Pathogenicity of *Venturia inaequalis* Strains of Race 6 on Apple Clones (*Malus* sp.)

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ABSTRACT

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About 40 cultivars derived from *Malus floribunda* 821 (Vf gene) are resistant to the five races of *Venturia inaequalis* previously described. Race 6, recently identified, is able to overcome the resistance of some selections carrying the Vf gene. Thirty-seven apple clones were tested for their susceptibility to different (races 1 and 6) strains of *Venturia inaequalis*. These clones represented a large sample of the resistance sources used by apple breeders throughout the world (selected clones and their ancestors). Conversely, race 6 induced symptoms on nearly all the Vf selections, and also on Nova Easygro (Vr), on a selection carrying Va, on Jonsib, and on a selection derived from *Malus atrosanguinea* 804. Race 6 did not attack susceptible cultivars such as Granny Smith, three selections from different polygenic sources of resistance, *Malus baccata jackii* (Vbj), R 127.40.7A (Vr), and PI 172623 (Va). The pedigrees of three hybrids selected for their Vf resistance were analyzed: all the resistant race 1 parents involved in these pedigrees were susceptible to race 6, except the ancestor *M. floribunda* 821 and one of its F_2 selected progeny (F_2 26829-2-2). The other F_2 (F_2 26830-2) was susceptible. These results confirmed the hypothesis of a complex genetic background for resistance to *Venturia inaequalis* in wild species, which has been partly lost during the breeding process. The variability of the resistance genes introgressed in recent selections could be lower than believed, and reduced to the Vf gene in most cases. Apple breeders should increasingly focus on finding polygenic sources of resistance in order to obtain a durable resistance to scab.

Several sources of resistance have been used in breeding for resistance to apple scab (*Venturia inaequalis* (Cooke) G. Wint.) (23). Six independent genes were identified: Vf from *Malus floribunda* Siebold ex Van Houtte 821; Va from Antonovka PI 172 623; Vb from *M. baccata* (L.) Borkh.; Vbj from *M. baccata jackii* Rehd.; Vr from *M. pumila* (L.) Mill. R127 40.7A; and Vm from *M. micromalus* Mak. (12). Jonsib was also classified as a monogenic source of resistance. In addition to these simple, inherited, complete resistances, partial resistance was identified in several species and cultivars. This partial resistance is considered to be under polygenic control.

The most well-known source of resistance, Vf, was identified at the beginning of the program (10). Over a period of 50 years, several cultivars derived from *M. floribunda* 821 were selected after successive backcrosses involving different recurrent parents. The first of these cultivars, named Prima, was released in 1970. Today, around 40 scab-resistant cultivars have been released (2–4) but none is widely planted due to commercial considerations.

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In western Europe, the cultivars Florina for fresh market and Judeline for juice, derived from *M. floribunda* 821, are the most widely grown. Judeline is only grown in the northwest of France, but Florina is cultivated in France, Switzerland, Rumania, and northern Italy.

In the last 40 years, four races have been identified and distinguished from race 1 on the basis of their pathogenicity on a range of different species of *Malus* used in breeding programs (20,22). Recently, a new scab race was identified in Germany (15). This race, race 6, is able to overcome the resistance of the recently released Vf cultivars and therefore could nullify the breeding efforts of half a century.

Vf resistance has been thought to be a complex resistance, based both on the variable results of the segregations between resistant and susceptible seedlings according to the progenies, and also on the different classes of symptoms that indicate a continuum from hypersensitivity to susceptibility (1,11,19). These characteristics suggest that the original level of resistance was due to a group of rather closely linked genes in addition to independent minor genes. This resistance, effective for 50 years, was qualified as a durable resistance.

The emergence of race 6 is a major event for the breeding programs. The pathogenicity of this new race must be studied before new breeding strategies can be determined. Studies need to clarify the reaction of the main scab-resistant cultivars to race 6 and also the reaction of ancestors up to *M. floribunda* 821 itself. It is also important to know the behavior of the other independent monogenic or polygenic sources of resistance. This work will be very helpful in defining new breeding strategies that take race 6 into account.

This study concerns the pathogenicity of race 6 strains compared with a reference strain of race 1 on several *Malus* clones, representing most of the resistance sources used in the breeding programs for scab resistance.

MATERIALS AND METHODS

Strains of *V. inaequalis* and inoculum preparation. Six monoconidial strains were tested. Their origin and characteristics are described in Table 1. The method employed to characterize the pathogenicity of the strains was described by Parisi et al. (16).

