Adaptation of *Phytophthora infestans* to Partial Resistance in Potato: Evidence from French and Moroccan Populations

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ABSTRACT

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The use of partially resistant cultivars should become an essential component of a sustainable management strategy of potato late blight, caused by *Phytophthora infestans*. It is therefore important to determine to what extent *P. infestans* populations can be selected for increased aggressiveness by potato cultivars with different levels of partial resistance. To this end, we sampled *P. infestans* populations from France and Morocco, chosen as locations where late blight occurs regularly but which differ in the distribution of potato cultivars. Cross-inoculation experiments were used to determine the aggressiveness of all populations to potato cvs. Bintje (prevalent in France but not grown in Morocco) and Désirée

(popular in Morocco but cultivated to a very small extent in France). French populations were more aggressive on cv. Bintje than on cv. Désirée, irrespective of the site they were sampled from. Their aggressiveness increased between early and late samplings, suggesting that both cultivars selected for increased aggressiveness during epidemics. By contrast, Moroccan populations were more aggressive on Désirée, regarded as partially resistant in Europe, than on Bintje, highly susceptible under European conditions. These data indicate that *P. infestans* populations adapt to locally dominant cultivars, irrespective of their resistance levels, and can therefore overcome polygenic, partial resistance. This adaptive pattern may render partial resistance nondurable if not properly managed.

Additional keywords: durability, pathogenicity, resistance erosion, *Solanum tuberosum*.

Late blight, caused by *Phytophthora infestans* (Mont.) de Bary, is the most destructive disease of potato (*Solanum tuberosum* L.) worldwide. It recently re-emerged as an important disease in many countries (11), increasing the need for effective and durable control strategies. While late blight control currently relies heavily on pesticide applications, both in developed and developing countries, the sustainability of this approach is highly questionable, both because isolates resistant to systemic fungicides appear rapidly wherever these products are used (16), and because sustainable, organic and subsistence agriculture require low or no synthetic inputs and have to rely on renewable means of control.

Genetic resistance to late blight is available in a wide range of genetic resources (20,35,36,41), but has shown limitations for effective or durable control of late blight. *P. infestans* is a highly variable pathogen, especially for virulence, making race-specific resistance genes almost useless for durable disease control in the field (31,41). Polygenic partial resistance may contribute to disease control, but breeding cultivars with sufficient resistance is difficult and cumbersome. Furthermore, the durability of partial resistance, often postulated from its polygenic inheritance, remains to be ascertained. Several reports provided evidence for isolate specificity in the response of several partially resistant cultivars in controlled inoculation experiments (5,6,8,9,22). These

suggest that adaptation for aggressiveness (i.e., quantitative components of pathogenicity) (2,37) can take place in *P. infestans* populations and result in the progressive erosion of partial resistance. However, since part of this isolate specificity might be due to environment heterogeneity (26), and since other workers did not observe isolate specificity or preferential adaptation (21), the question of the extent and conditions in which adaptation to partial resistance can occur remains open.

From an evolutionary standpoint, answering this question equates to investigating whether *P. infestans* populations show general adaptation (i.e., adapt to the prevailing resource), local adaptation to individual niches (in this case, different cultivars), or local maladaptation (i.e., higher pathogenicity on cultivars not present locally). This key issue in host-parasite coevolution has been much debated recently in several pathosystems (15,24,25). Theoretical models show that general adaptation and local adaptation or maladaptation can occur, depending on the extent of relative gene flow (migration) in the host and pathogen, mutation rates, recombination, population size, and generation time (1,12-14). Unfortunately, these parameters are poorly quantified in many host-parasite systems, and their relative importance is likely to differ from site to site; for instance, in *P. infestans*, the amount of recombination is probably very different in populations dominated by one of the two mating types than in populations where both mating types are present at almost equal frequencies. Experimental evidence is thus needed to validate theoretical expectations in populations with different life histories. Recent work on French *P. infestans* populations sampled from cultivars with various types and levels of resistance showed that the susceptible

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cv. Bintje hosted a more aggressive population than the partially resistant cv. Désirée, without differential adaptation to these two cultivars for aggressiveness (30). Because cv. Désirée is rarely grown in France and cv. Bintje is one of the prevailing cultivars there, this finding could reveal general adaptation rather than an effect of cultivar resistance levels.

