Genetics of Resistance to *Uromyces phaseoli* in a *Phaseolus vulgaris* Line Resistant to Most Races of the Pathogen

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ABSTRACT

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Tests of F_1, F_2, and F_3 progeny from crosses of the rust-resistant bean (*Phaseolus vulgaris*) breeding line B-190 with the moderately susceptible snap bean cultivar Green Giant 447 to each of eight races of *Uromyces phaseoli*, applied simultaneously, indicated that the resistance to each race was controlled by a monogenic dominant gene. For seven of these races, resistance (R) in B-190 was expressed as a limitation of uredinium size to less than 0.3 mm in diameter. To the eighth race, B-190 had high resistance (HR), in which small necrotic spots, containing no urediniospores, were the only visible symptom; a single gene also governed the response of B-190 to this race. Two of the seven R genes appeared to be allelic, but evidence was obtained that the rest of the R genes and the HR gene were closely linked to one another. The tested monogenic R genes in B-190 were independent of the dominant single genes conditioning R or HR in the pinto cultivar Olathe. The genes in Olathe that conditioned the HR reaction against three races were closely linked to one another and epistatic to the genes that conditioned R against the same races in B-190. B-190 and Olathe each had a single dominant gene for the R reaction to races to which one was resistant and the other susceptible. B-190 and its parent, Mexico 309, have many genes for rust resistance but probably only one for each of the races tested to which they were resistant or highly resistant. Implications of these results for breeding rust-resistant beans are discussed.

Rust, caused by *Uromyces phaseoli* (Reben) Wint., has been severely epidemic in beans (*Phaseolus vulgaris* L.) in the United States in recent years (14,32). Many pathogenic races have been reported for the bean rust fungus since the first systematic identification of races in 1941 (3,4,13,23,28,31). Considerable pathogenic variability in the U.S. collections of the fungus has recently been shown (28). Most field collections of urediniospores contain more than one race (3,28). This high degree of pathogenic variability is not surprising, since *U. phaseoli* is autoecious and macrocyclic and has functional teliospores in at least some major bean production areas (12,31).

Inseparably linked to the existence of many pathogenic races is the existence of many host resistance genes. Most bean cultivars are resistant to at least one or a few races (3,4,7,8,13,26,28). Only a few of the many tested cultivars, however, are resistant to most or all races (4,7,8,26,28). One such cultivar, black-seeded Mexico 309, was resistant to all known races in 1974 (3) and was susceptible at two and at one of the 17 locations in the 1976 and the 1977–1978 International Bean Rust Nurseries, respectively (7,8). Three U.S. races virulent on Mexico 309 were recently identified (28). Mexico 309 was used as a parent in developing a high-yielding Puerto Rican breeding line, B-190, that is immune to *U. phaseoli* there and was resistant to all known continental U.S. races at the time of its release in 1979 (9,30). Eighteen races of the pathogen were recently identified in Puerto Rico (23).

B-190 and Mexico 309 have identical reactions (28) to the 20 recently identified U.S. races, which strongly suggests that their resistance is controlled by identical genes (18,28). To 15 of these 20 races, B-190 and Mexico 309 are resistant, not immune (28). After inoculation they develop minute uredinia, smaller than 0.3 mm in diameter. Field symptoms and yield reduction with this kind of resistance are negligible (20). There has been considerable unpublished speculation that resistance to each race in these lines might be controlled by more than one gene.

Numerous reports have been published on the genetics of resistance to certain races of *U. phaseoli* in certain cultivars of beans (2,3,5,6,15,21,31,33). All of these studies have indicated oligogenic (simple) control of rust resistance in beans (17). Ballantyne (3) determined the genetics of several kinds of rust resistance, using Australian races of the pathogen. Her data gave strong evidence that resistance in beans to single races of *U. phaseoli* is controlled by monogenic dominant factors, regardless of how resistance is expressed. At the time an abstract of the present study was published (25), Kolmer and Groth (15) reported the monogenic dominant control of a minute uredinium reaction in the differential cultivar Kentucky Wonder 814. Christ and Groth (6) have shown a gene-for-gene relationship between virulence in *U. phaseoli* and resistance in beans.

A major objective of the Beltsville bean rust research effort has been to introduce broadly effective rust resistance into breeding lines of the major types of beans grown in the contiguous United States. Because of the high degree of pathogen variability, lines such as B-190 are attractive sources of such resistance. The purpose of the research reported here was to determine the genetics of the rust resistance in B-190.