For each strain, a conidial suspension was first obtained with Keitt and Palmiter's technique (13). This conidial suspension was applied to young seedlings from a cross between two susceptible cultivars, Golden Delicious and Granny Smith. For each strain, leaves with abundant sporulation were collected, dried at laboratory temperature, and frozen at –18°C. A conidial suspension was obtained from these leaves and adjusted at 2 to 2.5 × 10^5 conidia/ml to inoculate grafted plants.

Source of plant materials and methods for assessing pathogenicity. Scionwood was collected from the INRA repository and grafted onto seedling rootstock. As a whole, 37 clones were grown in pots in the greenhouse (Table 2). Only plants with growing shoots and young leaves were inoculated. The mean number of leaves per shoot was 10 to 13 when inoculation was performed.

All experiments were carried out in a growth chamber. Conidial suspensions were applied to runoff with a manual sprayer (Clause, Brétigny-sur-Orge, France). Plants were incubated for 48 h in the dark at 18°C, with constant leaf wetness maintained by a plastic sheet or a humidifier. After incubation, the plants were grown at 17 to 19°C, under a 16-h photoperiod of 70 μE s^{-1} m^{-2} with relative humidity (RH) 85 to 95%. Temperature and RH monitoring was performed with a thermohygrograph (Jules Richard & Pékly, Argenteuil, France). Symptoms on potted trees were assessed 14 days after inoculation. Disease severity was assessed on all leaves on each shoot, according to a previously published grading scale (15) derived from those of Croxall et al. (5). Disease severity was determined for each potted tree by the median obtained from the scores of all scabbed leaves; disease incidence was the percentage of scabbed leaves. For each strain, an average of four trees was evaluated (representing 5 to 14 shoots and 52 to 182 leaves per clone).

Experimental design and statistical analysis. The incidence of disease on the different clones was transformed in arcsin√percentage. The homogeneity of variances was tested by Bartlett's test. When possible, an analysis of variance was made and when F values were significant, means were compared by Duncan's multiple range test at $P = 0.05$.

Because of plant availability and growth chamber size, it was not possible to test more than two strains on the apple clones each year. The experiments were carried out principally in 1992 and 1993, and some recently introduced clones were tested in 1994. Each year, the Golden Delicious cultivar was tested as a reference scab-susceptible control of the repeatability of the results.

RESULTS

The pathogenicity of the reference strain of race 1 and two race 6 strains (302 and 305) was first evaluated on 28 apple clones, representing a large sample of the resistance sources used by apple breeders throughout the world (Table 3). The set of clones also included some cultivars representing different ranges of susceptibility to scab in French orchards (17), and the differential host range of the five other scab races previously identified (20,22). For this experiment, the Bartlett test indicated that the variance values were not homogeneous; the analysis of variance was not possible with all the values. Only the values obtained with Golden Delicious and Gala were compared. The results showed no significant difference with the Golden Delicious control cultivar tested in three different years, indicating the reproducibility of the results. Golden Delicious appears significantly less susceptible than Gala to the two strains 104 and 302 (Table 3).

The results showed that the race 1 strain 104 only induced symptoms on Gala, Golden Delicious, Reinette Clochard, and TN 10-8, a polygenic resistant hybrid. Unlike strain 104 (race 1) the two race 6 strains induced symptoms not only on Gala, Golden Delicious, and nearly all the Vf recently released cultivars, but also on Nova Easygro (Vr resistant), on a Va-resistant hybrid, on Jonsib, and on a selection from *M. atrosanguinea* 804 (OR 45T132). But many other cultivars or hybrids remained resistant to the race 6 strains: Akane, Granny Smith, Reinette Clochard, Antonovka, TN 10-8, X7218 (Vbj resistant), 91/19-64 (a selection from Prima), and P35R11-34 (a selection from Jonsib). In addition, *M. floribunda* 821, Evereste, *M. pumila* R127.40.7A, and the clone PI 172623 were also resistant to the two race 6 strains (Table 3). The three strains tested in this experiment could not induce symptoms on the range of differential hosts used for races 2 to 5.

