Inheritance of a Minute Uredinium Infection Type of Bean Rust in Bean Breeding Line 814

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ABSTRACT

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Uromyces appendiculatus isolate S1-5 produces an infection type characterized by a minute uredinium on bean line 814. Cultivars Early Gallatin and Pinto 111 are moderately and fully susceptible, respectively, to S1-5. S1-5 produced the minute uredinium on the F_1 of 814 × Pinto 111. The F_2 segregated in a 3:1 ratio for minute- :large-uredinia infection types. Early Gallatin has a single dominant gene conditioning hypersensitive resistance to *U. appendiculatus* isolate P10-1. The F_1 from 814 × Early Gallatin were resistant to both S1-5 and P10-1. The F_2 segregated in a 9:3:3:1 ratio for resistance to isolates P10-1 and S1-5: resistance only to P10-1: resistance only to S1-5: susceptibility to both isolates. Bean cultivar US#3 has a single dominant gene conditioning a large, sometimes sporulating fleck, when inoculated with S1-5. F_1 progeny of 814 × US#3 produced minute necrotic flecks when inoculated with S1-5. The F_2 segregated in a 12:3:1 ratio: progeny with minute, non-necrotic uredinia grading into minute necrotic flecks: sporulating uredinia surrounded by large areas of necrosis: and large non-necrotic uredinia, respectively. Segregations in the F_3 families of 814 × US#3 agreed with the F_2 segregations. The gene conditioning the minute uredinium infection type in 814 appears to be epistatic to the gene conditioning the necrotic fleck in US#3.

Additional key words: *Phaseolus vulgaris*, specific resistance.

Wingard (5) was the first to study the inheritance of resistance in beans (*Phaseolus vulgaris* L.) to *Uromyces appendiculatus* Fries. He observed in two different crosses that a single dominant gene conditioned resistance. Harter and Zaumeyer (4) identified 20 races of *U. appendiculatus* by using a differential set of seven cultivars. In a later study, Zaumeyer (6) found that single dominant factors commonly conditioned resistance to most of the races of *U. appendiculatus* that he used. He dealt primarily with the hypersensitive type of resistance. The F_2 progeny of a cross between a resistant cultivar and a susceptible cultivar segregated in a 3:1, resistant:susceptible, ratio. However, in the F_3 progeny derived from a heterozygous F_2 plant, variation within the resistant class was observed. Most of the resistant F_3 plants displayed the hypersensitive infection type, while a few had minute-uredinium infection types. Environmental factors were eliminated as the source of variation within the resistant class. Zaumeyer and Harter (6) concluded that a major genetic factor may govern resistance, and that others may govern variation within the range of susceptibility. They stated that variation within the susceptible and resistant class could be accounted for by the presence of segregating background factors which have an effect on infection type.

Bean line 814, when inoculated with *U. appendiculatus* isolate S1-5, produces an infection type 3 (uredinium diameter, 100 μm) based on the scale of Groth and Shrum (3), which is characterized by a minute uredinium. This interaction is readily distinguished from hypersensitive-resistant flecks and susceptible infection types (uredinium diameter, 500 μm). The infection type 3 is unique because of the lack of necrosis associated with the minute uredinium.

Cultivar Early Gallatin has a single dominant gene, designated by Christ and Groth (2) as (Up_2), which conditions a type 1 infection, a minute hypersensitive fleck, in response to isolate P10-1 of *U. appendiculatus*. Early Gallatin is moderately resistant (infection type 4) to isolate S1-5. Cultivar US#3 has a single dominant gene designated by Christ and Groth (2) as (Up_1) which conditions a type 2 resistant infection (small sori with both urediniospores and flecks) in response to isolate S1-5 (3). Cultivar Pinto 111 is susceptible to both S1-5 and P10-1.

The objectives of this research were to determine the inheritance of the minute-uredinium infection type 3 in bean line 814; determine if the resistance in 814 is independent from, linked, or identical to that in US#3, and if resistance in 814 to S1-5 is independent of, or linked with resistance in Early Gallatin to isolate P10-1.

MATERIALS AND METHODS

Seeds of the bean cultivars Early Gallatin, Pinto 111, US#3, and line 814 were germinated in vermiculite, then transplanted to 30.5-cm-diameter pots filled with soil and grown in the greenhouse. Each week, 0.3 g of 10% aldicarb insecticide granules and 12-12-12

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(N-P-K) fertilizer were applied to the soil.

Line 814 was crossed with cultivars Pinto 111, Early Gallatin, and US#3 by the hooking method (1). A tag was looped around the flowers indicating the parents and the date the cross was made. All flowers that were not involved in crosses were removed from plants. Seeds resulting from a cross were harvested when pods were dry.

