Resistance to Common Bacterial Blight among *Phaseolus* Species and Common Bean Improvement

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ABSTRACT

Common bean (*Phaseolus vulgaris* L.) is highly susceptible to common bacterial blight (CBB), caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye. High levels of cultivar resistance would minimize yield losses, reduce bactericide use and production costs, and facilitate integrated disease-and-crop management and the production and distribution of pathogen-free seed. We aimed to (i) assess the levels of CBB resistance of different *Phaseolus* species in the tropics, (ii) determine the CBB reaction of resistant cultivars and advanced breeding lines, and (iii) report on CBB resistance of lines developed from *P. vulgaris* × *P. acutifolius* (tepary bean) hybridization and gene pyramiding at CIAT. Between 1994 and 1998, we evaluated, in the field, 162 accessions of tepary, scarlet runner (*P. coccineus*), lima (*P. lunatus*), and common beans, 119 CBB-resistant cultivars and advanced breeding lines of common bean, and six lines recently developed by interspecific hybridization and gene pyramiding. For inoculation, we used aspersion, surgical blades, and/or multiple needles. The highest levels (scores of 1.2–2.0) of CBB resistance were found in *P. acutifolius* accessions, G40029 and G40156, followed by *P. lunatus* (scores of 4.2–6.2), *P. coccineus* (scores of 4.8–5.5), and *P. vulgaris* (scores of 4.5–6.4). Resistance available in *P. coccineus* and *P. vulgaris* landraces has already been transferred to common bean. But resistance transferred from *P. acutifolius* was much lower (scores of 3.8–4.5) than those available. Gene pyramiding produced lines with high CBB resistance (scores of 1.5–2.4), and is thus, a suitable method for developing CBB-resistant cultivars of different market classes.

COMMON BEAN is a legume crop of worldwide significance (Singh, 1992). In the tropics and subtropics, it is frequently and severely attacked by CBB, a systemic (Burkholder, 1921), seed-transmitted (Aggour et al., 1989b) disease caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye (*Xcp*) (Saettler, 1989; Schuster and Coyne, 1981).

CBB is widespread in Latin America, particularly in northwestern Argentina, south central Brazil, Venezuela, Central America and Cuba, and coastal Mexico. These regions typically grow small-seeded, susceptible cultivars of the common bean race Mesoamerica (Singh et al., 1991).

The pathogen attacks all aerial plant parts, including leaf petioles, pods, and seeds, but the characteristic symptoms of chlorotic borders around the necrotic lesions are more severe and conspicuous on leaves of susceptible cultivars. Similarly, the movement of bacterial populations through vascular tissue may depend on the level of CBB resistance (Goodwin et al., 1995). Susceptible cultivars accumulate larger bacterial populations, these moving faster through vascular tissues, than do CBB-resistant genotypes. CBB-infected seeds with visible symptoms can lose their color or are stained and their value is thus lowered. However, planting infected seeds does not necessarily result in systemic transmission of the bacteria from the vascular tissues of the grown plants to the new seeds (Aggour et al., 1989b).

Bacteria can survive for months on plant debris left on the soil and in seeds (Gilbertson et al., 1990). Severity of yield losses varies according to cultivar, levels of infection, environment, and stage of crop growth. Heavy and early infection, high humidity, temperatures fluctuating between <20 and >25°C, and alternately dry and wet weather can cause more than 40% yield loss in susceptible cultivars (Serracin et al., 1991). Other factors influencing disease severity are photoperiod (Arnaud-Santana et al., 1993a), inoculation method and bacterial concentration (Aggour et al., 1989a), and stage of crop maturity at infection (Coyne and Schuster, 1974). A *Phaseolus* genotype may also show resistance in leaves, but susceptibility in pods, or vice versa; it may also be resistant to some strains of the bacterium but susceptible to others (Aggour et al., 1989a).

Disease incidence can be reduced by intercropping, for example, with maize (*Zea mays* L.) (Fininsa, 1996) or by chemicals such as copper hydroxide and potassium methyldithiocarbamate, particularly when applied early. However, chemical control does not significantly reduce pod infection nor is seed yield increased (Weller and Saettler, 1976). Cultivar resistance is thus the most effective strategy, and is pivotal to all other CBB control measures, including integrated disease-and-crop management practices.

Moderate resistance to CBB has been found in common bean; comparatively higher levels in some scarlet runner bean (*P. coccineus*) accessions and the highest levels in tepary bean (*P. acutifolius*) (Coyne and Schuster, 1973; Mohan, 1982; Yoshii et al., 1978). Although more than 80% of *P. acutifolius* cultivars are highly resistant to CBB, fewer than 25% of wild *P. acutifolius* accessions possess similar resistance (CIAT, 1996).

In common bean, a single recessive gene controls CBB resistance in trifoliolate leaves of an induced mutant, Bulgarian snap bean line A-8-40 (Adams et al., 1988). CBB resistance is also inherited quantitatively, with predominance of additive gene action and low to high heritability (Arnaud-Santana et al., 1994; Silva et al., 1989). Eskridge and Coyne (1996), using inbred-backcross data, estimated that between one and five genes control CBB resistance. Studies involving DNA-based (RAPD, RFLP) markers support the existence

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Abbreviations: CBB, common bacterial blight; cfu, colony forming units; GNN #1 Sel 27, Great Northern Nebraska #1 Selection 27; QTLs, quantitative trait loci; *Xcp*, *Xanthomonas campestris* pv. *phaseoli*.

of two to six quantitative trait loci (QTLs) responsible for CBB resistance in common bean (Jung et al., 1996; Nodari et al., 1993).

In *P. acutifolius*, three linked dominant genes (one for a different isolate of *Xcp*) were identified as controlling CBB resistance (Dursun et al., 1996; Freytag, 1989). But Drijfhout and Blok (1987), after crossing resistant (PI 319443) and susceptible (Oaxaca 88 and PI 313488) *P. acutifolius*, reported a single dominant gene to be responsible for CBB resistance in leaves and pods.

