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Inheritance of resistance to bacterial blight in common bean

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Summary. Inheritance of resistance to common bacterial blight in the trifoliate leaf, plant canopy, and pods was controlled by a single major gene. Additive followed by dominance effects were more important than epistatic interactions. Narrow-sense heritability values ranged from 0.18 to 0.87 for trifoliate leaf, from 0.26 to 0.76 for canopy, and from 0.11 to 0.36 for pods. Observed gains from selection for resistance were higher than expected gains. Implications of these results in breeding for resistance are discussed.

Key words: *Phaseolus vulgaris* – *Xanthomonas campestris* pv *phaseoli* – Genetics of resistance – Genetic gain

Introduction

Common bacterial blight, caused by *Xanthomonas campestris* pv *phaseoli* (Smith) Dye (Xcp), is an economically important disease of common bean (*Phaseolus vulgaris* L.) in tropical and subtropical areas, characterized by high relative humidity and mean growing temperature of ca. 24 °C (Yoshii 1980). The bacteria attack aerial parts of the plant, including leaves, petioles, pods, and seeds. The extent of loss of seed yield and quality caused by Xcp depends upon weather conditions, disease pressure, and degree of susceptibility of cultivars grown. Moreover, the pathogen is transmitted in the seed and, hence, seriously affects germ plasm distribution between and within countries. This also serves as the initial inoculum that starts the disease in subsequent crops. Most commercial cultivars of common bean grown in Latin America are highly susceptible to Xcp, and chemical control is either not completely effective or it is not economical to bean growers.

Sources of resistance to Xcp have been reported in tepary bean, *Phaseolus acutifolius* (Drijfhout and Blok 1987; Schuster et al. 1983; Valladares-Sánchez et al. 1979), runner bean, *Phaseolus coccineus* (Mohan 1982; Park and Dhanvantari 1987), and common bean (Pompeu and Crowder 1972; Rava et al. 1987; Schuster et al. 1983; Valladares-Sánchez et al. 1983; Webster et al. 1980). Resistance from tepary bean (Honma 1956; McElroy 1985; Scott and Michaels 1988) and runner bean (Freytag et al. 1982; Park and Dhanvantari 1987) has successfully been transferred to common bean. However, most of these original and derived sources of resistance are poorly adapted in tropical conditions. At CIAT, resistance from common bean accession PI 207262 and common bean Great Northern cultivars Tara and Jules, which derive their resistance from tepary bean, has been incorporated into a series of tropically adapted lines, including XAN 40 and XAN 112. The objectives were to study the inheritance of resistance of bean lines XAN 40 and XAN 112 to Xcp in different plant parts and to measure genetic gains from selection.

Materials and methods

Common bean cultivars Catu, Ouro, and Rio Doce from Brazil were used as susceptible parents. Lines XAN 40 and XAN 112 were used as sources of resistance to common bacterial blight. Three crosses, Catu × XAN 40, Ouro × XAN 112, and Rio Doce × XAN 112 were made in 1985. Agronomic characteristics of the five parents used in these crosses are given in Table 1. From these crosses two separate experiments were conducted. In one study, the parents, F_1, F_2, and the backcrosses of the F_1 to each parent (BC_1 and BC_2) were evaluated for estimation of gene effects, genetic variances, gene number, degree of dominance, and heritability. In another study, randomly derived F_3 and F_4 families were evaluated for estimation of heritability, and expected and realized gains from selection. Details of each of these experiments follow.

Table 1. Agronomic characteristics of five bean lines used at CIAT-Colombia to study inheritance of resistance to *Xanthomonas campestris* pv *phaseoli*

Identification	Pedigree	Growth habit[a]	Grain type	100-seed weight (g)	CBB reaction[b]
Rio Doce (A 247)	Carioca × BAT 76	II	Cream striped	22	S
Ouro (A 295)	A 30 × Aete 1/37	III	Beige	19	I
Catu (G 15416)	Rio Minas × Preto Común	II	Cream	23	S
XAN 40	BAT 4 × BAT 93	II	Black	24	R
XAN 112	XAN 18 × (G 4495 × G5476)	II	Black	24	R

[a] Growth habits II and III correspond to indeterminate upright bush and indeterminate prostrate, respectively

[b] Reaction of lines to common bacterial blight (CBB) pathogen under field conditions in Colombia: R, I, and S = resistant, intermediate, and susceptible, respectively, based on a 1–9 scale, where 1 is free of symptoms and 9 is severely diseased