The present study is based on aggressiveness measurements on the same two potato cultivars (Bintje and Désirée) of *P. infestans* populations collected in France and in Morocco, chosen to represent contrasting situations in terms of cultivar distributions (and hence of selection pressures). In both countries, late blight is a major constraint for potato cropping (7,33). Potato acreage in Morocco ranges from 50,000 to 60,000 ha annually; potatoes are grown in coastal areas during the autumn and winter for export, and inland during the spring and autumn for local fresh market consumption (19). Late blight severity fluctuates from year to year depending on climatic conditions, but also depends on host susceptibility and pathogen genetic diversity. In the coastal areas, the main cultivar is Nicola, while inland production areas are grown primarily to cv. Désirée and to a lesser extent cv. Spunta. The first population surveys of *P. infestans* in Morocco have only recently been performed. A national survey in 1996 to 1998 revealed the occurrence of a limited number of genotypes, although the presence of both mating types was ascertained (33). A more focused investigation over 2 years (1999–2000 and 2000–2001) in two areas of potato cropping, the northern plain around Larache and the Middle Atlas area around Meknès, showed a clear regional structure. Populations from Larache consisted mainly of isolates belonging to the A1 mating type and to complex pathotypes (5.5 virulence factors per isolate on average), whereas populations from Meknès predominantly included A2 isolates belonging to simple pathotypes (2.85 virulence factors per isolate) (17). In France, potato is grown mainly in the northern half of the country, where late blight is often a problem, as shown by the 12 to 18 annual sprays applied to commercial crops to combat the disease (32). The surveys done in the 1990s and early 2000s indicate that the French *P. infestans* populations almost exclusively consist of A1 isolates belonging to rather complex races (3,4,28,30).

The aims of the present study were thus to determine whether populations of *P. infestans* were more aggressive (i) in locations with long-term cultivation of partially resistant potato cultivars than in locations with long-term cultivation of susceptible cultivars, and (ii) at the end than at the start of epidemics.

MATERIALS AND METHODS

Isolate collection and isolation. In France, isolates were collected in the spring of 1999 from cvs. Bintje and Désirée grown at two locations in Brittany (Le Rheu, 48°01'N, 1°43'W; Ploudaniel, 48°30'N, 4°19'W). At both locations and for both cultivars, two series of isolates were collected: the first sampling was 1 week after the first symptoms were observed in the field, and the second sampling was 2 to 3 weeks later. In Morocco, infected leaf samples were collected from potato crops in farmers' fields in the autumns of 1999 and 2000 in the area of Meknès (33°54'N, 05°33'W), and in the winters of 1999–2000 and 2000–2001 around Larache (35°11'N, 06°09'W). In each site, the collection area included several fields in a 15 to 20 km radius. Infected material was taken from one to five plants per field and brought back to the laboratory for isolation. Unlike in France, the identity of cultivars from which the samples were taken could not be systematically ascertained; however, the foliage and tuber characteristics of the crops sampled leave little doubt that almost all isolates from Meknès came from cv. Désirée, while most isolates from Larache came from cv. Nicola.

In both countries, single lesion isolates were established as described by Lebreton and Andrivon (27). Briefly, small portions

(0.25 to 1 cm²) of diseased tissue were excised from the margin of active lesions, deposited on slices of susceptible potato tubers, and incubated in a humid chamber for 8 to 10 days. Mycelium growing on the surface of the tuber slices was then aseptically transferred to pea agar containing nystatin (80 mg liter⁻¹) and ampicillin (160 mg liter⁻¹). Cultures were subsequently maintained on pea agar at 15 to 18°C. Overall, 63 Moroccan isolates from 29 different fields (11 isolates from eight fields in Meknès, 1999; 12 isolates from five fields in Larache, 1999; 21 isolates from nine fields in Meknès, 2000; and 19 isolates from seven fields in Larache, 2000), and 57 French isolates (18 from Bintje in Le Rheu, 9 from Désirée in Le Rheu, 16 from Bintje in Ploudaniel, and 14 from Désirée in Ploudaniel) were used in the experiments.

Aggressiveness tests. Tests were performed on leaves of cvs. Bintje and Désirée, detached from plants grown in the glasshouse for 6 to 8 weeks. Désirée is a red-skin cultivar, which has been popular in Mediterranean regions for at least a decade, but is not widely grown (except for seed production destined to export) in Western Europe where it displays a moderate level of partial resistance to late blight in the field (European Cultivated Potato Database, provided online by the Scottish Agricultural Science Agency). Bintje is a yellow-skin cultivar, widely grown in continental Western Europe where it is highly susceptible to late blight (European Cultivated Potato Database), but is not grown to any extent in Morocco. Nicola, from which the blight samples from Larache presumably originated, is a yellow-skin, early cultivar rated as moderately susceptible in Europe (European Cultivated Potato Database).

