Inheritance and Nature of Resistance in Beans to *Fusarium oxysporum* f. sp. *phaseoli*

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ABSTRACT

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Strains of *Fusarium oxysporum* f. sp. *phaseoli*, representing two distinct pathogenic races, were used to study the mode of inheritance and the nature of yellows resistance in beans. Analysis of progenies of each of the crosses between four resistant cultivars and a susceptible cultivar indicated that a single gene controls resistance to each race. Resistance to a race from Brazil appears to be controlled by a dominant gene tentatively designated as *Fop 1*. This gene is present in the cultivars Tenderette, Pintado, and possibly Early Gallatin. Resistance to a race from the United States appears to be controlled by an incompletely dominant gene tentatively designated as *Fop 2*. The heterozygous F_1 progeny of the cross of resistant (Preto Uberabinha) and susceptible cultivars displayed a degree of resistance to the U.S. race lower than that of the resistant parent. Resistance to both races of the fungus is expressed by a restriction of distribution and/or growth of the pathogen in the vascular system of inoculated plants.

Additional key words: Fusarium yellows, *Phaseolus vulgaris,* vascular wilt.

Fusarium oxysporum (Schlecht.) f. sp. *phaseoli* Kendrick and Snyder is the causal agent of a vascular wilt of beans (*Phaseolus vulgaris* L.) called Fusarium yellows (10). It has been reported from several regions of the United States (1, 10, 16) but apparently has not reached economic significance. In Brazil, however, Fusarium yellows is regarded as an important disease, especially in certain southeastern areas (6–8).

In a Rhode Island experimental field plot, bean cultivars differed in their reaction to a disease with symptoms of Fusarium yellows (9). Cruz et al (7) found resistance in snap and dry bean cultivars to strains of the fungus isolated in the state of São Paulo, Brazil.

Cardoso (4) in Brazil first indicated the existence of naturally occurring pathogenic races of the Fusarium yellows organism. We recently found new sources of resistance in beans to *F. oxysporum* f. sp. *phaseoli*, identified two races of the pathogen, and listed cultivars as differentials for these races (13).

The work of Cruz et al (7) showed possibilities of controlling Fusarium yellows through host resistance, and breeding of resistant snap beans for the infested areas of Brazil is in progress. This article reports the results of investigations concerning the mode of inheritance and some aspects of the nature of resistance in *P. vulgaris* to *F. oxysporum* f. sp. *phaseoli*. A preliminary report on some of the research has been published (14).

MATERIALS AND METHODS

Two strains of *F. oxysporum* f. sp. *phaseoli* were used: strain 2107-A isolated from diseased specimens of dry bean in Rio de Janeiro, Brazil, and strain ATCC 18131 originally isolated from beans in South Carolina (1). These strains represent distinct pathogenic races of the fungus (13).

Bean seedlings were inoculated by a root-dip technique (13). Unless otherwise specified, the inoculum consisted of suspensions containing about 3×10^5 washed microconidia per milliliter. The cultures were grown on potato dextrose agar (PDA) and were initiated by mass transfers from monoconidial isolates stored in soil tubes. The same tubes were used as sources of inoculum throughout the work. Inoculated plants were kept in an air-conditioned greenhouse at 18–24 C. As reported (13), a relatively cool temperature of incubation (20 C) increased disease severity and prevented escapes in susceptible cultivars. Noninoculated, susceptible checks were included in all tests. Results were recorded after 30 days, and the reactions of individual plants were scored by a disease severity rating (DSR) that ranged from 1 to 5 (13). Plants with a DSR of 1 or 2 were rated resistant, those with a DSR of 4 or 5 were rated susceptible, and those with a DSR of 3 were rated intermediate in reaction.

To estimate the progression of the pathogen within resistant and susceptible plants, stem sections serially taken from the soil level upward were plated on PDA for reisolation of the fungus. Streptomycin sulphate (250 ppm final concentration) was added to the culture media to minimize contamination by bacteria.

Cultivar Bush Blue Lake 274 (BBL 274), susceptible to both races of the pathogen (13), was used as the female parent. Cultivars Tenderette, Early Gallatin, and Pintado are resistant to the Brazilian race (13,14). The cultivar Pintado, a dry bean grown commercially, also is resistant to strains of the organism occurring in São Paulo (7), but it is completely susceptible to the U.S. race (13). These three cultivars were selected as male parents for crosses with BBL 274. The progenies derived from the crosses were used to test the inheritance of resistance to the Brazilian race of *F. oxysporum* f. sp. *phaseoli*.

The cultivar Preto Uberabinha (PUb), another dry bean commonly planted in Brazil, is susceptible to the Brazilian race but highly resistant to the U.S. race (13). Progenies of BBL 274 × PUb were used to test the inheritance of resistance to the U.S. race of the organism.