In a second experiment, several steps of the long breeding process from the first cross between *M. floribunda* 821 and Rome Beauty and the recently released Vf-resistant cultivars were tested with the same three strains. This experiment included the two F_2 hybrids derived from the first cross (Fig. 1A), and some hybrids from the genealogy of Florina (Fig. 1B), K1R27-18 (Fig. 1C), and Judeline (Fig. 1D). For this experiment, the analysis of variance indicated that no significant difference existed between the results of the 2 years with the Golden Delicious clone (Table 4). The comparison of incidence values obtained with the other clones is indicated in Figure 1.

All the hybrids or cultivars tested, except Golden Delicious, were resistant to the race 1 strain. With the race 6 strains, only the progenitor *M. floribunda* 821 and the F_2 26829-2-2 were resistant (Fig. 1B); all the other clones were susceptible to differing degrees. Nevertheless, the comparison of the incidence values obtained at each step of the breeding process with strain 302 showed that significant differences were obtained only on the pedigree of K1R27-18 (Fig. 1C).

The differential susceptibility of the two F_2 hybrids from the cross *M. floribunda* 821 × Rome Beauty was confirmed by the test with three other race 6 strains (312,

Table 1. Origin and characteristics of the six *Venturia inaequalis* strains tested on apple cultivars

Strain	Origin	Host cultivar or hybrid	Characteristics
104	Saint Lézin, France,1978	Golden Delicious	Race 1 reference strain
302	Ahrensburg, Germany, 1988	81/11-22[a]	Race 6
305	Ahrensburg, 1988	81/11-22	Race 6
312	Ahrensburg, 1988	81/11-22	Race 6
600	Ahrensburg, 1990	81/11-3[b]	Race 6
635	Ahrensburg, 1990	81/11-3	Race 6

[a] Tree No. 22 of the progeny Prima × A143/24.
[b] Tree No. 3 of the progeny Prima × A143/24.

Table 2. Characteristics of 37 apple clones inoculated with race 1 and race 6 strains of *Venturia inaequalis*

Clone	Name or code number	Characteristic reaction
X 2836	Akane	Scab susceptible
X 4712	Gala	Scab susceptible
X 972	Golden Delicious	Scab susceptible
X 3069	Granny Smith	Scab susceptible
X 1725	Reinette Clochard	Scab susceptible
X 7187	Antonovka	Polygenic resistant
X 4732	Generos	Polygenic resistant
X 4442	TN 10-8	Polygenic resistant
X 7217	PI 172623	Va resistant
X 2594	CCR3T11	Va resistant, seedling from PI 172633
X 7218	*Malus baccata jackii*	Vbj resistant
X 6518	*Malus floribunda* clone 821	Progenitor of the Vf selections
X 6771	F_2 26829-2-2	F_2 selection from M.*floribunda* 821, Vf resistant
X 6772	F_2 26830-2	F_2 selection from M.*floribunda* 821, Vf resistant
X 2881	Coop8	Vf resistant
X 4205	Coop11	Vf resistant
X 2596	Prima	Vf resistant
X 6607	Ahra	Vf resistant, seedling from Prima
X 6608	81/19-64	Vf resistant, seedling from Prima
X 2814	Priam	Vf resistant
X 2774	Judeline	Vf resistant, seedling from Priam
X 2033	OR53T52	Vf resistant
X 2775	Florina	Vf resistant, seedling from OR53T52
X 4982	P6R28A39	Vf resistant, seedling from Florina
X 2042	O54T184	Vf resistant
X 4638	TNR 11-62	Vf resistant, seedling from O54T184
X 6688	K1R27-18	Vf resistant
X 2241	*Malus pumila* R 127.40.7A	Progenitor of the Vr selections
X 4077	Nova Easygro	Vr resistant
X 2369	Evereste	Scab resistant, ornamental crabapple
X 7188	Jonsib	Scab resistant
X 7125	P35R11-34	Selection from Jonsib, scab resistant
X 1926	OR45T132	Scab resistant from *Malus atrosanguinea* 804
X 2250	TSR34T132	Differential host for race 2 (h2)
X 2253	Geneva	Differential host for race 3 (h3)
X 2249	TSR33T239	Differential host for race 4 (h4)
X 2225	9-AR2T196	Differential host for race 5 (h5)

600, and 635). The F_2 26829-2-2 was resistant and the F_2 26830-2 susceptible to these three strains (Table 5).

DISCUSSION

This work showed an important difference in pathogenicity between the two race 6 (302 and 305) strains principally studied and the reference race 1 strain 104. These differences concerned not only the cultivars or hybrids carrying the Vf gene, but also several other sources of monogenic and polygenic resistance and even some cultivars known as susceptible, based on their orchard behavior (Table 3).

