Heritability and Sources of Ascochyta Blight Resistance in Common Bean

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ABSTRACT

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Common bean germ plasm (*Phaseolus vulgaris*) with intermediate Ascochyta blight (caused by *Phoma exigua* var. *diversispora*) resistance has been identified at CIAT. The heritability and inheritance of resistance to this pathogen were studied in three resistant climbing bean sources. Narrow-sense heritability estimates determined by the regression of the F_2-derived F_4 line means on F_2-derived F_3 line means from crosses Carioca (S) × G 10817 (R) and G 10088 (S) × G 10747 (R) were low to moderate (0.19–0.64), depending on the cross and character measured. A generation means analysis of resistant parents G 10817 and G 10823 crossed with the susceptible parent G 12488 indicated that additive, dominance, and epistatic effects were important in the inheritance of resistance. Evaluation of lines for resistance should be conducted in advanced generations in replicated trials.

Additional keywords: black node disease

Ascochyta blight (AB), caused by *Phoma exigua* var. *diversispora* (Bubak) Boerema, can be an economically important foliar disease of common bean (*Phaseolus vulgaris* L.) grown in mid- to high-altitude regions of eastern and central Africa, and Central and Andean America (11,12). The pathogen is favored by a relative humidity greater than 80% and temperatures between 15 and 20 C. Infection of all aerial plant parts can occur, and symptoms include black or brown concentric lesions 1–3 cm in diameter (1) on leaves and pods, as well as collapsed and black nodes, petioles, and stems (1,11). Schwartz et al (11) estimated seed yield losses of about 40% due to AB under moderate disease pressure in a trial in Colombia. Generally, seed yield losses are more severe following early infection and premature defoliation (1).

Genetic variation within common bean and wild *P. vulgaris* for AB resistance is reported to be nonexistent or very low (1,5,10). Greater resistance, including immunity, exists in other *Phaseolus* species, particularly in *P. polyanthus* Greenman (5,9), but attempts to transfer resistance from the secondary gene pool into common bean while maintaining acceptable agronomic characteristics have not been successful. Recently, CIAT researchers evaluated the AB reaction of a large number of common bean germ plasm accessions and breeding lines in the field at Popayán, Colombia, where AB is endemic. Common bean genotypes with intermediate levels of resistance were identified (CIAT, 1989, Bean Program Annual Report, Cali, Colombia). Information on the heritability and inheritance of resistance would facilitate the design of an efficient selection program.

The objectives of this study were to estimate the heritability and gene action of AB resistance in several common bean accessions and to report on additional sources of AB resistance.

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MATERIALS AND METHODS

Heritability. Populations derived from the following crosses were studied: Carioca × G 10817 and G 10088 × G 10747. Resistant parents G 10817 (growth habit IV [2], medium-seeded, pink) and G 10747 (growth habit IV, medium-seeded, black) have consistently scored 4–5 on a 1 (no disease symptoms) to 9 (severely diseased) scale in previous testing at Popayán; G 10747 was also observed to have relatively high AB resistance in Uganda (12). Carioca (growth habit III, medium-seeded, cream) and G 10088 (growth habit I, large-seeded, cream) were AB susceptible. G 10088 × G 10747 generated a few plants with determinant growth habits, but almost all segregants were of indeterminate growth habits III or IV.

F_2 seeds of each cross were sown at Popayán in April 1990, and random F_2 plants were harvested individually in August to begin F_2-derived F_3 ($F_{2:3}$) lines. Sufficient seed to conduct the experiment was the only criterion for choosing $F_{2:3}$ lines; Carioca × G 10817 and G 10088 × G 10747 were represented by 73 and 52 lines, respectively. The $F_{2:4}$ generation was planted from seed bulk harvested from $F_{2:3}$ plants. Crosses were planted 4 October 1990 and 3 April 1991 at Popayán. An experimental unit consisted of a one-row plot, 2 m long. Spacing was 60 cm between rows and 25 cm within rows. Lines were replicated twice and arranged in a randomized complete-block design. Within crosses, parental lines appeared twice in each replication. Plots were fertilized at planting with 10-30-10 (NPK) at a rate of 300 kg ha^{-1} plus 5 kg ha^{-1} Klip Boro B: 20.5%, B_2O_3: 66.1%), 25 kg ha^{-1} $ZnSO_4$, and 10 kg ha^{-1} $MnSO_4$. Seeds were dusted with carboxin at a rate of 2.5 g kg^{-1} seed.

