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Evolution of resistance against powdery mildew in winter wheat populations conducted under dynamic management. II. Adult plant resistance

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Abstract The evolution of adult plant resistance towards powdery mildew (caused *by Blumeria graminis* f. sp. *tritici*) was investigated in 11 wheat populations cultivated for 10 years in a French network for dynamic management (DM) of wheat genetic resources. The aims of the study were to compare the evolution of resistance in sites submitted to different powdery mildew pressure and to investigate the implication of specific resistance gene action in adult plant resistance. For this, 7 of the 11 populations were characterized for their composition of specific resistance genes (results presented in a former paper). Even though no population differed significantly from the initial PA0 pool for mean adult plant resistance, divergence appeared among the final populations. The populations with the highest adult plant resistance level originated from sites where powdery mildew pressure is known to be high (Vervins, Le Rheu), whereas populations with the lowest adult plant resistance corresponded to areas with no, or very low, powdery mildew pressure (Toulouse, Montreuil-Bellay). A residual effect of defeated specific resistance genes was hypothesized, as lines accumulating at least two specific resistance genes appeared more resistant. Additional quantitative resistance seemed to be involved in adult plant resistance. DM lines appeared then as an interesting source of variability for resistance towards powdery mildew. Moreover, as these lines had been grown in mixed populations they may be appropriate as components of a composite cultivar.

Keywords Composite populations · *Triticum aestivum* · *Blumeria* (*Erysiphe*) *graminis* f. sp. *tritici* · Residual resistance effects · Quantitative resistance

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Introduction

An experiment on dynamic management (DM) of the genetic resources of bread wheat (*Triticum aestivum* L.) was initiated in France in 1984 (Henry et al. 1991). Three segregating populations (refered to as pools), derived from the crossing of varieties and lines of various origins (two predominantly selfing pools and one outcrossing due to a male sterility gene) constituted the initial gene pools. Samples of these gene pools were distributed throughout a French network and were cultivated without human selection or deliberate migration (seed or pollen exchange) between the populations. After 10 years of cultivation, short plants were selected from the different populations of the network and inbred lines were derived from those plants. The aim was to characterize the evolution of the populations and to investigate the variability present in a sample of short lines that would be the most apropriate for possible use in breeding programs.

Studying the evolution of pathogen resistance in DM is a way to test the ability of DM populations to respond to biotic pressures, and to investigate the kind of mechanisms maintained or naturally selected in those populations. Powdery mildew of wheat [caused by *Blumeria graminis* (DC.) Golovin ex Speer (syn. *Erysiphe graminis* DC.*)* f. sp. *tritici* Em. Marchal)] is of economic importance in regions with high rainfall and with a maritime or

semi-continental climate (Bennett 1984). In France, high inoculum pressure is observed in the North of the country, whereas this pressure is very low in the South. Powdery mildew resistance was studied in the sample of short lines derived from one of the selfing pools, called PA. In a separate paper (Paillard et al. 2000), we have shown that the changes in the frequency of some specific resistance genes were certainly due to selection in some populations, although all the considered genes were defeated (see Nass et al. 1981). The efficiency of DM to maintain the diversity of powdery mildew specific resistance genes was demonstrated, which corroborated previous observations made by Le Boulc'h et al. (1994) on earlier generations and on the three different pools.

In this paper, we focus on adult plant resistance, its evolution in the different populations and the links that can be established between adult plant resistance and specific resistance expressed from the seedling stage. A residual effect of defeated specific resistance genes was already postulated by several authors (Martin and Ellingboe 1976; Nass et al. 1981; Royer et al. 1984: Negassa 1987; Chantret et al. 1999; Keller et al. 1999) and we address the question of whether this mechanism may explain a part of the adult plant resistance in the DM populations and contribute to the maintenance of defeated genes in some of the populations. The interest of DM material as a potential source of diversity for resistance to powdery mildew, and its possible use in breeding, is discussed. Particularly, as DM populations are heterogeneous, some of the variability selected may be of interest for the breeding of composite cultivars.

