Horizontal and Vertical Resistance in *Vicia faba* to Chocolate Spot Caused by *Botrytis fabae*

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ABSTRACT

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Of the 1,730 germ plasm lines tested for resistance to chocolate spot in Syria, 353 showed resistance in 1979 and 1980. Nineteen of these resistant lines were tested during two consecutive seasons in Syria, Egypt, England, and the Netherlands. Lines BPL 710, 1196, and 1179-1 were consistently resistant in all countries. Lines BPL 261, 266, 274, 470, 1055, 1058, 1278, 1390, 1543, 1544, 1547, 1548, and 1550 were resistant in Syria and Egypt but susceptible in England and the Netherlands. In tests repeated twice, BPL 710, 1196, and 1179-1 revealed no differential interaction, whereas BPL 1763, 1821, and ILB 1814 consistently revealed a significant differential interaction when inoculated with 12 isolates of *Botrytis fabae* from Syria. Therefore, BPL 710, 1196, and 1179-1 seemed to carry genes for a broad-based horizontal resistance compared with those for a narrow-based vertical resistance in BPL 1763, 1821, and ILB 1814. On the basis of their interactions with BPL 1763, 1821, and ILB 1814, the 12 isolates of the pathogen were classified into four groups representing races 1, 2, 3, and 4. These races seemed to be more common in England and the Netherlands than in Egypt and Syria.

Chocolate spot, caused by *Botrytis fabae* Sard., is one of the most important diseases of faba bean (*Vicia faba* L.) throughout the Middle East, North Africa, and Europe (2,8,10,13,14,16). Yield losses as high as 75% have been reported from areas where extended periods of wet weather conditions prevail (4,5).

Disease management today is based mainly on expensive fungicides and modified cultural practices, which provide only partial protection. Therefore, effective disease control strategies should include resistant cultivars as a major component. Unfortunately, chocolate spot-resistant sources are limited (2,3,5). The only two cultivars, Purple Pod and Hmelnikie, that have been reported relatively resistant are from the USSR (13).

Large germ plasm collections could vary for both vertical or specific and horizontal or general resistance (15). Therefore, selection for the latter requires certain procedures to differentiate between the two (10,11,15). In these procedures, the suppression of vertical resistance is attempted to enhance the expression of horizontal resistance (11). Some reports suggested using wide mixtures of isolates (12) or virulent races (1) to avoid selecting plants with highly race-specific or vertical resistance, whereas another report (11) indicated that mixtures tend to confound vertical with horizontal resistance and therefore recommended using a single race with the broadest possible virulence spectrum. Vanderplank (15) suggested, however, that the two types of resistance can be distinguished by the presence or absence of differential interactions between genotypes of the host and those of the pathogen.

Although different isolates of *B. fabae* can vary considerably in their virulence (6,9), no evidence has been provided for the existence of physiological races in the pathogen. However, in the recent multilocation testing of several chocolate spot-resistant lines conducted in 1982 and 1983 by the International Center for Agricultural Research in Dry Areas (ICARDA), certain faba bean lines were found susceptible at some locations and resistant at others (7). These findings indicated possible physiological specialization in *B. fabae*.

The objectives of this work were to 1) identify new sources for resistance to chocolate spot by local and international evaluation of the faba bean germ plasm collection of ICARDA, 2) study the race situation in *B. fabae*, and 3) differentiate lines with genes for vertical from those with genes for horizontal resistance.

MATERIALS AND METHODS

Local evaluation. Local evaluation was made in 1979 and 1980 in the field at ICARDA's subsite in Lattakia in northern Syria. In October of each year, 20 seeds of faba bean per line were planted in single rows 2 m long and 50 cm apart. A Syrian faba bean local land race (ILB 1814) was planted as a standard check every 10 test entries.