Popayán is located at lat. 2°27′ N, long. 76°36′ W; mean yearly temperature and rainfall are 19 C and 1,830 mm, respectively. Plants were inoculated each season by backpack sprayer at a concentration of 1.2×10^6 spores per milliliter with the Col 10 isolate of *P. e. diversispora,* an isolate originally collected from a diseased common bean plant at Popayán, to promote early disease development. Inoculum production was carried out as described by Schwartz et al (11). $F_{2:3}$ lines were inoculated 29 and 42 days after planting, and $F_{2:4}$ lines were inoculated 30 and 37 days after planting. Percent leaf area affected by AB was estimated for each experimental unit (eight plants) beginning at flowering and continued every 10–21 days (five evaluations). The last evaluation (LE), taken at mid-pod fill, and the area under the disease progress curve (AUDPC) according to Vanderplank (14) were analyzed. AUDPC made use of all disease measurements, while LE was the largest dis-

ease score observed on each experimental unit. Narrow-sense heritability estimates for AUDPC and LE were determined as the regression of $F_{2:4}$ line means on $F_{2:3}$ line means. These heritability estimates are biased upward by small fractions of dominance and dominance epistatic components (13), and are predictive for selection based on $F_{2:3}$ line means without recombination between parental and progeny generations (6).

Generation means. Gene action conditioning AB resistance was studied in two AB-resistant climbing genotypes: G 10817 and G 10823 (growth habit IV [2], medium-seeded, cream). Each resistant parent was crossed as the male with the susceptible G 12488 (growth habit IV, large-seeded, cream) to produce F_1 hybrids. F_1 plants were backcrossed with both resistant and susceptible parents, and selfed to obtain F_2 seed. Parents, F_1, F_2, BC_1, and BC_2 of each cross were evaluated at Popayán from October 1991 to January 1992. Entries were sown on 17 October in 2-m rows spaced 0.6 m apart with 10 plants per row in a completely randomized design replicated twice. Row number per plot differed depending on population size. One row of G 12488 was planted every fifth row to monitor disease distribution and severity. Plants were inoculated as described previously on 15 and 26 November 1991. Percent leaf area affected by AB was estimated on each plant beginning on 16 December and every 11–18 days thereafter until mid-pod fill (five evaluations). Genetic parameters for each cross were estimated for LE and AUDPC by using the coefficients given by Gamble (4) after application of the joint-scaling test of Rowe and Alexander (8).

Germ plasm evaluation. Several thousand common bean accessions and advanced lines were tested for AB reaction in field trials at Popayán, beginning in 1985. Bush types (growth habits I–III) and climbing types (growth habit IV) were evaluated in separate trials. Initially, entries were included in a preliminary trial with 200–400 entries. Bush types were planted in single rows 3 m long, spaced 0.5 m apart; climbing entries were planted in two-row plots 2 m long, spaced 1 m apart. Resistant bush entries were reevaluated in subsequent seasons in four-row plots 2 m long. Resistant climbing types were also reevaluated in additional trials, but plot size remained the same as in the preliminary trials. All trials were replicated twice in a randomized complete-block design. Experimental fields were fertilized at planting with 10-30-10 (NPK) at a rate of 300 kg ha^{-1} plus 25 kg ha^{-1} sodium borate and 25 kg ha^{-1} zinc sulfate; 1 t ha^{-1} dolomitic lime (36% Ca, 20% Mg) was broadcast on the experimental fields before planting every 2 yr. Seeds were dusted with carboxin at 2.5 g kg^{-1} seed, and linuron, metaclor, and glyphosate were applied at recommended rates to control weeds. Plants were inoculated two-to-three times each season as described previously at preflowering and flowering stages, and scored for AB symptoms every 7–10 days after the appearance of symptoms with the CIAT 1 (immune) to 9 (highly diseased) scale (2).

RESULTS

Heritability. AB levels on G 10817 and G 10747 were significantly less than those of the susceptible parents as measured by AUDPC and LE (Table 1). Diseased leaf area of resistant parents was about 10% at mid-pod fill. Significant genetic variation existed in these lines for the traits measured (Table 2). Line-by-season interactions were not significant in crosses and traits except for LE in Carioca × G 10817. Overall, lines performed similarly over seasons. Distributions of line means for AUDPC and LE were continuous in both crosses (*data not shown*). LE means (Table 1) were skewed toward the resistant parent, while AUDPC population means were skewed slightly toward the susceptible parent.

