Resistance to *Colletotrichum lindemuthianum* Isolates from Middle America and Andean South America in Different Common Bean Races

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ABSTRACT

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A total of 20,144 common bean (*Phaseolus vulgaris*) accessions were evaluated in the field at CIAT-Popayán, Colombia, with a mixture of local isolates of the anthracnose pathogen, *Colletotrichum lindemuthianum*. Of these, 4,939 (24.5%) accessions were resistant, and another 4,410 (21.9%) showed an intermediate reaction between resistant and susceptible. These accessions were then inoculated at the seedling stage in the screenhouse at the same site with the same mixture of isolates. The 3,778 accessions showing resistance were subsequently challenged in a greenhouse at the seedling stage, with a mixture of isolates from Middle America and separately with a mixture from Andean South America. Resistance to all isolates was found in 1,270 accessions, and of these, 350 (1.7% of total) were immune. These sources of resistance included representatives from all six races of cultivated common bean and showed variation for growth habit, maturity, seed color and size, adaptation traits, and geographical origin. Also, 68 resistant accessions were wild common beans from Middle America and Andean South America.

The common bean (*Phaseolus vulgaris* L.) is a very important and cheap source of protein, natural fiber, and calories in eastern and southern Africa and tropical America (13). Nearly 10 million tons of dry common bean are harvested annually in the world on over 13 million hectares. In Latin America and sub-Saharan Africa where more than 70% of beans are produced, diseases, pests, soil fertility problems, and drought adversely affect yield. One of the most widespread and severe diseases of the common bean is anthracnose, caused by the fungus *Colletotrichum lindemuthianum* (Sacc. & Magnus) Lams.-Scrib. (15). It thrives in relatively cool and wet regions of the tropics and subtropics, and is endemic in southern and central Brazil, the highlands of Peru, Ecuador, Colombia, Costa Rica, Nicaragua, Honduras, Guatemala, Mexico, and Central and East Africa. The pathogen is seedborne, and planting infected seed usually results in poor germination and infected seedlings. Most aerial parts of the plant, especially pods, seeds, leaf petioles, and lower surfaces of leaflets, including veins, are infected. When susceptible cultivars are grown in the presence of *C. lindemuthianum,* yield losses, reduced pod and seed quality, and the consequent economic losses can be extremely severe (9,19). There are many races of *C. lindemuthianum;* thus, as prevailing races shift, cultivars resistant in one year or location may be killed in another (1,5,11). Resistance mechanisms have been identified in the common bean (16), and extremely high levels of genetic resistance, controlled by a single or few major genes, have been reported (12,17). Cultivars resistant to some races are available (3,11,15,22,25). However, because of the highly variable nature of the pathogen, which results in the emergence of new races, this resistance is not durable and new sources of resistant germ plasm are continually needed (2,5,11,18). Schwartz et al (18) systematically evaluated over 13,000 accessions of common bean, and found 30 to be resistant, under field conditions at CIAT-Popayán, Colombia, and in the greenhouse, to other selected Latin American and European isolates of the pathogen.

At the time of the study by Schwartz et al (18), information about patterns of variation found in common bean and its races and gene pools was not available. Since then CIAT's Genetic Resources Unit has processed new common bean accessions, making them available to researchers. Considerable information has also been accumulated on the origin, domestication, evolution, and races of common bean (6–8, 21,23). Similarly, much more is known now about the virulence diversity of *C. lindemuthianum* in Latin America, and on its likely evolution with the cultivated common bean (4; M. A. Pastor-Corrales, *unpublished*). The virulence phenotype (race) of more than 600 isolates of *C. lindemuthianum* from 12 Latin American countries has been characterized. Based on virulence, these isolates can also be grouped into gene pools analogous to those found on the cultivated common bean (4,23).

Our objective was to learn how the common bean varied in its reaction to representative *C. lindemuthianum* isolates from CIAT-Popayán, where anthracnose is endemic, and from Middle America and Andean South America, where anthracnose is significant and where the bean's centers of domestication and genetic diversity are located (6–8). We also report on new sources of anthracnose resistance.