A mixture of 60 isolates of *B. fabae* was composited from a wide range of naturally infected faba bean leaves of chocolate spot-susceptible local land races in major production regions in Syria. Infected leaves were surface-disinfected in a 10% Clorox solution for 2 min, plated on FDA medium (extracts of 200 g of faba bean seeds, 20 g of dextrose, and 18 g of agar), incubated at room temperature (20 ± 2 C) for 7 days, and subcultured until pure isolates of *B. fabae* were obtained. These isolates were incubated in the dark for 48 hr, exposed to three cycles of 12 hr of darkness and 12 hr of ultraviolet light to induce sporulation (14), then propagated at room temperature. After 12 days, all cultures were blended together in equal amounts, passed through two layers of cheesecloth, and diluted with tap water until 600,000 spores per milliliter were obtained. This inoculum was applied in the evening (6:00–8:00 P.M.) to the foliage of 8-wk-old plants with a knapsack sprayer, using 20 ml of inoculum per plant. Inoculated plants were then covered with polyethylene sheets supported by metal frames 2.0 × 0.9 × 6.0 m. After 12 hr, plants were uncovered and sprinkled twice a day with water (at 9:00 A.M. and 6:00 P.M.), then covered again in the evening. This procedure was continued until susceptible lines developed severe chocolate spot symptoms (15 days after inoculation).

A new two-cycle screening technique was adopted. In the first screening cycle (1979 season), 1,730 germ plasm lines were evaluated using the mixed inoculum of *B. fabae* mentioned earlier. Some of the resistant lines, detected in the first cycle, developed few coalesced-sporulating lesions 3 wk after inoculation. These lesions were believed to have been induced by unusual highly virulent forms (6,9) that seemed to occur at low frequencies in local populations of the pathogen. To subject resistant materials to a rigorous evaluation, 60 isolates of *B. fabae* obtained from such lesions were mixed in equal proportions, and then, in a second screening cycle in 1980, inoculated back to progenies of the resistant lines identified the previous season.

The 60 isolates used to composite the mixed inoculum (A) of the first screening cycle were designated A_1 to A_{60}; the 60 isolates used to composite the mixed inoculum (B) of the second screening cycle were designated B_1 to B_{60}.

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International evaluation. On the basis of local screening at Lattakia, 19 chocolate spot-resistant faba bean lines (Table 1) were included in the Faba Bean International Chocolate Spot Nursery (FBICSN) for testing in Syria, Egypt, England, and the Netherlands, where chocolate spot has long been known to be endemic. Lines 1–16 were resistant to inocula A of the first and B of the second screening cycles, whereas lines 17–19 were resistant to inocula A only and susceptible to B (Table 1). In each country, seeds were planted in rows 1 m long and 30 cm apart with two replicates. Local standard checks were repeated every four test entries. The 19 entries in the FBICSN were evaluated twice (1982 and 1983) with the help of ICARDA's cooperators at Giza Research Station in Egypt, the Plant Breeding Institute, Cambridge, England, and the Nickerson Zwaan Seed Company in the Netherlands.

Pathogenicity tests. A modification of the detached-leaf technique (6) was employed to conduct two pathogenicity tests in the laboratory. The first test was carried out to study differences in the frequency distribution of virulence between inocula A of the first and B of the second screening cycle. On the basis of their reactions in the FBICSN, two faba bean lines were selected for this study. Fully expanded single leaflets of similar age were detached from the fifth nodes of healthy plants of the faba bean lines BPL 710 (resistant at all locations) and ILB 1814 (resistant in Egypt but susceptible in Syria, England, and the Netherlands). These leaflets were laid flat on a 2-cm-thick moist sponge that lined the bottoms of galvanized metal pans 90 × 40 × 5 cm. The upper laminal surfaces of leaves were inoculated with an Eppendorf digital pipette (Brinkmann Instruments, Westbury, NY) to deposit 0.1-ml droplets of a suspension containing 600,000 spores of *B. fabae* per milliliter. One droplet was placed on each half of each leaflet, and pans were covered immediately and incubated at room temperature. This test was repeated twice with treatments replicated four times.

The secondary laboratory test was carried out to check the presence or absence of differential interactions and thus be able to distinguish lines with horizontal from those with vertical resistance. On the basis of the frequency distribution of virulence revealed from the first laboratory test, 12 isolates (A_{10}, A_{13}, A_{19}, A_{20}, A_{36}, A_{46}, B_1, B_6, B_7, B_9, B_{44}, and B_{47}) representing the widest possible range of virulence spectra in the mixed inocula A and B were selected. These isolates were used separately to inoculate leaflets from six faba bean lines selected on the basis of their reactions at different locations. These lines were BPL 710, 1196, and 1179-1 (resistant across all locations) and BPL 1763, 1821, and ILB 1814 (resistant in Egypt only but susceptible in Syria, England, and the Netherlands). This test was repeated twice, with treatments replicated four times in a split-plot design. Host materials were placed in the main plot and isolates of *B. fabae* in the subplot. Disease readings were made 6 days after inoculation in both tests.