McElroy (1985) concluded that one major and a few minor genes controlled resistance in lines XAN 159, XAN 160, and XAN 161, which were developed at CIAT from a *P. vulgaris* × *P. acutifolius* (PI 319443) population received from the University of California-Riverside. Kolkman and Michaels (1994) reported that both tepary bean accessions PI 319443 and PI 440795 carried identical genes for CBB resistance. But in F_2 populations among crosses of OAC 88-1 (CBB resistance introgressed from PI 440795 at the University of Guelph, ON, Scott and Michaels, 1992), XAN 159, and XAN 161, segregation for susceptibility was observed, suggesting that a different gene for resistance was probably transferred from the *P. acutifolius* in each of these genotypes. Nonetheless, CBB resistance in OAC 88-1 and XAN 159 is linked to the same RAPD marker (P.N. Miklas, 1997, personal communication).

All breeding and genetic studies on CBB resistance in Latin America have been carried out within the last 25 yr. The sources of CBB resistance often used were those initially introgressed from tepary bean at the University of Nebraska, Lincoln, for example, GNN #1 Sel 27, Tara, and Jules (Coyne and Schuster, 1969, 1970). But because photoperiod and temperature are known to affect common bean's reaction to CBB (Arnaud-Santana et al., 1993a) and because these Nebraska sources of CBB resistance are poorly adapted to the tropics (Webster et al., 1983), better tropical adaptation was sought (Beebe and Pastor-Corrales, 1991; Mohan and Mohan, 1983). A major breakthrough in breeding for CBB resistance was achieved when lines XAN 159, XAN 160, XAN 161, and OAC 88-1 were developed from new *P. vulgaris* × *P. acutifolius* crosses.

CBB-resistant lines have also been developed from *P. vulgaris* × *P. coccineus* crosses in Puerto Rico (Freytag at al., 1982; Miklas et al., 1994) and Canada (Park and Dhanvantari, 1987). Recently, CBB resistance from GNN #1 Sel 27, PI 207262, and XAN 159 have been combined with other resistance genes at CIAT and in Brazil, Puerto Rico, and USA. These sources of CBB resistance are also being transferred into common bean cultivars of different market classes.

Hybridization between *P. vulgaris* and *P. acutifolius*, by embryo rescue, was initiated at CIAT, Palmira, Colombia, in 1989 (Mejía-Jiménez et al., 1994). More than 10 000 advanced-generation progenies were obtained from recurrent and congruity backcrosses (i.e., backcrossing alternately to either species) of the interspecific F_1 hybrids and gene pyramiding (i.e., combining different sources of CBB resistance genes). For the last 5 yr, these progenies have been systematically screened under field conditions at CIAT's Quilichao Experiment Station, Colombia, giving rise to six CBB-resistant lines.

This paper compares the levels of CBB resistance available in some promising accessions of four *Phaseolus* species, the levels of CBB resistance introgressed from the primary, secondary, and tertiary gene pools into common bean lines and cultivars, and the levels of CBB resistance of lines developed from gene pyramiding. It also discusses difficulties faced so far and suggests alternative breeding strategies and methods for future needs.

MATERIALS AND METHODS

All germplasm screening and breeding studies for CBB resistance were carried out in the field at Quilichao. Between 1994 and 1998, 162 promising germplasm accessions of common (38 accessions), lima (35), scarlet runner (55), and tepary (34) beans were systematically screened for CBB reaction. Also screened were 70 advanced breeding lines from different programs around the world and reported CBB-resistant lines derived from interspecific crosses (16 lines) and gene pyramiding (33 lines). The outstanding genotypes from these groups were also compared with six CBB-resistant lines: VAX 1, VAX 2, VAX 3, VAX 4, VAX 5, and VAX 6 (Table 1), recently developed at CIAT from interspecific hybridization of *P. vulgaris* and *P. acutifolius* and gene pyramiding.

To develop the six VAX lines, the common bean cultivar ICA Pijao was crossed with tepary bean accession G 40001

Table 1. Parents used to develop common bacterial blight-resistant common bean breeding lines VAX 1 to VAX 6 from *P. vulgaris* × *P. acutifolius* interspecific hybridization and gene pyramiding at CIAT, Colombia, 1989–1997.

	Parent lines					
Breeding line	Jules ↓ XAN 87 ↓ A 769	PI 207262 and Jules ↓ XAN 112 ↓ A 775	ICA Pijao	G 40001†	G 40020† ↓ XAN 159 ↓ XAN 263	PI 207262, Tara and G 40020 ↓ XAN 90 and XAN 263 ↓ XAN 309
VAX 1	X	X	X	X		
VAX 2	X	X	X	X		
VAX 3	X	X	X	X		X
VAX 4	X	X	X	X	X	
VAX 5	X	X	X	X	X	
VAX 6	X	X	X	X		X

† *Phaseolus acutifolius*; all others are *P. vulgaris*. Common bean cultivars Jules and Tara derive their CBB resistance from *P. acutifolius* (Coyne and Schuster, 1969, 1970).

in 1989 by embryo rescue (Mejía-Jiménez et al., 1994). The F_1 of the interspecific hybrid was then crossed, first with the advanced common bean line A 775 and then with line A 769. This was followed by three generations of inbreeding before conducting intensive screening and selection for CBB resistance. By 1995, this resulted in common bean lines VAX 1 and VAX 2 (Table 1). An advanced CBB-resistant sister line (PVPA 9576-1) of these two was crossed with previously developed CBB-resistant CIAT lines XAN 263 and XAN 309, resulting in lines VAX 4 and VAX 5, and VAX 3 and VAX 6, respectively (Table 1).

An unreplicated, 2-m-long, single-row plot was first used. The spacing between rows was 60 cm with about 10 cm between plants within a row. Susceptible and resistant checks of known CBB reaction were planted throughout the nurseries. The nurseries were inoculated by spraying the canopy with back-pack solo sprayers, two to four times at 7- to 10-d intervals, beginning about 3 wk after sowing. A bacterial concentration of 10^7 to 10^8 cfu/mL was used.

All common bean genotypes were evaluated on a 1-to-9 scale, as described by Schoonhoven and Pastor-Corrales (1987). Genotypes receiving scores of 1 (no visible symptoms) to 3 (about 2% of leaf surface covered by small CBB lesions) were considered resistant; those receiving scores of 4 (<5% of the leaf area covered by small CBB lesions) to 6 (<10% leaf area covered by medium-sized and large CBB lesions) were classified as intermediate; and those with scores of 7 (about 10% leaf area affected) to 9 (>25% leaf area affected by CBB) were susceptible.

