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Inheritance; Low Correlations of Leaf, Pod, and Seed Reactions to Common Blight Disease in Common Beans; and Implications for Selection

Eladio Arnaud-Santana[1], D.P. Coyne[2], K.M. Eskridge[3], and A.K. Vidaver[4]
University of Nebraska, Lincoln, NE 68583-0724

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Abstract. **The heritability of leaf, pod, and seed reactions; stem color and abaxial leaf pubescence; and the association of these traits were studied in advanced dry bean recombinant inbred lines derived from the *Phaseolus vulgaris* crosses 'PC-SO' × XAN-159, 'PC-50' × BAC-6, and 'Venezuela 44' × BAC-6. The reaction to *Xcp* was quantitatively inherited in all three plant organs. Qualitative inheritance was found for stem color and leaf pubescence. Low to intermediate heritability values were obtained for the leaf and seed reactions to *Xcp.* Heritability estimates were consistently low for the pod reaction to *Xcp.* Low nonsignificant Pearson correlations were detected between leaf and pod reactions, leaf and seed reactions, and pod and seed reactions, except for the latter two correlations, which were low and significant in lines from the cross 'PC-50' × XAN-154. Genetic correlations between leaf and pod reactions and leaf and seed reactions were low and significant in lines from all crosses, except for Venezuela 44 × BAC-6 in the latter case. Genetic correlations between pod and seed reactions were low and nonsignificant, except in the cross 'PC-50' × XAN-159, for which a low significant correlation was observed. No significant association was found between *Xcp* leaf reaction and stem color or leaf pubescence. A breeding strategy for improving resistance to *Xcp* in *P. vulgaris* is discussed.**

Common blight (CB), caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye *(Xcp), is an* important disease of dry beans *(Phaseolus vulgaris* L.) worldwide (Saettler, 1989; Zaumeyer and Thomas, 1957). The pathogen is transmitted by seeds (Weller and Saettler, 1980; Zaumeyer, 1930). High temperature (25 to 30C), high relative humidity, frequent rains, and susceptibility are major factors favoring epidemics of this disease (Goss, 1940; Saettler, 1989).

Using dry bean varieties resistant to the *Xcp* pathogen has been suggested as the most effective measure to control this disease (Schwartz and Galvez, 1981). Disease-resistant bean varieties can enable commercial production in regions where this disease is a major production constraint. Some bean varieties and lines resistant to *Xcp* have been developed, and the inheritance of the leaf and pod reaction to *Xcp* has been reported (Coyne and Schuster, 1969; Mohan, 1981; Valladares-Sanchez et al., 1979). A differential reaction of leaves and pods to *Xcp* has been detected in some germplasm (Aggour et al., 1989; Valladares et al., 1979, 1983). However, high positive correlations between leaf and pod reactions to *Xcp* have also been observed in some segregating populations (Rava et al., 1987).

Internal and external seed infections with *Xcp* have been implicated as major sources of inocula causing CB epidemics (Weller and Saettler, 1980; Zaumeyer and Thomas, 1957). The use of seeds free from *Xcp* has been recommended as an important control practice (Weller and Saettler, 1980; Zaumeyer and Thomas, 1957). The process of seed infection and transmission with *Xcp* has been reported (Weller and Saettler, 1980; Zaumeyer, 1930), but there are no reports on the inheritance and heritability of seed reaction in common beans or its inheritance with any bacterial pathogen in any legume.

The major objective of this research was to study the inheritance and heritability of leaf and pod reactions and seed infection to *Xcp* in diverse crosses. The inheritance and association of stem color and leaf pubescence, two easily observed markers, with reaction to *Xcp* were also investigated, since the parents differed in these traits.