RESULTS AND DISCUSSION

Chocolate spot reactions varied considerably among different faba bean lines in both first and second screening cycles. Of the 1,730 lines tested in the first cycle, 1,285 were rated resistant and the remaining 445 lines were rated susceptible. Chocolate spot scores on plants of the local check ILB 1814 in this cycle ranged between 3 and 5 with an average of 3.3, indicating a uniform disease pattern throughout this test. Of the 1,285 resistant lines identified in the first cycle and retested more rigorously in the second cycle, only 353 lines remained resistant and 932 lines were rated susceptible. However, chocolate spot scores on plants of ILB 1814 in this cycle ranged between 7 and 9 with an average of 7.4.

The increase in average disease score on plants of ILB 1814 from 3.3 in the first to 7.4 in the second cycle, and the decrease in the number of resistant lines from 1,285 in the first to only 353 in the

Table 1. Faba bean (*Vicia faba*) reactions to *Botrytis fabae* at different locations

Line no.	Germ plasm identification	Origin	Disease reaction[a]								
			Syria[b]				Egypt		England		Netherlands
			1979	1980	1982	1983	1982	1983	1982	1983	1983
1	BPL 710	Colombia	R	R	R	R	R	R	R	R	R
2	BPL 1196	Spain	R	R	R	R	R	R	R	R	R
3	BPL 1179-1	Colombia	R	R	R	R	R	R	R	R	R
4	BPL 261	Greece	R	R	R	R	R	R	S	S	S
5	BPL 266	Greece	R	R	R	R	R	R	S	S	S
6	BPL 274	Holland	R	R	R	R	R	R	S	S	S
7	BPL 470	Lebanon	R	R	R	R	R	R	S	S	S
8	BPL 1055	Turkey	R	R	R	R	R	R	S	S	S
9	BPL 1058	Turkey	R	R	R	R	R	R	S	S	S
10	BPL 1278	Syria	R	R	R	R	R	R	S	S	S
11	BPL 1390	Turkey	R	R	R	R	R	R	S	S	S
12	BPL 1543	Unknown	R	R	R	R	R	R	S	S	S
13	BPL 1544	Unknown	R	R	R	R	R	R	S	S	S
14	BPL 1547	Unknown	R	R	R	R	R	R	S	S	S
15	BPL 1548	Unknown	R	R	R	R	R	R	S	S	S
16	BPL 1550	Unknown	R	R	R	R	R	R	S	S	S
17	BPL 1763	Ethiopia	R	S	S	S	R	R	S	S	S
18	BPL 1821	Ethiopia	R	S	S	S	R	R	S	S	S
19	ILB 1814[d]	Syria	R	S	S	S	R	R	S	S	S
20	Rebaya-40[d]	Egypt	NT[c]	NT	NT	NT	S	S	NT	NT	NT
21	Maris Bead[d]	England	NT	NT	NT	NT	NT	NT	S	S	NT
22	Optica[d]	Netherlands	NT	NT	NT	NT	NT	NT	NT	NT	S

[a] Resistance (R) denotes 1, 3, or 5 and susceptibility (S) denotes 7 or 9 on a disease rating scale of 1–9, where 1 = no disease symptoms, or very few lesions covering up to 1% of leaf surface; 3 = few small discrete lesions covering 1.1–2% of leaf surface; 5 = lesions common, some coalesced, covering 2.1–5% of leaf surface, and poor sporulation; 7 = large coalesced sporulating lesions covering 5.1–10% of leaf surface, some defoliation, and intermediate sporulation; and 9 = extensive lesions on leaves covering more than 10% of leaf surface, severe defoliation, abundant sporulation, stem girdling, and death of most plants.

[b] In Syria, evaluations in 1979 were made with the mixed inoculum A of the first screening cycle, whereas evaluations in 1980, 1982, and 1983 were made with the mixed inoculum B of the second screening cycle.

[c] NT = not tested.

[d] Local faba bean cultivar in respective countries.