Thus, all common bean genotypes that received scores of 1 to 6 were evaluated in replicated trials by the same procedure in subsequent plantings. All susceptible genotypes were eliminated. The three leaflets of the first or second trifoliolate leaf of all those genotypes still resistant or intermediate were then inoculated with twin surgical blades (Pastor-Corrales et al., 1981) about 3 wk after sowing. Subsequently, all entries were also inoculated three to five times (at weekly intervals) by spraying the canopy to verify the CBB reaction.

Promising entries thus identified and reported in this article were compared with each other in a final trial with two replicates between 1996 and 1998. Plot size, distance between and within rows, and inoculation and evaluation methods were similar to those of previous years. However, in addition to inoculating the canopy and trifoliolate leaf, developing pods were also inoculated with a hypodermic needle, multiple needles (florist's frog), and/or surgical blades.

Trifoliolate leaves inoculated with surgical blades were evaluated 7 to 15 d after inoculation. Spray-inoculated canopies were evaluated periodically from when the first symptoms appeared on the susceptible check—common bean cultivar ICA Pijao—until leaves senesced or the crop matured. The pods were evaluated about a week after inoculation. Also, growth habit (Singh, 1982) and seed size and color were recorded for all entries. All data were analyzed by SAS (SAS Institute Inc., 1985).

RESULTS

CBB Resistance in *Phaseolus* Species

Table 2 indicates the number of promising accessions evaluated, and the ranges and means for CBB reaction in leaves inoculated in two ways for four *Phaseolus* species. While susceptible accessions were found in all *Phaseolus* species, the lowest levels of resistance were recorded in *P. coccineus*, *P. lunatus*, and *P. vulgaris*. Table 3 shows that the highest CBB resistance (scores of 1.2–2.0), as determined by all three inoculation methods, were recorded for *P. acutifolius*, accessions G 40029 and G 40156. But not all *P. acutifolius* accessions possessed high levels of resistance; some were intermediate (e.g., G 40022) and others highly susceptible (e.g., G 40110). Some *P. lunatus* accessions exhibited scores of 4.2 to 6.2; *P. coccineus* had scores of 4.8 to 5.5; and the three most promising *P. vulgaris* landraces had scores of 4.5 to 6.4. The susceptible cultivar ICA Pijao had scores of 8.0 to 8.9.

Introgression of CBB Resistance from Wild Populations and Landraces of the Primary, Secondary, and Tertiary Gene Pools of *P. vulgaris*

Examples of use of CBB resistance genes from only the wild or cultivated germplasm forming the primary gene pool of *P. vulgaris* are rare indeed. As far as we know, the only line that derives such resistance (from a landrace accession G 4399, also known as Tamaulipas 9-B, from Mexico) is XAN 91, developed at CIAT more than a decade ago (Beebe and Pastor-Corrales, 1991). Its resistance is intermediate (scores of 5.2–6.3).

Table 4 includes the CBB reaction of the most promising common bean lines that derive their resistance from *P. acutifolius* and *P. coccineus*. Both groups of lines, in general, exhibited intermediate levels of CBB reaction.

Table 2. The ranges and means for reaction to common bacterial blight (CBB) in leaves of promising accessions of different *Phaseolus* species and of advanced breeding common bean lines derived from interspecific hybridization and gene pyramiding. Two inoculation methods were used: surgical blade and aspersion. CIAT-Quilichao, Colombia, 1994–1998.

Germplasm identification	Number evaluated	CBB score†			
		Surgical blade		Aspersion	
		Range	Mean	Range	Mean
P. acutifolius	34	1.0–9.0	3.0	1.0–9.0	2.9
P. coccineus	55	5.0–9.0	7.0	4.8–9.0	6.2
P. lunatus	35	6.2–9.0	6.3	4.2–9.0	5.6
P. vulgaris landraces	38	5.9–9.0	6.8	6.0–9.0	6.8
Lines or cultivars	70	4.1–9.0	6.5	3.4–9.0	5.8
Lines from *P. vulgaris* × *P. acutifolius*	5	3.8–7.0	5.8	4.3–5.0	4.6
Lines from *P. vulgaris* × *P. coccineus*	11	5.2–7.0	6.7	4.2–7.0	5.8
Lines from gene pyramiding	33	1.5–7.0	4.5	2.0–7.0	3.9
LSD (0.05)		1.3	0.3	1.6	0.4

† Scores: 1 = immune with no visible symptoms; 3 = about 2% leaf surface covered by small CBB lesions; 5 = about 5% leaf surface covered by small and medium-sized CBB lesions; 7 = about 10% leaf area affected; 9 = >25% leaf area diseased (Schoonhoven and Pastor-Corrales, 1987).

Table 3. Origin, growth habit, seed color and size, and common bacterial blight reaction of promising *Phaseolus acutifolius*, *P. coccineus*, *P. lunatus*, and *P. vulgaris* accessions. Three inoculation methods were used; CIAT-Quilichao, Colombia, 1994–1998.