Experiment 1. The parents, F_1, F_2, BC_1, and BC_2 of each of the three crosses were evaluated at CIAT-Quilichao, Colombia, during the April–July season of 1987. A randomized complete block design with three replications was used. Each plot consisted of 4 rows, 5 m long and spaced 0.6 m apart; within-row spacing was 8–10 cm. Inoculum was prepared with strain Xcp 123 from Cali, Colombia. Inocula were prepared from 48-h cultures grown on a yeast extract-dextrose-$CaCO_2$-agar medium. The bacterial growth was suspended in tap water and the inoculum was standardized photometrically to 0.3 at 500 μm wavelengths, to approximate a density of 5×10^8 CFU/ml. This suspension was diluted to give a final inoculum potential of approximately 5×10^7 CFU/ml. The fully expanded first or second trifoliate leaf was inoculated 25 days after planting, using the twin-razorblade method (Pastor-Corrales et al. 1981). Plant canopies were inoculated in the late afternoons by a manual backpack sprayer at 40, 47, and 54 days after planting. Young pods were inoculated with a hypodermic needle at three points (Rava et al. 1987). Disease evaluations were made approximately 2 weeks after inoculations. Trifoliate leaves, plant canopy, and pods were evaluated using a 1–9 scale, where 1 = immune and 9 = very susceptible (CIAT 1987). For the twin-razorblade method, an area of 4 cm^2 bordering the inoculation site was used to measure percent area infected. An automatic leaf area meter (Hayashi Denkah model AAC 400) was used to calculate percentage of plant canopy affected by the disease. Similarly, actual infected area on pods was measured to obtain disease scores. Disease scores in each of the three plant parts were transformed into percentage of disease severity by multiplying each disease score by its mean of class intervals. The number of plants scored varied from treatment to treatment (Table 2).

For estimation of genetic parameters, the additive-dominance model of Mather and Jinks (1971) was used. Data were subjected to the individual and joint scaling tests (Mather and Jinks 1971; Singh and Chaudhary 1985) to test the validity of the model. Only data satisfying the digenic model were subjected to further analyses. The same set of data was also used to estimate degree of dominance, narrow-sense heritability, and number of genes controlling the inheritance of resistance, according to Warner (1952).

Experiment 2. The F_2 generations of each of the three crosses used in Experiment 1 were space-planted at CIAT-Palmira, Colombia. Each plot consisted of 12 rows, 7 m long with two replications. Rows were spaced 60 cm apart; spacing between plants within rows was 10 cm. A total of 64, 81, and 121 single plants were randomly harvested from crosses Ouro × XAN 112, Rio Doce × XAN 112, and Catu × XAN 40, respectively. The F_3 families were planted at CIAT-Quilichao, Colombia, in partially balanced lattice designs of 8 × 8, 9 × 9, and 11 × 11 with two replications for the three crosses, respectively. Each plot consisted of a single row, 1 m long with 10-cm spacing between plants within the row. The same amount of seed from each family was saved for planting the next semester. Disease inoculation and evaluation of the trifoliate leaf and plant canopy were the same as in Experiment 1. However, data were taken on five competitive plants in each plot. At maturity, all plants within each plot were harvested in bulk by taking a single pod from each plant. In the subsequent semester, the F_3 and F_4 family lines were planted simultaneously at CIAT-Quilichao in paired plots, using a similar experimental design as in the previous semester for disease inoculations and evaluations. Narrow-sense heritability was calculated by the parent-offspring (F_3–F_4) method of regression (Fernández and Miller 1985), with F_3 and F_4 grown in the same and different semester. The regression coefficients (b values) were then adjusted for inbreeding effects (Smith and Kinman 1965). Realized and expected gains from selection (10% selection intensity) were calculated according to Frey and Horner (1955).

Results

From the individual scaling tests (data analysis not shown), it was found that data for the reaction to Xcp of trifoliate leaves and pods for Rio Doce × XAN 112, of trifoliate leaves and canopy for Catu × XAN 40, and of pods for Ouro × XAN 112 satisfied the additive-dominance digenic model. The additive × additive for plant canopy and additive × dominance interactions for trifoliate leaf were significant ($P < 0.05$) for Ouro × XAN 112. For Rio Doce × XAN 112, additive × additive, additive × dominance, and dominance × dominance interactions were significant ($P < 0.01$) for canopy reaction.