Materials and Methods

Crosses, lines, and experiments. Four experiments were conducted under greenhouse conditions at the Univ. of Nebraska, Lincoln. One hundred F_6 lines from the dry bean cross 'PC-50' × XAN-159 and 100 F_6 lines from the cross 'Venezuela 44' × BAC-6 were planted in separate experiments. These F_6 lines were developed using the single-seed descent (SSD) breeding method. Accession 'PC-50' from the Dominican Republic is a red mottled variety susceptible to *Xcp;* XAN- 159 (from the Centro Internacional de Agricultural Tropical) is resistant to *Xcp* (McElroy, 1985); and 'Venezuela 44' (from Venezuela) is a black-seeded variety commercially grown in the Dominican Republic and susceptible to *Xcp.* Accession BAC-6 (from Brazil) is a line resistant to *Xcp* (Mohan, 1981).

Sixty-four F_3BC_2 lines from each of the crosses 'PC-50' × XAN- 159, and' PC-50' × BAC-6 were planted in separate experiments. These lines were developed sequentially using the backcross (BC) and SSD breeding methods (Baker, 1978; Wehrhahn and Allard, 1965). Sixty-four BC_1 pods were obtained by crossing each of the F_1s of the above crosses to the recurrent parent 'PC-50'. One BC plant derived from a seed of each of the 64 pods was randomly selected for backcrossing to the recurrent female parent to obtain another set of 64 BC_2 pods for each cross. The planting process and selection were repeated. Advanced lines (F_3BC_2) were then developed using SSD for two generations. The seeds from

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[1]Former PhD graduate student, Dept. of Horticulture, Current address: Arroyo Loro Experiment Station, San Juan de la Maguana, Dominican Republic.
[2]George Holmes Regents professor, Dept. of Horticulture.
[3]Associate professor, Biometry.
[4]Professor and head, Dept. of Plant Pathology.

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each plant were harvested separately to test lines for leaf, pod, and seed reaction to *Xcp.*

Design. The lines and parents in each experiment were arranged on greenhouse benches in a randomized complete-block design with two replications. The experimental unit consisted of three plants per 15-cm clay pot containing 1.8 liters of a mixture of equal parts (by volume) of sand, peatmoss, vermiculite, and soil (Sharpsburg silty clay loam). The plants were fertilized weekly with 200 ppm of 9N–3.5P–16.5K fertilizer containing trace elements. Greenhouse temperatures ranged between 25 and 28C, and the natural day length ranged from 12 to 16 h from April to July 1991.

Bacterial strains and inoculation procedures. Bacterial strains V_3S_8 and V_4S_1 (source: Dominican Republic) were grown on MXP medium (a semi-selective medium for *Xcp)* (Claflin et al., 1987) for 24 to 48 h. Bacterial growth was transferred to 25 ml of 0.01 M potassium phosphate buffer (PB), pH 7.1, and diluted to read 0.1 on a spectrophotometer (Spectronic 20; Bausch and Lomb, Rochester, N. Y.) at 640 nm. Further dilutions were transferred into 250 ml of PB to give a concentration of 10^7 colony-forming units/ml.

Inoculations were conducted within 30 min after bacterial suspensions were prepared. For leaf inoculations, two leaflets of the first fully expanded trifoliolate leaf of each plant were inoculated using the multiple needle method (Andrus, 1948). A buffered saline solution was used as the control in the remaining third leaflet foliate of each trifoliolate. For seed inoculations, a puncture was made with a dissecting needle at the beginning of the pod suture (as far as possible from the first seed) on each fully expanded green pod (two pods per plant) containing completely developed seeds. Then, 10 µl of bacterial suspension was deposited through the puncture inside the pod using a pipette tip of a Pipetteman (Rainin Instrument Co., Brighton, Mass.). A new pipette tip was used to inoculate each line in each replication. This method ensured that a similar amount of the inoculum suspension was deposited inside each pod.

Leaves were inoculated 20 days after planting (9 Apr. 1991). Pods were inoculated at different times due to differences in flowering date and stage of pod development of the lines. Symptoms of CB such as necrosis, water soaking, and chlorosis appeared on the leaves 5 to 6 days after inoculation and were restricted to the inoculated area. Variable sizes of water-soaked areas on the inoculated pods appeared 5 to 6 days after inoculation. Symptoms occurred along the pod suture or along the sides of the pod walls.