F_1 seeds were germinated in vermiculite, then transplanted to 305-mm-diameter plastic pots containing steamed soil. Primary leaves of the plants were inoculated before full leaf expansion with *U. appendiculatus* isolates S1-5, P10-1, or both (on separate leaves). The inoculation method of Groth and Shrum (3) was used. The plants were treated with fertilizer and insecticide in the same manner as the parental plants. The F_1 plants were allowed to self-fertilize. The F_2 seeds were removed from the F_1 plants when the plants were dry. The F_2 seeds were germinated and inoculated in 25–20 seedling lots in steel flats containing vermiculite. The infection types on the F_2 plants were determined 12 days after inoculation.

Selected F_2 plants from Pinto 111 × 814, and US#3 × 814, were transplanted to 30.5-cm-diameter pots and were allowed to self-fertilize. The infection types of the families of F_3 progeny were determined as described above.

RESULTS

Two F_1 seeds obtained from the cross of Pinto 111 (susceptible to S1-5) × 814 (resistant to S1-5) produced a resistant type 3 uredinium when inoculated with isolate S1-5 (Table 1). The segregation of the combined F_2 progeny from both families approximated a 3:1 ratio (Table 1). Progeny with infection types 3 and 4 were classed as resistant; those that developed infection types 5 to 8 were classed as susceptible. Although variation from the parental types were observed within resistant and susceptible classes, a discrete difference in uredinium size between infection types 4 and 5 was found, and progeny were readily classed as resistant or susceptible.

Five F_2 plants of 814 × Pinto 111, selected on the basis of their infection type with S1-5, were allowed to self-fertilize to obtain F_3 families. Two of the families derived from resistant F_2 plants that had an infection type 3 did not segregate when inoculated with S1-5; all of their F_3 progeny were resistant. Two other families derived from resistant F_2 families did segregate into an approximate 3:1 ratio when inoculated with S1-5. The fifth F_3 family derived from a susceptible F_2 plant did not segregate; all progeny were susceptible to S1-5 (Table 1).

Three F_1 plants obtained from US#3 × 814 were all resistant to S1-5 and produced minute necrotic flecks. The F_2 generation of the families segregated into three discrete infection types when inoculated with S1-5: minute type 1 flecks grading into type 3 uredinia; uredinia surrounded by large necrotic zones; types 5–8 uredinia. These infection types were grouped according to the observed discontinuity in sizes of uredinia and the presence or absence of necrosis. In this manner, two different resistant classes and one susceptible class were obtained. Progeny with type 1 flecks, minute type 3 uredinia with necrosis, and minute type 3 uredinia were grouped together on the basis of minute infection types into the largest resistant class. Variation within this class was continuous. Infection types with large sporulating uredinia with large areas of necrosis were grouped into the second resistant class. Continuous variation in uredinia size and necrotic area was also observed in this class. The numbers of the F_2 plants in the two resistant and one susceptible classes approximated a 12:3:1 ratio (Table 2).

Two F_2 plants of US#3 × 814, selected on the basis of their infection type with S1-5, were allowed to self-fertilize to obtain F_3 families. One of the families, derived from an F_2 plant with an infection type 3, had progeny that exhibited only minute flecks surrounding a minute uredinium. The other family, also derived from an F_2 with an infection type 3, segregated for the two resistant classes in an approximate 3:1:0 ratio (Table 2).

The cross between 814 and Early Gallatin resulted in an F_1 plant that was resistant to both P10-1 and S1-5. The F_2 progeny of the family segregated consistent with a 9:3:3:1 ratio for resistance to both isolates P10-1 and S1-5: resistance only to P10-1: resistance only to S1-5: susceptibility to both isolates (Table 3).

TABLE 1. Segregation for resistance to *Uromyces appendiculatus* isolate S1-5 in two F_2 families (pooled) and five F_3 families from the cross of bean cultivars 814 (infection type 3) × Pinto 111 (infection type 7)

Family type	Numbers of progeny: Observed Resistant[a]	Observed Susceptible	Expected Resistant	Expected Susceptible	Ratio	*P* value
F_2	83	34	87.75	29.25	3:1	0.3
F_3[b]	20	0	20.0	0.0	1:0	···
F_3[b]	25	0	25.0	0.0	1:0	···
F_3[b]	7	4	8.25	2.75	3:1	0.4
F_3[b]	9	5	10.5	3.5	3:1	0.4
F_3[c]	0	15	0.0	15.0	0:1	···

[a] Infection types 3 and 4 indicate resistance; infection types 5–8 indicate susceptibility.
[b] F_2 Parental plant resistant (infection type 3) to isolate S1-5.
[c] F_2 Parental plant susceptible (infection type 7) to isolate S1-5.