MATERIALS AND METHODS

Cultivars and races. Seed of rust-resistant B-190 was obtained from G. F. Freytag, Tropical Agricultural Research Center, Mayagüez, PR. B-190 was crossed with two cultivars: Green Giant 447, a snap bean, and Olathe, a pinto bean. Seed of these two cultivars were obtained from their respective breeders, J. E. McCully, Green Giant Co., Le Sueur, MN, and D. R. Wood, Colorado State University, Fort Collins.

U. phaseoli races 39, 40, 41, 42, 43, 45, 46, and 52 (28), all obtained from snap bean production areas, were used in testing the Green Giant 447 × B-190 F_1 hybrids and progeny. The selection of Green Giant 447 that was used here is moderately susceptible to all but one of the races used to inoculate its hybrids and progeny. To races 40, 41, 42, 43, 45, 46, and 52 (28), it develops uredinia

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predominantly 0.3–0.5 mm in diameter; some are larger than 0.5 mm and an occasional one is smaller than 0.3 mm. To these same races, B-190 develops uredinia smaller than 0.3 mm on the abaxial leaf surface and similar small uredinia as well as small necrotic spots less than 0.3 mm in diameter on the adaxial surface. The small uredinia predominate on the adaxial surface. These reactions of B-190 and Green Giant 447 are distinct and easily differentiated. To race 39, B-190 develops necrotic spots less than 0.3 mm in diameter and Green Giant 447 develops larger necrotic spots and small uredinia. So both parents are resistant to race 39, although the resistance is expressed by two distinct, readily differentiated reactions.

On the hybrids and progeny from the Olathe crosses, races 44 and 50 (28) were substituted, respectively, for races 39 and 43. Olathe and B-190 have opposite reactions to two of the races that were used. Olathe develops small uredinia when infected with race 50 and B-190 develops large ones, whereas the reverse is true with race 52. To races 40, 41, and 44, Olathe produces only a necrotic reaction, no uredinia; this reaction is distinctly different from the small uredinium reaction of B-190 to these races. To the remainder of the tested races—42, 45, and 46—the reaction of Olathe is very similar, although not identical, to that of B-190.

Green Giant 447 has white seed and flowers and green stems, whereas B-190 has black seed and purple flowers and stems. Olathe has typical brown and light tan mottled pinto seed, white flowers, and green stem pigmentation. These characters were recorded for all hybrid and progeny plants.

Plant propagation, inoculation, and hybridization. The methods used for seeding, growing, and inoculating the plants for this study were the same as those described previously (27). All seedlings were kept in a rust-free greenhouse until after inoculation and overnight incubation in a dew chamber. Care was taken to inoculate plants only when the primary leaves were 35–65% expanded, which often required inoculating portions of populations seeded at the same