Disease rating scales. The rating scales used to evaluate the symptoms on the leaves and pods were as follows: a) leaves: percentage of inoculated area with symptoms; b) pods: resistant= $0 \leq x < 1$ mm (x = length of water-soaking lesion from the point of inoculation), slightly resistant = $1 \leq x < 2$ mm, slightly susceptible =$2 \leq x < 3$ mm, susceptible= $3 \leq x < 4$ mm, and highly susceptible = $x > 4$ mm.

Dissecting-scalpel blades and forceps were used to open the pods and remove the seeds in sequential order from the pedicel end. Seed infection was assessed by aseptically plating the seeds obtained from the inoculated pods (when dried on the plant) of each entry in a 150- × 15-mm petri dish containing MXP medium. Seeds were plated on one side only. Seeds were incubated for 4 to 5 days at 28C in the dark. Each seed was rated as positive (+) *(Xcp* present on the medium) or negative (-) *(Xcp* not detected). The presumptive *Xcp* colonies were pale yellow, convex, and mucoid and were surrounded by a zone of starch hydrolysis.

Other traits. Stem color, red (complete or partial) vs. green, of the F_6 lines was recorded in two experiments. Abaxial leaf pubescence of the F_3BC_2 lines were rated in two experiments as 1 = glabrous to 9 = highly pubescent (Oviedo et al., 1989).

Statistical analysis. The number of genes determining traits in the inbred-BC populations was calculated using the inbred-BC method as described by Wehrhahn and Allard (1965). "The expected number of inbred-backcross lines carrying a specific gene from the donor parent and forming a non-parental class is NP where N is the number of inbred-backcross lines, P is approximately $(1/2)^{K+1}$, and K is the number of backcrosses" (Baker, 1978). The approximate 95% confidence interval for the observed number of lines in the nonparental class is NP ± 2[NP(1 – P)] (Wehrhahn and Allard, 1965). In the two inbred populations tested here, K= 2, N = 64, P = 1/8, and NP = 8, with an approximate 95% confidence interval of 8 ± 5.29. "The probability is $(1/2)^{2K+2}$ that two specific but unlinked genes will be incorporated into a line" (Wehrhahn and Allard, 1965). In this case, P = 1/64 and NP = 1, with an approximate 95% confidence interval of 1±2.0. Using the additive rule of probability, the probability of at least one of two specific unlinked genes being incorporated into-a line is $2(1/2)^{K+1}$ - $(1/2)^{2K+2}$. Thus P = 15/64 and NP = 15, with an approximate 95% confidence interval of 15 ± 6.78. Similar reasoning was used to determine 95% confidence intervals for the number of lines incorporating at least one of three specific unlinked genes (21 ± 7.93) and at least one of four specific unlinked genes (26* 7.86). To apply the method of Wehrhahn and Allard (1965), it was necessary to count the number of lines that showed a significant resistance improvement over the recurrent parent, 'PC-50'. Such lines were identified as those with mean responses more than $\sqrt{MSE}$ units below the mean reaction of 'PC-50'.

Analysis of variance were conducted using the Statistical Analysis System (SAS, 1982). The chi-square test was used to assess goodness-of-fit of genetic ratios in predicting responses of discrete traits. Heritabilities of the reactions to *Xcp* in the different plant organs were calculated using the components of variance method (Fehr, 1987; Hallauer and Miranda, 1988). Heritability of the *Xcp* seed reaction was based on the proportions of infected seeds per replicate and line. The associations of discrete traits were tested using the chi-square goodness-of-fit procedure. The association of quantitative traits was assessed using Pearson and genetic correlations for pairs of traits (Robertson, 1959; Steel and Torrie, 1980). Fisher's exact test (Steel and Tome, 1980) was used for each individual line to determine if the location of the seed in the pod (either next to the point of inoculation or not) was related to the presence or absence of infection.