The first experiment showed that Golden Delicious was less susceptible than Gala to two of the three strains tested. This result is consistent with orchard observations (17). No significant difference in aggressiveness was noted between the two race 6 strains and race 1 on these susceptible cultivars. Akane, classified as slightly susceptible to scab in field evaluation (17), appeared resistant to the three strains in this experiment; this could be interpreted as an expression of its polygenic resistance. Granny Smith was resistant to both strains 302 and 104, and Reinette Clochard susceptible to race 1 and resistant to race 6 strain 302. This last cultivar is considered slightly susceptible and Granny Smith moderately susceptible to scab (17). Sierotzki et al. (21) have recently demonstrated that most of the *V. inaequalis* strains from a cultivar were unable to infect some other susceptible cultivars. Although not formally demonstrated, this could be the result of the interaction between *V. inaequalis* unknown avirulence genes and ephemeral resistance genes of apple (8). Our strains were isolated from Golden Delicious and from Prima seedlings, and therefore could be specially adapted to these hosts and not to Granny Smith and Reinette Clochard, which were perhaps not present in their original orchards. Nevertheless, in a previous study, when the progeny of the Granny Smith × Golden Delicious cross was inoculated with both strains 104 and 302, we observed that all the progeny was susceptible to these two strains (16). Therefore, the resistance of Granny Smith to these two strains cannot be explained by the presence of a single resistance gene. Perhaps this phenomenon of adaptation between the scab population and the host has a more complex genetic background or involves genes not expressed at the seedling level.

The two polygenic resistant hybrids (Antonovka and Generos) included in this study remained entirely resistant to the three strains tested (Table 3). The third, TN 10-8, was moderately susceptible to the race 1 strain and resistant to the two race 6 strains. It is known that the expression of polygenic resistance is influenced by climatic conditions and inoculum pressure, and that leaf resistance is not always perfectly correlated with fruit resistance (14). Nevertheless, we consider these results to be a good indication of the interest in planting polygenic resistant hybrids in areas where race 6 is present, and of their use in breeding programs for scab resistance.

The resistance of Generos to race 1 and 6 strains should also be underlined. Generos is a cultivar from Rumania, with *M. kaido* in its parentage. It is slightly susceptible to scab in field conditions in Rumania (N. Braniste, personal communication). But in other experiments carried out in our research program, the study of Generos progeny segregation indicated that this cultivar did not exhibit a polygenic resistance. In the greenhouse, its resistance is expressed by a very clear hypersensitive response, and could be coded by two major genes (F. Laurens, Y.

Table 3. Pathogenicity of race 1 and race 6 of *Venturia inaequalis* strains on 28 clones of apple

	Strain 104 (race 1)		Strain 305 (race 6)		Strain 302 (race 6)	
Clones	Incidence	Severity	Incidence	Severity	Incidence	Severity
Akane	0	0	0	0	0	0
Gala	47.9 a[y]	2	NT[z]	NT	61.2 a	5
Golden Delicious						
1992	22.6 b	4	21.5 b	3	NT	NT
1993	25.7 b	3	14.5 b	3.5	30.7 b	3
1994	30 b	2	NT	NT	25.7 b	2
Granny Smith	0	0	NT	NT	0	0
Reinette Clochard	15.1	4	NT	NT	0	0
Antonovka	0	0	0	0	0	0
Generos	0	0	0	0	0	0
TN 10-8						
1992	2.3	1	0	0	NT	NT
1993	0	0	NT	NT	0	0
PI 172623	0	0	0	0	0	0
CCR3T11	0	0	5.7	2	11.1	2
M. baccata jackii	0	0	0	0	0	0
M. floribunda. 821	0	0	0	0	0	0
Coop 8	0	0	NT	NT	6.2	3
Coop 11	0	0	NT	NT	24.1	4
Prima	0	0	19	3	24.4	3
Ahra	0	0	1.3	2	30.8	3
81/19-64	0	0	0	0	0	0
M. pumila R 127.40.7A	0	0	0	0	0	0
Nova Easygro	0	0	18.8	2	28.8	3
Evereste	0	0	0	0	0	0
Jonsib	0	0	16.5	2	35.5	2
P35R11-34	0	0	0	0	0	0
OR45T132	0	0	17.8	3	24.7	3
TSR34T132 (h2)	0	0	0	0	0	0
Geneva (h3)	0	0	0	0	0	0
TSR33T239 (h4)	0	0	0	0	0	0
9-AR2T196 (h5)	0	0	0	0	0	0

[y] Percentages followed by the same letter are not significantly different according to Duncan's multiple range test ($P = 0.05$); only the cvs. Gala and Golden Delicious have been compared.
[z] Not tested.