Identification	Origin†	Growth habit‡	Seed		Mean bacterial blight score§		
			Color	Size	ASP	SRB	MNP
P. acutifolius							
G 40001	MEX	III	White	Small	1.9	3.0	4.0
G 40022	USA	III	Beige	Small	4.1	2.5	3.0
G 40029	USA	III	Cream speckled	Small	1.2	1.4	2.0
G 40034	MEX	III	White	Small	1.4	1.2	3.5
G 40035	MEX	III	Black	Small	3.0	1.8	5.0
G 40038	MEX	III	Cream	Small	1.7	1.8	3.0
G 40110¶	MEX	III	Black	Small	8.0	7.3	7.0
G 40155	MEX	III	White	Small	2.0	2.3	2.0
G 40156	MEX	III	White	Small	1.3	1.7	2.0
P. coccineus							
G 35006	GTA	III	Variable	Large	6.3	6.2	–
G 35007	GTA	III	Variable	Large	6.1	6.2	–
G 35016	MEX	III	Variable	Large	6.7	5.3	–
G 35066	MEX	III	Gray speckled	Large	5.5	4.9	–
G 35105	MEX	III	Variable	Large	5.0	6.2	–
G 35113	MEX	III	Variable	Large	6.2	5.3	–
G 35116	MEX	III	Variable	Large	5.8	5.3	–
G 35121	MEX	III	Variable	Large	6.4	5.6	–
G 35148	MEX	III	Variable	Large	5.5	4.8	–
G 35157	MEX	III	Variable	Large	5.4	5.4	–
P. lunatus							
G 25254	GTA	I	Pink	Small	6.8	6.1	–
G 25835	PER	III	Cream	Large	6.8	6.9	–
G 25890	CLB	III	Pink mottled	Small	6.2	4.2	–
G 25947	PER	III	Gray speckled	Large	6.6	6.0	–
G 26007	USA	I	White	Medium	6.8	6.8	–
P. vulgaris							
G 6772	MEX	III	Beige	Small	6.4	6.1	4.5
G 1320	MEX	III	Beige	Small	6.8	6.8	5.3
G 4399	MEX	III	Beige	Small	6.4	6.4	7.5
ICA Pijao¶	CLB	II	Black	Small	8.7	8.9	8.0
LSD (0.05)					1.6	1.3	1.6

† CLB = Colombia; GTA = Guatemala; MEX = Mexico; PER = Peru; and USA = United States of America.
‡ I = determinate upright; II = indeterminate upright; and III = indeterminate, prostrate, semiclimbing (Singh, 1982).
§ Mean of three crop seasons, evaluated on a scale of 1 = immune with no visible symptoms; 3 = about 2% leaf surface covered by small CBB lesions; 5 = about 5% leaf surface covered by small and medium-sized CBB lesions; 7 = about 10% leaf area affected; 9 = >25% leaf area diseased (Schoonhoven and Pastor-Corrales, 1987). Inoculation methods: ASP = aspersion, SRB = surgical blade (for leaves only), MNP = multiple needles (for pods only).
¶ Susceptible check.

Table 4. Origin, growth habit, seed color and size, and common bacterial blight (CBB) reaction of some common bean cultivars and breeding lines developed by introgression of CBB resistance from *P. autifolius* and *P. coccineus* into *P. vulgaris*. Three inoculation methods were used; CIAT-Quilichao, Colombia, 1994–1998.

Identification	Origin†	Growth habit‡	Seed		Mean bacterial blight score§		
			Color	Size	ASP	SRB	MNP
P. vulgaris × *P. acutifolius*							
GNN #1 Sel 27	UNE	III	White	Medium	6.1	5.0	3.0
Jules	UNE	III	White	Medium	5.6	5.0	2.8
Tara	UNE	III	White	Medium	6.4	4.9	1.8
OAC 88-1	UGC	II	White	Small	6.2	4.3	4.7
XAN 159	CIAT	I	Gray speckled	Large	3.8	4.0	5.3
P. vulgaris × *P. coccineus*							
ICB 3	UPR	II	Black	Small	5.2	4.2	3.3
ICB 6	UPR	II	Red	Small	6.6	5.6	4.5
ICB 11	UPR	II	Black	Small	7.0	6.7	4.5
ICB 37	UPR	II	White	Small	7.0	6.4	6.0
I 9365-1-9	UPR	II	Beige	Small	6.7	5.9	6.0
I 9365-5-DR	UPR	II	Red	Small	6.9	6.6	6.5
TARS VCI-4B	TARS	III	Pinto	Medium	4.5	3.8	3.0
XR 235-1-1	MITA	III	White	Small	6.8	5.8	3.5
ICA Pijao¶	ICA	II	Black	Small	8.7	8.9	8.0
LSD (0.05)					1.6	1.3	1.6

† CIAT = Centro Internacional de Agricultura Tropical; ICA = Instituto Colombiano Agropecuario; MITA = Mayaguez Institute of Tropical Agriculture; TARS = Tropical Agricultural Research Service; UGC = University of Guelph, Canada; UNE = University of Nebraska; UPR = University of Puerto Rico.
‡ I = determinate upright; II = indeterminate upright; and III = indeterminate, prostrate, semiclimbing (Singh, 1982).
§ Mean of three crop seasons, evaluated on a scale of 1 = immune with no visible symptoms; 3 = about 2% leaf surface covered by small CBB lesions; 5 = about 5% leaf surface covered by small and medium-sized CBB lesions; 7 = about 10% leaf area affected; 9 = >25% leaf area diseased (Schoonhoven and Pastor-Corrales, 1987). Inoculation methods: ASP = aspersion, SRB = surgical blade (for leaves only), MNP = multiple needles (for pods only).
¶ Susceptible common bean cultivar.

Table 5. Origin, growth habit, seed color and size, and common bacterial blight (CBB) reaction of some common bean breeding lines obtained by pyramiding resistance genes from different sources. Three inoculation methods were used; CIAT-Quilichao, Colombia, 1994–1998.

Identification	Origin†	Growth habit‡	Seed		Mean bacterial blight score§		
			Color	Size	ASP	SRB	MNP
BAC 31	IAPAR	III	Pinto	Small	5.0	8.0	8.0
WBB-20-1	UPR	I	White	Small	6.2	4.4	2.5
G 17341	CU	III	Pinto	Small	3.6	3.2	2.3
NY 79-3776-1	CU	III	Pinto	Small	3.7	3.4	2.5
Wilk. 2	CU	I	White	Small	3.1	3.3	4.8
XAN 263	CIAT	II	Red	Small	2.8	2.8	4.0
XAN 309	CIAT	II	Red	Small	2.9	2.7	2.5
XAN 328	CIAT	II	Red	Small	4.4	4.2	4.0
XAN 330	CIAT	II	Red	Small	4.8	3.6	4.0
XAN 332	CIAT	II	Red	Small	4.4	3.6	2.5
VAX 1	CIAT	III	Cream striped	Small	3.6	2.6	3.4
VAX 2	CIAT	III	Cream	Small	3.0	3.0	3.3
VAX 3	CIAT	II	Red	Small	2.0	2.0	2.4
VAX 4	CIAT	II	Cream	Small	1.5	2.4	2.4
VAX 5	CIAT	II	Black	Small	2.6	2.7	2.7
VAX 6	CIAT	II	Red	Small	1.8	2.0	2.4
ICA Pijao¶	ICA	II	Black	Small	8.7	8.9	8.0
LSD (0.05)					1.6	1.3	1.6