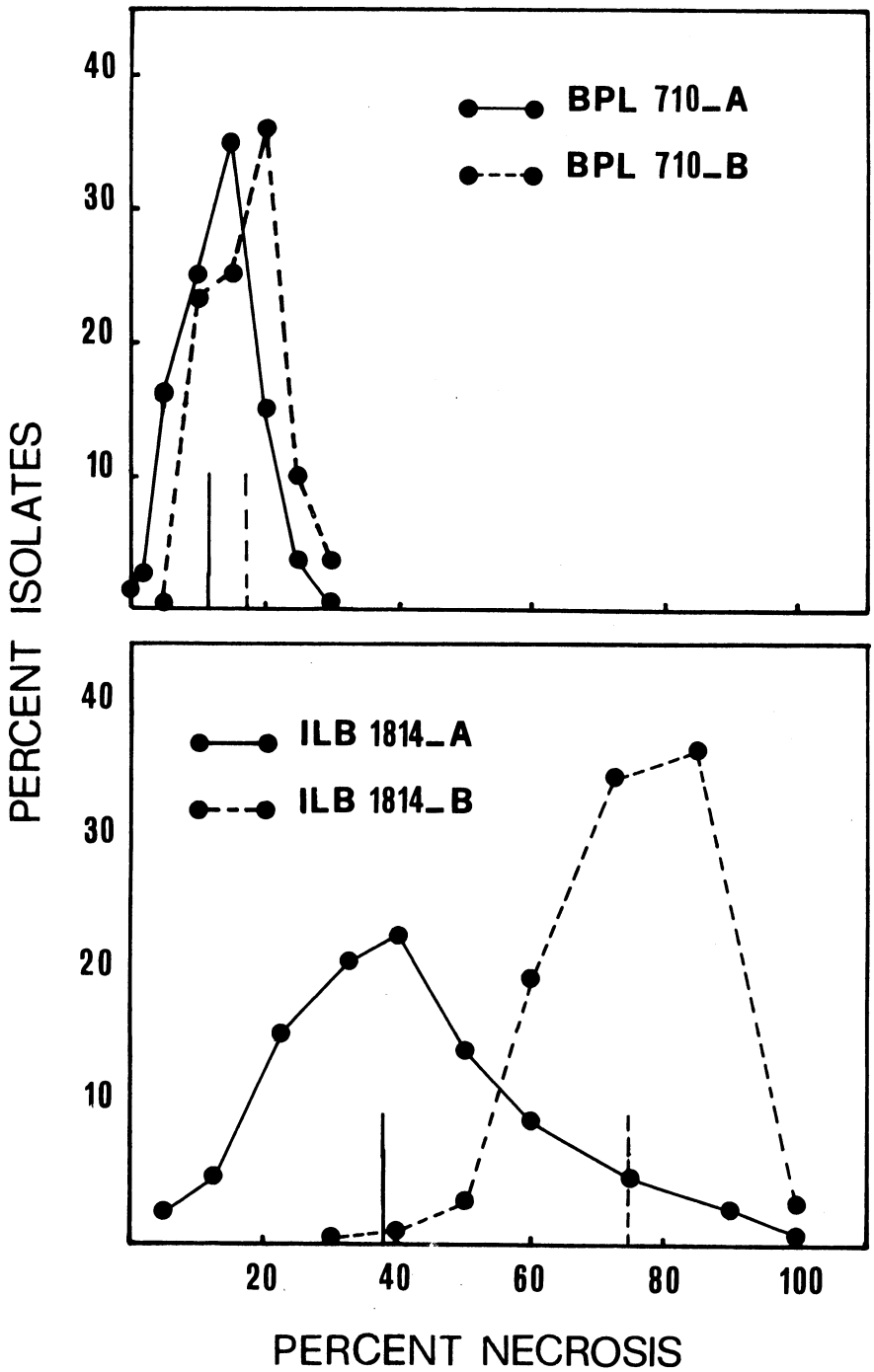

Fig. 1. Frequency distributions of virulence among isolates of *Botrytis fabae* in the mixed inocula A of the first and B of the second screening cycles on faba bean lines BPL 710 and ILB 1814. Means are indicated by solid lines for inoculum A, and broken lines for inoculum B. (Means, standard deviations, ranges, and variances for above curves are shown in Table 2.)