Heritability estimates (Table 2) were low to moderate, depending on the cross and the trait measured. Heritabilities were greater in G 10088 × G 10747 than in Carioca × G 10817. In both crosses, LE estimates exceeded twice their standard errors and were higher than the corresponding estimates for AUDPC. Phenotypic correlations between AUDPC and LE were +0.67 for Carioca × G 10817 and +0.82 for G 10088 × G 10747. LE may have had a higher heritability because disease distribution in the canopy increased at the end of the season when evaluation was easier and perhaps more precise.

Generation means. Both G 10817 and G 10823 developed less disease than G 12488, although resistance was greater in G 10817 than in G 10823 (Table 3). Similarly, the F_2 means of G 12488 × G 10817 for AUDPC and LE were less than those of G 12488 × G 10823. In both crosses, F_1 generation means for LE and AUDPC were at or slightly above the midparent value, but F_2 means fell below the midparent value. Models including the simplest set of genetic effects for both crosses and characters are presented (Table 3). In the case of LE for

Table 1. Parental means, midparent values, and combined $F_{2:3}$ and $F_{2:4}$ population means for two common bean crosses evaluated for Ascochyta blight reaction at Popayán, Colombia

Population/Parent	AUDPC[a]	LE[b]
Carioca (P_1)	661.0 ± 135.0	48.8 ± 11.7
G 10817 (P_2)	108.1 ± 41.9	9.2 ± 4.0
$P_1 - P_2$	552.9**[c]	39.6**
Midparent value	384.6	29.0
$F_{2:3}$ and $F_{2:4}$ mean	410.6 ± 166.9	25.7 ± 7.9
G 10088 (P_1)	568.7 ± 192.3	37.9 ± 4.5
G 10747 (P_2)	331.8 ± 85.2	10.8 ± 4.7
$P_1 - P_2$	236.9**	27.1**
Midparent value	450.3	24.4
$F_{2:3}$ and $F_{2:4}$ mean	538.8 ± 273.7	22.6 ± 12.0

[a] Area under the disease progress curve.
[b] Last evaluation = % leaf area affected at mid-pod fill.
[c] ** = Difference between parents significant at $P = 0.01$ according to t test. Except for the variable LE for G 10088 × G 10747, t tests were performed after data transformation with square root or $\log_{10}$ to homogenize parental variances. Differences between nontransformed means are shown.

Table 2. Line, line-by-season, and error mean squares of the combined $F_{2:3}$ and $F_{2:4}$ generations and narrow-sense heritabilities for two common bean crosses evaluated for reaction to Ascochyta blight at Popayán, Colombia

Evaluation	Carioca × G 10817	G 10088 × G 10747
AUDPC[a]		
Line	27853.5**[b]	74900.9**
Line × season	19434.6	34171.6
Error	16229.9	35122.2
Heritability[c]	0.19 ± 0.11	0.50 ± 0.17
LE[d]		
Line	63.2*	143.6**
Line × season	40.7*	56.6
Error	29.0	50.7
Heritability	0.29 ± 0.13	0.64 ± 0.19

[a] Area under the disease progress curve.
[b] * = Significant at $P = 0.05$; ** = significant at $P = 0.01$.
[c] Values are the regression coefficients ± the standard error.
[d] Last evaluation = % leaf area affected at mid-pod fill.

cross G 12488 × G 10823, the data did not satisfactorily fit the additive-dominance model or any model including the epistatic effects. Because a square root transformation did not improve the fit, the best fitting model for the nontransformed data is given. Additive, dominance, and epistatic effects were important in both crosses for the characters measured. Of the epistatic effects, additive-by-additive effects were significant in both crosses and for both characters. Additive-by-dominance effects were important in G 12488 × G 10823 for LE and AUDPC, and a significant dominance-by-dominance interaction was found for LE in the cross G 12488 × G 10817.