RESULTS

Resistance to the Brazilian race (strain 2107-A). In the F_1 progenies of BBL 274 × Tenderette, BBL 274 × Early Gallatin, and BBL 274 × Pintado, all individuals were resistant. The degree of resistance of the F_1 plants was comparable to that of the resistant parents. The pathogen was reisolated from the basal parts of the stems of resistant individuals but not from the upper parts. Conversely, it was distributed throughout the entire vascular system of the stems of the most susceptible plants (Table 1). In some instances, resistant individuals showed a slight amount of stunting and chlorosis, but virtually no leaf dropping occurred. Usually they recovered almost completely from the symptoms. Under similar

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testing conditions, susceptible plants were killed at the seedling stage.

The F_2 progenies from selfed F_1 plants of the three crosses segregated in a 3:1 (resistant/susceptible) ratio (Table 2). In backcrosses of BBL 274 × Tenderette and BBL 274 × Early Gallatin to the susceptible cultivar, the F_1 populations segregated in a 1:1 (resistant/susceptible) ratio.

The resistant cultivars Tenderette and Pintado also were crossed. In the F_1 progeny (50 inoculated individuals) all plants were rated as resistant (DSR = 1.3). No segregation occurred in the F_2 progeny because all 125 inoculated plants were resistant (DSR = 1.2) to the fungus.

Resistance to the U.S. race (strain ATCC 18131). This race also infected resistant plants (cultivar PUb), but the fungus (similar to the Brazilian race) was reisolated only from the basal portions of stems. Resistant plants sometimes displayed a shock reaction (stunting and cholorosis), but remission of symptoms eventually occurred. Under the standard testing conditions, all the plants in the F_1 progeny of BBL 274 × PUb behaved as resistant. The degree of resistance of the F_1 individuals was apparently lower (DSR = 1.9), however, than that of the resistant parent (DSR = 1.1). This difference in behavior was fully demonstrated by increasing the inoculum dosage to 3×10^6 conidia per milliliter. With this higher dosage, the F_1 plants showed a variable degree of wilting symptoms (DSR = 2.8), whereas plants of the cultivar PUb still exhibited highly resistant response (DSR = 1.4).

The inoculum dosage of 3×10^5 conidia per milliliter was used to screen the F_2 progeny of BBL 274 × PUb; the F_2 population segregated in a 3:1 (resistant/susceptible) ratio (Table 3). Twenty resistant F_2 plants were selected and allowed to self; seeds were harvested separately from each plant, and the respective F_3 lines subsequently tested (20–25 plants per line). Eight of these F_3 Lines contained resistant plants only; the remaining 12 lines contained both resistant and susceptible individuals. The overall segregation pattern for these 12 segregating lines approximated the 3:1 (resistant/susceptible) ratio. Of 268 inoculated plants, 198 were resistant and 70 were susceptible ($\chi^2 = 0.089$ and $P = 0.80$–0.90 for the hypothesis of 3R:1S).

TABLE 1. Recovery of *Fusarium oxysporum* f. sp. *phaseoli* (Brazilian race) from PDA-plated stem sections of inoculated bean cultivars and crosses

Cultivar and cross	Reaction	Positive recovery (%), soil level		
		to 3 cm	3–6 cm	6–9 cm
Early Gallatin	R[a]	50[b]	30	0
Tenderette	R	45	25	0
BBL 274[c]	S	100	95	85
F_1 (BBL 274 × Early Gallatin)	R	50	30	0
F_1 (BBL 274 × Tenderette)	R	55	35	0

[a]R = resistant. S = susceptible.
[b]Values from 20 plants, 30 days after inoculation.
[c]BBL 274 = Bush Blue Lake 274.

DISCUSSION

The analysis of segregation in the crosses indicated that single genes condition resistance to the races of the organism. The reaction of the F_1 progenies indicated complete dominance over susceptibility to the Brazilian race. The segregation ratios of the F_2 progenies indicated that one dominant gene controls resistance to this race in cultivars Tenderette, Pintado, and Early Gallatin. In cultivars Tenderette and Early Gallatin, the hypothesis was further supported by the segregation ratios observed in the populations of the backcrosses to the susceptible parent. Lack of segregation in the F_2 progeny of Tenderette × Pintado indicated that the same gene for resistance to the Brazilian race operates in both of these cultivars.