Materials and methods

Plant material

Single-seed descent lines derived from the initial PA0 pool (Thomas et al. 1991) and samples of short inbred lines derived from 11 populations of the network were studied for adult plant resistance. The 11 populations had been cultivated for 10 years (8 in the case of Rennes) in six locations of the network (for further information and a map of the network see Paillard et al. 2000): Toulouse (TOE and TOI) and Montreuil-Bellay (MBE and MBI), where powdery mildew pressure is low, Le Moulon (LME and LMI) and Châlons-sur-Marne (CHA), with intermediate powdery mildew pressure, and Rennes (LRE and LRI) and Vervins (VVE and VVI), which are subject to high powdery mildew pressure. "I" corresponds to the modern intensive agricultural method used in the neighbourhood of the site and "E" to a practice with no foliar fungicide treatment and a low nitrogen fertilizer supply (1/3 of the "I" method). In Châlons-sur-Marne only one population was available, for which "I" or "E" status was not taken into account because of changes in its management during the first 10 years. Among the 11 DM populations, seven have been characterized for powdery mildew specific resistance genes (Paillard et al. 2000): the populations originating from Châlons-sur-Marne, Rennes, Toulouse and Vervins.

Experimental design

Adult plant resistance was evaluated in 2 consecutive years in Rennes (1996, 1997) and 1 year in Le Moulon (1997). These three experiments will be further referred to as Ren96, Ren97 and Mou97. In Rennes, the experimental design consisted of hillplots with no replication. About 30 seeds of the same inbred line were sown in each plot. In Le Moulon, a complete randomized block design with two replications was applied. In each replication, a genotype was represented by a 1.5 m-long row plot of 30 plants. The number of lines of the populations scored in the different experiments are presented in Table 1. A 1–9 scale was used for the notation of the powdery mildew severity of each plot, with 1 for no visible symptoms and 9 for a high density of sporulating pustules up to the last leaf.

In the three experiments, the virulence composition of pathogen populations was investigated using a set of differential host seedlings according to the method described by Le Boulc'h et al. (1994). Ten-day old disease-free seedlings with known resistance profiles were left for 1 day in the plots and were scored for powdery mildew development after a 10-day incubation period in glasshouse.

Table 1 Number[a] of wheat lines from the initial PA0 population and DM populations scored for adult plant resistance to natural powdery mildew populations

Population	Rennes 96	Rennes 97 Le Moulon 97
PA0	20	69
CHA	20	17
LME	14	11
LMI	12	10
LRE	19	15
LRI	17	12
MBE	12	10
MBI	22	20
TOE	27	23
TOI	18	14
VVE	15	10
VVI	21	18
Total	217	229

[a] For PA0, all the lines observed in 1996 were included in the 1997 experiments. For the DM populations, all the lines observed in 1997 were included in the 1996 experiment

Statistical analysis

Evolution of adult plant resistance

A global analysis of variance (ANOVA) was performed on all the populations in the three experiments, followed by separated ANOVAs for each experiment (Ren96, Ren97 and Mou97). To test the site and farming-methods effects and their interaction, populations CHA and PA0 were not taken into account. In the ANOVAs including CHA and PA0, a population effect was tested, corresponding to the combinations of site and farming-method for the sites where the two farming-methods were available. The population effect for adult plant resistance was tested with different models depending on the experimental design. In all cases the genotype within-population effect was declared as a random effect and an adequate test for the between-population comparisons was performed. For each pair of populations, mean adult plant resistance was compared using a corrected *t*-test.

Relationship between adult plant resistance and specific resistance

For each of the three experiments and for the seven populations already characterized for powdery mildew specific resistance genes, the effect of specific resistance genes on adult plant resistance was tested in a multivariate regression. The specific resistance genes *Pm2*, *Pm4b*, *Pm6*, *Pm8*, *Pmx* and *Mlar* were declared as the re-

Table 2 *F* values and significance for ANOVA carried out on three experiments comparing DM wheat populations for adult plant resistance towards powdery mildew

Experiment	Population[a] effect		Site effect	Farming-method effect	Site×farming-method interaction
	With CHA[b]	Without CHA			
Mou97	2.1*	2.22*	2.42*	4.33*	1.25
Ren96	3.58***	4.14***	5.05***	0.85	2.24
Ren97	2.6**	1.83(*)	2.16(*)	1.91	1.03

(*) $P<0.1$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$
[a] Corresponds to the different combinations of sites and farming methods
[b] CHA=population of Châlons-sur-Marne for which I or E status is not defined

Table 3 Comparison of mean adult plant resistance towards powdery mildew between the DM wheat populations, including the initial PA0 population