Germ plasm evaluation. Twenty-five *P. vulgaris* entries consistently showed AB-resistant reactions based on three or more seasons of evaluation (Table 4). One *P. polyanthus* accession, G 35182, and AB-susceptible common bean lines G 12488 and A 150 are included for comparison. In addition, all the resistant accessions or lines in Table 4 carry anthracnose (caused by *Colletotrichum lindemuthianum* (Sacc. & Magnus) Lams.-Scrib.) resistance; anthracnose is a serious disease of common bean, and it commonly occurs in regions where AB is a problem. AB scores of the resistant common bean lines/accessions ranged from 3.5 to 5.3 on the 1–9 scale and would be classified as intermediate (2).

DISCUSSION

Boerema et al (1) observed plant death due to AB in pod fill and earlier growth stages in Germany and the Netherlands. However, AB did not kill plants prematurely here, even though two inoculations were applied prior to flowering. This may be because of differences in pathogen strains, the way plants became infected, or environmental conditions. In both seasons, symptoms appeared on plants 7–10 days after inoculation. The disease remained mostly in the lower canopy during the vegetative stages and affected less than 5% of the leaf area. During pod fill, AB severity increased rapidly on susceptible plants, covering the entire canopy and producing necrosis on leaves, pods, and petioles, and eventual plant defoliation. The stage of host development was an important factor affecting disease levels; symptoms were most severe in pod fill and much less severe in earlier growth stages, even though environmental conditions favored the pathogen. Evaluation during pod fill is important, and in crosses where segregation for AB resistance and maturity occur, it is necessary to observe late-maturing lines for disease in mid-pod fill.

Although plants in the experiment were inoculated with the same isolate, Pinzón Perea (7), in a study of pathogenic variation among 40 Latin American isolates of *P. e. diversispora,* observed differences among isolates in host symptom severity but no significant host genotype by isolate interaction. Consequently, we would not expect significant rank changes among the F_2-derived lines, even if one or more additional isolates had been included in the study. Because the experiment was conducted in the field at Popayán, natural infection by other isolates of the AB pathogen was probable.

Resistance in *P. polyanthus* is greater than that found in common bean. G 35182, a *P. polyanthus* accession and a resistant check in AB trials, had an average score of 1.6 (highly resistant) over

Table 3. Generation means with standard errors and estimates of genetic effects for two common bean crosses measured for Ascochyta blight resistance at Popayán, Colombia

Generation	Generation means		Genetic effects		
	LE[a]	AUDPC[b]		LE	AUDPC
G 12488 (P_1)	40.9 ± 8.1	687.6 ± 154.1	m[c]	17.3 ± 0.9	311.8 ± 12.9
G 10817 (P_2)	7.1 ± 2.0	131.5 ± 51.8	a	17.1 ± 0.5	281.2 ± 9.7
F_1	28.1 ± 7.4	420.0 ± 111.6	d	13.0 ± 4.7	216.8 ± 51.3
F_2	17.3 ± 9.6	311.7 ± 144.3	aa	9.0 ± 4.5	207.8 ± 36.6
BCP_1	30.4 ± 10.3	529.9 ± 179.1	ad	...	...
BCP_2	10.6 ± 2.6	213.5 ± 74.6	dd	17.5 ± 6.8	...
			χ^2[d]	2.4	1.2
			P	0.25–0.1	0.75–0.5
G 12488 (P_1)	40.9 ± 8.1	687.6 ± 154.1	m	24.0 ± 0.9	381.0 ± 12.7
G 10823 (P_2)	12.3 ± 3.9	232.5 ± 50.3	a	7.0 ± 1.8	87.8 ± 27.0
F_1	25.0 ± 6.5	481.4 ± 74.9	d	9.2 ± 4.9	231.8 ± 61.8
F_2	22.9 ± 9.2	373.7 ± 132.3	aa	7.4 ± 3.1	197.0 ± 40.8
BCP_1	31.2 ± 7.9	496.7 ± 156.5	ad	−7.3 ± 1.9	−140.7 ± 28.6
BCP_2	24.5 ± 8.7	395.6 ± 103.0	dd	...	...
			χ^2	8.5	1.8
			P	< 0.01	0.25–0.1

[a] Last evaluation = % leaf area affected at mid-pod fill.
[b] Area under the disease progress curve.
[c] m = Mean, a = additive, d = dominance, aa = additive × additive, ad = additive × dominance, and dd = dominance × dominance effects.
[d] Chi-square value for model goodness of fit.

