 cultivars, Champtal, Friedland and Nougat appeared to possess gene *Pm2* combined with *Pm6*. The response pattern of cultivar Damier was characteristic for the presence of genes *Pm2* and *Pm8*. Cytological analysis of the root tip mitoses in Damier also showed 2 satellited chromosome. Reactions of cultivar Divio indicated the presence of both genes *Pm4b* and *Pm5*. However, there was a mixed reaction to isolate No 14 with some plants possessing only gene *Pm4b*.

The cultivars Abo, Aristide and Courtot exhibited reaction patterns characterized by resistance to isolate No 2 and differing from the patterns of known major resistance genes.

In addition to the identification of resistance genes in commercial cultivars the reaction patterns of 7 wheat strains present in their pedigrees were determined (table III). Accessions of the cultivars Etoile de Choisy, Vilmorin 27, strain 293, Hybrid 40 and US (60) 43 appeared to possess no known major resistance gene. The response pattern of the Finnish wheat cultivar Lontoï which was already described by Goujon (1965), corresponded well with the pattern of Ulka/8*CC, indicating the presence of gene *Pm2*. Strain VPM1 which was widely used in French wheat resistance breeding was characterized by a reaction pattern indicative of the presence of *Pm4b*.

DISCUSSION

The response patterns of distinct host lines after inoculation with a collection of differential isolates of the pathogen have been interpreted on the basis of Flor's classical gene-for-gene hypothesis (Flor, 1955). These reactions do not always give clearcut results. Different background effects and possible interaction of modifying genes may complicate interpretation. By using the method described above it is possible to detect qualitatively inherited gene effects when low disease reactions (< ≈ 30% infection) to at least 1 isolate were obtained. However, quantitative gene effects could not be ruled out in reactions showing

Table III. Reactions of 7 parent lines of cultivars after inoculation with 12 differential isolates of *E graminis tritici* (*r* = resistant, *i* = intermediate, *s* = susceptible, – not tested).

Parent line	*Postulated major resistance gene(s)*	E graminis tritici *isolates*												*Growth habit*
		2	*5*	*6*	*9*	*10*	*12*	*13*	*14*	*15*	*16*	*17*	*19*	
Etoile de Choisy	None	s	s	s	s	s	s	s	s	s	s	s	–	A
293	"	i	s	s	s	s	s	s	s	s	s	s	s	W
Hybride 40	"	s	s	s	s	s	s	s	s	s	s	s	s	A
US (60) 43	"	s	s	s	s	s	s	s	s	s	s	s	s	W
Vilmorin 27	"	s	s	s	s	s	s	s	s	s	s	s	–	W
Lontoï	*Pm2*	s	r	r	i,s	r	s	s	s	r	s	s	–	W
VPM 1	*Pm4b*	s	r	s	r	r	r	s	s	r	s	s	–	W

infection > 30%. Therefore available information on the response patterns of the corresponding parent lines, the pedigrees and descendent advanced breeding lines were used in addition to determine the resistance gene(s) in the cultivars tested.

In cultivars Capitole, Champlein, Darius, Festival, Fidel, Frandoc, Moisson, Promentin and Rescler intermediate reactions to certain isolates were observed. Thus there was no evidence for any known *Pm* resistance genes in these cultivars.

Table IV. Genealogies of French cultivars tested.

Cultivar	*Pedigree*
Abo	Etoile de Choisy / Yaktana // 8.2/2.3/3/81-12 / Bezostaja
	8.2 = Lobau / Etoile de Choisy // Cappelle /3/ Méxique 50 / B21
	2.3 = Line 90 / Etoile de Choisy
Aristide	Boulmiche / Sister line of Courtot
Austerliz	US (60)43 / Capest // Courtot /3/ Argent
Beauchamp	Capitole / Palmaress
Berlioz	Maris Ranger / Hardi // Capitole
Camp-Remy	362 / Atou // Hardi
Capitole	Cappelle // 80-3 / Etoile de Choisy
Champlein	Yga Blondeau / Tapesi Benoist
Champtal	Maris Huntsman / H76267 (line from C Benoist)
Courtot	Mexique 50/B21
Damier	Maris Huntsman/Clement
Darius	Capitole /3/ Heurtebise // 293-1-6(1) / Heurtebise
Divio	Ducat // VPM / Moisson
Festin	Chrismar / Cappelle // Fec 28
	Chrismar = US line // Champlein / Mont Ferrier (T durum)
	Fec 28 = Fortunato / Etoile de Choisy
Festival	11.804 / Talent
Fidel	Horizon / Frontana // Capitole /3/ Major
Frandoc	Chrismar / Capitole // USA 402
Friedland	Maris Huntsman // 146 // Champlein / Reso
Gerbier	VPM / Moisson // US (60)43 / Prieur
Goelent	Goya x Talent
Iena	Champlein / Courtot
Moisson	Cappelle // H 80-3 / Etoile de Choisy
Nougat	Maris Hunstman / 022 453 / R 3669 / Poggy
Pernel	V 81-12 // US (60)43 / Prieur /3/ VPM / Moisson
	V 81-12 = Etoile de Choisy s / YGA // 80-3 / Etoile de Choisy
	YGA = Vilmorin 27 / Red Five
Petrel	B49 / Hardi
Promentin	Promesse / Clement // Lutin
Recital	Mexican line 267 /4/ 81.12 / Heine VII // Nord / Tadorna /3/ 9369
Rescler	N 2-7 / Cappelle // D48 /3/ Mexique 50 / B21
	N 2-7 = 90-2 / Etoile de Choisy
	Mexique 50 = Mayo 54 // Norin 10 / Brevor
	B21 = 68-2 / YGA // 90-2 / Etoile de Choisy (old Versailles line)
Roazon	*Aegilops ventricosa* / *T persicum* // Marne*3 /3/ Moisson
Scipion	Champlein // Cappelle x Magdalena /3/ Moisson // Cappelle / Magdalena
	Magdalena = K8 / Szeckacz // Providence
Talent	Champlein /3/ Thatcher / Vilmorin 27 // Fortunato
Tarasque	Florence Aurore / Magdalena // Triticale 8-3 (CIMMYT)
Tenor	348 / 2361 // Capitole /3/ 10491
	348 = Thatcher / Vilmorin 27 // Petit Quiquin / Hybride 40
	2361 = Thatcher / Vilmorin 27 // Fortunato
	10491 = Sister line of Talent
Thesée	B1731 x Maris Huntsman
US(60)43	Complex cross with Chinese, Hope, Fultz, Purdue line
Voyage	RPB 72-85A / Armada
VPM 1	*Aegilops ventricosa* / *T persicum* // Marne *3
293	80 / Etoile de Choisy