Results

Number of genes affecting leaf, pod, and seed resistance to Xcp. For the F_3BC_2 'PC-50' × BAC-6 cross, there were 19 lines that showed a significant improvement in leaf resistance over that of 'PC-50' for both strains of *Xcp,* Since 19 fell within the three confidence intervals of 15 ± 6.78, 21 ± 7.93, and 26 ± 7.86, this result indicated that the presence of at least one of two, three, or four major unlinked genes was necessary before a line expressed leaf resistance. For the F_3BC_2 'PC-50' × XAN- 159 cross, there were nine and 32 lines that showed a significant improvement of leaf resistance over that of 'PC-50' for strains V_3S_8 and V_4S_1, respectively. Since nine fell in the confidence intervals 8 ± 5.29 and 15 ± 6.78, it seemed that at least one of one or two major genes must be present before leaf resistance was observed for the V_3S_8 strain. Thirty-two fell inside 26* 7.86, a result indicating that at least one of four major genes was necessary before leaf resistance to *Xcp* strain V_4S_1 was present. For the F_3BC_2 'PC-50' × BAC-6 cross, 25 lines showed a significant improvement of pod resistance over that

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of 'PC-50', while the F_3BC_2 'PC-50' × XAN-159 cross had nine lines with significantly Improved pod resistance. Since nine fell in the confidence intervals 8 ± 5.29 and 15± 6.78, pod resistance for the 'PC-50' × XAN-159 cross seemed to be controlled by the presence of at least one of one or two major genes. The 25 improved lines in the 'PC-50' × BAC-6 cross indicated the presence of at least one of three or four major genes before pod resistance was present, Twenty-three and 18 lines showed significant improved seed resistance over 'PC-50' for the F_3BC_2 'PC-50' × W-159 and 'PC-50' × BAC-6 crosses, respectively. These values fell in confidence intervals, a result that indicated that at least one of two, three, or four genes win-needed for seed resistance in the 'PC-50' × BAC-6 cross, while at least one of three or four genes was needed for seed resistance in the 'PC-50' × XAN-159 cross.

Heritability of reactions in different plant parts to Xcp. Due to a wide range of responses, quantitative inheritance patterns were determined for the leaf, pod, and seed reactions of the F_3BC_2 and F_6 lines to one or more strains of *Xcp*. The distributions of the leaf and pod reactions of the lines were skewed toward susceptibility, except in the F_6 'Venezuela 44' × BAC-6 cross, for which the leaf reactions were skewed toward the resistant class (data not shown) (Arnaud-Santana, 1992). Low heritability values for leaf and pod reactions were found, except that intermediate values were detected for leaves of F_6 'PC-50' × XAN-159 (0.35 and 0.41) (Table 1). For seed infection, moderate heritabilities were found for the F_6 (0.53) and F_3BC_2 (0.44) 'PC-50' × XAN-159 and the F_6 'Venezuela 44' × BAC-6 (0.36) (Table 2). Several resistant F_3BC_2 lines (rating classes 2 and 3) were identified, a result indicating that lines with a high level of resistance in leaves and pods can be obtained using the inbred BC method.

Lines were grouped into three reaction classes (Table 2). A low number (11 and 3) of resistant lines occurred in the F_3BC_2 lines,

Table 1. Mean ratings (X), heritabilities (H), Pearson correlations (r), and genetic correlations (r_g) for leaf and pod common blight disease reactions after inoculation with strains of *Xanthomonas campestris* pv. *phaseoli (Xcp)* for lines from several dry bean crosses (greenhouse, Lincoln, Neb., 1991).