Rennes 96			**Rennes 97**			**Le Moulon 97**		
Population	LSMean	*t*-test grouping[a]	Population	LSMean	*t*-test grouping	Population	LSMean	*t*-test grouping
VVI	2.48	A	CHA	3.24	A	VVI	2.83	A
TOE	3.67	B	VVI	3.67	AB	LME	2.95	AB
LRE	3.74	B	LRE	3.73	ABC	LRE	3.13	ABC
VVE	3.75	B	LME	3.82	ABC	VVE	3.15	ABC
PA0	**3.80**	**B**	**PA0**	**4.05**	**ABCD**	CHA	3.16	ABC
LRI	3.82	B	VVE	4.10	ABCD	**PA0**	**3.40**	**ABCD**
CHA	4.00	B	LRI	4.50	BCD	TOE	3.42	ABCD
TOI	4.06	B	TOE	4.64	CD	MBE	3.59	ABCD
LMI	4.25	B	MBE	4.78	BCD	LMI	3.66	BCD
LME	4.29	B	TOI	4.79	CD	MBI	3.77	CD
MBI	4.36	B	LMI	4.90	BCD	LRI	3.84	CD
MBE	4.42	B	MBI	4.95	D	TOI	3.99	D
DM[b]	3.84		DM	4.27		DM	3.40	
PA0	3.80	NS[c]	PA0	4.05	NS	PA0	3.40	NS

[a] Populations with different letters differed at the 5% level (corrected *t* test)
[b] Mean of the 11 DM populations for adult plant resistance
[c] Non-significant contrast of mean DM populations and PA0

gressor variables with two possible values at each locus: 0 for a susceptible allele and 1 for a resistant allele. The STEPWISE option of the SAS regression procedure was used so that only regressors that explained a reasonable proportion of the variance ($P<0.15$) were entered step by step in the model.

A complementary ANOVA was performed to test the effect of cumulative specific genes on adult plant resistance. Three levels were considered: 0 for the lines with no detected gene, 1 for the lines with one postulated gene, and 2 for the lines with at least two genes. The least square means of adult plant resistance of these three groups of lines were compared with a corrected *t* test.

All statistical analyses were performed using SAS software (1988).

Results

Evolution of adult plant resistance

The global analysis of variance revealed strong interaction effects between experiment and population, and between year and population ($P<0.01$, data not shown). It was then decided to perform all the analyses for each experiment separately. The ANOVA carried out on all the populations showed a significant population effect in the three experiments. The strongest effect was revealed in the Ren96 experiment (Table 2). As the I or E status of CHA was unknown, the ANOVA with farming-method and site effects was carried out on a subset of data excluding this population. A site effect was detected in the three experiments and a farming-method effect was detected only in the Mou97 experiment. Unlike the specific resistance gene frequencies (Paillard et al. 2000), these two effects were not associated with a significant interaction between site and farming-method effects.

The contrast between the mean adult plant resistance of PA0 and the mean DM population was not significant in any of the three experiments, indicating no gain but also no loss in the global level of adult plant resistance (Table 3). The corrected student test revealed that none of the populations differed significantly from PA0 for adult plant resistance, except for VVI, which was more resistant than PA0 in the Ren96 experiment (Table 3) and was always among the most resistant populations in all three experiments. Some of the 11 DM populations significantly differed from one another in each of the three experiments, indicating a differentiation for adult plant resistance among populations within the DM populations after 10 years of cultivation. LRE, which was always among the three most-resistant populations, appeared significantly more resistant than the most-susceptible populations in two experimentations (MBI in Ren97 and

Table 4 Results for multivariate stepwise regression, testing the effect of specific resistance genes on adult plant resistance. The threshold level for the introduction of a variable was set to $P<0.15$. No gene effect was found significant for the Mou97 experiment

Experiment	Gene	Partial R^2	Model R^2	*F*	Prob>*F*
Ren96	*Mlar*	0.15	0.15	12.89	0.0006
	Pm4b	0.09	0.24	8.28	0.0053
	Pmx	0.04	0.28	4.21	0.0438
Ren97	*Pm2*	0.0732	0.0732	4.97	0.0293

Table 5 Effect of specific resistance gene accumulation on adult plant resistance. Classes with different letters present significantly different mean adult plant resistance (corrected *t* test, $P<0.067=0.05/3$)

Experiment	*F* value for global test	Least-square mean resistance of lines with		
		0 gene	1 gene	2 genes or more
Mou97	5.05**	3.55 **A**	3.54 **A**	2.72 **B**
Ren96	9.05***	4.13 **A**	3.64 **A**	2.73 **B**
Ren97	3.26*	4.43 **A**	4.27 **A**	3.41 **B**

* Significant at the 5% level, ** sign. at the 1% level, *** sign. at the 0.1% level

TOI in Mou97). TOI and MBI were among the most-susceptible populations in the three experiments. Except for VVE and VVI in the Ren96 experiment, two populations of the same site were never found significantly different for mean adult plant resistance, which is consistent with a significant site effect and no farming-method effect nor interaction (Table 2).