Estimates of gene effects for disease reaction in different plant parts for data satisfying the digenic model are given in Table 3. From the mean genetic effect (*m*), it could be concluded that the Ouro × XAN 112 was the best cross for resistance to Xcp. Additive (*d*) and dominance (*h*) effects were significant ($P < 0.05$) for all plant parts and crosses studied, except for the dominance effect in the trifoliate leaves of Catu × XAN 40. Moreover, the additive effects were greater in the trifoliate leaves for all three crosses, in leaf canopy for Catu × XAN 40, and in

Table 2. Number of plants evaluated and mean reaction to *Xanthomonas campestris* pv *phaseoli* in different plant parts in three crosses of common bean at CIAT-Quilichao, Colombia, 1987

Generation	Plant part	Rio Doce (P_1) × XAN 112 (P_2)		Ouro (P_1) × XAN 112 (P_2)		Catu (P_1) × XAN 40 (P_2)	
		No. of plants	Disease score (%)	No. of plants	Disease score (%)	No. of plants	Disease score (%)
P_1	Trifoliate leaf	220	59.4	221	20.8	229	50.8
	Canopy	202	61.8	196	12.2	162	58.4
	Pod	115	2.5	152	2.4		
P_2	Trifoliate leaf	208	9.6	240	7.3	228	15.7
	Canopy	186	4.2	202	4.3	164	8.0
	Pod	106	1.6	122	1.2		
F_1	Trifoliate leaf	145	31.4	185	14.7	201	32.5
	Canopy	136	40.4	176	11.0	165	53.2
	Pod	102	2.3	102	1.5		
F_2	Trifoliate leaf	457	32.5	504	14.5	482	34.5
	Canopy	435	28.0	481	11.7	341	39.6
	Pod	245	2.2	386	1.6		
BC_1[a]	Trifoliate leaf	139	43.1	181	19.6	214	40.8
	Canopy	138	35.8	175	14.9	158	53.0
	Pod	92	2.4	128	2.0		
BC_2[b]	Trifoliate leaf	146	21.3	188	12.6	219	24.2
	Canopy	139	12.1	173	11.9	171	32.0
	Pod	88	2.1	114	1.5		

[a] BC_1 Backcross to parent P_1

[b] BC_2 Backcross to parent P_2

Table 3. Estimates of mean genetic (*m*), additive (*d*), dominance (*h*), additive × additive (*i*), and dominance × dominance (*l*) interaction effects for reaction to *Xanthomonas campestris* pv *phaseoli* in trifoliate leaf, canopy, and pod for three crosses of common bean at CIAT-Quilichao, Colombia, 1987

Cross	Plant part	*m*	*d*	*h*	*i*	*l*	*P*[a]
Rio Doce	Trifoliate leaf	34.2±0.7	24.6±0.7	−3.1± 1.5			0.75
×	Canopy	43.7±6.6	28.4±0.7	−59.8±16.7	−11.2±6.6	56.4±10.7	0.05
XAN 112	Pod	2.1±0.1	0.4±0.1	0.2± 0.1			0.75
Ouro	Trifoliate leaf	14.0±0.4	6.7±0.4	4.5± 2.1			0.25
×	Canopy	8.2±0.4	3.9±0.4	14.0± 2.4		−3.8± 2.2	0.25
XAN 112	Pod	1.8±0.1	0.6±0.1	−2.3± 0.1		−11.2± 2.8	0.50
Catu	Trifoliate leaf	33.3±0.6	17.6±0.6	−0.2± 1.3			0.75
×	Canopy	32.5±0.8	24.5±0.8	19.0± 1.9			0.75
XAN 40							

[a] *P* is the probability level for the fitness of the additive-dominance digenic model

pods for Rio Doce × XAN 112. Values for dominance effects were negative in trifoliate leaves and canopy reactions for Rio Doce × XAN 112, and in pods for Ouro × XAN 112. For canopy in cross Ouro × XAN 112, dominance effects were positive and greater than additive effects. Additive × additive and dominance × dominance interaction effects in canopy for Rio Doce × XAN 112 and dominance × dominance in canopy and pods for Ouro × XAN 112 were also significant.

Degree of dominance, number of genes controlling the trait, and narrow-sense heritability estimates are given in Table 4. Partial dominance of resistance in trifoliate leaves and pods for the Rio Doce × XAN 112 and in canopy for Catu × XAN 40, complete dominance in trifoliate leaves for Catu × XAN 40, and overdominance in pods for Ouro × XAN 112 were observed. Wherever estimation was possible in all three crosses, only a single major gene was found to be controlling inheritance of resistance in different plant parts studied. Whether it was the same or a different gene was not determined in this study.

