Phaseolin Variability among Wild and Cultivated Common Beans (*Phaseolus vulgaris*) from Colombia[1]

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*Phaseolin seed protein variability in a group of 8 wild and 77 cultivated common bean (*Phaseolus vulgaris*) accessions was determined using 1-dimensional SDS/PAGE and 2-dimensional IEF-SDS/PAGE. Wild common bean accessions exhibited the 'CH' and 'B' patterns, previously undescribed among either wild or cultivated common beans. The cultivated genotypes showed (in decreasing frequency) the previously described 'S,' 'T,' and 'C' phaseolin patterns as well as the new 'B' pattern similar to the pattern identified in a Colombian wild common bean accession. In the northeastern part of the Colombian bean-growing region, the cultivars exhibited almost exclusively an 'S' phaseolin type, while in the southwestern part, the 'T' and 'C' phaseolin cultivars were more frequent. Seed size analysis indicated that 'T' and 'C' phaseolin cultivars had larger seeds than 'S' and 'B' phaseolin cultivars. Our results suggest that Colombia is a meeting place for Andean and Middle American common bean germplasms, as well as a domestication center for the common bean.*

Phaseolin constitutes the major seed-storage protein of the common bean, *Phaseolus vulgaris* L. It accounts for 35–50% of total seed nitrogen (Ma and Bliss, 1978). One-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS/PAGE) and 2-dimensional isoelectric focusing SDS/PAGE (IEF-SDS/PAGE) revealed 3 predominant banding patterns—'S' ('Sanilac'), 'T' ('Tendergreen'), and 'C' ('Contender')—among cultivars of the common bean. Crossing experiments have shown that the genes coding for the different polypeptides of each phaseolin pattern are tightly linked and inherited as a single Mendelian unit with the alleles being co-dominant (Brown et al., 1981a,b, 1982).

Further screenings of phaseolin variability among Middle American and Andean wild and cultivated common beans by means of SDS/PAGE and IEF-SDS/PAGE, have provided evidence for multiple, independent domestications of the common bean in Middle America and the Andes (Gepts et al., 1986). While the Middle American wild beans showed 'S' and 'M' phaseolin types, the Andean wild beans (originating in Peru and Argentina) exhibited exclusively the 'T' phaseolin type. Most of the Middle American landraces had an 'S' phaseolin type, while a majority of the Andean cultivars had a 'T' phaseolin type. In addition, some Andean cultivars exhibited either a 'C' or the previously undescribed 'H' or 'A' phaseolin types (Gepts et al., 1986). In both regions, cultivars with a 'T' phaseolin type had larger seeds than 'S' phaseolin cultivars. In the Andes, no significant differences in seed size were observed among 'T,' 'C,' 'H,' and 'A' phaseolin cultivars. Based on these results, 2 major centers of domestication for the common

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bean were hypothesized: one in Middle America, leading to small-seeded, 'S' phaseolin cultivars, and the other in the Andes, giving rise to large-seeded, 'T' phaseolin-type cultivars (Gepts et al., 1986).

Colombia, located in the northwestern part of South America, might possibly be a meeting place for the Middle American and Andean common bean germplasms. On the other hand, the description by Brücher (1968), Berglund-Brücher and Brücher (1976), and Brücher (1977) of wild-growing beans on the eastern slope of the Andes in Colombia raises the possibility that the common bean might have been domesticated there also in addition to Middle America and the southern Andes.

In order to determine whether the common bean cultivars from Colombia represent introductions from Middle American and Andean domestication centers or local domesticates, we have analyzed the electrophoretic variation of phaseolin in a collection of wild and cultivated common bean accessions from Colombia. Determining the genetic relationships among common bean genotypes may have important consequences for the management of genetic resources and breeding programs.

MATERIALS AND METHODS

Plant materials

The sample of wild common beans consisted of 8 accessions from the Departamento of Cundinamarca. These accessions were collected by Dr. Leroi, Université de Tours, France, and were made available by Dr. R. Maréchal, Faculté des Sciences Agronomiques, Gembloux, Belgium. Their identification and the location and altitude of the collection sites are indicated in Table 1.