The inoculation protocol was described previously (29). Leaves were detached from the plants (fifth to seventh node from the base) just prior to inoculation. They were placed abaxial face up on moist filter paper in large clear plastic boxes, with a wet cotton bud on the petiole to maintain sufficient turgidity in the leaf tissue throughout the experiments.

Sporangial suspensions of the isolates were prepared by gently scraping the surface of 2-week-old cultures on pea agar after flooding with 5 ml of sterile water. The concentration of the suspensions was adjusted to 5×10^4 sporangia ml⁻¹ with a hemacytometer. For each isolate, a 20- μ l drop of spore suspension was deposited on each of the five leaflets of two complete leaves per cultivar. Inoculated leaves were incubated for 7 days in a climate chamber under a 16-h dark/8-h light photoperiod with respective temperatures of 15 and 18°C. Disease severity was recorded on each inoculated leaflet 7 days after inoculation through the measurement of lesion diameters on two orthogonal directions (L_1 for width and L_2 for length). Spore production (SP) on each leaflet was assessed by collecting the spores in 5 ml of sterile water and measuring the concentration of the resulting suspension with a hemacytometer.

For practical reasons, tests were performed as a series of batches, each including 10 to 15 isolates from the same origin. Isolates from Ploudaniel were tested in the summer of 2000, while isolates from Le Rheu and Morocco were tested in the summer of 2001. All tests were performed in the same facilities.

Data collection and analysis. Two aggressiveness components were assessed 7 days after inoculation. Lesion size was calculated as $LS = (\pi \times L_1 \times L_2)/4$, i.e., assuming the lesion was elliptic, and SP was assessed as the total number of spores produced per leaflet. Although statistically significant due to the large number of observations in the data set, the linear correlation between both variables proved weak ($r^2 = 0.207$), suggesting that LS and SP are largely independent components of aggressiveness.

Since our experimental design was not intended to directly compare the aggressiveness of French and Moroccan isolates, data were analyzed separately for France and Morocco, and site effects were included within countries. Data for each aggressiveness variable (LS and SP) were submitted to analyses of variance

(ANOVA) using the general linear models (GLM) procedure of the SAS statistical software, version 8.1 (SAS Institute, Cary, NC). Shapiro-Wilk and Kolmogorov-Smirnov tests showed that data sets had nonnormal distributions due to longer tails than expected for a strictly normal distribution. Transforming the data reduced the deviation of residues from normality, but did not suppress it. The statistical effects of variables generated by ANOVA on transformed and nontransformed data were similar, although the significance levels varied. An ANOVA performed on the ranks rather than on the aggressiveness variables (suggested to be a more robust method) also yielded the same results. We take this as evidence that the effects of test cultivars, sites, and sampling dates/years were strong enough to be detected in all cases, and to suggest that the slight deviations of the distributions of residuals from normality in our data sets did not skew ANOVA comparisons of effects to any marked extent. Whenever significant effects were detected, means were compared using the Student-Newman and Keuls test ($\alpha = 0.05$).

RESULTS

Selection for aggressiveness according to cultivar use. ANOVA revealed significant effects of test cultivar on LS and SP in French populations, and on SP in Moroccan populations (Tables 1 and 2). The comparison of means indicated that French populations produced significantly larger lesions and higher numbers of sporangia on leaflets of cv. Bintje (the prevalent cultivar in France) than on leaflets of cv. Désirée, whereas Moroccan populations produced slightly larger lesions (7.22 versus 6.88 cm²; $P = 0.069$) and significantly more sporangia on leaflets of cv. Désirée (the prevalent cultivar in Morocco) than on leaflets of cv. Bintje (Fig. 1). Site-test cultivar and sampling date-test cultivar interactions were not significant for the French populations (Table

TABLE 1. Analysis of variance for lesion size (LS) and spore production (SP) in French populations of *Phytophthora infestans* collected in two sites (Le Rheu and Ploudaniel) in 1999 at two different sampling date

Source	LS		SP	
	F^a value	$P > F$	F value	$P > F$
Site	181.59	<0.0001***	19.63	<0.0001***
Test cultivar	89.14	<0.0001***	94.68	<0.0001***
Site-test cultivar	0.67	0.4142	0.60	0.4401
Sampling date	0.31	0.5758	20.50	<0.0001***
Sampling date-site	0.36	0.5474	0.05	0.8245
Sampling date-test cultivar	3.42	0.0648	2.87	0.0906

^a Sources of variation are the site effect, the test cultivar effect, the sampling date effect, and all two-way interactions between these variables. The statistically significant effects are indicated by asterisks (*, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$).