Table 2. Occurrence and distribution of virulence in inocula A of the first and B of the second screening cycles on leaves detached from the faba bean lines ILB 1814 and BPL 710 in the laboratory

Host-pathogen combinations	Disease severity (% necrosis)[y]			
	Mean[z]	SD	Range about mean ($P = 0.05$)	Variance
ILB 1814-B	74.23 a	12.50	49.41–98.85	254.82
ILB 1814-A	39.97 b	18.84	2.86–77.08	355.10
BPL 710-B	17.10 c	5.44	6.39–27.81	29.63
BPL 710-A	12.82 d	5.88	1.24–24.40	34.58

[y] Necrosis on leaves: 0% = no necrosis and 100 = 100% of leaf tissue necrotic.
[z] Pairs of means for each line followed by different letters are significantly different at $P = 0.01$ ($t = 26.88$ for ILB 1814 and 11.31 for BPL 710).

second cycle, were apparently due to certain differences in the frequency distribution patterns for virulence among isolates of inoculum A as compared to inoculum B.

Results from the first pathogenicity test indicated that inoculum B, with greater frequencies of highly virulent isolates of *B. fabae* (Fig. 1) and narrower variation for virulence (Table 2), induced significantly greater disease levels on ILB 1814 and BPL 710 compared with inoculum A. Differences between inocula A and B (Fig. 1, Table 2) were obviously due to the concentration of highly virulent isolates from resistant lines only in B compared with the wide mixture of isolates with high and low virulence (Fig. 1) from susceptible local land races only in inoculum A. The greater frequency of highly virulent isolates in B (Fig. 1) apparently represented a larger sector of the more virulent forms of *B. fabae*, compared with A. Therefore, inoculum B much more efficiently suppressed the expression of all genes for resistance in the 932 lines that had escaped suppression by inoculum A in the first cycle. However, inoculum B did not seem efficient enough to suppress resistance of any of the remaining 353 lines that had also been rated resistant to inoculum A in the first cycle.

Therefore, it would be reasonable to conclude that the two-cycle screening technique, which employed inocula A and B with a wide and a narrow range of variation for virulence, respectively (Fig. 1, Table 2), was efficient in separating the 932 lines with resistance to inoculum A only from the 353 lines with resistance to both inocula A and B. Lines in the first group were believed to carry genes for a narrow-based resistance, compared with those for a broad-based resistance in lines of the second group.

These results agree with those reported by other workers who indicated that mixtures with a wide range of variation for virulence tend to confound narrow-based vertical resistance with broad-based horizontal resistance (11) and that the use of virulent pathogen races for screening the most resistant individuals helps detect new sources for broad-based horizontal resistance (1).

On the basis of local screening, 19 lines representing broad-based and narrow-based resistance were included in the FBICSN to determine their resistance spectra across different geographical regions (Table 1). Of the 19 lines included in this study, only three (BPL 710, 1196, and 1179-1) were rated resistant across all locations, indicating a broad-based resistance to the pathogen. Although lines BPL 261, 266, 274, 470, 1055, 1058, 1278, 1390, 1543, 1544, 1547, 1548, and 1550 were rated resistant in Syria and Egypt, they were rated susceptible in England and the Netherlands, indicating an intermediate range of resistance and

that populations of *B. fabae* in Middle Eastern regions apparently had a narrower range for virulence spectra than those in Northern Europe. However, the remaining three lines (BPL 1763, 1821, and ILB 1814), which were resistant in Egypt only, were rated susceptible in Syria, England, and the Netherlands, indicating a narrow-based resistance to the pathogen and that populations of *B. fabae* in Egypt apparently had the narrowest range for virulence spectra compared with those in other regions.

Results from the FBICSN (Table 1) confirmed findings obtained from the local two-cycle screening technique in Syria. Lines with resistance to both inocula A and B in Syria were either resistant at all four locations (lines 1–3) or at least at two locations (lines 4–16), whereas lines with resistance to inoculum A only in local screening were resistant in Egypt only and susceptible at the remaining three locations (lines 17–19). Therefore, the two-cycle-screening technique and international evaluation helped identify different groups of faba bean lines with narrow-, intermediate-, and broad-based resistance to *B. fabae* that were lacking in the past. These sources have been provided by ICARDA to several national programs and institutions around the world to help stabilize faba bean production, particularly in areas where chocolate spot is serious.