Generation	Plant organ	*Xcp* strain	No. of lines	X	H	r Leaf/pod	r_g Leaf/pod
P_1 PC-50	Leaves[z]	V_3S_8	1	48.8[z]			
P_2 XAN-159	Leaves		1	0.5			
F_3BC_2 P_1 x P_2 lines	Leaves		64	47.3	0.32		
P_1 PC-50	Leaves	V_4S_1	1	75.0			
P_2 XAN-159	Leaves		1	3.0			
F_3BC_2 P_1 x P_2 lines	Leaves		64	49.4	0.14	0.16	0.27*
P_1 PC-50	Pods[y]	V_4S_1	1	4.0			
P_2 XAN-159	Pods		1	1.2			
F_3BC_2 P_1 x P_2 lines	Pods		64	2.9	0.12		
P_1 PC-50	Leaves	V_3S_8	1	75.0			
P_3 BAC-6	Leaves		1	3.0			
F_3BC_2 P_1 x P_3 lines	Leaves		64	55.5	0.08		
P_1 PC-50	Leaves	V_4S_1	1	75.0			
P_3 BAC-6	Leaves		1	3.0			
F_3BC_2 P_1 x P_3 lines	Leaves		64	58.0	0.15	0.06	−0.25*
P_1 PC-50	Pods	V_4S_1	1	4.0			
P_3 BAC-6	Pods		1	1.0			
F_3BC_2 P_1 x P_3 lines	Pods		64	3.4	0.10		
P_1 PC-50	Leaves	V_3S_8	1	52.5			
P_2 XAN-159	Leaves		1	3.0			
F_6 P_1 x P_2 lines	Leaves		100	49.6	0.35		
P_1 PC-50	Leaves	V_4S_1	1	37.5			
P_2 XAN-159	Leaves		1	0.5			
F_6 P_1 x P_2 lines	Leaves		100	53.5	0.41	0.13	0.23*
P_1 PC-50	Pods	V_4S_1	1	4.4			
P_2 XAN-159	Pods		1	1.0			
F_6 P_1 x P_2 lines	Pods		100	2.4	0.13		
P_3 BAC-6	Leaves	V_3S_8	1	3.0			
P_4 Venezuela 44	Leaves		1	63.8			
F_6 P_3 x P_4 lines	Leaves		100	18.4	0.30		
P_3 BAC-6	Leaves	V_4S_1	1	3.0			
P_4 Venezuela 44	Leaves		1	37.5			
F_6 P_3 x P_4 lines	Leaves		100	34.6	0.23	0.09	0.30*
P_3 BAC-6	Pods	V_4S_1	1	1.0			
P_4 Venezuela 44	Pods		1	3.2			
F_6 P_3 x P_4 lines	Pods		100	2.0	0.27		

[z]Leaf rating scale: percentage of inoculated area with symptoms.

[y]Pod rating scale for length of water-soaking lesion (x): resistant = $0 \le x < 1$ mm, slightly resistant = $1 \le x < 2$ mm, slightly susceptible = $2 \le x < 3$ mm, susceptible = $3 \le x < 4$ mm, and very susceptible = $x > 4$ mm.

*Significant at $P \le 0.05$.

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Table 2. Frequency distributions of F_6 and F_3BC_2 lines and parents for *Xanthomonas campestris* pv. *phaseoli (strain* V_4S_1) seed reaction rating classes, mean of diseased seed probabilities (X), LSD values and heritabilities (H) of seed reaction, and Pearson *(r)* and genetic *(r_g)* correlations for disease reactions in leaf, pod, and seed for lines derived from three bean crosses (greenhouse, Lincoln, Neb., 1991).

	No. of lines										
	Seed reaction classes[z]			No. of				r		r_g	
Generation	1	2	3	lines	X	H	LSD	1	2	1	2
P_1 PC-50			1	1	0.7						
P_2 XAN-159	1			1	0.1						
F_6 P_1 x P_2 lines	24	33	43	100	0.6	0.53	0.3	0.30*	0.26*	0.38*	0.33*
P_1 PC-50			1	1	1.0						
P_2 XAN-159	1			1	0.1						
F_3BC_2 P_1 x P_2 lines	11	20	33	64	0.6	0.44	0.3	0.23	0.01	0.38*	0.04
P_1 PC-50			1	1	0.9						
P_3 BAC-6	1			1	0.1						
F_3BC_2 P_1 x P_3 lines	3	22	39	64	0.5	0.26	0.4	–0.15	–0.11	–0.40*	–0.14
P_4 Venezuela 44			1	1	0.9						
P_3 BAC-6	1			1	0.1						
F_6 P_3 x P_4 lines	54	35	11	100	0.2	0.36	0.4	0.07	0.02	0.13	0.12

[z]Seed reaction classes based on the following range of probabilities for seed infection: 1(resistant)is 0 to 0.111; 2 (moderately susceptible) is 0.112 to 0.3; 3 (susceptible) is ≥ 0.311.
[y]1 = Correlation between leaf and seed reactions. 2 = pod and seed reaction.
*Significant at $P \leq 0.05$.

while the expected higher number of resistant lines (24 and 54) occurred in the F_6 lines from the two crosses. The line distributions were skewed toward susceptibility, except in the cross 'Venezuela 44' × BAC-6, for which they were skewed toward resistance.