TABLE 2. Analysis of variance for lesion size (LS) and spore production (SP) in Moroccan populations of *Phytophthora infestans* collected in two sites (Larache and Meknès) in two consecutive cropping seasons (1999–2000 and 2000–2001)

Source	LS		SP	
	F^a value	$P > F$	F value	$P > F$
Site	16.98	<0.0001***	25.13	<0.0001***
Test cultivar	3.30	0.0696	12.27	0.0005***
Site-test cultivar	4.80	0.0288*	0.17	0.6763
Year	33.39	<0.0001***	24.04	<0.0001***
Year-site	7.62	0.0059**	0.16	0.6884
Year-test cultivar	6.12	0.0136*	0.01	0.9170

^a Sources of variation are the site effect, the test cultivar effect, the sampling date effect, and all two-way interactions between these variables. The statistically significant effects are indicated by asterisks (*, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$).

1), indicating that French populations were more aggressive on Bintje than on Désirée in both sites and at both sampling dates. The site-test cultivar and year-test cultivar interactions were not significant for SP in Moroccan populations (Table 2), so Moroccan populations were more aggressive on Désirée than on Bintje in both sites and in each of the 2 years.

Selection for aggressiveness during the epidemic. ANOVA on French data revealed a significant effect of sampling date on SP (Table 1). The means comparison indicated that isolates collected at the start of the epidemic were less aggressive than those sampled at the end of the epidemic (Fig. 2). This result was true in both French sites (no interaction between sampling date and site) and on the two test cultivars (no interaction between sampling date and test cultivar).

Aggressiveness according to sample origin. In both French and Moroccan populations, a highly significant site effect on aggressiveness components was detected in the ANOVA (Tables 1 and 2). The lack of statistically significant interactions between sites and all other main factors indicates that the adaptive pattern to locally dominant cultivars was independent of the mean aggressiveness levels of local populations (high in Ploudaniel and Larache, low in Le Rheu and Meknès).

In France, populations collected from the susceptible cultivar (Bintje) proved the most aggressive on both test cvs. Bintje and Désirée (data not shown), suggesting that differential adaptation of *P. infestans* populations to cultivars did not occur. This is consistent with a previous report using the same two cultivars (30).

DISCUSSION

The data from aggressiveness measurements in both French and Moroccan *P. infestans* populations are consistent with the hypothesis that these populations are adapted to the locally dominant resources (in this case, cultivars), irrespective of the resistance characteristics of these cultivars. Although the results concerning the adaptation of Moroccan populations to the partially resistant cv. Désirée seem at first glance to contradict previous reports from U.S. populations showing no evidence for erosion of partial resistance (21), this contradiction is only apparent, since the partially resistant cultivars included in the experiments had not been grown to any large extent in the United States at the time of the study. However, the pattern of general adaptation observed in both France and Morocco is not consistent with theoretical expectations based on local life histories of the pathogen in either country. Indeed, in France, pathogen populations are clonal (only one mating type present), but not geographically structured (28), which suggests extensive gene flow occurring through migration; conversely, in Morocco, populations are geographically structured and both mating types are present (17,33), which may indicate local recombination but limited gene flow between areas. The fact that in all cases adaptation to locally dominant cultivars was observed points to a prevailing influence of selection over other life history traits in shaping *P. infestans* populations, probably a consequence of the almost obligate biotrophic status of the pathogen.

Very few data exist regarding the pathogenicity characteristics of Moroccan populations of *P. infestans*. Hammi et al. (18) investigated the aggressiveness of seven isolates from tomato and 92 isolates from potato on detached leaflets of four potato cultivars (Désirée, Nicola, Spunta, and Kondor) and of one tomato cultivar (Daniela). Unfortunately, their paper only reports on the range of variation observed within and among the two groups of isolates on each host species, but does not provide any quantitative indication regarding differences between isolates on each potato cultivar. Our data clearly demonstrate (i) that Moroccan *P. infestans* populations are adapted to a partially resistant cultivar (Désirée) and (ii) that the variation for aggressiveness shows a regional structure that was also detected using virulence or other biological markers (mating type and metalaxyl sensitivity) (17).