DISCUSSION

We hypothesize that a single dominant gene, designated as (Up_3), conditions the minute uredinium resistance in bean line 814 to *U. appendiculatus* isolate S1-5. This hypothesis is the simplest explanation of the approximate 3:1, resistant:susceptible, ratio seen in the F_2 progeny of 814 × Pinto 111. Two F_3 families derived from resistant F_2 plants segregated in approximate 3:1, resistant:susceptible, ratios when inoculated with S1-5. This indicates that both F_2 plants were heterozygous for resistance at a single locus. Two other F_3 families derived from resistant F_3 plants had only progeny resistant to S1-5. This indicates that both of these F_2 plants were homozygous for resistance. The final F_3 family, derived from a susceptible F_2 plant, had only susceptible progeny. This indicates that the F_2 plant was homozygous recessive for susceptibility.

The approximate 12:3:1 segregation pattern in the F_2 progeny of the cross between US#3 and 814 can be explained by considering that the types resistant to infection by S1-5 in the two parents are conditioned by independent dominant genes and by hypothesizing that (Up_3) is epistatic to (Up_1). A small-lesion infection type (either

TABLE 2. Segregation for resistance to *Uromyces appendiculatus* isolate S1-5 in three F_2 families (pooled) and two F_3 families from the cross of bean cultivars 814 (infection type 3) × US#3 (infection type 2)

Family type	Numbers of progeny: Observed Resistant$_1$[a]	Observed Resistant$_2$	Observed Susceptible	Expected Resistant$_1$	Expected Resistant$_2$	Expected Susceptible	Ratio	*P* value
F_2	179	46	20	183.75	45.9	15.31	12:3:1	0.60
F_3[b]	45	···	···	45.0	···	···	1:0:0	···
F_3[b]	27	11	···	28.5	9.5	···	3:1:0	0.65

[a] Resistant$_1$ = infection types 1 and 3; Resistant$_2$ = infection type 2; and Susceptible = infection types 5–8.
[b] F_2 Parent plant resistant (infection type 3) to *U. appendiculatus* isolate S1-5.

type 1 minute fleck or minute uredinium) characterizes the first and largest resistance class (Table 2). Three-fourths of the members of this class have both the resistance gene (Up_3) from 814 and (Up_1) from US#3. As the (Up_3) gene appears to be epistatic to the (Up_1) gene, resistance to S1-5 in plants with both resistance genes is expressed as the minute infection type characteristic of the gene (Up_3) in bean line 814, with varying degrees of necrosis. This was seen in both the F_1 and F_2 of 814 × US#3. The other resistant class in the F_2 progeny had the infection type 2 characteristic of US#3 (Table 2). The members of this class were either homozygous or heterozygous for the gene (Up_1). The resistance gene (Up_3) was not present. Although variation was seen in all three classes, discrete differences in size of infection type enabled the progeny to be readily assigned to one of the two resistance classes, or to the susceptible class.

Variation within the three segregating classes in the F_2 of 814 × US#3 could have been due to either genetic or environmental sources. Segregating background genes with an effect on expression of infection type may be responsible for the variation seen within the three classes. Environmental variation may also have been present due to differing amounts of fertilizer, sunlight, and water which the F_2 progenies received.

The two F_3 families of 814 × US#3 were consistent with the F_2 results. The genotype of the F_2 plant from which the homozygous resistant F_3 family was derived is hypothesized as ($Up_1 - up_2up_2Up_3Up_3$). The genotype of the F_2 plant from which was derived the F_3 family segregating for resistance is hypothesized as ($Up_1Up_1up_2up_2Up_3up_3$).

The segregation in the F_2 of 814 × Early Gallatin indicates that (Up_2), the gene in Early Gallatin that conditions resistance to isolate P10-1, and (Up_3), the gene in 814 are independent of each other (Table 3).

The suggested genotypes of US#3, Early Gallatin, and 814 are ($Up_1Up_1up_2up_2up_3up_3$), ($up_1up_1Up_2Up_2up_3up_3$), and ($up_1up_1up_2up_2Up_3Up_3$), respectively.

TABLE 3. Parental infection types and segregation for infection types with *Uromyces appendiculatus* isolates S1-5 and P10-1 in one F_2 family from the cross of bean cultivars 814 × Early Gallatin

Bean cultivar	Infection type for: P10-1	S1-5	Numbers of progeny: Observed	Expected	Expected ratio[a]
Early Gallatin	1	4			
814	6	3			
	1	3	29	29.25	9
	1	4	7	9.75	3
	6	3	11	9.75	3
	6	4	5	3.15	1

[a] $P = 0.6$.

The effect of segregating background genes can be seen readily in the variation within the F_2 resistant and susceptible classes of Pinto 111 × 814, and US#3 × 814. It is evident that single genes may condition resistance or susceptibility, while background genes may play a role in the manner in which the resistance is expressed.

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