Table 4. Characteristics of selected common bean accessions and lines resistant to *Phoma exigua* var. *diversispora* at Popayán, Colombia

Accession/ line	Origin	Growth habit[a]	Primary seed color	100-seed weight (g)	Seasons evaluated (no.)	AB score[b] ($\bar{x}$)
A 525	CIAT	II	Cream	18	4	4.4
A 643	CIAT	II	Cream	15	4	5.3
AND 398	CIAT	III	White	23	4	4.3
LSA 42	CIAT	II	Cream	50	3	4.9
LSA 112	CIAT	III	Red	41	4	5.0
G 4032	Costa Rica	III	Cream	17	7	4.4
G 7199	Venezuela	III	Black	22	6	5.3
G 10859	Guatemala	III	Black	26	6	3.9
G 18990A	Guatemala	III	Red	28	4	4.2
G 19237A	Ethiopia	III	Red	26	3	4.2
AFR 262	CIAT	IV	Red	19	9	5.1
ASC 1	CIAT	IV	Black	17	8	4.9
ASC 39	CIAT	IV	White	27	4	4.5
ASC 42	CIAT	IV	White	37	4	4.3
G 3367	Mexico	IV	Cream	16	5	4.4
G 6040	Guatemala	IV	Black	20	6	5.2
G 10485	Guatemala	IV	Purple	26	5	5.0
G 10539	Guatemala	IV	Red	22	4	4.5
G 10580	Guatemala	IV	Black	41	5	5.2
G 10747	Guatemala	IV	Black	27	6	4.1
G 10817	Guatemala	IV	Pink	32	4	4.7
G 10823	Guatemala	IV	Cream	26	4	4.5
G 12356	Ecuador	IV	Cream	40	6	4.3
G 12582	Peru	IV	Pink	56	4	4.8
G 20783	Rwanda	IV	Red	28	4	3.5
A 150 (check)		I	Yellow	17	...	7.2
G 12488 (check)		IV	Cream	58	...	7.6
G 35182 (*P. polyanthus*)		IV	Red	79	...	1.6

[a] I = Determinate, II = indeterminate upright bush, III = indeterminate prostrate, and IV = indeterminate climbing.
[b] Average ($\bar{x}$) score based on 1–9 scale where 1 is disease free and 9 is severely diseased.

12 seasons at Popayán (CIAT, 1990, Bean Program Annual Report, Cali, Colombia). CIAT and the University of Gembloux in Belgium have attempted to incorporate resistance from *P. polyanthus* into common bean by interspecific crosses and recurrent selection (9). This approach has so far failed to yield *P. vulgaris* segregants with both high AB resistance and suitable agronomic characters. More information is needed to determine whether the intermediate levels of AB resistance in common bean are high enough to prevent significant yield reductions or to require the assistance of fungicides. If resistance is not high enough, the potential gains from incorporating AB resistance from *P. polyanthus* should be further explored. It may also be possible to increase resistance levels in *P. vulgaris* by selection within populations developed from crossing AB-resistant lines. Exploiting AB resistance within common bean is easier than resorting to interspecific crosses. The germ plasm listed in Table 4 should provide a pool of parents to begin a recurrent selection program to increase resistance. Genetic variability for resistance in climbing types was demonstrated in this experiment. But because heritabilities in F_2-derived lines were moderate to low, and dominance and epistatic effects are perhaps important in conditioning resistance, selection may be best postponed until the F_3 or F_4 generations, when dominance and epistatic effects involving dominance would decrease.

It is noteworthy that nine of the 16 germ plasm accessions (with prefix G) and the *P. polyanthus* accession, G 35182, originated in Guatemala (Table 4); in addition, CIAT-bred lines ASC 39, ASC 42, and AND 398 include Guatemalan parents in their pedigrees. Mounting evidence suggests that common bean land races coevolved with some pathogens or pathogen strains in particular environments (3); perhaps such an interaction occurred between common bean and *P. e. diversispora* in the Guatemalan highlands where AB is endemic. Evaluation of additional highland Guatemalan germ plasm accessions or bred lines descended from crosses involving Guatemalan parents may reveal more resistant germ plasm. Nevertheless, resistant common bean genotypes were also found in a range of germ plasm, including large- and small-seeded materials and beans with bush and climbing growth habits originating in a range of countries.

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