Narrow-sense heritability values (h^2) calculated from variance components varied between 0.18 and 0.54 for trifoliate leaves, from 0.34 to 0.76 for canopy, and from 0.11 to 0.36 for pods (Table 4). Estimates of h^2 obtained from parent-offspring regression varied between 0.28 and 0.87 for trifoliate leaves and from 0.26 to 0.69 for canopy (Table 5). In all but one case, values were lower when the F_3 and F_4 generations were grown in the same season as opposed to when the two generations were grown in different seasons. Heritability values were lower for the parent-progeny regression method compared with estimates obtained from components of variance for Rio Doce × XAN 112. The opposite was found for Ouro × XAN 112 and Catu × XAN 40.

Expected genetic gains ranged from 2.5 to 4.5 for trifoliate leaves and from 3.8 to 6.3 for canopy (Table 5). The cross Catu × XAN 40, on the average, gave the lowest values. Also, in most cases, observed gains were higher than expected values.

Simple phenotypic correlation coefficients between disease reaction in trifoliate leaves and canopy, trifoliate leaves and pods, and canopy and pods were 0.83**, 0.78**, and 0.65**, respectively.

Table 4. Estimates of degree of dominance (R), number of effective factors (k), and narrow-sense heritability (h^2) for reaction to *Xanthomonas campestris* pv *phaseoli* in different plant parts of common bean at CIAT-Quilichao, Colombia, 1987

Cross	Plant parts	R	k	h^2
Rio Doce	Trifoliate leaf	0.7	0.9	0.54
×	Canopy			0.76
XAN 112	Pod	0.5	1.1	0.11
Ouro	Trifoliate leaf			0.33
×	Canopy			0.34
XAN 112	Pod	1.9	0.6	0.36
Catu	Trifoliate leaf	1.2	1.5	0.18
×				
XAN 40	Canopy	0.7	1.1	0.34

Table 5. Mean scores in trifoliate leaf and plant canopy for common bacterial blight of unselected and selected F_3 and F_4 families grown in different and same seasons, narrow-sense heritability (h^2) from regression of the F_4 on F_3, and expected (GE) and observed (GO) gains from selection in common bean at CIAT-Quilichao, Colombia, 1987

Cross	Plant part[a]	Year and generation	Mean disease score (%)		h^2	GE	GO	% of F_3 mean
			Unselected	Selected (10%)				
Rio Doce	Trifoliate	1986 F_3	11.5	4.8	0.51	3.4	–	29.8
×	leaf	1987 F_4	17.2	12.8	–	–	4.4	25.6
XAN 112		1987 F_3	16.7	4.5	0.37	4.5	–	27.1
		1987 F_4	–	10.4	–	–	6.8	39.4
	Canopy	1986 F_3	23.6	4.7	0.26	4.9	–	20.8
		1987 F_4	21.9	13.3	–	–	8.6	39.4
		1987 F_3	16.2	2.5	0.46	6.3	–	38.9
		1987 F_4	–	10.8	–	–	11.1	50.7
Ouro	Trifoliate	1986 F_3	8.9	4.1	0.87	4.2	–	47.2
×	leaf	1987 F_4	13.1	9.5	–	–	3.6	27.5
XAN 112		1987 F_3	9.9	3.3	0.57	3.7	–	37.8
		1987 F_4	–	6.6	–	–	6.5	49.7
	Canopy	1986 F_3	11.3	2.1	0.63	5.8	–	51.6
		1987 F_4	14.3	5.4	–	–	8.9	62.4
		1987 F_3	10.6	1.3	0.41	3.8	–	35.8
		1987 F_4	–	7.8	–	–	6.5	45.7
Catu	Trifoliate	1986 F_3	11.7	5.6	0.41	2.5	–	21.6
×	leaf	1987 F_4	19.4	15.6	–	–	4.0	20.4
XAN 40		1987 F_3	22.4	11.2	0.28	3.1	–	14.0
		1987 F_4	–	13.0	–	–	6.6	33.8
	Canopy	1986 F_3	10.4	4.4	0.69	4.1	–	39.7
		1987 F_4	22.8	12.8	–	–	9.9	43.7
		1987 F_3	15.6	3.8	0.37	4.4	–	27.9
		1987 F_4	–	13.1	–	–	9.6	42.3

[a] Inoculated by twin-razorblades in the trifoliate leaf and by aspersion method using a backpack sprayer in plant canopy, respectively

Discussion

Presence of significant interaction effects, especially for plant canopy for Rio Doce × XAN 112 and Ouro × XAN 112, influenced the estimates of additive and dominance effects and did not permit inferences about degree of dominance and gene number. This would require a more complete genetic model and more generations than actually used in this study. Nonetheless, in most cases the additive-dominance digenic model provided a good fit.