Gene *Pm2* in cultivar Austerliz appears to have been derived from Argent (table IV), a British wheat strain expressing the same response pattern (unpublished results). However, it is not known which parent has donated *Pm2* to cultivar Berlioz.

Resistance gene *Pm4b* was identified in cultivars Gerbier, Pernel and Roazon (table II). All these cultivars have strain VPM1 in their pedigree (table IV). VPM1 was first described by Maia (1967) and is a selection of a cross involving *Triticum carthlicum* = *T persicum* (table IV). It is very likely that *T carthlicum* accessions possess a single gene (*Mle*, Wolfe, 1963; later designated *Pm4b* by The *et al,* 1979) and that this gene has been introduced into VPM1 (table III; Doussinault, McIntosh, personal communication).

Cultivars Talent and Tarasque possess gene *Pm5*. The origin of this resistance gene could not be deduced, neither from their pedigrees (table IV) nor from additional data of some progenitors. However, cultivars Champlein, Hybrid 40 and Vilmorin 27 can be excluded as possible donors due to susceptible reactions (tables II, III) as well as Thatcher (Heun and Friebe, 1990). Moreover, Talent appears to possess some additional resistance indicated by intermediate reactions to isolates Nos 2 and 15, and, in part, to isolates Nos 5, 6 and 13.

Two cultivars, Voyage and Damier, are characterized by the presence of resistance gene Pm8, located on the short arm of rye chromosome 1R. Whether this chromosome segment arose from a 1B/1R wheat-rye translocation or a whole chromosome (1B)1R substitution requires further cytological analysis. According to the pedigree of Voyage, *Pm8* must come from line RPB 72–85a (table IV) since Armada (table I) carries only gene *Pm4b*. It appears that Damier inherited *Pm2* from Maris Huntsman and *Pm8* from Clement, possessing the 1B/1R translocation or substitution.

It is evident that cultivars Champtal, Friedland and Nougat possess the gene combination *Pm2* and *Pm6*. This combination can be traced to Maris Hunstman (table I) which is in the pedigree of all 3 cultivars (table IV). However, Thesée which also originated from a cross with Maris Huntsman carries only *Pm6* as revealed by intermediate reactions to corresponding isolates.

Cultivar Divio, which carries 2 resistance genes, *Pm4b* and *Pm5*, may have inherited *Pm4b* from strain VPM1 (table III). The source of *Pm5* most probably is cultivar Ducat (table IV), since Moisson does not appear to possess any known major resistance gene (table II).

It is remarkable that the resistance in cultivars Abo, Aristide and Courtot could be detected only by means of isolate No 2. All other isolates showed susceptible reactions (table II). The resistance is tentatively designated *Mlar* (Aristide). Although there is a pedigree relationship between Aristide and Courtot (table IV), the origin of *Mlar* is unknown.

Up to the present, at least 6 major genes have been used in French wheat breeding for mildew resistance. These are mainly genes also used in resistance breeding in Czechoslovakia (Lutz *et al,* 1992) in Germany (Heun and Fischbeck, 1987a,b; Schneider *et al,* 1991), in Scandinavian countries (Hovmøller, 1989) and in Switzerland (Winzeler *et al,* 1991).

There is little genetic diversity of wheat mildew resistance in Europe. In addition, the genes used so far provide little protection against the contemporary pathogen populations (Limpert *et al,* 1987; Felsenstein *et al,* 1991). Therefore novel sources of resistance are urgently needed. They can be found in common wheat itself, in cultivated and wild *Triticum* relatives, such as emmer wheat, Einkorn, *Aegilops* and rye. Moreover, it is necessary to consider improved strategies to make better use of the valuable resources.

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