MATERIALS AND METHODS

Isolates. All 14 *C. lindemuthianum* isolates used in this study (Table 1) were obtained during 1976–1992 from naturally infected, domesticated, common bean plants that showed anthracnose symptoms. Monosporic cultures of each isolate were grown and maintained for short periods on potato-dextrose agar in glass petri dishes, incubated at 19–21 C in darkness. For medium-term storage, conidia from sporulating colonies were harvested in a sterile solution of 10% peptone and 20% sucrose and the resulting spore suspension impregnated on sterile pieces of filter paper. The papers were desiccated over sterilized silica gel for about 8 days and then stored. The race (virulence phenotype) of each isolate was characterized, using a set of 12 common bean differential cultivars or lines (14): the small-seeded Michelite, Cornell 49242, PI 207262, AB 136, and G 2333 belong to the Mesoamerica common bean race; the medium-seeded Widusa, Mexico 222, TO, and TU to the Durango race; the large-seeded Michigan Dark Red Kidney and Kaboon to the Nueva Granada race; and Perry Marrow to the Chile race (23). Both the Mesoamerica and Durango bean races were domesticated in Middle America, while races Nueva Granada and Chile were domesticated in Andean South America (23). Seven local isolates, belonging to five different races of *C. lindemuthianum,* were used to inoculate common bean accessions in the field and screenhouse at CIAT-Popayán. Isolates belonging to seven different races of the anthracnose pathogen (three from Middle America and four from Andean South America), were used to inoculate bean accessions in the greenhouse at CIAT-Palmira, Colombia (Table 1).

Germ plasm evaluation. Twelve seeds of each of 20,144 common bean accessions, obtained from the CIAT germ

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plasm bank, were sown in hill plots at CIAT's experiment farm located about 9 km west of Popayán (latitude 2° 27′ N; longitude 76° 34′ W; 1,750 m elevation; mean growing temperature of 18 C; annual rainfall of >2,000 mm). All common bean accessions and check cultivars known for their anthracnose reaction at CIAT-Popayán were inoculated with a mixture of seven isolates of the pathogen collected from CIAT-Popayán in previous cropping seasons. Approximately equal amounts of spores for each isolate were used. These seven isolates belonged to four different races of *C. lindemuthianum* (Table 1). The methods described by Schwartz et al (18) were used to obtain abundant sporulation, prepare and quantify inoculum, and to inoculate the common bean accessions under field conditions. Four inoculations were made, beginning 3–4 wk after sowing when most plants were in the second or third trifoliolate leaf stage, and repeating every 10 days.

The anthracnose reaction was evaluated on the foliage and pods of adult plants. Pods were evaluated several times, beginning with early pod development and ending at harvest maturity, using a 1 to 9 severity scale in which 1 = no visible symptoms (i.e., immune) and 9 = severely diseased (26). All susceptible accessions (scores 7 to 9) were discarded. Accessions with a resistant (scores 1 to 3) or an intermediate (scores 4 to 6) field reaction were reevaluated in replicated plots in subsequent cropping seasons, using the same procedures. The 9,349 accessions that were consistently resistant or intermediate during several cropping seasons were evaluated again in the screenhouse at CIAT-Popayán. Ten 7-day-old seedlings of each accession were inoculated with the same mixture of isolates used for the field evaluations. All accessions with a susceptible (4,060) or an intermediate (1,511) reaction were eliminated.

Individual members of one set of the 3,778 accessions resistant at Popayán were inoculated in a greenhouse at CIAT-Palmira with an equal ratio mixture of pathogen isolates obtained from Middle America, and members of another set with a mixture from Andean South America (Table 1). For abundant production of spores, each isolate was grown separately on previously sterilized young bean leaves placed flat over on potato-dextrose agar in petri dishes, at 19–21 C or until abundant sporulation was observed in about 8 days. A conidial suspension with a concentration of 1.2×10^6 conidia per milliliter of sterile distilled water was prepared for each isolate by washing and scraping the dishes. Equal volumes of conidial suspension of each isolate from a given region were mixed and the mixture used to inoculate 7-day-old seedlings in the greenhouse. Inoculated seedlings were kept for 7 days in a chamber at 21±1 C with 95–100% relative humidity. The chamber was placed in a greenhouse with a 12-hr photoperiod per day. Individual plants were then evaluated, using the same 1–9 scale (26).

All accessions found resistant under field and screenhouse conditions at CIAT-Popayán were also grown in plots under field conditions at Popayán for characterization of morphological marker traits (23). All plants in the field plots were protected from diseases, insect pests, and noxious weeds with fungicides, insecticides, and herbicides, respectively. Also, plots were corrected for soil fertility problems with chemical fertilizers. Data were recorded for growth habit, days to maturity, shape of the flower bracteole and central leaflet of the trifoliolate leaf, presence or absence of stripes at the outer base of flower standards, pod beak position, seed color, seed shape, and 100-seed weight (g). These data were used to identify and assign each accession to its appropriate common bean race (23). All available passport data were also used to determine the country of origin of each accession.