Table 4. Pathogenicity of race 1 and race 6 of *Venturia inaequalis* strains on 12 clones of apple

	Strain 104 (race 1)		Strain 305 (race 6)		Strain 302 (race 6)	
Clones	Incidence	Severity	Incidence	Severity	Incidence	Severity
Golden Delicious						
1992	38.1 a[y]	4	NT[z]	NT	38 a	5
1993	33.8 a	3	24.2 a	3	NT	NT
M. floribunda. 821	0	0	0	0	0	0
F_2 26829-2-2	0	0	0	0	0	0
F_2 26830-2	0	0	NT	NT	22.6	3
Priam	0	0	NT	NT	19.3	3
Judeline	0	0	2.1	1	27.3	3
OR53T52	0	0	6.7	3	26.9	3
Florina	0	0	9.9	1	27.1	3
P6R28A39	0	0	13.7	3	38.6	3
O54T184	0	0	6.1	2	18.6	3
TNR 11-62	0	0	4.4	1	0	0
K1R27-18	0	0	3.6	1	8.7	4

[y] Percentages in rows followed by the same letter are not significantly different according to Duncan's multiple range test ($P = 0.05$). Only the comparison of the results with the Golden Delicious clone is indicated; for the other susceptible clones, see Figure 1.
[z] Not tested.