Relationship between adult plant resistance and specific resistance

The specific resistance genes that were identified in the populations (*Pm4b*, *Mlar*, *Pm2* and *Pm6*) have now been overcome, while *Pm4b*, *Mlar* and *Pm2* had already been overcome at the start of the DM program (Doussinault, personnal communication). Moreover, local analysis of the virulence frequencies of the pathogen populations carried out at Rennes in 1996 and 1997 and at Le Moulon in 1997 within the experimental plots showed that the virulences corresponding to all these genes were highly frequent (higher than 50%, data not shown). *Pmx*, the resistance factor recently identified in one of the parents of the PA pool, appeared defeated at the time of the experiments (1996, 1997), but the corresponding virulence frequency could not be estimated. Investigating a possible residual effect of these genes on adult plant resistance, we found that regressions of adult plant resistance on variables indicating the presence of specific genes showed a significant effect of some genes for Ren96 and Ren97, but not for Mou97. The genes involved in each of the Rennes experiments were not the same in 1996 and 1997 (Table 4).

In all three experiments, we found that the lines that had accumulated at least two specific resistance genes, whatever the genes involved, were on average significantly more resistant than the ones with only one gene or with no postulated gene (Table 5).

Discussion

Significant differentiation between populations was found for adult plant resistance. Such a structure has already been observed for specific resistance genes (Paillard et al. 2000) and revealed divergent evolution for specific resistance gene frequencies, even for populations originating from the same site. In the case of adult plant resistance the site effect appeared stronger and no interaction was observed between site and farming-method effects. This means that, even though specific resistance gene frequencies were different in the two populations of a site, these two populations did not diverge strongly for mean adult plant resistance. The best illustration of this is given by the two populations of Vervins: our results on specific resistance genes revealed a strong divergence between VVI and VVE ($Fst=0.41$), whereas this divergence was not observed for adult plant resistance (Table 3). This suggests that specific resistance is not the only mechanism involved in adult plant resistance in the DM populations. An interesting point is that VVI and LRE, which appear among the most-resistant populations in all three experiments, originate from areas where powdery mildew pressure is high. Conversely, Toulouse, located in the South of France, and Montreuil-Bellay, in a wine-producing area, have low powdery mildew pressure. Indeed TOI and MBI were always among the most susceptible populations in all three experiments.

Our results showed that, even if defeated, specific resistance genes seemed to have a positive effect on adult plant resistance. A so-called residual effect of defeated major genes was recently postulated for *Pm5* (Keller et al. 1999) and *MlRE* (Chantret et al. 1999). Nass et al. (1981) found residual effects for *Pm3c* and *Pm4b* but did not find any residual effect for *Pm2* and *Pm5*. Other authors (Martin and Ellingboe 1976; Royer et al. 1984; Negassa 1987) also gave evidence that *Pm* genes which had been overcome by virulent isolates still contributed to partial resistance. This effect of defeated specific resistance genes could be attributed to a residual expression of the gene itself (Nelson 1978), but the hypothesis of strong linkage with quantitative resistance genes can not be excluded. Several studies showed that specific resistance genes were grouped in clusters (for a review see Michelmore and Meyers 1998). This was also shown for resistance towards different diseases (Witsenboer et al. 1995). It was therefore hypothesized that some specific and quantitative resistance genes may be grouped in

clusters (Leonards-Schippers et al. 1994). In our study, in the Ren96 experiment, *Pm4b*, *Mlar* and *Pmx*, the three most-frequent genes in DM populations, proved to have a significant effect on adult plant resistance (Table 4). In the same experiment, the lines with only one resistance gene did not appear significantly more resistant than lines with no postulated gene, whereas the lines harbouring two or more genes were found significantly more resistant on average than the lines with a 0 or 1 postulated resistance gene (Table 5). Note that this phenomenon can be described as complementary epistasis. Moreover, VVI and LRE appeared among the most-resistant populations in all three experiments and were the populations with the highest proportions of multi-resistant lines (52.4% of lines for VVI, and 41.2% for LRE, compared with all the other populations containing from 0 to 26.7% multi-resistant lines). Three hypotheses, not mutually exclusive, can be formulated to explain this advantage conferred by harbouring several defeated resistance genes. Firstly if we suppose that residual effects are additive, the effect of one gene might not be detectable in our experiments because of a too-small sample size. Secondly, possessing several defeated resistance genes could be an advantage if the frequency of races of the pathogen harbouring the corresponding virulence alleles was low enough so that the multi-resistant lines appeared more tolerant. Unfortunately, information concerning the composition of pathogen populations was not precise enough concerning complex races because of a lack of appropriate differential hosts. A third hypothesis is that pathogen races harbouring the virulences overcoming the studied specific resistance genes might be less aggressive because the loss of several avirulence alleles reduced their selective value (i.e. they were less competitive on non-resistant hosts).