In spite of the presence of dominance gene action in some cases, additive gene effects predominated. This suggested that selection for resistance to Xcp should be effective and the performance of parents should be a good indicator of the potential of their crosses for breeding purposes. Predominance of additive gene effects in common bean was also reported by Rava et al. (1987) and Valladares-Sánchez et al. (1983), and in tepary bean by McElroy (1985).

One major gene was found to be controlling disease reaction to Xcp in different plant parts. These results are in agreement with those reported by Adams et al. (1988) for a mutant derived from a *P. vulgaris* snap bean cultivar and by Drijfhout and Blok (1987) in tepary bean. However, Scott and Michaels (1988) reported two complementary dominant genes controlling resistance to Xcp in common bean lines that had derived their resistance from tepary bean.

Narrow-sense heritability estimates for reactions in different plant parts varied from low to moderately high. Similar results were also reported by Coyne et al. (1965) and Rava et al. (1987). Nonetheless, heritability values for two out of three crosses were higher for parent-offspring regression than those obtained from components of variance. In addition to the differences between the two methods of estimation, the higher values for the parent-offspring method could be due to increased homozygosity because of using the F_3 and F_4 generations versus using earlier generations for the components of variance method. In the parent-offspring method, higher heritability estimates were observed when the parent (F_3) and offspring (F_4) generations were grown in different seasons than when both generations were grown in the same season. The former should have reduced environmental effects on disease development and interaction between pathogen and environment, thus causing higher heritability as found in our experiment.

Variation in values of expected response from selection for reaction in different plant parts was often proportional to the differences in their respective heritability values. Moreover, observed gains were often higher than expected values, thus supporting the earlier results of Pompeu and Crowder (1972).

We can make several points regarding inheritance of resistance to common bacterial blight. A single major gene was involved and additive effects were often more important than dominance and epistatic interactions. Narrow-sense heritability estimates were moderately high, and relatively larger observed gains than expected were obtained. All this may suggest that any method of selection would be effective for incorporating Xcp resistance into susceptible common bean cultivars. But there should be ample genetic variation among and within the crosses and a uniform and adequate pressure of the disease in the nurseries. However, since significant dominance and epistatic interactions were found in some cases, and heritability values and expected and realized gains were higher when using F_3 and F_4 generations than when using the parents, F_1, F_2, and backcross generations, this may suggest that in practice bean breeders might be better off delaying selection until F_3 and F_4. In addition, evaluation and selection based on progeny-row performance would be more reliable than selection based on single plants in the F_2. In the latter generations, selection for seed characteristics and other agronomic traits, especially those controlled by recessive genes, might also be facilitated.

It was not clear whether high positive association obtained for disease reaction in different plant parts was due to the pleiotropic effect of the same gene or to tight linkage among genes controlling reactions in different plant organs. Nonetheless, similar results were also reported in tropical and subtropical environments by Webster et al. (1980) and Rava et al. (1987), when they used PI 207262 and/or Mexico 168 as sources of resistance. Rava et al. (1987) and Valladraes-Sánchez et al. (1979, 1983), on the other hand, found independent segregation for disease reactions in pods versus trifoliate leaves in some crosses.

Among the three crosses, Ouro × XAN 112 was found to be the best, followed by Rio Doce × XAN 112 for breeding for resistance to Xcp. The cross Ouro × XAN 112 exhibited transgressive segregations for higher resistance. Several dozen resistant lines possessing commercial seed types have been derived from these two crosses, all involving XAN 112 as a source of resistance. The line XAN 112 derives its resistance from two different parents: PI 207262 and Great Northern Jules from Nebraska, USA. The latter in turn derives its resistance from tepary bean. Since the line XAN 112 itself possesses higher levels of resistance than its parents (S. Beebe, personal communication), this indirectly suggests that the gene(s) for resistance found in common bean accession PI 207262 is different from those occurring in tepary bean, that both groups of genes are complementary, and that they could be combined. This supports the conclusions of Coyne and Schuster (1974). Hence, there is definite merit in searching for newer and different sources of resistance in common bean and its related species, and in making efforts to combine them in currently grown susceptible cultivars.

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