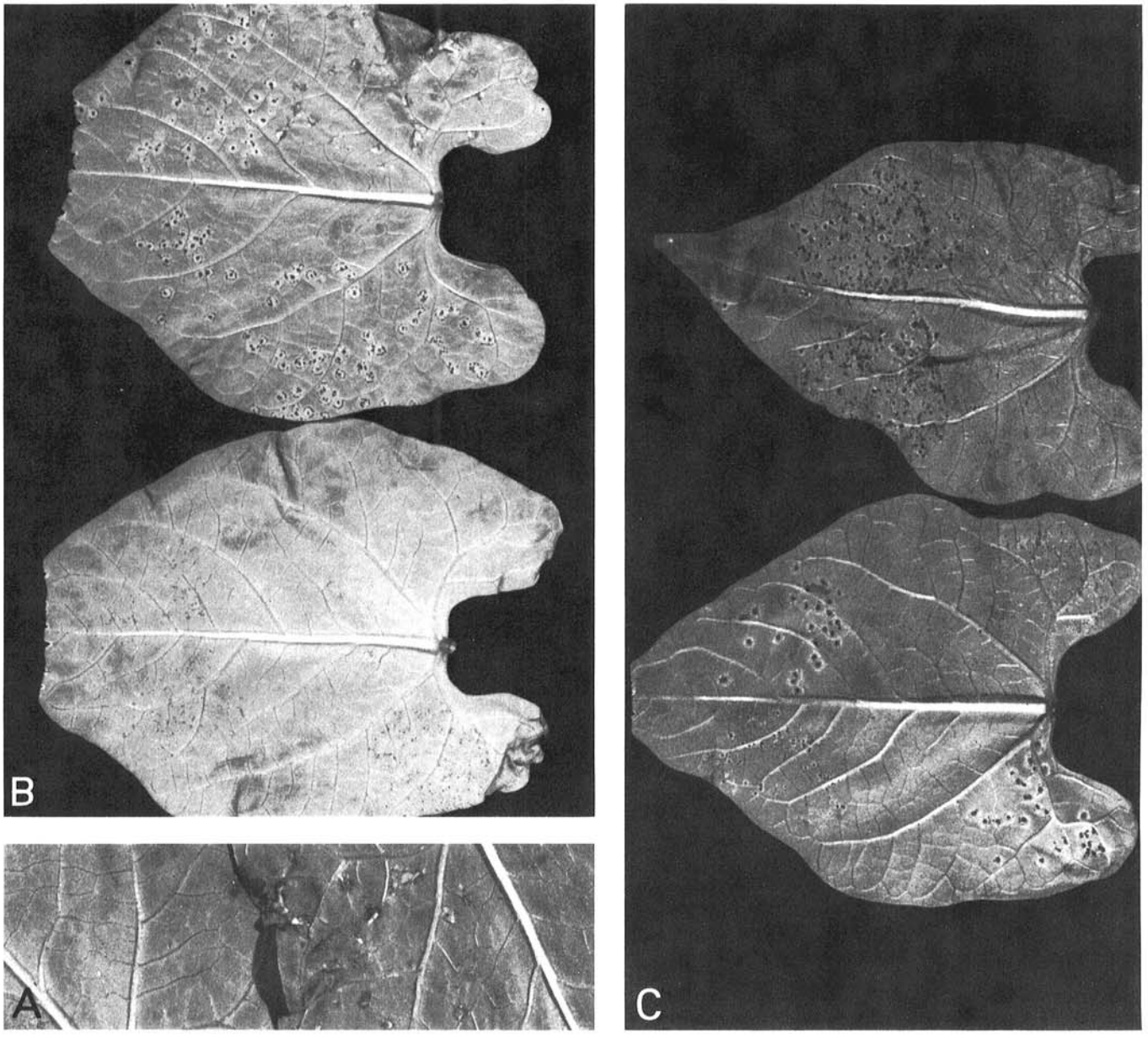

Fig. 1. Bean rust symptoms 15 days after inoculation of Green Giant 447 × B-190 F_2 or F_3 plants with multiple races of *Uromyces phaseoli*. **A,** Barely visible, tiny necrotic spots of the B-190 reaction (left) and large necrotic lesions and small uredinia of the Green Giant 447 reaction (right) in F_2 plants inoculated with race 39. **B,** Monofoliolate leaves from F_2 plants, the upper one from a plant having reactions like the more susceptible Green Giant 447 parent and the lower one, like B-190. Races in each leaf quadrant (clockwise from upper right) are 39, 43, 40, and 41. **C,** Leaves from a recombinant F_3 plant; upper leaf inoculated (clockwise from upper right) with races 39, 43, 40, and 41 and lower leaf, with races 42, 45, 52, and 46. This population of plants had the B-190 reaction to races 42, 43, and 52 and the Green Giant 447 reaction to the other races, as did their F_2 parent. Uredinia with race 52 are slightly larger than those with the other races.

time on two or three different days. The multiple inoculation technique (27) was used for all plants. Eight races were tested simultaneously on each plant. At least four plants of each parent were included in each inoculation. Results were recorded 15 days after inoculation and are reported here according to the grading scale developed at a recent Bean Rust Workshop and used to describe the races (28,29).

All cross-pollinations were done in the greenhouse. Because the bean flower is naturally self-fertilized before the corolla opens, the corollas were opened and the flowers emasculated before the anthers had dehisced. At the time of emasculation, appropriate pollen was applied by touching a dehisced anther to the stigma. The pollinated stigma was then placed back inside the corolla. After being tested for rust reactions, several F_1 and many randomly selected F_2 plants were repotted into 20-cm-diameter clay pots and kept in a greenhouse to obtain selfed seed from each plant. The progeny from each plant were tested separately and records were kept so that each F_3 plant could be traced back to the appropriate F_2 and F_1 parent plants. For establishing the genotypes of individual F_2 plants, results from a minimum of 20 or 14 F_3 plants were required before assuming homozygosity or heterozygosity, respectively.