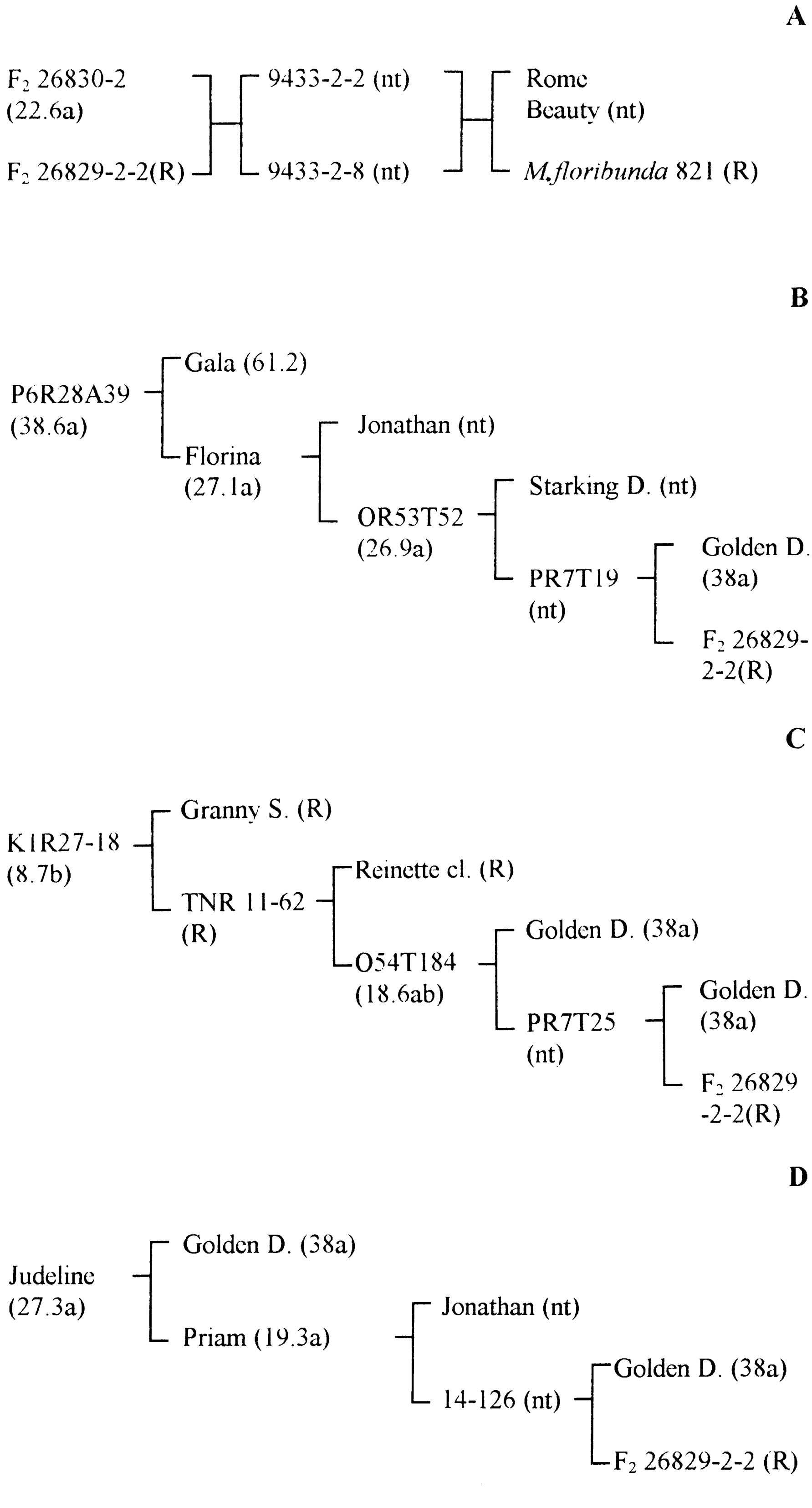

Fig. 1. Pedigrees of different apple clones and incidence (in parentheses) of the race 6 strain 302 of *Venturia inaequalis* on each susceptible clone. Percentages followed by the same letter are not significantly different according to Duncan's multiple range test ($P = 0.05$). R = resistant to the strain 302; nt = not tested. **(A)** Pedigree of the two F_2 from *Malus floribunda* 821, from which all the recently released Vf cultivars are derived. **(B)** Pedigree of the hybrid P6R28A39. Gala was not included in the comparison of clones because tested in a different experiment (Table 3). **(C)** Pedigree of the hybrid K1R27-18. **(D)** Pedigree of Judeline apple. (Golden D = Golden Delicious; Granny S. = Granny Smith; Reinette cl. = Reinette Clochard; Starking D. = Starking Delicious)

Lespinasse, and L. Parisi, unpublished data).

Concerning the sources of monogenic resistance studied, other than Vf resistance, the main result is that the two race 6 strains showed pathogenicity on Nova Easygro (Vr resistant) and on CCR3T11, a hybrid supposed to be Va resistant, but the sources of resistance, *M. pumila* R127.40.7A and PI172623, remained resistant to race 6. Apparently, a part of the initial resistance of the two clones has been lost during the breeding process, and their resistance was more complex than a single gene. One hypothesis is that the two clones contain several (at least two) resistance genes, one of them being the Vf gene. During the selection process, most of these genes have been lost, and only Vf kept. The resistance of the clone R127.40.7A, for example, is more complex than one major resistance gene (6). From this clone originated the two sets of seedlings si and s'i, designated as differential hosts for race 2 and 4, which indicates that at least three different resistance genes segregate in its progenies (only Vr was resistant to races 1 to 5) (23). But Dayton and Williams showed that the Vr gene was nonallelic to the Vf gene (7). Nevertheless, random amplified polymorphic DNA (RAPD) molecular markers of the Vf gene are successful in marking the cv. Nova Easygro; with a cleaved amplified polymorphic sequence (CAPS) marker derived from a RAPD marker of the Vf gene, Gianfranceschi et al. (9) studied the progeny of the Florina × Nova Easygro cross and showed that these two genes are tightly linked, or may be the same gene. Only molecular markers could answer the question of the presence of the Vf gene in the clone R127.40.7A

A similar but more speculative hypothesis concerns the Va resistant clone. In fact, it is not clearly demonstrated that the parental clone PI172633 possesses the Va gene of resistance. It is the clone PI172623 that was named Va resistant; the two clones gave the same resistance reaction in greenhouse tests (E. B. Williams, personal communication). The genetic background of this clone resistance is therefore not clear. The use of molecular markers will also be useful in clarifying this situation.

Another monogenic resistance, that of Jonsib, was overcome by race 6 strains. Interestingly, a descendant of Jonsib, the clone P35R11-34, recovered a resistance to the race 6 strains. P35R11-34 originated from an open-pollinated descendant of Jonsib, the clone PI12171, crossed with Empire. Therefore, this clone may have one or several resistance genes from its unknown male parent, different from that of Jonsib, which explains its resistance to race 1 and race 6.