Table 1. Identification, country of origin, and race characterization of *Colletotrichum lindemuthianum* (CL) isolates used in the sequential evaluation of 20,144 common bean accessions

CL isolate	Country of origin	Differential common bean cultivars or lines[a]												CL race[b]
		A	B	C	D	E	F	G	H	I	J	K	L	
CIAT-Popayán[c]														
CL 2	Colombia	+	+	+	−	−	−	−	−	−	−	−	−	7
CL 20	Colombia	+	−	−	+	−	−	−	−	−	+	−	−	521
CL 27	Colombia	+	−	−	+	−	−	−	−	−	+	−	−	521
CL 39	Colombia	+	+	+	−	−	−	−	−	−	−	−	−	7
CL 56	Colombia	+	+	+	+	−	−	−	−	−	−	−	−	15
CL 94	Colombia	+	−	−	+	−	−	−	+	−	−	−	−	137
CL 111	Colombia	+	−	−	+	−	−	−	−	−	+	−	−	521
Middle America[d]														
CL 2	Guatemala	−	−	+	−	−	+	−	−	−	+	+	−	1,572
CL 15	Mexico	+	−	−	−	−	−	+	+	+	−	+	−	1,473
CL 46	Mexico	+	+	−	−	−	−	−	−	−	−	−	−	3
Andean South America[d]														
CL 4	Peru	+	−	−	+	−	−	−	−	−	−	−	−	9
CL 27	Ecuador	−	−	+	−	−	−	−	−	−	−	−	−	4
CL 28	Ecuador	−	+	−	−	−	−	−	−	−	−	−	−	2
CL 105	Colombia	+	+	+	−	−	−	−	−	−	−	−	−	7

[a]Letters A to L designate differential common bean cultivars used to type races of *C. lindemuthianum* (14). Their identification, followed by their binary value in parentheses: Michelite (1), Michigan Dark Red Kidney (2), Perry Marrow (4), Cornell 49242 (8), Widusa (16), Kaboon (32), Mexico 222 (64), PI 207262 (128), TO (256), TU (512), AB 136 (1,024), and G 2333 (2,048).
[b]Race designation obtained by adding binary values of susceptible differential common bean cultivars (14).
[c]Isolates used in field and screenhouse at CIAT-Popayán, Colombia.
[d]Isolates used in greenhouse at CIAT-Palmira, Colombia.

Table 2. Reaction of common bean accessions to mixtures of isolates of *Colletotrichum lindemuthianum* from CIAT-Popayán, Middle America, and Andean South America

Anthracnose reaction[a]	CIAT-Popayán[b]		CIAT-Palmira, screenhouse[c]		
	Field	Screenhouse	Middle America	Andean South America	Both[d]
Resistant	4,939	3,778	1,667	2,806	1,270
Intermediate	4,410	1,511	693	392	37
Susceptible	10,795	4,060	1,418	580	191

[a]Evaluation based on 1–9 scale: 1 = no visible anthracnose symptoms; 9 = severely diseased; grades 1, 2, and 3 are resistant; 4, 5, and 6 intermediate; 7, 8, and 9 susceptible.
[b]20,144 common bean accessions were evaluated under field conditions. Only 9,349 accessions were resistant or intermediate to anthracnose; these were then evaluated in the screenhouse. In both field and the greenhouse, accessions were inoculated with a mixture of isolates from CIAT-Popayán: CL 2 and CL 39 (race 7), CL 56 (race 15), CL 94 (race 137), and CL 20, CL 27, and CL 111 (race 521). All race characterization of isolates was done on a set of 12 differential common bean cultivars or lines (14).
[c]The 3,778 accessions resistant in the CIAT-Popayán screenhouse were evaluated in the CIAT-Palmira greenhouse. The Middle American isolates: CL 46 (race 3) and CL 15 (race 1473) from Mexico, and CL 2 (race 1572) from Guatemala. The Andean South American isolates: CL 27 (race 4) and CL 28 (race 2) from Ecuador, CL 4 (race 9) from Peru, and CL 105 (race 7) from Colombia.
[d]Accessions that were separately resistant, intermediate, or susceptible to both groups of isolates.