A collection of 77 cultivated common bean lines was obtained from Dr. R. Hannan, USDA-Western Regional Plant Introduction Station, Pullman, Washington, USA. To this collection were added line NI645, obtained from Dr. R. Maréchal, and Rubona 5, obtained from Dr. J. Davis, CIAT, Cali, Colombia. For the analysis of the results, we have included lines analyzed previously: Cargamanto and Nariño 23 (Gepts et al., 1986), and PI207227 (Brown et al., 1982). The identification of these accessions is shown in Table 2.

Preparation of flour samples for electrophoresis

Four seeds of each wild bean accession and 5 seeds of each cultivated genotype were analyzed by 1-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS/PAGE). A flour sample from the raphe end of each seed was suspended at room temperature for at least 0.5 h in a mixture consisting of equal volumes of a 0.5 M NaCl solution and cracking buffer (0.625 M Tris-HCl, pH 6.8; 2 mM EDTA; 2% (w/v) SDS; 40% (w/v) sucrose; 1% (v/v) 2-mercaptoethanol; and 0.01% bromophenol blue marker dye (Brown et al., 1981a). The mixture was then heat-treated at 100°C for 5 min, centrifuged, and the supernatant was submitted to electrophoresis.

Electrophoresis

One-dimensional SDS/PAGE was performed according to the method of Laemmli (1970) modified by Ma and Bliss (1978). Electrophoresis was carried

TABLE 1. IDENTIFICATION, ORIGIN, AND PHASEOLIN TYPE OF WILD BEANS FROM THE DEPARTAMENTO OF CUNDINAMARCA, COLOMBIA.

Identification[a]	Location		Altitude (m)	Phaseolin type[b]
NI922	Ubaqué	N4.29; W73.56	1,900	CH
NI926	Choachí	N4.32; W73.55	1,800	S
NI928	Manta	N5.01; W73.33	1,600	CH
NI937	Tena	N4.40; W74.24	1,560	CH
X634	Ubaqué	N4.29; W73.56	1,750	CH
X636	Machetá	N5.05; W73.37	1,900	B
X643	Choachí	N4.32; W73.55	1,900	CH
X654	Manta	N5.01; W73.33	1,900	CH

[a] NI and X, introduction numbers of the wild *Phaseolus* collection, Faculté des Sciences Agronomiques, Gembloux, Belgium.
[b] B, 'B' phaseolin; CH, 'CH' phaseolin; S, 'S' phaseolin-banding patterns.

out in 0.75 mm thick, 15% (w/v) polyacrylamide slab gels. Two-dimensional isoelectric focusing SDS/PAGE (IEF-SDS/PAGE) was carried out as described by Brown et al. (1981a), except that 15% polyacrylamide slab gels were used for the second (SDS) dimension. The phaseolin types, as determined by 1-dimensional SDS/PAGE and 2-dimensional IEF-SDS/PAGE, are listed in Table 1 for the wild common beans and in Table 2 for the cultivated common beans.

Seed size

Seed size of cultivars was determined as indicated previously (Gepts et al., 1986) and is listed in Table 2. The statistical significance of seed-size differences was assessed by analysis of variance and by Duncan's multiple range test (Dagnelie, 1969).

RESULTS

Phaseolin variability among wild common bean accessions

Using 1-dimensional SDS/PAGE, 4 different banding patterns were observed among the wild common bean lines (Fig. 1). Accession NI926 was similar to the 'S' banding pattern, described previously among wild common bean accessions of Middle America and among common bean cultivars. The 3 other banding patterns, represented by NI922, NI937, and X636, differed from the 'S' banding pattern, especially among the lower molecular-weight phaseolin bands.

Two-dimensional IEF-SDS/PAGE confirmed that NI926 had an 'S' phaseolin type (not shown). The patterns of NI922 (representative for NI928 and X643) and of NI937 (representative for X634 and X654) showed some similarities, but were different from any of the 'M' types described earlier as well as from any of the phaseolin patterns described among cultivars (Brown et al., 1981a; Gepts et al., 1986).