RESULTS

Reactions. The most resistant reaction was a necrotic spot, less than 0.3 mm in diameter, produced by race 39 on B-190 and on most of the F_2 plants (Fig. 1A). This reaction was considered highly resistant (HR) because of the lack of sporulation. Reactions in which uredinia less than 0.3 mm in diameter were present with necrotic spots or predominated in the presence of uredinia up to 0.5 mm in diameter were classified as resistant (R). Reactions in which uredinia 0.3–0.5 mm in diameter predominated, usually accompanied by uredinia up to 0.8 mm in diameter and with a few uredinia smaller than 0.5 mm, were considered moderately susceptible (MS). In susceptible (S) reactions, uredinia larger than 0.8 mm were present, and in very susceptible (VS) reactions, these large uredinia predominated. These reaction classes were consistent in the greenhouse environment employed for this research (28) and from generation to generation in host cultivars. On B-190, Green Giant 447, and Olathe, the same reactions occurred on the trifoliolate leaves in the field at Beltsville as on the monofoliolate leaves in the greenhouse.

F_1 and F_2 from Green Giant 447 × B-190. All 17 F_1 plants from Green Giant 447 × B-190 reacted to each race in the identical manner as the B-190 parent. From three of these F_1 plants, 160 F_2

TABLE 1. Phenotypic reactions to eight races of *Uromyces phaseoli* of the parents, F_1, and 160 F_2 bean plants from Green Giant 447 × B-190 and the genotypic composition of 57 of the F_2 plants as indicated by tests of F_3 progeny from single F_2 plants

Generation[a]	No. of plants	*U. phaseoli* races, host reactions,[b] and tentative genotypes[c]							
		39	40	41	42	43	45	46	52
P_1	55	2^{++},2^{+},3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3
P_2	55	2	3,2	3,2	3,2	3,2	3,2	3,2	3,2
F_1	3	2	3,2	3,2	3,2	3,2	3,2	3,2	3,2
Parental types									
F_2	119	2	3,2	3,2	3,2	3,2	3,2	3,2	3,2
F_3	11	Ur_AUr_A	Ur_BUr_B	Ur_CUr_C	Ur_DUr_D	Ur_EUr_E	Ur_FUr_F	Ur_GUr_G	Ur_HUr_H
F_3	25	Ur_Aur_A	Ur_Bur_B	Ur_Cur_C	Ur_Dur_D	Ur_Eur_E	Ur_Fur_F	Ur_Gur_G	Ur_Hur_H
F_3	1	Ur_Aur_A	Ur_Bur_B	Ur_Cur_C	Ur_Dur_D	Ur_Eur_E	Ur_Fur_F	Ur_Gur_G	Ur_HUr_H
F_3	1	Ur_AUr_A	Ur_Bur_B	Ur_Cur_C	Ur_Dur_D	Ur_Eur_E	Ur_Fur_F	Ur_Gur_G	Ur_Hur_H
F_2	25[d]	2^{++},2^{+},3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3
F_3	8	ur_Aur_A	ur_Bur_B	ur_Cur_C	ur_Dur_D	ur_Eur_E	ur_Fur_F	ur_Gur_G	ur_Hur_H
Recombinant types									
F_2	2	2^{++},2^{+},3	4,3	4,3	3,4	3,4	4,5,3	4,5,3	3,4
F_3	2	ur_Aur_A	ur_Bur_B	ur_Cur_C	Ur_Dur_D	Ur_Eur_E	ur_Fur_F	ur_Gur_G	Ur_Hur_H
F_2	1	2^{++},2^{+},3	4,5,3	4,5,3	3,4	3,4	4,5,3	4,5,3	3,2
F_3	1	ur_Aur_A	ur_Bur_B	ur_Cur_C	Ur_Dur_D	Ur_Eur_E	ur_Fur_F	ur_Gur_G	Ur_Hur_H
F_2	2	2^{++},2^{+},3	3,2,4	4,3	3,2,4	3,4	4,5,3	4,5,3	3,2,4
F_3	2	ur_Aur_A	Ur_Bur_B	ur_Cur_C	Ur_Dur_D	Ur_Eur_E	ur_Fur_F	ur_Gur_G	Ur_Hur_H
F_2	1	2	3,2	3,2	3,2	3,2	4,5,3	3,2	3,2
F_3	1	Ur_AUr_A	Ur_BUr_B	Ur_CUr_C	Ur_DUr_D	Ur_EUr_E	ur_Fur_F	Ur_GUr_G	Ur_HUr_H
F_2	1	2^{++},2^{+},3	4,3	4,3	3,2,4	3,2	4,5,3	4,5,3	3,4
F_3	1	ur_Aur_A	ur_Bur_B	ur_Cur_C	Ur_Dur_D	Ur_Eur_E	ur_Fur_F	ur_Gur_G	Ur_HUr_H
F_2	2	2^{++},2^{+},3	4,5,3	4,5,3	4,5,3	3,4	4,3	4,5,3	4,5,3
F_3	1	ur_Aur_A	ur_Bur_B	ur_Cur_C	ur_Dur_D	Ur_Eur_E	ur_Fur_F	ur_Gur_G	ur_Hur_H
F_2	2	2^{++},2^{+},3	4,5,3	4,5,3	3,2	3,2,4	4,5,3	4,5,3	3,2
F_3	2	ur_Aur_A	ur_Bur_B	ur_Cur_C	Ur_Dur_D	Ur_Eur_E	ur_Fur_F	ur_Gur_G	Ur_Hur_H
F_2	1	2	3,2	4,3	3,2	3,2	4,5,3	4,5,3	3,2,4
F_2	1	2^{++},2^{+},3	4,5,3	5,4,6	4,5,3	3,4	4,5,3	4,5,3	3,2
F_2	2	2^{+},3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3
F_2	1	5,6,4	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3	4,5,3
F_3	1	ur_Aur_A	ur_Bur_B	ur_Cur_C	ur_Dur_D	ur_Eur_E	ur_Fur_F	ur_Gur_G	ur_Hur_H
Highly resistant		123	0	0	0	0	0	0	0
Resistant		36	124	120	129	132	119	120	130
Moderately susceptible or susceptible		1	36	40	31	28	41	40	30
χ^2		0.30	0.53	0	2.70	4.80	0.03	0	3.33
P		>0.50	>0.30	>0.99	>0.10	>0.02	>0.80	>0.99	>0.05