RESULTS

Of the 20,144 common bean accessions that were evaluated in the field at CIAT-Popayán with a mixture of local isolates

of the anthracnose pathogen, 4,939 (24.5%) were resistant and 4,410 (21.9%) were intermediate (Table 2). When these 9,349 accessions were inoculated in the seedling stage, in the screenhouse at the same site, only 3,778 accessions were resistant and 1,511 were intermediate. When the 3,778 anthracnose-resistant accessions under field and screenhouse conditions at Popayán were evaluated in the CIAT-Palmira greenhouse, more accessions (2,806 versus 1,667) were resistant to the mixture of Andean South American isolates than to the mixture from Middle America (Table 2). Conversely, more accessions (1,418 versus 580) were susceptible to the mixture of isolates from Middle America than to those from Andean South America. More than one-third (1,270) of accessions were resistant to both Middle American and Andean South American *C. lindemuthianum* isolates.

The 1,270 common bean accessions resistant to both groups of isolates were separated according to their region of domestication, common bean race, anthracnose reaction, growth habit, and flower color (Table 3). The Mesoamerica bean race had the highest number of resistant accessions, followed by races Nueva Granada and Durango. Race Peru, followed by race Chile, had the lowest number of resistant accessions. Although a preponderance of resistant common bean accessions had growth habits III and IV (20), the majority of resistant accessions from the Nueva Granada race had growth habit I. Growth habit II had the lowest number of resistant accessions. Most resistant accessions also had nonwhite flowers. Of the 1,270 accessions resistant to both groups of isolates, 68 were wild common bean, the immediate ancestor of the cultigens. The 1,270 resistant accessions were also grouped according to country of collection, often referred as the country of origin. For example, Mexico was the origin for 379 accessions, Guatemala 163, Brazil 93, Netherlands 82, Malawi 73, Colombia 39, Peru and Rwanda 38 each, Burundi 29, Honduras 25, United States of America 22, Ecuador 21, Cameroon and Japan 17 each, Costa Rica, Nicaragua, Haiti, and Zambia 15 each, Zaire 10, Turkey 9, and Kenya, India, and Germany 8 each. The remaining 131 accessions were obtained from 24 other countries.

Thus, of the 20,144 accessions evaluated, 1,270 were resistant to local isolates in the field and screenhouse at CIAT-Popayán, and to isolates from Middle America and Andean South America in the CIAT-Palmira greenhouse. Furthermore, 350 of these accessions were immune to all isolates tested. A group of 60 resistant accessions was selected to represent different bean races, growth habit, country of origin, and seed type (Table 4).

DISCUSSION

The relatively cool and humid conditions prevalent at CIAT-Popayán were conducive to pathogen infection and anthracnose development, facilitating the evaluation of 20,144 common bean accessions. In all, 9,349 accessions were identified as resistant or intermediate, and 10,795 (53.6%) were eliminated as susceptible. Of the 4,939 accessions resistant to anthracnose in the field, only 3,778 were resistant as seedlings in the CIAT-Popayán screenhouse. Because the growing environment in the screenhouse was similar to that of the field, the 1,161 susceptible accessions were either escapes or possessed only adult-plant resistance (16). Repeated screenings of the bean accessions under field conditions for 8 yr (1985–1992) should have minimized escapes. These accessions, therefore, are likely candidates for further evaluation and identification of adult-plant resistance, if desired. Because of the relatively large number of resistant accessions and our interest in resistance in all stages of plant growth and development, we did not attempt to identify accessions possessing only adult-plant resistance.

The composition of *C. lindemuthianum* populations occurring at CIAT-Popayán is monitored systematically. Isolates are collected periodically from susceptible common bean genotypes of both Andean and Middle American origins for race characterization and artificial inoculations of common bean germ plasm and breeding lines under field conditions. The *C. lindemuthianum* isolates from Popayán, which is located in the northern Andes, have virulence characteristics that are intermediate between the isolates from Middle America and those from the Andes of South America (M. A. Pastor-Corrales, *unpublished*). This mirrors the pattern of the cultivated and wild common bean genotypes from the northern Andes and adjoining regions of Middle America, which often possess intermediate characteristics of the common bean between the two extremes of its range of domestication (8,10,24). The ample virulence diversity of the anthracnose pathogen present in Popayán helped eliminate a high number of accessions with susceptible anthracnose reaction.