† CIAT = Centro Internacional de Agricultura Tropical; CU = Cornell University; IAPAR = Instituto Agronômico do Paraná; ICA = Instituto Colombiano Agropecuario; UPR = University of Puerto Rico.
‡ I = determinate upright; II = indeterminate upright; and III = indeterminate, prostrate, semiclimbing (Singh, 1982).
§ Mean of three crop seasons, evaluated on a scale of 1 = immune with no visible symptoms; 3 = about 2% leaf surface covered by small CBB lesions; 5 = about 5% leaf surface covered by small and medium-sized CBB lesions; 7 = about 10% leaf area affected; 9 = >25% leaf area diseased (Schoonhoven and Pastor-Corrales, 1987). Inoculation methods: ASP = aspersion, SRB = surgical blade (for leaves only), MNP = multiple needles (for pods only).
¶ Susceptible common bean cultivar.

The line XAN 159 had higher levels of CBB resistance in leaves but lower resistance in pods, compared with the initial Nebraska lines GNN #1 Sel. 27, Jules, and Tara. Table 4, in conjunction with Tables 2 and 3, also shows that, while the highest levels of CBB resistance available in *P. vulgaris* and *P. coccineus* have been introgressed into common bean, those for *P. acutifolius* still remain to be achieved (e.g., *P. acutifolius* accessions G 40029 and G 40156, Table 3).

Pyramiding CBB Resistance Genes from Across *Phaseolus* Species

Only limited efforts have been made to systematically recombine and accumulate CBB resistance from different *Phaseolus* species into a common bean genotype. For example, GNN #1 Sel 27, Jules, and/or Tara, which derive their resistance from *P. acutifolius*, were crossed with common bean accessions such as PI 207262 (Beebe and Pastor-Corrales, 1991; Mohan and Mohan, 1983). This resulted in lines BAT 93, XAN 112, IAPAR BAC 20, IAPAR BAC 31 (Table 5), and IAPAR BAC 44, among others.

Subsequently, concerted efforts to combine different CBB resistance genes were made by R.E. Wilkinson of Cornell University in the 1980s, and at CIAT. Although, the exact pedigree and germplasm used at Cornell University are not known, Wilkinson seems to have combined CBB resistance genes from all three species: *P. vulgaris*, *P. coccineus*, and *P. acutifolius*, including line XAN 159 or its sisters. The three most promising genotypes from this work, G 17341, NY 79-3776-1, and Wilkinson 2, are listed in Table 5.

Table 5 shows that, over the years, steady progress has been made in raising the levels of CBB resistance, and the common bean lines obtained from gene pyramiding at the Cornell University and CIAT possess, by far, the highest levels of CBB resistance. Moreover, VAX 3, VAX 4, and VAX 6 possess levels of CBB resistance that are as high as those found in *P. acutifolius* accessions. These lines also possess much better tropical adaptation, plant type, and seed color (Table 5).

Transfer of CBB Resistance into Cultivars

For some time, in USA (Coyne and Schuster, 1969, 1970), Brazil (Mohan and Mohan, 1983), and Colombia (Beebe and Pastor-Corrales, 1991), the initial source of CBB resistance, GNN #1 Sel 27, was used for cultivar development. Subsequently, line XAN 159 (or its sisters), and other sources of resistance have been used in breeding programs in Brazil (Rava et al., 1996), Canada (Park and Dhanvantari, 1994), Colombia (Beebe and Pastor-Corrales, 1991), and USA (Arnaud-Santana et al., 1993b). Table 6 summarizes the CBB reaction of some promising common bean lines and cultivars of different commercial classes that were available to us. This level of CBB resistance is comparable with, or slightly better than, those introgressed from *P. coccineus* and *P. acutifolius* (Table 4).

DISCUSSION

Our comparative study of the four species of *Phaseolus* in tropical Colombia demonstrated the occurrence of the highest levels of CBB resistance in some *P. acutifolius* accessions. The levels of CBB resistance in *P. coccineus*, *P. lunatus*, and *P. vulgaris* were intermediate. These findings agree with levels of resistance in these species reported earlier (Coyne and Schuster, 1973; Mohan, 1982). We evaluated only a very small number of accessions of the four *Phaseolus* species and

Table 6. Origin, growth habit, seed color and size, and common bacterial blight (CBB) reaction of some common bean breeding lines. Three inoculation methods were used; CIAT-Quilichao, Colombia, 1994–1998.

Identification	Origin†	Growth habit‡	Seed		Mean bacterial blight score§		
			Color	Size	ASP	SRB	MNP
Race Mesoamerica							
A 716	CIAT	II	Black	Small	5.2	4.0	4.0
AND 915	CIAT	II	Cream	Small	5.6	4.2	7.0
APN 137	CIAT	III	Brown	Small	6.5	4.7	3.5
BAT 93	CIAT	II	Beige	Small	6.8	5.2	4.5
G 18484	GTA	II	Black	Small	5.4	3.8	2.5
MUS 105	CIAT	II	Black	Small	4.8	4.3	2.3
XAN 91	CIAT	II	Gray	Small	6.3	5.2	6.0
XAN 200	CIAT	II	Black	Small	5.5	3.4	2.5
BAC 14	IAPAR	II	Cream striped	Small	5.7	4.1	2.0
ICA Pijao¶	ICA	II	Black	Small	8.7	8.9	8.0
Race Durango							
Chase	USA	III	Pinto	Medium	6.0	7.8	4.5
MAM 48	CIAT	III	Pinto	Medium	4.9	6.7	5.8
Pinto UI 114¶	USA	III	Pinto	Medium	8.0	7.7	6.8
Race Nueva Granada							
AFR 603	CIAT	II	Red mottled	Large	5.4	5.4	2.5
AND 1071	CIAT	I	Cream mottled	Large	6.6	6.2	2.0
BLM 85	CIAT	I	White	Medium	6.4	5.3	4.6
CAL 123	CIAT	I	Red mottled	Large	6.1	5.6	8.0
DRK 120	CIAT	II	Red	Large	5.9	5.3	2.3
G 4079	USA	I	Pink	Large	6.2	6.9	8.0
G 4081	USA	I	Red	Large	5.9	6.8	5.0
G 18168	HTI	I	Red	Large	6.1	6.8	5.0
G 18221	KYA	I	Red mottled	Large	6.5	6.0	7.5
G 20539	KYA	II	Cream mottled	Large	6.7	6.5	7.5
SUG 131	CIAT	II	Cream mottled	Large	6.3	5.1	7.5
SUG 135	CIAT	II	Cream mottled	Large	5.4	5.4	7.5
ZAA 91	CIAT	I	Purple mottled	Large	4.1	4.0	7.0
ZAA 93	CIAT	I	Purple mottled	Large	6.0	5.9	2.0
Montcalm	USA	I	Red	Large	6.0	8.0	3.0
Diacol Calima¶	CLB	I	Red mottled	Large	8.0	9.0	8.0
LSD (0.05)					1.6	1.3	1.6