[a] P_1 = Green Giant 447, P_2 = B-190.

[b] Rust reaction grades are based on a 1–6 scale: 1 = immunity; 2 = necrotic spots without sporulation; 2^{+} and 2^{++} = necrotic spots 0.3–1.0 mm and 1.0–3.0 mm in diameter, respectively; 3 = uredinia smaller than 0.3 mm in diameter; 4 = uredinia 0.3–0.5 mm in diameter; 5 = uredinia 0.5–0.8 mm in diameter; 6 = uredinia larger than 0.8 mm in diameter. Where more than one is given, grades are listed in order of predominance. A 3,2 grade is actually 3,2/3, the abaxial surface being the only one with necrotic spots.

[c] *Ur* = dominant, *ur* = recessive, subscripts A through H = tentative genes from B-190 that condition resistance to each race.

[d] Size 6 uredinia present on two of these plants inoculated with races 45 and 46 and on three inoculated with race 41.

plants were obtained and each was simultaneously tested with eight *U. phaseoli* races (Table 1). The F_2 populations from each of the three F_1 plants reacted similarly, so the data from all three have been combined. In a few cases, infection with one or more of the races was absent or too light to be considered reliable. In all such cases, the F_2 plants were saved and the F_3 from them was used to establish the missing F_2 phenotype. Thus, reactions of all 160 F_2 plants to all eight races were obtained. When the reactions of all F_2 plants to all races except 39 were placed into R or MS-S reaction classes, the segregation ratios gave an acceptable fit to a 3:1 ratio, indicating monogenic resistance to each race. The only possible exception was for race 43, with an excess of resistant plants (Table 1). The reactions of the F_2 plants to race 39 also fit a 3:1 ratio. One F_2 plant, however, had an S reaction to race 39 (Table 1), suggesting epistasis by the gene conditioning HR in B-190 to the gene conditioning R in Green Giant 447 (Fig. 1A) and that these two genes are located in the same chromosomal region. The reactions of 119 and 25 of these F_2 plants to all eight races were identical to the reactions of the B-190 and Green Giant 447 parents, respectively (Table 1 and Fig. 1A,B).