In this work, 13 Vf-resistant selections, plus their progenitor and the two F_2 hybrids from their pedigrees were tested. The results obtained with the two monoconidial

Table 5. Pathogenicity of a race 1 and three race 6 strains of *Venturia inaequalis* on the two F_2 hybrids derived from the cross Rome Beauty × *Malus floribunda* 821 apples

	Strain 104 (race 1)		Strain 312 (race 6)		Strain 600 (race 6)		Strain 635 (race 6)	
Clones	I[y]	S[z]	I	S	I	S	I	S
Seedlings from the cross Golden Delicious × Granny Smith	44.1	4	50	5	40	5	66.6	5
F_2 26829-2-2	0	0	0	0	0	0	0	0
F_2 26830-2	0	0	18	2	35.2	4	18.8	2

[y] Incidence.
[z] Severity.

race 6 strains confirmed the first results obtained with a mixed inoculum called Ahrensburg (15). Nearly all the recently released Vf selections were susceptible to race 6; the only exception was the clone 81/19-64, a descendant of Prima selected at IZZ (Ahrensburg, Germany). The resistance of the progenitor *M. floribunda* 821 was also confirmed. Its original resistance was eroded or lost during the breeding process. The study of the behavior of the two F_2 hybrids with the race 6 strains clearly showed that one of them was resistant and the other susceptible. Nearly all the recently released selections originated from the resistant one, the F_2 26829-2-2. So, the original resistance was eroded or lost after this step. The study of all the available parents involved in the pedigree of three Vf-resistant hybrids showed that the resistance was always lost after the second backcross (Fig. 1); race 1 resistant selections from the first backcrosses were definitively lost. Furthermore, on the pedigree of the hybrid K1R27-18, a partial resistance is recovered after two backcrosses with the cvs. Granny Smith and Reinette Clochard, both being resistant to the race 6 strain 302. In the other pedigrees, no significant difference of susceptibility to the strain 302 was noticed between the different steps of the breeding process. From the race 6 susceptible F_2 26830-2, only three Vf-resistant selections were obtained; two of them, Coop 8 and Coop 11, were susceptible to race 6 strain 302 in our study.

These results showed that not only the Vf gene of the recently released selections, but also the Vr, Va, and Jonsib genes were overcome by the race 6 strains from the Ahrensburg orchard. Nevertheless, this work points out two other findings. The first is that the resistance to scab of three different progenitors used in breeding programs was more complex than a single gene and partly lost during the breeding process. The second is that the genetic background of the selections' resistance to scab is not always well known, and when the resistance is supposed to be monogenic the resistance gene itself is not always identified. This situation needs to be clarified for the efficiency of the breeding programs. In fact, the variability of resistance genes that are introgressed in modern cultivars may be lower than supposed. In addition, the high level of resistance of the progenitors has been lost.

This work also showed the continuing effectiveness of several polygenic resistant hybrids and commercial cultivars considered susceptible to the disease. If confirmed by other tests, these results should encourage breeders to take greater account of host variability in their programs. These cultivars or hybrids can confer a very interesting partial resistance level to scab, which could be associated with major resistance genes.

This work concerned only a small part of the variability of the fungus. Recently, Roberts and Crute (18) showed that the resistance of *M. floribunda* 821 was overcome by *V. inaequalis* strains different from race 6 in their pathogenicity. On the other hand, we have no data on the frequency of race 6 virulence in *V. inaequalis* populations. This basic work needs certain tools that are not yet available in our model, i.e., test of pathogenicity on a small scale, and identification and molecular marking of avirulence genes. When available, these tools could be useful for epidemiological work on the occurrence, distribution, and speed of emergence of virulences in *V. inaequalis* populations. Also, these data could provide valuable information to establish breeding strategies aimed at obtaining a durable resistance to scab.