The behavior of the F_1 progeny of the BBL 274 × PUb cross indicated that resistance to the U.S. race is incompletely dominant

TABLE 2. Tests for resistance to *Fusarium oxysporum* f. sp. *phaseoli* (Brazilian race) in progenies of crosses between resistant (Tenderette, Early Gallatin, and Pintado) and susceptible (Bush Blue Lake 274) bean cultivars

Cultivar and cross	Plants tested (No.)	Phenotypic segregation		χ^2	P
		Expected ratio	Observed number		
Tenderette	50	All R[a]	50R:0S	···	···
Early Gallatin	50	All R	50R:0S	···	···
Pintado	50	All R	50R:0S	···	···
BBL 274[b]	50	All S	0R:50S	···	···
F_1 (BBL 274 × Tenderette)	72	All R	72R:0S	···	···
F_2 (BBL 274 × Tenderette)	248	3R:1S	188R:60S	0.09	0.70–0.80
BC_1 (BBL 274 × [BBL 274 × Tenderette])	80	1R:1S	38R:42S	0.20	0.60–0.70
F_1 (BBL 274 × Early Gallatin)	72	All R	72R:0S	···	···
F_2 (BBL 274 × Early Gallatin)	248	3R:1S	191R:57S	0.54	0.40–0.50
BC_1 (BBL 274 × [BBL 274 × Early Gallatin])	80	1R:1S	35R:45S	1.25	0.20–0.30
F_1 (BBL 274 × Pintado)	75	All R	75R:0S	···	···
F_2 (BBL 274 × Pintado)	224	3R:1S	158R:66S	1.84	0.15–0.20

[a]R = resistant. S = susceptible.
[b]BBL 274 = Bush Blue Lake 274.

TABLE 3. Tests for resistance to *Fusarium oxysporum* f. sp. *phaseoli* (U.S. race) in progenies of a cross between resistant (Preto Uberabinha) and susceptible (Bush Blue Lake 274) bean cultivars

Cultivar and cross	Plants tested (No.)	Phenotypic segregation		χ^2	P
		Expected ratio	Observed number		
Preto Uberabinha	50	All R[a]	50R:0S	···	···
BBL 274[b]	50	All S	0R:50S	···	···
F_1 (BBL 274 × Preto Uberabinha)	75	All R	75R:0S	···	···
F_2 (BBL 274 × Preto Uberabinha)	215	3R:1S	156R:59S	0.68	0.40–0.50

[a]R = resistant. S = susceptible.
[b]BBL 274 = Bush Blue Lake 274.

over susceptibility, but highly concentrated spore suspensions were required to demonstrate this incomplete dominance unequivocably. At least for practical purposes, therefore, resistance to this race might be regarded as dominant, because under natural field conditions inoculum would rarely approximate the critical levels.

The segregation ratio of F_2 progeny of BBL 274 × PUb indicated that resistance to the U.S. race also is conditioned by a single gene. This hypothesis was further supported by the segregation pattern of the F_3 lines from resistant F_2 individuals. Although the number of plants inoculated was not large, the results indicated that some F_3 lines originated from homozygous resistant and some from heterozygous resistant F_2 plants.

To conform with the gene nomenclature used by Netzer et al (12) and Risser et al (15) for resistance to vascular wilt Fusaria in cucurbits, we propose that: (i) the alleles conferring resistance and susceptibility to the Brazilian race be designated as *Fop 1* and *Fop* $^{+}$*1*, respectively, and (ii) the alleles conferring resistance and susceptibility to the U.S. race be designated as *Fop 2* and *Fop* $^{+}$*2*, respectively. That these two genes are race-specific was evidenced clearly by the fact that certain cultivars (eg, PUb and Pintado) highly resistant to one race were completely susceptible to the other (13).

The results of the attempts at serial reisolation indicated that resistance to both races of the fungus is expressed as a marked restriction of the distribution of the pathogen in the infected plants. This type of resistance has been associated with other Fusarium wilts (2,3); in such cases, the response was partially attributed to the rapid formation of occlusions in the xylem (gels, gums, tyloses, etc.) that reduced or prevented distribution of the pathogen in the host. In other instances, alternative mechanisms of resistance have been proposed. In Fusarium wilt of sweet potatoes, Collins and Nielsen (5) indicated that the pathogen reached the upper portion of resistant plants but that its multiplication was inhibited by a fungistatic condition prevailing in the vessels. Their results agree with those of Mace et al (11) who investigated the mode of resistance in tomatoes to *F. oxysporum* f. sp. *lycopersici*. In the case of Fusarium yellows of beans, serial recovery of the causal agent was performed at a late stage only (30 days after inoculation); hence, the possibility cannot be ruled out that systemic spread of the fungus was unrestricted initially but that fungistasis occurred in the vessels to prevent its further multiplication in resistant plants. The resistance mechanism in beans seemed to operate more efficiently at warm temperatures (24 C or above). Cool temperature (about 20 C), which delayed the growth of the bean plant, also favored the development of external symptoms in some resistant cultivars (13).

The high degree of resistance to *F. oxysporum* f. sp. *phaseoli* present in bean cultivars, along with its simple inheritance, leads to the reasonable assumption that incorporation of resistance into snap bean cultivars adapted to southeastern Brazil should not be too difficult. On the basis of the "long life" of single genes for race-specific resistance to vascular wilt Fusaria in other crops, we believe that control of Fusarium yellows of beans by genetic resistance may be regarded as a promising approach.

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