These results about the possible residual effect of defeated resistance genes and the interest of harbouring these genes do not preclude that another quantitative variability for resistance to powdery mildew has also been selected. Selection for independent quantitative resistance could explain that VVE presented an adult plant resistance very similar to PA0 (Table 3), corresponding to an intermediate level of resistance, whereas it was the population with the lowest frequency of specific resistance genes: half of the lines of this population were found susceptible (no specific resistance gene detected) and very few lines exhibited any gene combinations (Paillard et al. 2000). The good level of resistance found in VVE could also be due to the presence of a specific resistance gene that our isolate collection was not able to detect.

Since specific genes were defeated, the selection of more quantitative resistance was possible in all populations. This is of interest, because specific resistance genes towards powdery mildew are known to be quickly overcome due to the rapid evolution of the pathogen (Bennet 1984; Felsenstein et al. 1987). Pyramiding several non-defeated *Pm* genes in one cultivar did not even provide durable resistance (Brown et al. 1997). McIntosh (1998) proposed that breeding strategies aimed at the avoidance of highly susceptible genotypes may be as effective as one aimed at complete resistance based on genes conferring non-durable resistance. As defeated genes might confer residual resistance, harbouring several defeated genes and at the same time alleles at other loci that are involved in quantitative resistance could be an efficient strategy for building durable resistance. The development of appropriate markers linked to specific resistance genes and resistance QTLs would greatly enhance the feasibility of such a strategy. Even though we could not estimate the respective parts of these two mechanisms (qualitative and quantitative resistance) in the DM populations, we know that the conditions were favourable to allow for the selection of quantitative resistance. Because we showed that for certain lines the combination of different defeated specific genes enhanced adult plant resistance, the interplay between selection on specific and non-specific resistance mechanisms appeared complex.

The present study was carried out on a sample of DM lines that are suitable for use in breeding programs because of their short height. These inbred lines could represent an interesting source of variability for quantitative resistance to powdery mildew. Moreover as DM populations are mixtures of genotypes, these lines could be of interest in the development of composite cultivars. They might be used as mixture components since they may combine ability for association with a good tolerance towards powdery mildew and possibly other diseases. McDonald et al. (1988) studied the ability of two-, three- and four-component barley mixtures to control scald disease caused by the fungus *Rynchosporium secalis* (Oud) Davis. The mixtures were composed of parents of the experimental population of barley Composite Cross II (CCII) grown at Davis, and of lines derived from the 45th generation of CCII. They showed that lines from the 45th generation of CCII interacted to reduce the incidence of scald more often than parental lines. These results led us to think that the variability for powdery mildew resistance available in the wheat DM populations could be a source of interesting material for creating cultivar mixtures since there is generally an interest in populations evolving under natural conditions as sources of lines for mixtures.

The interest of cultivar mixtures for decreasing the impact of different fungal diseases has been demonstrated in different studies on wheat (Mahmood et al. 1991; Manthey and Fehrmann 1993; Gacek et al. 1997), barley (Kolster et al. 1989; Newton and Thomas 1992), and other crops. The major problem is to find components that would also provide a sufficient and stable yield: this could be obtained only with lines presenting a good ability for association. Because today's cultivars had never been selected for this trait, they might not be the most appropriate to become components of mixtures. The interest of DM lines as mixture components should be further investigated, even if they may not be of a direct interest for pure-stand cultivation. The inbred lines of this

study are now being evaluated for other agronomic traits (yield, earliness, resistance to other diseases, quality). The next step will be to compare the behaviour of some of these characterized lines in different mixtures and in pure-stand conditions.

Because of too-small sample sizes, the mechanisms implied in adult plant resistance could not be precisely characterized in our experiment. It would then be of a great interest to carry out a similar study on a smaller number of appropriate populations but with larger sample sizes per population.

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