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LITERATURE CITED

1. Chevalier, M., Lespinasse, Y., and Renaudin, S. 1991. A microscopic study of the different classes of symptoms coded by the Vf gene in apple for resistance to scab (*Venturia inaequalis*). Plant Pathol. 40:249-256.
2. Crosby, J. A., Janick, J., Pecknold, P. C., Goffreda, J. C., and Korban, S. S. 1994. "Enterprise" apple. HortScience 29:825-826.
3. Crosby, J. A., Janick, J., Pecknold, P. C., Goffreda, J. C., and Korban, S. S. 1994. "GoldRush" apple. HortScience 29:827-828.
4. Crosby, J. A., Janick, J., Pecknold, P. C., Korban, S. S., O'Connor, P. A., Ries, S. M., Goffreda, J. C., and Voordeckers, A. 1992. Breeding apples for scab resistance: 1945 - 1990. Fruit Var. J. 46:145-166.
5. Croxall, H. E., Gwynne, D. C., and Jenkins, J. E. E. 1952. The rapid assessment of apple scab on leaves. Plant Pathol. 1:39-41.
6. Dayton, D. F., Shay, J. R., and Hough, L. F. 1953. Apple scab resistance from R 12740-7A, a Russian apple. Proc. Am. Soc. Hortic. Sci. 62:334-340
7. Dayton, D. F., and Williams, E. B. 1970. Additional allelic genes in *Malus* for scab resistance of two reaction types. Proc. Am. Soc. Hortic. Sci. 95:735-736.
8. Gessler, C. 1994. Biology and biotechnology in strategies to control apple scab. Norw. J. Agric. Sci. 17:337-354.
9. Gianfranceschi, L., Koller, B., Seglias, N., Kellerhals, M., and Gessler, C. Molecular selection in apple for resistance to scab caused by *Venturia inaequalis*. Theor. Appl. Genet. (In press.)
10. Hough, L. F. 1944. A survey of the scab resistance of the foliage on seedlings in selected apple progenies. Proc. Am. Soc. Hortic. Sci. 44:261-272.
11. Hough, L. F., Shay, J. R., and Dayton D. F. 1953. Apple scab resistance from *Malus floribunda* Sieb. Proc. Am. Soc. Hortic. Sci. 62: 805-820.
12. Hough, L. F., Williams, E. B., Dayton, D. F., Shay, J. R., Bailey, C. H., Mowry, J. B., Janick, J., and Emerson, F. H. 1970. Progress and problems in breeding apples for scab resistance. Pages 217-230 in: Proc. Eucarpia Fruit Sec. Symp., Tree Fruit Breed. INRA Ed., Versailles.
13. Keitt, G. W., and Palmiter, D. H. 1938. Heterothallism and variability in *Venturia inaequalis*. Am. J. Bot. 25:338-345.
14. Lespinasse, Y. 1989. Breeding pome fruits with stable resistance to diseases. Genes, resistance mechanisms, present work and prospects. Pages 100-115 in: Integrated Control of Pome Fruit Diseases, Vol II. C. Gessler, D. J. Butt, and B. Koller, eds. No publisher given, Zurich.
15. Parisi, L., Lespinasse, Y., Guillaumes, J., and Krüger, J. 1993. A new race of *Venturia inaequalis* virulent to apples with resistance due to the Vf gene. Phytopathology 83:533-537.
16. Parisi, L., Lespinasse, Y., Guillaumes, J., and Krüger, J. 1994. A new race of *Venturia inaequalis* overcomes apples resistance due to the Vf gene. Norw. J. Agric. Sci. 17:95-104.
17. Parisi, L., and Trillot, M. 1993. Variétés de pommier: Résistance et sensibilité à la tavelure, à l'oïdium et aux maladies de conservation. INFOS-CTIFL 89:29-30.
18. Roberts, A. L., and Crute, I. R. 1994. Apple scab resistance from *Malus floribunda* 821 (Vf) is rendered ineffective by isolates of *Venturia inaequalis* from *Malus floribunda*. Norw. J. Agric. Sci. 17:403-406.
19. Rousselle, G. L., Williams, E. B., and Hough, L. F. 1974. Modification of the level of resistance to apple scab from the Vf gene. Pages 19-20 in: Proc. Int. Hortic. Congr., 19th, Vol. III. Int. Soc. Hortic. Sci. Ed., Warsaw.
20. Shay, J. R., and Williams, E. B. 1956. Identification of three physiologic races of *Venturia inaequalis*. Phytopathology 46:190-193.
21. Sierotzki, H., Eggenschwiler, M., Boillat, O., McDermott, J. M., and Gessler, C. 1994. Detection of variation in virulence toward susceptible apple cultivars in natural populations of *Venturia inaequalis*. Phytopathology 84: 1005-1009.
22. Williams, E. B., and Brown, A. G. 1968. A new physiologic race of *Venturia inaequalis*, incitant of apple scab. Plant Dis. Rep. 52:799-801.
23. Williams, E. B., and Kuc, J. 1969. Resistance in *Malus* to *Venturia*. Annu. Rev. Phytopathol. 7:223-246.