From the spectra of their reactions to the eight races, 16 of the F_2 plants were apparently recombinant types (Table 1 and Fig. 1C). Among these 16 plants were 15 F_2 host-race combinations in which the uredinial size suggested a slightly less resistant reaction than that of B-190. One, one, zero, four, five, zero, zero, and three such reactions (Fig. 1C) occurred with races 39, 40, 41, 42, 43, 45, 46, and 52, respectively (Table 1). Among these 15 plants were also eight host-race combinations that appeared to be slightly less susceptible than that of Green Giant 447 because of the absence of grade 5 uredinia. Two, four, one, and one of these occurred with races 40, 41, 45, and 52, respectively.

Green Giant 447 × B-190 F_3. Seed were obtained from as many of the apparently recombinant F_2 plants as possible, as well as from many random plants having the B-190 reactions and several having the Green Giant 447 reactions. The F_3 results confirmed and supplemented those obtained with F_2 plants (Table 1). The F_3 populations having a total of 173 plants from eight F_2 plants having the Green Giant 447 reactions all gave the same reactions as Green Giant 447. The F_3 populations from 36 F_2 plants having the B-190 reactions segregated 11 homozygous and 25 heterozygous to all races. In two cases, one with race 39 and one with race 52, plants were homozygous HR or R to one race and heterozygous R or HR to the other seven races (Table 1, rows 7 and 8).

The F_3 progeny from the one plant that was susceptible to race 39 (Table 1, row 28) were confirmatory, and two more plants susceptible to race 39 were found in F_3 progeny from heterozygous F_2 plants. Among the other 15 apparently recombinant F_2 plants, F_3 results were obtained for 10 (Table 1). Two of these populations proved to be homozygous for reaction to those races to which they were resistant, and the remaining were heterozygous. The results from these F_3 populations confirmed the F_2 in all cases of suspected recombination. In those cases where the F_2 reaction was apparently MS but lacked grade 5 uredinia, at least a few of these slightly larger uredinia were found on most of the F_3 plants. In those cases where the F_2 phenotype lacked the necrotic grade 2 reaction and included a few grade 4 uredinia, however, this also occurred in the F_3.

Tentative rather than permanent symbols have been assigned to the genes identified here, owing to the lack of sufficient information about their relationship to the already named rust resistance genes in beans (Table 1) (3). I have used the *Ur* symbol approved by the Germ Plasm Committee of the Bean Improvement Cooperative (22) and used in assigning permanent or tentative symbols to more than a dozen rust resistance genes by Ballantyne (3).

Chi-square values were calculated for goodness of fit of all eight of the *Ur Ur* and *Urur* genotypes (Table 1) to a 1:2 ratio. The *urur* group was not included for a 1:2:1 ratio because the number of MS-S F_2 plants from which F_3 progeny were tested was not entirely random. All these chi-squares were less than 1.0, giving probabilities greater than 0.30.

Linkage data for B-190 resistance genes. If inheritance of any two of the B-190 genes for R or HR to specific races of *U. phaseoli* had been completely independent, 90 of the 160 F_2 plants would have been expected to be resistant to both races, 60 to be resistant to one or the other but not both races, and only 10 to be susceptible to both races. The occurrence of 119 plants with the B-190 reactions and 25 plants with the Green Giant 447 reactions *to all eight races* along with only 25 plants resistant to one or more races and susceptible to the remainder (Table 1) indicates that the genes for R and HR in B-190 are inherited as a closely linked group.

The population sizes tested here were too small to allow precise determination of values for the percent recombination among genes in order to construct a linkage map. Trial calculations, using the method of maximum likelihood (1), suggest that at least three to four times as many F_2 plants would need to be tested. The F_3 results confirmed recombinations that indicate seven linked loci for the resistance genes of B-190 to seven of the eight races tested (Table 1). The single exception was the lack of recombinants for Ur_C and Ur_G that condition resistance to races 41 and 46. Calculations based on the data in Table 1 indicate that the greatest distance between any two of the genes occurred between Ur_A and Ur_E, with a recombination value of 9.16%. In a few cases, the calculations gave a rather high chi-square value for goodness of fit to a coupled, random, four-class segregation. The highest was for the recombination percentage between Ur_E and Ur_F, giving a chi-

TABLE 2. Reactions to *Uromyces phaseoli* of bean line B-190, bean cultivar Olathe, and F_2 plants from reciprocal crosses between them