We suggest that these patterns be designated as 'CH' patterns after the pre-Colombian Chibcha civilization of this region of Colombia, which includes the Departamentos of Boyacá, Cundinamarca, and Santander.

Phaseolin variability among cultivated common bean accessions

When analyzed by 1-dimensionalSDS/PAGE, the cultivated accessions showed the phaseolin-banding patterns—'S,' 'T,' and 'C'—identified previously among

TABLE 2. IDENTIFICATION, PHASEOLIN TYPE, AND SEED SIZE OF COLOMBIAN COMMON BEAN CULTIVARS.

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or name		Length	Height	Width
	Cargamanto	T	12.9	9.5	7.2
NI645		C	11.4	8.9	7.6
PI207227		S	8.5	5.7	4.4
PI313571*	Antioquia 6	T			
PI313572	Antioquia 12	S	9.4	5.8	4.0
PI313573*	Antioquia 18	T			
PI313574*	Antioquia 25	S, T			
PI313575*	Antioquia 26	S, C			
PI313576*	Antioquia 34	S, T, C			
PI313577*	Antioquia 36	S, C			
PI313578*	Antioquia 64	S			
PI313579	Antioquia 94	S	10.9	6.4	4.1
PI313580*	Antioquia 106	T			
PI313581*	Antioquia 140	S, C			
PI313582*	Atlántico 1	S			
PI313583	Atlántico 6	S	10.0	6.6	4.5
PI313584	Boyacá 1	S	9.7	6.3	5.2
PI313585	Boyacá 4	S	10.1	6.9	4.7
PI313586	Boyacá 5	S	11.8	6.8	4.9
PI313587	Boyacá 6	S	10.1	6.7	4.5
PI313588	Boyacá 8	S	10.8	6.3	5.0
PI313589*	Boyacá 21	S			
PI313590*	Boyacá 22	B, S			
PI313591	Boyacá 30	S	11.5	7.3	4.8
PI313592*	Boyacá 101	S			
PI313593*	Boyacá 104	S			
PI313594	Cauca 15	S	9.5	5.9	4.2
PI313595	Cauca 31	S	9.3	6.3	5.1
PI313596*	Cauca 33	S			
PI313597	Cauca 36	T	16.1	8.6	6.1
PI313598	Cauca 38	T	14.3	8.4	5.8
PI313599	Cauca 39	S	9.7	6.5	4.8
PI313600*	Cauca 41	S			
PI313601	Cundinamarca 11	T	13.2	7.4	5.7
PI313602	Cundinamarca 17	S, C			
PI313603*	Cundinamarca 45	S, C			
PI313604	Cundinamarca 47	T	15.4	8.6	6.2
PI313605*	Cundinamarca 65	S, C			
PI313606*	Cundinamarca 112	S, C			
PI313607	Cundinamarca 115	S	10.5	6.5	4.7
PI313608	Cundinamarca 116	S	10.4	6.7	4.6
PI313609	Cundinamarca 120	T	16.4	9.0	6.2
PI313610*	Cundinamarca 137	S, T			
PI313611*	Cundinamarca 138	S, C			
PI313612*	Cundinamarca 140	S, C			
PI313613*	Cundinamarca 146	S, T, C			
PI313614*	Huila 2	S, C			
PI313615	Huila 5	S	10.5	7.4	4.8
PI313616*	Huila 6	S, C			
PI313617*	Huila 7	S, C			
PI313618	Huila 9	T	12.1	7.0	5.3
PI313619	Huila 12	T	12.9	8.8	6.8

TABLE 2. CONTINUED.