The relation of *Xcp* seed infection to the position of seeds within the pods was different in each experiment. A Fisher exact test was conducted for each line (data not shown); however, the test could not be computed for some lines since some lines did not express presence and absence of infection. In the two F_6 populations, 73% and 75% of the lines from the two crosses did not show a significant association (data not shown). In the two F_3BC_2 populations, 87% and 78% of the lines from both crosses also failed to show a significant association, a result indicating that seed location within the pod was not an important factor for *Xcp* seed infection among those lines. However, seed position in a pod was an important factor in the two resistant parent lines and for the resistant lines in all of the populations from the different crosses.

Inheritance of other traits. A good fit to a 3:1 ratio ($X^2 \approx 0.00$, $P > 0.99$; $X^2 = 0.33$, $P > 0.5$) of green to red stem color was obtained in the F_6 lines 'PC-50' × XAN-159 and 'Venezuela 44' × BAC-6, respectively, a result indicating qualitative inheritance. It is hypothesized that green stem color is controlled by each of two different dominant genes, with red being recessive.

F_3BC_2 lines 'PC-50' × BAC-6 and 'PC-50' × XAN-159 separated into glabrous (10, 10) and pubescent (54, 54) leaf classes, respectively, for both crosses. A good fit to a 1:9 ratio of glabrous to pubescent lines ($X^2 = 1.67$, $P > 0.10$) was obtained for both crosses. It is hypothesized that a single dominant gene primarily determined pubescent leaves, with glabrous being recessive.

Association between leaf, pod, and seed reactions. No significant Pearson correlations were found between the leaf and pod reactions to *Xcp* in any population; however, small significant *(P* < 0.05) genetic correlations were found for all populations (Table 1). Small significant Pearson correlations were detected between the leaf and pod and seed reaction (Table 2). Small significant genetic correlations between leaf and seed infection were found for most populations, while only one genetic correlation was significant for pod and seed infection (Table 2). This result suggested somewhat independent genetic control of these two reactions in seeds and pods.

Association between leaf reaction to Xcp and other traits. No significant correlations were observed in the F_6 lines 'PC-50' × XAN-159 and 'Venezuela 44' × BAC-6 between the leaf reactions to the bacterial strains and stem color. No significant associations were observed between leaf reactions to *Xcp* and leaf pubescence in the F_3BC_2 lines 'PC-50' × XAN-159 and 'PC-50' × BAC-6.

Discussion

Leaves and pods. The quantitative inheritance of the leaf reactions to the two *Xcp* strains tested agrees with previous reports (Aggour et al., 1989; Valladares-Sanchez et al., 1979; Webster et al., 1983). The general finding that several major genes were involved in leaf and pod reactions seems to agree in part with the results of McElroy (1985), who reported that resistance to *Xcp* seemed to be under simple genetic control in the segregating populations from which XAN- 159 was selected. Other authors found that, in common bean, the leaf reaction to *Xcp* was determined by minor genes (Mohan, 1981; Valladares-Sanchez et al., 1979).

The heritability estimates for leaf reactions ranged from low to intermediate values. Low to moderately high heritability values for leaf reaction to *Xcp* have been reported by other researchers (Aggour et al., 1989; Coyne et al., 1965; Valladares-Sanchez et al., 1979). Pod-reaction heritability estimates were generally low in our populations. Aggour et al. (1989) and Valladares-Sanchez et al. (1983) also reported low heritability estimates for pod reaction to *Xcp* in common beans, The latter group of authors used two of the genotypes reported here in crosses. In general, pod reaction heritability estimates were nearly similar to the leaf reaction heritability estimates.