Cultivar or hybrid	Reaction[a]	Pathogenic race, number of plants, χ^2, and P							
		40	41	42	44	45	46	50	52
B-190	HR	0	0	0	0	0	0	0	0
	R	48	48	48	48	48	48	0	48
	MS-VS	0	0	0	0	0	0	48	0
Olathe	HR	48	48	0	48	0	0	0	0
	R	0	0	48	0	48	48	48	0
	MS-VS	0	0	0	0	0	0	0	48
F_2[b]	HR	131	143	0	132	0	0	0	0
	R	43	49	185	39	177	179	142	149
	MS-VS	17	8	15	20	14	17	58	51
χ^2 and P									
3:1	χ^2							1.7067	0.0267
	P							>0.10	>0.98
12:3:1	χ^2	4.6370	5.4733		5.8547				
	P	>0.05	>0.05		>0.05				
15:1	χ^2			0.5333		0.3801	1.9646		
	P			>0.30		>0.50	>0.10		

[a] HR (highly resistant) = necrotic spots without sporulation; R (resistant) = uredinia smaller than 0.3 mm in diameter predominating, often also with necrotic spots; MS-VS (moderately susceptible to very susceptible) = uredinia larger than 0.3 mm in diameter predominating.

[b] Pooled data from 110 plants of B-190 × Olathe and 90 plants of Olathe × B-190. A few plants escaped infection with races 40, 44, 45, and 46.

square of 13.4625, with a probability only greater than 0.001. This high chi-square value was due to the occurrence of only a one-way recombination between the dominant allele of Ur_F and the recessive allele of Ur_E (Table 1).

B-190, Olathe. Olathe and B-190 were each resistant or highly resistant to seven of the eight races used to test the F_1 and F_2 progeny from reciprocal crosses between them. The F_2 segregation patterns obtained from the reciprocal crosses fit the expected ratios for each race, so the data were pooled (Table 2).

The reactions of Olathe and B-190 to all races were controlled by independent, monogenic dominant genes. Reactions of Olathe, B-190, and most of their progeny to races 42, 45, and 46 were so similar that they could not be reliably distinguished on segregating F_2 plants. These reactions could readily be grouped into a distinct R category that included all reactions in which uredinia smaller than 0.3 mm predominated and a second MS-VS category in which uredinia larger than 0.3 mm predominated (Table 2). With all three races, the F_2 chi-square values indicated a good fit to a 15:1 ratio. This ratio suggests that each parent contributed an independent, monogenic dominant resistance gene. With races 40, 41, and 44, three distinct categories occurred: the R and MS-VS reactions and the HR necrotic reaction without sporulation. The F_2 chi-square values for races 40, 41, and 44 all fit a 12:3:1 ratio, again indicating independent single resistance genes from Olathe and B-190. In these cases, the genes conditioning the necrotic reaction type of Olathe were epistatic to the genes conditioning the small uredinium of B-190. Olathe contains a single dominant gene for resistance to race 50 and B-190 contains a single dominant gene for resistance to race 52 (Table 2).

With the Olathe × B-190 crosses, F_3 populations were tested from only 22 of the F_2 plants. These all supported the hypothesized genotypes of their F_2 parents and gave the expected genotypic ratios.

Although the primary purpose for making the Olathe × B-190 crosses was to determine the relationship of the genes in B-190 to the genes in Olathe, the data could be used to determine the existence of linkage among the genes conditioning HR in Olathe. The similarity of the resistance to races 42, 45, and 46 in B-190 and Olathe permitted F_2 plants with recombinant reactions to these races to have come from either parent. The largest number of recombinations occurred between the genes for resistance to races 42 and 45, with five plants being R to one of these races and MS-VS to the other. Three were R to race 42 and MS-VS to race 45 and two were R to race 45 and MS-VS to race 42. Where a 12:3:1 ratio occurred, recombinations for both the Olathe HR genes and the B-190 R genes could be detected. For the Olathe genes for HR to races 40, 41, and 44, evidence of close linkage rather than allelism was found in two plants differing in reaction to races 40 and 44 and in one differing in reaction to 40 and 41. Recombinant F_2 plants also occurred for the B-190 R to races 40, 41, and 44. One F_2 plant gave an R reaction to race 52, an S reaction to race 45, and a reaction to race 44 that indicated the gene in B-190 conditioning an R reaction to race 44 is separate but linked to the other B-190 R genes.