Of the relatively large number of common bean accessions resistant to all isolates of *C. lindemuthianum* utilized in this study, many were from the Middle American races of common bean, especially the Mesoamerica race. Among the accessions from Andean South America, the Nueva Granada race had the largest number of resistant accessions. This may be partly because of the proportionately larger representation of the Mesoamerica and Nueva Granada races in the CIAT germ plasm bank. Another factor may be the extensive cultivation of bean landraces derived from the Mesoamerica and Nueva Granada races (22) and, hence, their proportionately wider exposure to *C. lindemuthianum* over millennia and resultant natural selection for resistance. Within the common bean's range of domestication, anthracnose has traditionally been endemic and more severe in Middle America (Costa Rica, Nicaragua, Honduras, Guatemala, and Mexico) than in Andean South America.

Worth noting is the higher susceptibility of some of the differential cultivars of Andean origin to the isolates of *C. lindemuthianum* from Popayán and other Andean South American isolates, compared with those from Middle America (Table 1). These cultivars are Michigan Dark Red Kidney, and Perry Marrow. Although it possesses all mor-

Table 3. The 1,270 common bean accessions resistant to *Colletotrichum lindemuthianum* (CL) isolates from both Middle America and Andean South America categorized by region of domestication, race, CL reaction type, growth habit, and flower color

Domestication region and race of bean accession[a]	Number of bean accessions							
	CL reaction[b]		Growth habit[c]				Flower color	
	1.0	1.1-3.0	I	II	III	IV	White	Others
Middle America								
Mesoamerica	161	322	53	39	223	168	80	403
Durango	20	100	0	0	105	15	29	91
Jalisco	25	64	0	0	6	83	16	73
Andean South America								
Nueva Granada	58	197	178	11	54	12	54	201
Peru	1	10	0	0	0	11	2	9
Chile	4	16	0	0	19	1	4	16
Wild beans	30	38	0	0	3	65	1	67
Uncharacterized	51	173	...	...	...	...	...	...
Total	350	920	231	50	410	355	186	860

[a] According to classification by Singh et al (23).
[b] Evaluation based on 1–9 scale: 1 = no visible anthracnose symptoms; and 9 = severely diseased; grades 1, 2, and 3 are resistant; 4, 5, and 6 intermediate; 7, 8, and 9 susceptible.
[c] According to classification by Singh (20): I = determinate; II = indeterminate erect; III = indeterminate, prostrate, semiclimbing; IV = indeterminate climbing.

phological characteristics of the Mesoamerica race, Cornell 49242 is from Venezuela where it probably originated from wild common bean populations occurring in the northern Andes. Similarly, the other differential common bean cultivars of Middle American origin (letters G–L, Table 1) were usually immune to the Andean South American isolates. This suggests a high degree of specificity with *C. lindemuthianum*. The CIAT germ plasm bank has a proportionately higher number of accessions from Middle America, this may also explain the relatively higher number of accessions resistant to the Andean South American isolates of the anthracnose pathogen (Table 2). This information should help in gene deployment and pyramiding for developing more effective and stable anthracnose resistance in common bean cultivars.

There are fewer than 1,000 accessions of wild common bean in the CIAT germ plasm bank. While not all were available at the beginning of the study, of the 510 accessions evaluated, 68 were resistant to pathogenic populations from both Andean South America and Middle America. Cultigens easily hybridize with wild forms and no apparent barriers to gene exchange exist. Wild forms should therefore serve as valuable germ plasm for further breeding and selection studies.

To identify host resistance, researchers are often confined to greenhouse evaluations of bean seedlings (2,5,11) and thus cannot identify adult-plant resistance or evaluate other agronomic traits. Sequential evaluations, first in the field and screenhouse at wet and high elevations, and then in the greenhouse with mixed pathogen isolates allowed more information to be obtained. However, screening all 20,144 accessions to individual isolates from Andean South America and Middle America would have been a monumental task and prohibitively expensive.

Only a small number of *C. lindemuthianum* isolates, selected from several hundred available from around the world, were used in this study; thus, the 1,270 common bean accessions identified as resistant need to be challenged with other isolates to verify the broader resistance. The exchange and dissemination of common bean among regions within the Americas and between the Americas and other parts of the world, suggest possible duplication exists among the 1,270 resistant accessions. These need to be identified and eliminated. Nonetheless, occurrence of anthracnose resistance across different common bean races varying in seed and plant types, adaptation traits, and geographical origin should facilitate and maximize chances for identifying and using different resistant genes.