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a] and/or name			Length	Height	Width
PI313620	Huila 14	S	10.3	7.0	4.7
PI313621	Huila 17	S	9.9	5.9	4.1
PI313622*	Huila 19	S			
PI313623	Huila 23	S	11.1	7.4	5.0
PI313624	Magdalena 3	B	9.5	6.6	5.0
PI313625	Magdalena 11	S	10.2	6.4	4.8
PI313626	Magdalena 12	T	14.4	7.6	5.8
PI313627*	Nariño 2	S, T			
PI313628	Nariño 4	T	11.7	8.4	6.3
PI313629	Nariño 7	S	11.0	7.0	5.1
PI313630*	Nariño 11	S			
PI313631*	Nariño 12	T			
	Nariño 23, Matahambre	S	11.0	6.6	4.2
PI313632*	Nariño 24	S			
PI313633	Nariño 47	C	12.1	7.1	6.1
PI313634	Nariño 50	B	10.4	6.1	4.5
PI313635	Santander del Norte 1	S	10.3	6.4	4.7
PI313636	Santander del Norte 3	S	10.7	6.2	4.8
PI313637*	Santander del Norte 6	S			
PI313638	Santander 9	S, T			
PI313639	Tolima 17	S	11.5	6.9	5.1
PI313640*	Tolima 35	S, T			
PI313641	Tolima 39	T	15.7	8.1	6.1
PI313642	Valle 3	T, C			
PI313643	Valle 4	C	11.6	7.2	6.0
PI313644	Valle 10	S	10.2	6.1	4.5
PI313645	Valle 15	S	8.1	5.2	4.5
PI313646	Valle 16	C	11.5	8.1	7.2
PI313647	Valle 17	T	14.1	7.7	5.4
	Rubona 5	T	12.9	8.2	5.9

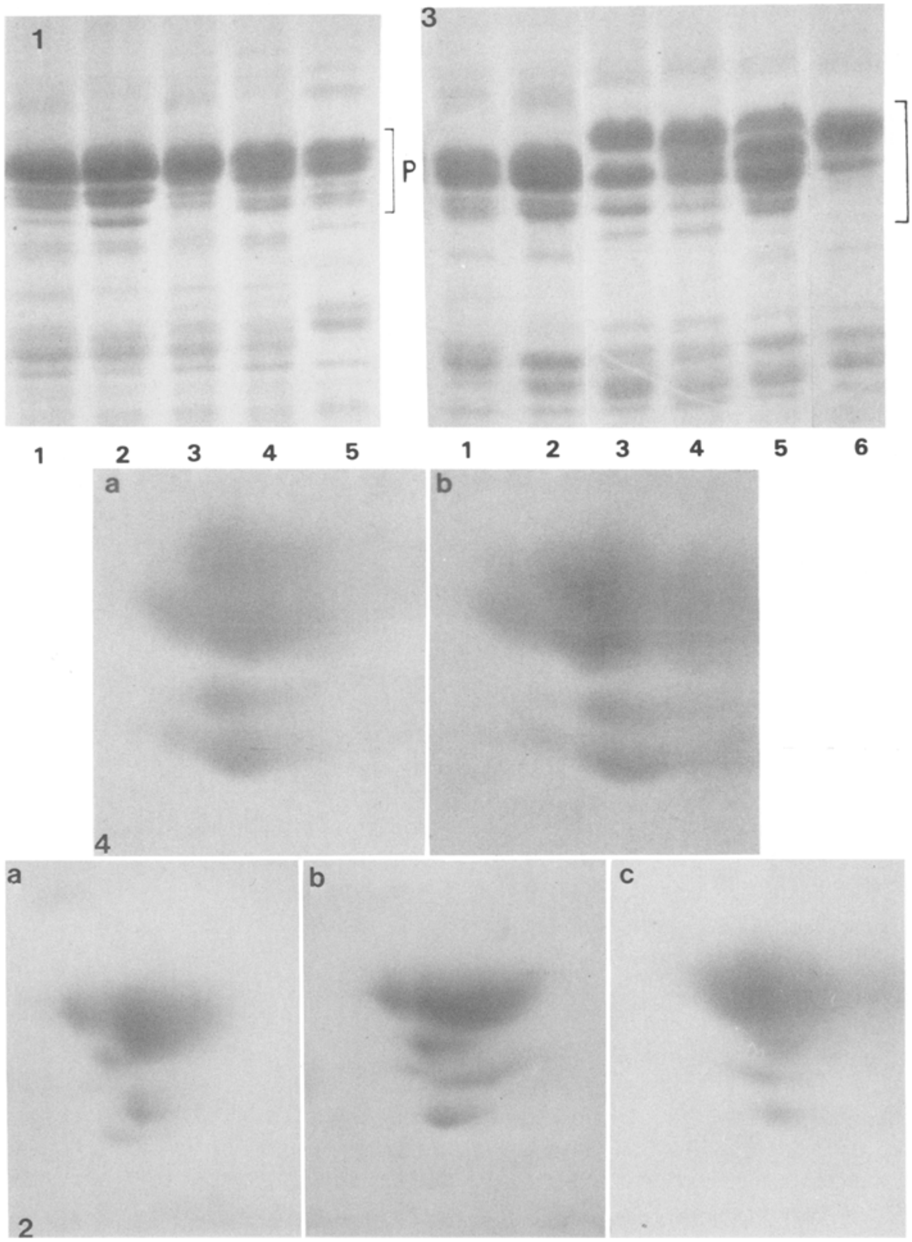
[a] The asterisk indicates accessions heterogenous for seed type.
[b] A, 'Ayacucho'; B, Boyacá 22; C, 'Contender'; H, 'Huevo de huanchaco'; S, 'Sanilac'; T, 'Tendergreen' phaseolin types.
[c] Only seed sizes of accessions homogenous for seed and phaseolin type were included.