† CIAT = Centro Internacional de Agricultura Tropical; CLB = Colombia; GTA = Guatemala; HTI = Haití; IAPAR = Instituto Agronômico do Paraná; ICA = Instituto Colombiano Agropecuario; KYA = Kenya; and USA = United States of America.

‡ I = determinate upright; II = indeterminate upright; and III = indeterminate, prostrate, semiclimbing (Singh, 1982).

§ Mean of three crop seasons, evaluated on a scale of 1 = immune with no visible symptoms; 3 = about 2% leaf surface covered by small CBB lesions; 5 = about 5% leaf surface covered by small and medium-sized CBB lesions; 7 = about 10% leaf area affected; 9 = >25% leaf area diseased (Schoonhoven and Pastor-Corrales, 1987). Inoculation methods: ASP = aspersion, SRB = surgical blade (for leaves only), MNP = multiple needles (for pods only).

¶ Susceptible common bean cultivar.

some *P. acutifolius* had accessions with much higher levels of CBB resistance than those so far reported and used in common bean breeding programs. A strong justification therefore exists for more systematic and exhaustive screening of all available accessions from wild and cultivated populations of the primary, secondary, and tertiary gene pools of *P. vulgaris*.

Because *Xcp* races have been identified from some bean-growing environments (Rava, 1984; Schuster et al., 1973), an international CBB nursery must be established to evaluate pure lined, resistant accessions of different *Phaseolus* species (and breeding lines and cultivars of common bean) across sites endemic to CBB and in the greenhouse for their reaction in canopy, trifoliolate leaf, and pods, and for their overall usefulness before being used in breeding and genetic studies.

In *P. acutifolius*, most cultivars are resistant to CBB, whereas most of the wild populations available at CIAT are highly susceptible (CIAT, 1996). This may indicate a founder effect, where most cultigens originate from a few wild populations. As far as we know, only the *P. acutifolius* landraces PI 319443 and PI 440795 have been tested for allelism; both were found to possess the same CBB-resistant gene (Kolkman and Michaels, 1994). This was further confirmed by the presence of the same RAPD marker in common bean lines XAN 159 and OAC 88-1, derived, respectively, from the two *P. acutifolius* accessions (P.N. Miklas 1997, personal communication). Thus, a test of allelism against specific *Xcp* isolates needs to be performed between different CBB-resistant *P. acutifolius* accessions before using them in interspecific hybridization and gene pyramiding for common bean improvement.

Tables 3, 4, and 6 show that, although the levels of CBB resistance available in landraces of *P. vulgaris* and *P. coccineus* have been successfully transferred into cultivated common bean, some *P. acutifolius* accessions still possess much higher levels of resistance. Thus, in the common bean lines that derived from interspecific hybridization with *P. acutifolius*, most likely not all the CBB-resistant genes or QTLs were introgressed. Lack of information about the specificity between *Xcp* isolates and different QTLs conferring resistance makes the task of recovering all QTLs from tepary bean and transferring them to common bean relatively difficult. Thus, the identification and use of tightly linked molecular markers for each QTL should facilitate gene transfer and pyramiding. Moreover, *P. acutifolius* accessions possessing the highest levels of CBB resistance (e.g., G 40029 and G 40156, Table 3) must be used in interspecific hybridization.

Although interspecific hybridization and gene pyra-

Table 7. Variation observed for common bacterial blight reaction within advanced breeding lines of common bean, CIAT-Quilichao, Colombia, 1994–1998.

Identification	Common bacterial blight score¶
XAN 309	2, 3, 4, 5, 7
VAX 1	2, 3, 4, 5, 6, 7
VAX 2	2, 3, 4, 5, 7
VAX 3	1, 2, 5, 7
VAX 4	1, 2, 4
VAX 5	1, 2, 3, 5, 7
VAX 6	1, 2, 3, 5, 6

† Recorded on single plants: 1 = immune with no visible symptoms; 3 = about 2% leaf surface covered by small CBB lesions; 5 = about 5% leaf surface covered by small and medium-sized CBB lesions; 7 = about 10% leaf area affected; 9 = >25% area of trifoliolate leaves diseased (Schoonhoven and Pastor-Corrales, 1987). The surgical blade method of inoculation was used.

miding have often been carried out without knowing the underlying genetics of CBB resistance, Table 5 shows that substantial progress has been made for CBB resistance breeding through gene pyramiding. These results, especially the performance of lines VAX 3, VAX 4, and VAX 6 developed at CIAT, suggest that the soundest strategy for breeding for CBB resistance is to pyramid resistance genes from several different *Phaseolus* species.

Although the initial transfer of partial CBB resistance from tepary to common bean was achieved with lines of commercial or near-commercial seed types (e.g., GNN #1 Sel 27), lines developed from wide crosses and gene pyramiding were often not of commercial seed type (e.g., BAT 93, XAN 91, XAN 159, VAX 1, VAX 4, and VAX 6). Neither did the lines and cultivars presented in Table 6 have the levels of CBB resistance found in pyramided resistant lines (Table 5). This high, pyramided resistance must therefore be transferred to, and combined with, other desirable traits in cultivars of different market classes.