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Table 4. Characteristics of 60 selected common bean accessions resistant to local isolates of *Colletotrichum lindemuthianum* in the field and screenhouse at CIAT-Popayán, Colombia, and to a mixture of isolates from Middle America and Andean South America in the greenhouse at CIAT-Palmira, Colombia

Accession no.	Race[a]	GH[b]	Country of origin[c]	Seed color[d]	Seed size[e]	Accession no.	Race[a]	GH[b]	Country of origin[c]	Seed color[d]	Seed size[e]
G 813	M	IV	Mexico	3	S	G 7499	NG	I	Neth.	1	M
G 929	M	II	Honduras	6	S	G 7958	NG	I	Brazil	6	L
G 2052	M	III	Nicaragua	4	S	G 8877	NG	I	Neth.	1	S
G 2241	M	IV	Guatemala	8	M	G 13610	NG	IV	Mexico	6	M
G 2333	M	IV	Mexico	6	S	G 13921	NG	I	Colombia	6, 2	M
G 3817	M	I	Mexico	2	S	G 14175	NG	II	U.K.	7	L
G 9807	M	II	Mexico	2	S	G 20524	NG	III	Zaire	2, 7	M
G 10850	M	III	Guatemala	8	M	G 20555	NG	III	Kenya	2, 6	M
G 18642	M	I	Brazil	7	S	G 12688	C	III	Colombia	2, 6	M
G 21212	M	I	Colombia	8	S	G 13106	C	III	India	1	M
G 2280	D	IV	Mexico	2	L	G 13107	C	III	India	1	M
G 2385	D	III	Mexico	2	L	G 13772	C	III	Zambia	6	M
G 10029	D	III	Neth.	1	L	G 14221	C	III	Yugoslavia	1	L
G 11396	D	III	Mexico	2, 4	M	G 15928	C	III	Neth.	1	S
G 17420	D	III	USA	1	M	G 19189	C	III	Haiti	1	L
G 19096	D	IV	Mexico	2, 3	L	G 21361	C	III	Bulgaria	1	L
G 19993	D	III	USA	4	M	G 1032	P	IV	Yugoslavia	1	L
G 20835	D	IV	Rwanda	5, 4	M	G 7380	P	IV	Colombia	2, 6	L
G 21994	D	IV	Brazil	7	S	G 12668	P	IV	Colombia	7	M
G 877	J	IV	Mexico	5	M	G 14788	P	IV	Haiti	2, 6	L
G 10500	J	IV	Guatemala	1	M	G 14983	P	IV	Colombia	7	L
G 10648	J	IV	Guatemala	1	L	G 9989	W	IV	Mexico	2, 4	S
G 11087	J	IV	Mexico	9, 8	M	G 10005	W	IV	Mexico	9, 8	S
G 15629	J	IV	Turkey	1	L	G 11023	W	III	Mexico	8	M
G 16085	J	IV	Mexico	2, 5	M	G 12873	W	IV	Mexico	9, 8	S
G 19035	J	IV	Mexico	5	M	G 12916	W	IV	Mexico	8	S
G 19921	J	IV	Mexico	6	M	G 13015	W	IV	Mexico	4, 8	S
G 20804	J	IV	Rwanda	7	M	G 13566	W	IV	Mexico	2, 7	S
G 3094	NG	I	USA	1	L	G 23418	W	IV	Costa Rica	9, 4	S
G 7342	NG	I	Peru	3	L	G 23519	W	IV	Mexico	2, 9	S

[a] According to classification by Singh et al (23): M = Mesoamerica, D = Durango, and J = Jalisco, from the Middle American region of domestication; NG = Nueva Granada, C = Chile, and P = Peru, from the Andean South American region of domestication; W = wild common bean.

[b] Growth habits as classified by Singh (20): I = determinate; II = indeterminate erect; III = indeterminate, prostrate, semiclimbing; IV = indeterminate climbing.

[c] Country where the common bean accession was collected.

[d] First number refers to primary and second to secondary seed color: 1 = white, 2 = cream-beige, 3 = yellow, 4 = brown-maroon, 5 = pink, 6 = red, 7 = purple, 8 = black, 9 = others.

[e] Seed size and weight of 100 seeds: S = small, <25 g; M = medium, 25–40 g; L = large, 40 g.

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