In our tests, cv. Désirée was more susceptible to Moroccan isolates of *P. infestans* than cv. Bintje, regardless of the aggressiveness component considered. While this was more obvious for SP than for LS, for which the probability associated with the *F* test (0.069) was marginally significant, the trend was consistent for both aggressiveness variables. This result is consistent with the fact that cv. Désirée is used extensively in Morocco (and more generally in northern Africa), whereas cv. Bintje is not grown to any extent in this part of the world. It was, however, surprising at first, because (i) the relative susceptibility to late blight of these two cultivars in western Europe, where they were bred, is exactly the opposite and (ii) no strong genotype–environment interactions have been detected in a previous multilocal, multi-year trial involving other sources of partial resistance to late blight (10). The high susceptibility of cv. Désirée in Morocco might thus be diagnostic of the erosion of the partial resistance of this cultivar, through adaptation to increased aggressiveness in local populations of the pathogen. Since the aggressiveness of French and Moroccan populations of *P. infestans* on cv. Bintje was comparable, the change in relative susceptibility between the two cultivars strongly suggests that adaptation to cv. Désirée in Moroccan populations was the result of selection of isolates with increased aggressiveness specifically to this cultivar rather than a consequence of selection for higher aggressiveness to all potato cultivars. It would be very worthwhile to confirm this hypothesis by testing in the field the relative susceptibility of a range of potato cultivars in Morocco and comparing it to that in other parts of the world.

The large statistical effect of geographical origin of isolates within countries on aggressiveness variables strongly suggests that the geographical structure previously observed in Moroccan populations of *P. infestans* could be related, at least in part, to pathogenicity. This hypothesis is consistent with the fact that

Fig. 2. Number of sporangia produced per leaflet by *Phytophthora infestans* isolates collected in France in 1999, according to sampling dates. The early sampling was 1 week after the first appearance of symptoms in the field; the late sampling was 3 weeks later. Different characters above bars represent the homogenous groups identified (Student-Newman and Keuls test, $\alpha = 0.05$).

Fig. 1. Lesion sizes and number of sporangia produced per leaflet on potato cvs. Bintje and Désirée by *Phytophthora infestans* isolates collected in France and in Morocco. Different characters above bars represent the homogenous groups identified (Student-Newman and Keuls test, $\alpha = 0.05$).

racés found in Larache, which showed the highest aggressiveness to potato, had complex virulence combinations, whereas the less aggressive isolates from Meknès belonged to simple races (17). Overall, isolates from Larache appear to be much specialized to potato, whereas isolates from Meknès might be more polyphagous, with a better ability to switch hosts between potato and tomato. This hypothesis is supported by the fact that most isolates from Meknès belonged to the A2 mating type, which was found to occur at higher frequencies on tomato than on potato in that area (18), but not in other places and years (33). The current situation in Meknès is reminiscent to the population structure observed in France (27,29).

The aggressiveness of the two French populations of *P. infestans* increased between the two dates of sampling, independently of the host genetic background. A similar result was observed in a population of *Blumeria graminis tritici* (39). This change in mean aggressiveness during the course of the epidemic shows that a selection for the isolates most aggressive exists. On a long-term basis, this selection could affect the durability of partial resistance, and might explain the progressive decrease in the resistance of partially resistant cultivars, such as 'Charlotte' in western Europe (F. Pilet and D. Andrivon, unpublished data; D. Michelante, *personnel communication*). However, partial resistance is usually long lasting, including in potato (38). If selection for aggressiveness is strong, the durability of this type of resistance supposes a strong counter-selection of the most aggressive isolates between two cropping seasons of production. One possible explanation for the counter-selection of highly aggressive isolates is related to the detrimental effect of increased pathogenicity on the persistence of host organs (such as tubers) the pathogen survives on. It has been argued that aggressive *P. infestans* strains that cause extensive rot in susceptible potato seed tubers may not survive the winter period, thus leading to a negative selection pressure upon aggressive strains of the pathogen (23,34,40). Another possibility, which has not been thoroughly tested experimentally so far, is that aggressiveness is determined in part by epigenetic factors, allowing some degree of phenotypic plasticity within isolates. In any case, the observation that isolates/lineages of the pathogen with low or medium aggressiveness persist in the population collected in Ploudaniel supports the view that higher aggressiveness is not the only determinant of long-term fitness in *P. infestans* populations.

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