Seed, flower, and stem pigmentation were not linked to the rust resistance reactions of either B-190 or Olathe.

DISCUSSION

The results obtained here indicate that the small uredinium reactions of B-190 to each of seven races of *U. phaseoli* as well as the HR reaction to race 39 are controlled by single dominant genes that are closely linked in coupling to one another. In only one case was recombination between genes for two of the races not detected—between Ur_C and Ur_G, which condition R to races 41 and 46, respectively. These two genes may be allelic. The F_3 results, however, confirmed only one recombinant plant for differentiating Ur_C from Ur_F and Ur_F from Ur_G, indicating tight linkage in this particular region. Hence, a larger population may have given a recombinant to separate Ur_C from Ur_G.

Perhaps most difficult to explain is the lack of numerical equability of reciprocal recombinants for certain races in the B-190 × Green Giant 447 progeny. This was most evident between Ur_E and Ur_F. No such strong imbalances occurred in the recombinations in the Olathe × B-190 F_2 populations.

The occurrence of a few F_2 plants with slightly larger uredinia than occurred on B-190 among the recombinant plants from Green Giant 447 × B-190 may be explained by considering possible effects of the remaining effective genes from the linked complement of genes from B-190. Similar reactions occurred with similar frequency in the Olathe × B-190 F_2 populations. Perhaps the B-190 genes specific for resistance to certain races of *U. phaseoli* enhance the effect of other specific genes, so that when certain of these genes are absent, the remainder are less effective. Another possibility might be that an undetected enhancer gene or genes might be linked in coupling so that in rare plants where the major specific gene is present in the absence of the enhancer, it is slightly less effective. In such an extensive group of linked genes as these results indicate, the possibility that two tightly linked genes could be controlling resistance cannot be eliminated because the number of recombinations between them would be so few that the ratios would still be close to an expected 3:1.

The resistance of B-190 and Mexico 309 to many races in addition to those used here suggests that many more resistance genes may occur in the chromosomal region carrying the genes identified in this study. The Brazilian bean cultivar 1458 reacts to the 20 recently identified U.S. races of *U. phaseoli* in the identical manner as Mexico 309 and B-190 react (28). The identical nature of this range of reactions is strong evidence that all three of these lines carry the same genetic complement for rust reaction (18,28). Carvalho et al (5) have shown that the immunity of 1458 to five Brazilian races is under monogenic dominant control.

Evidence is reported here that at least three individual genes conditioning the HR reaction in Olathe are closely linked but independent of the genes conditioning the R reaction in B-190. B-190 is being used as a source of rust resistance for snap beans as well as pinto beans. The results from the snap bean backcrossing program indicate that the HR of the cultivars BBL 47, Eagle, and Gator Green to the three races to which B-190 is susceptible is controlled by three linked genes (*unpublished*). It appears that linkage blocks of genes for resistance to bean rust may be fairly common. Possibly, repeated gene duplications have occurred in which each duplicate has one or a few changes in its nucleotide sequence.

Closely linked groups of resistance genes have been reported for several other host-pathogen interactions among the rusts and powdery mildews (10,11,16,19,24). Use of the recently reported technique (27) for inoculating individual bean plants with multiple races of *U. phaseoli* has facilitated detection of the recombinant plants that enable identification of such a linkage series.

Ramos (21) speculated that the small uredinium type of resistance to bean rust would be more stable than immunity or HR. The recent identification of three races virulent on B-190 and Mexico 309 suggests this resistance is not stable. My data indicate that this resistance is under monogenic or relatively simple control, which probably explains its lack of stability.

It might be concluded that the monogenic or relatively simple genetic control of the resistances studied here should eliminate them from consideration in breeding rust resistance into bean cultivars for widespread planting. If this is done, the breeder would need to resort to a considerably lower level of resistance, with no assurance that even this level of resistance would be controlled by polygenes for each race. In snap beans, where uredinium development is deleterious to pod quality, such resistance would need to be expressed at a higher level on the pods. Alternatively, the occurrence of more than one series of linked, apparently monogenic factors conditioning R or HR suggests that combining several such linkage groups would yield lines and cultivars with planned polygenic resistance to individual races. Alternatively, they could be individually backcrossed into one seed or pod type to create multilines. To accomplish these objectives, much additional research is needed on the genetics of the resistance of the other broadly resistant lines or cultivars (28), and as other groups of linked resistance genes are identified, the relationship among them should be determined.

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