The faba bean lines BPL 710, 1196, and 1179-1 with a broad-based resistance were believed to carry genes for horizontal resistance, whereas lines BPL 1763, 1821, and ILB 1814 with a narrow-based-resistance were believed to carry genes for vertical resistance (Table 1). This was confirmed by exposing these six lines to 12 isolates of *B. fabae* to check the presence or absence of differential interactions (15). In tests repeated two times, lines BPL 710, 1196, and 1179-1 with resistance to both inocula A and B in local screening (Table 1) and with a location-non-specific resistance were consistently rated resistant to all isolates and hence revealed no significant ($P = 0.01$) differential interactions (Table 3). However, lines BPL 1763, 1821, and ILB 1814 with resistance to inoculum A only and with a location-specific resistance (Table 1) revealed consistently significant ($P = 0.01$) differential interactions (Table 3) with different isolates of *B. fabae*. Therefore, it would be reasonable to conclude that lines BPL 710, 1196, and 1179-1 carry genes for a broad-based horizontal resistance and lines BPL 1763, 1821, and ILB 1814 carry genes for a narrow-based vertical resistance to *B. fabae* (15).

On the basis of their virulence on BPL 1763, 1821, and ILB 1814, the 12 isolates of *B. fabae* were classified into five groups, each with a distinct disease pattern (Table 3). Faba bean line BPL 1763 was resistant to all isolates except isolate B_6 in group 5. Line BPL 1821 was resistant to all isolates except those in groups 3 and 4. Line ILB 1814, however, was resistant to isolates in groups 1 and 3 but susceptible to those in groups 2, 4, and 5. Isolates in group 2, which can be distinguished from isolates in group 5 by using BPL 1763 and from those in groups 3 and 4 by using BPL 1821, represent race 1. Isolates in group 3, which can be distinguished from isolates in group 5 by using BPL 1763 or 1821 and from those in group 4 by using ILB 1814, represent race 2. Isolate B_1 in group 4 and isolate B_6 in group 5, which can be distinguished from each other by using BPL 1763 and 1821, represent races 3 and 4, respectively. It was not possible to designate a distinct race status for isolates in group 1 because of the similarity of their reactions across the six faba bean lines included in these tests. It should be noted that all the six isolates representing inoculum B were associated with significant ($P = 0.01$) differential interactions, whereas only two (A_{20} and A_{13}) of the six isolates representing inoculum A produced significant ($P = 0.01$) differential interactions on BPL 1763, 1821, and ILB 1814 (Table 3). Therefore, the greater frequency of genes for vertical virulence in inoculum B made it much more efficient than inoculum A in suppressing the expression of a wider range of genes for vertical resistance carried by lines such as BPL 1763, 1821, and ILB 1814 with a location-specific resistance (Table 1) and significant ($P = 0.01$) differential interactions (Table 3) with isolates of *B. fabae*.

The resistant reactions on BPL 1763, 1821, and ILB 1814 in Egypt and their susceptibility in England and the Netherlands (Table 1) indicated that races 1–4 are apparently much more common in Northern Europe than in the Middle East. Results in Table 1 indicated the possible presence of other races as well in Northern Europe. An in-depth race survey is now being conducted in Egypt. If races 1–4 are not present in that region, as indicated from the results shown in Table 1, then genes for vertical resistance in BPL 1763, 1821, and ILB 1814 can also be used, along with genes for horizontal resistance in BPL 710, 1196, and 1179-1, which are being used effectively. An in-depth survey is also needed in Northern Europe to determine if other races of *B. fabae* are common in that region.

Surveys in Syria indicated that races 1–4 are common in the Tartous, Akkar, Tel-Kalakh and Homs areas but not in the Lattakia area.

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Table 3. Chocolate spot reactions on detached leaves of seven faba bean lines to 12 isolates of *Botrytis fabae* from Syria (in the laboratory)

	Disease reactions to different isolates[a]											
	Group 1				Group 2 (race 1)				Group 3 (race 2)		Group 4 (race 3)	Group 5 (race 4)
Line	A10	A19	A36	A46	A20	B7	B9	B47	A13	B44	B1	B6
BPL 1763	HR	R	R	HR	R	R	R	R	R	R	R	HS
BPL 1821	HR	R	R	HR	R	R	R	R	HS	HS	S	R
ILB 1814	HR	R	R	R	HS	HS	HS	HS	R	R	HS	S
BPL 710	HR	HR	HR	HR	HR	HR	HR	HR	HR	HR	HR	HR
BPL 1196	HR	HR	HR	HR	HR	HR	HR	HR	HR	HR	HR	HR
BPL 1179-1	HR	HR	HR	HR	R	R	R	R	R	HR	HR	HR

[a] HR = highly resistant (1–25% necrosis), R = resistant (26–50% necrosis, very poor sporulation), S = susceptible (51–75% necrosis, intermediate sporulation), and HS = highly susceptible (76–100% necrosis, abundant sporulation).