To summarize, breeding for CBB resistance in the tropics can now be expedited by maximizing the use of the best pyramided sources of resistance (Table 5), DNA-based markers (Jung et al., 1996; Nodari et al., 1993), and different inoculation methods.

Problems for CBB Resistance Breeding

By far the most serious problem in CBB resistance breeding has been the instability of resistance (Table 7). Often, after more than a dozen generations of selfing, CBB-resistant lines continue to segregate. As far as we know, no line carrying high levels of CBB resistance is found to be true breeding, despite many generations of selfing and selection under severe disease pressure. Thus, to maintain high levels of CBB resistance, single-plant selections must be made under high disease pressure in each generation. The cause of instability is not known: the CBB-resistant gene(s) may be unstable; or, because three or more genes or QTLs are involved in controlling CBB resistance, the population size and number of single-plant selections made for pure lining are not large enough to provide a line that is homozygous for and contains all CBB resistance genes.

Another serious problem in breeding for CBB resistance in common bean is the differential CBB reaction of different plant organs (e.g., leaves versus pods), especially in large-seeded germplasm of Andean origin (Table 6; Beebe and Pastor-Corrales, 1991). Differences in leaf and pod reactions to CBB have also been observed in *P. acutifolius* (Table 3; Zaiter et al., 1989), the species with the highest CBB resistance. Other problems are low correlations of leaf, pod, and seed reactions (Arnaud-Santana et al., 1994); and apparent association of resistance with stages of plant development, indeterminate growth habit, and/or delayed maturity (Coyne and Schuster, 1974).

Breeding Strategies and Methods

Any common bean improvement program for CBB resistance should take into account that (i) different levels of CBB resistance are found in the common bean's primary, secondary, and tertiary gene pools; (ii) different inoculation methods and bacterial concentrations produce different CBB reactions; (iii) different strains of *Xcp* and strain-specific resistance are found, at least in temperate environments; (iv) differential CBB reactions occur according to plant organ; (v) CBB resistance may be associated with the stage of plant development, growth habit, and/or maturity; (vi) strain-specific CBB resistance may be controlled by a single recessive gene, single dominant gene, or inherited quantitatively with low to high heritability and involving one to six genes or QTLs; (vii) DNA-based linked markers are available for some QTLs responsible for CBB resistance; and (viii) CBB reaction is also affected by photoperiod and temperature.

CBB resistance is often screened by artificial wounding methods and higher *Xcp* populations than probably occur naturally in bean-growing environments. Also difficult to do is directly transferring CBB resistance from exotic sources into cultivars of different market classes and combining it with other desirable agronomic traits. Thus, all available sources of CBB resistance would need to be evaluated against the prevalent strains of *Xcp* by appropriate inoculation methods and bacterial concentrations. For integrated genetic improvement (Singh, 1997), parental recombination and selection activities may need to be divided into (i) introgression of CBB-resistance genes from common bean's primary (distantly related landraces and wild populations), secondary, and tertiary gene pools; (ii) parental development and breeding for CBB resistance per se (i.e., broadening the genetic base, gene pyramiding, and character improvement); and (iii) cultivar development, that is, simultaneous selection for multiple qualitative and quantitative traits for specific market classes and bean production regions from elite × elite populations (Kelly et al., 1998).

Introgression of CBB Resistance

Often separate hybridization and selection programs would be required to transfer CBB resistance from each wild population or distantly related landrace of common bean, and from the secondary and tertiary gene pool

accessions. Crosses with the tertiary gene pool require embryo rescue. Recurrent and congruity backcrossings (Mejía-Jiménez et al., 1994), followed by at least one or more generations of inbreeding, are needed before evaluation and selection for CBB resistance can begin.

Parental Development and Breeding for CBB Resistance Per Se

Different sources of CBB resistance available (e.g., G 1320, G 4399, G 6772) or introgressed (e.g., XAN 91) from the primary, secondary (e.g., XR-235-1-1, ICB 3, TARS VCI-4B), and tertiary (GNN #1 Sel 27, OAC 88-1, XAN 159) gene pools to common bean need to be systematically combined to pyramid different genes for CBB resistance. The genetic base would thus be broadened, and the levels and durability of resistance increased. Different CBB resistance genes within each species may need to be combined first, followed by that between *P. vulgaris* and *P. coccineus* genes because they possess comparatively lower levels of CBB resistance. Finally, this pyramided resistance would need to be combined with that of *P. acutifolius* sources. Access to the widest range of pathogenic variation in *Xcp*, availability of tightly linked molecular markers to CBB resistance genes from different sources, and recurrent selection would greatly aid this task.

Cultivar Improvement

The highest levels of CBB resistance available in pyramided lines would need to be combined with other major desirable traits such as seed size and color, canning and cooking quality, growth habit, maturity, and resistance to other biotic and abiotic stresses for specific groups of cultivars for each major bean-growing environment. The levels of CBB resistance in cultivars that would suffice under field conditions should be determined a priori. Multiple-parent elite × elite crosses within a gene pool and races would need to be made for simultaneous selection and improvement of all desirable traits. Marker-assisted gamete (Singh, 1994, 1998), F_2-derived family, and/or single-seed descent (Urrea and Singh, 1994) breeding methods could be used for this purpose. The choice of breeding method would depend largely on the resources and facilities available, and the resistance level required. While making multiple-parent crosses, breeders should ensure a sufficient genetic contribution of the CBB-resistant parents so that a comparatively larger frequency of desirable recombinants with CBB resistance are available in segregating populations and families. Thus, in a multiple-parent cross (three or more parents), preferably two CBB-resistant parents from different sources are used (Table 8). Moreover, donor parents for CBB resistance and all other desirable traits should be similar to the commercial cultivar under improvement in seed color and size, growth habit, maturity, and adaptation (Kelly et al., 1998). Recovering lines with high CBB resistance is often difficult when and if the genetic contribution of its donor parents is ≤25% in a multiple-parent cross (Table 8).