Seed infection. The large number of lines having significantly

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improved seed resistance compared to that of the recurrent parent 'PC-50' suggested that several major genes had a significant effect on *Xcp* seed infection. The number of lines in the more resistant parent class was five times more than those in the susceptible parent class. This difference in seed infection between these lines and the others agrees with the results for pod and leaf reactions (bacterial strains V_3S_8 and V_4S_1). Parent mean differences were significant in the four experiments ($P = 0.05$). Seed position analysis showed that the first seed in XAN- 159 and BAC-6 pods was generally infected with *Xcp.* Only on rare occasions was an infected seed found in the second position in a BAC-6 pod and never beyond that point. Sometimes all of the seeds in the susceptible 'PC-50' and 'Venezuela 44' pods were infected. Seed infection was higher in the two populations derived from XAN- 159 (resistant parent) than in the two populations derived from BAC-6 (other resistant parent) crosses, a result indicating that BAC-6 transmitted a higher level of resistance to seed infection. The intermediate heritability values suggest that high resistance to seed infection may be selected for by growing advanced lines in replicated trials inoculated with *Xcp* instead of selecting on a single-plant basis in earlier segregating generations.

Other traits. The inheritance pattern of stem color agrees with the findings of Coyne and Steadman (1977). One major dominant gene was found to control pubescence in both crosses, a result that agrees with the findings in some crosses by Zaiter et al. (1990). The uniformity of 'PC-50' for the pubescence trait indicated little influence of environment on its expression, a result that agrees with Oviedo et al. (1989) and Zaiter et al. (1990). Single-plant selection for pubescence or stem color would be expected to be effective in early segregating generations.

Association between traits. No significant associations were found between the leaf and pod reactions to *Xcp* strains in any of the lines tested. Pearson and genetic correlations between pod and seed reaction to *Xcp* were small, probably because it was possible to isolate *Xcp* from apparently clean seeds coming from symptomless pods. However, it was not possible to obtain clean seeds from severely infected pods (^{3} 4-mm lesions). Discoloration, typical of seeds infected with *Xcp,* came from visibly infected pods. These observations agree with those of Aggour et al. (1989), who reported the isolation of *Xcp* from apparently symptomless seeds. Small Pearson and genetic correlations indicated relative independence of reactions to *Xcp* in these different plant organs, a result suggesting that it should be possible to develop recombinant genotypes with resistance to *Xcp* in pods, seeds, and leaves.

The association of *Xcp* seed reaction with seed location in the pod was significant for some lines but not for others. However, the number of lines not showing a significant association was much larger than those that did. The lack of significant association indicates that the position of the seeds in the pod in relation to the point of pod inoculation was not an important factor in determining if the seeds would become infected. For example, in some cases it was observed that the first seed in the pod near the inoculation site was the only uninfected seed. For those lines showing a significant interaction, only certain seeds were infected. This observation was noted in the two resistant parents in which the first seed was generally the only one infected. Only on rare occasions did seeds in the second position in the pod become infected.

The lack of significant associations between leaf reaction to the bacterial strains with stem color and pubescence in the populations tested indicates that resistance to *Xcp* can be readily combined with these traits. Pubescence is associated with nonspecific resistance to the rust fungus (Shaik, 1985) and is currently being used in the Nebraska dry bean breeding program. The heritability estimates of the reaction to *Xcp can* be considered narrow-sense heritabilities, since nearly homozygous lines (F_6) were tested. Most of the genetic variance between lines would be additive and additive x additive. These heritability estimates are also biased upward since the populations were tested in only one environment. Experiments need to be conducted in different locations (nurseries) to obtain more precise estimates of heritabilities.

In summary, because of the low heritabilities of the reactions to *Xcp* in these plant organs and the low associations or near independence of reactions, it is necessary to test for the reactions to *Xcp* in the organs in replicated tests to isolate recombinant lines with high levels of resistance to *Xcp*. Breeding for resistance to *Xcp* and nonspecific resistance to rust due to leaf pubescence should not be difficult because of the independence of these traits in inheritance.

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