Because of the relatively larger costs and resources required for inoculating trifoliolate leaves with razors or surgical blades, or multiple or hypodermic needles, sequential screening methods, like those currently in use at CIAT, can be adopted: all early generation, large-scale, field-grown, segregating populations and families should be initially inoculated by aspersion for canopy and pod evaluations. The trifoliolate leaves of advanced generation families and lines uniform for CBB resistance in canopy and pods should then be inoculated with either razors, surgical blades, or multiple needles. Those still resistant should then be screened for pod reaction to CBB against specific *Xcp* strains in both field and greenhouse, using any of the inoculation methods used for trifoliolate leaf screening, but preferably multiple needles. Greenhouse screening would be required when and if the field screening is not reliable and chances for escapes are real, and when screening against *Xcp* strains originating from outside the bean production region. Under the warm tropical environments of Colombia, greenhouse screening is not required.

For simultaneous selection for other desirable characters, including resistance to other diseases, insects, and abiotic stresses, a separate series of complementary nurseries may need to be grown, either at the same location or at different locations, and in the same or different cropping seasons (Singh et al., 1998). For ex-

Table 8. Number of common bean F_1-derived F_2 families that were resistant, intermediately resistant, or susceptible to common bacterial blight (CBB). The families were derived from populations obtained when using 0, 1, 2 or 5 CBB-resistant parents. The range and mean values of these families reaction to CBB are also given; CIAT-Quilichao, Colombia, 1994–1998.

Population identification	No. of CBB-resistant parents	No. of F_1-derived F_2 families				CBB scores†	
		Resistant	Intermediate	Susceptible	Total	Range	Mean
Catrachita/J 117//A 429/EMP 473	0	0	0	29	29	7–9	8.0
Catrachita/G 2883//G 3017/Othello	0	0	0	88	88	7–9	8.3
Catrachita/RM 35//G 17341/De Celaya	1	0	6	21	27	5–9	7.2
XAN 309/A 193//MAR 3/G 5653	1	0	9	12	21	4–8	6.7
MAM 38/G 17341//J 117/XAN 159	2	0	13	1	14	3–7	5.5
VAX 2///A 429/J 117//G 17341/G 3017	2	1	43	18	62	3–9	5.9
VAX 1////J 117///PVPA 9576-14/XAN 159//PVPA 9576-21/G 17340	5	11	27	9	47	2–8	4.8
VAX 1////SEA 7///XAN 330/ XAN 265//PVPA 9576-21/G 17341	5	56	125	7	188	3–8	4.3

† Scored on a 1 = immune with no visible symptoms; 3 = about 2% leaf surface covered by small CBB lesions; 5 = about 5% leaf surface covered by small and medium-sized CBB lesions; 7 = about 10% leaf area affected; 9 = >25% diseased leaf canopy (Schoonhoven and Pastor-Corrales, 1987). The aspersion method of inoculation was used.

ample, for leafhopper (*Empoasca kraemeri* Ross & Moore) screening, warm dry environments are required, whereas the development and spread of CBB in breeding nurseries require warm temperatures, high relative humidity, intermittently dry and wet weather, and high winds.

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Comparative Response of Two Reciprocal Recurrent Selection Methods in BS21 and BS22 Maize Populations

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ABSTRACT

Reciprocal recurrent selection (RRS) has not been widely adopted by maize (*Zea mays* L.) breeders because pedigree selection methods were effective in developing improved inbred lines. RRS as been used successfully, but modified reciprocal recurrent selection (MRRS) uses elite inbred lines as testers, which may be more useful in applied breeding programs. A study was conducted to compare responses to selection via RRS and MRRS in the BS21 and BS22 maize populations. After six cycles of RRS and MRRS, an experiment was conducted to determine the direct and the indirect responses to selection. The populations themselves, testcrosses to inbred testers, and crosses between BS21 and BS22 were evaluated at four locations for 2 yr. Grain yield increased significantly in all population crosses. Direct response to selection was greater for the RRS method than for the MRRS method: 4.4% cycle^{-1} for BS21(R) × BS22(R); 2.8% cycle^{-1} for BS21(HI) × A632; and 1.6% cycle for BS22(HI) × H99. RRS was as effective as MRRS for improving grain yield of BS21(R) and BS22(R) in crosses with A632 and H99, but MRRS was not as effective as RRS in the improvement of the BS21(HI) × BS22(HI) cross populations: 1.6%$^{-1}$ cycle for BS21(HI) × BS22(HI) vs. 4.4% cycle^{-1} for BS21(R) × BS22(R). There was no evidence that the genetic variation among testcrosses for grain yield was greater with use of inbred lines as testers compared with use of populations as testers.

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RECIPROCAL RECURRENT SELECTION methods have been successful for improvement of population crosses and to increase the heterosis expressed in population crosses. RRS has not been widely adopted by commercial breeders because it is not as efficient at recovering inbred lines as other selection methods of inbred line development. Use of elite inbred lines as testers, instead of the opposite population as reciprocal testers, in a modified RRS (MRRS) scheme could overcome, to some extent, the limitations of RRS for inbred line development. The use of inbred lines as testers was suggested by Russell and Eberhart (1975) as an alternative to the RRS method proposed by Comstock et al. (1949).

Russell et al. (1973), Russell and Eberhart (1975), and Horner et al. (1973, 1989) reported that maize populations improved for specific combining ability (SCA) with use of inbred lines as testers also had improved performance of the populations in crosses with other testers. Darrah (1985) and Horner et al. (1973, 1989) reported greater genetic variance among testcrosses with use of an inbred line as tester compared with use of a population as tester. Russell and Eberhart (1975) expected greater genetic gain with use of inbred lines as testers. Comstock (1979) compared both types of testers in terms of expected change in gene frequency on the basis of testcross progeny selection. Comstock (1979) assumed that the use of an inbred line derived

Abbreviations: RRS, reciprocal recurrent selection; HS, half-sib families; MRRS, modified reciprocal recurrent selection with use of inbred lines as testers; FS, full-sib families; TC, testcrossess; SCA, specific combining ability; G × E, genotype by environment interaction; GDU, growing degree units; h_r^2, realized heritability; S, selection differential; R, response to selection.