cultivated forms of the common bean (Ma and Bliss, 1978; Brown et al., 1981a; Brown et al., 1982) and a new banding pattern, the 'B' pattern after the Colombian landrace Boyacá 22 in which it was first observed (Fig. 3). Twenty-one accessions of 82 (26%) were heterogeneous for phaseolin type, showing 2 or more phaseolin patterns. Among 61 cultivars homogenous for phaseolin type, 62% had an 'S' phaseolin type, 28% a 'T' type, 7% a 'C' type, and 3% a 'B' type.

Two-dimensional IEF-SDS/PAGE confirmed that the 'B' phaseolin type had a unique 2-dimensional pattern not identified previously among cultivated common beans (Fig. 4a). However, the 'B' pattern closely resembled the pattern displayed by X636 as indicated by 2-dimensional IEF-SDS/PAGE of a mixture of the 2 phaseolins (Fig. 4b). Therefore, based on 2-dimensional IEF-SDS/PAGE, X636 also has a 'B' phaseolin type.

Geographic distribution of phaseolin types

The different phaseolin types were unequally distributed over the bean-growing region of Colombia (Table 3, Fig. 5). In the northeastern part of the bean-growing



Figs. 1-4. Fig. 1. One-dimensional SDS/PAGE of phaseolin (P) of wild common bean accessions from Colombia. Lane 1, 'CH' phaseolin of NI922; lane 2, 'CH' phaseolin of NI937; lane 3, 'B' phaseolin of X636; lane 4, 'S' phaseolin of NI926; lane 5, reference 'S' phaseolin of cultivar 'Sanilac'. Fig. 2. Two-dimensional IEF-SDS/PAGE of phaseolin from selected wild common bean lines from Colombia. a, 'CH' phaseolin of NI922; b, 'CH' phaseolin of NI937; c, 'B' phaseolin of X636. Fig. 3. One-dimensional SDS/PAGE of 'B' phaseolin and previously described 'S,' 'T,' 'C,' 'H,' and 'A' phaseolins (P). Lane 1, 'S' phaseolin of 'Sanilac'; lane 2, 'B' phaseolin of Boyacá 22; lane 3, 'T' phaseolin of 'Tendergreen'; lane 4, 'C' phaseolin of 'Contender'; lane 5, 'H' phaseolin of G12588 ('Huevo de huanchaco'); lane 6, 'A' phaseolin of 'Ayacucho.' Fig. 4. Two-dimensional IEF-SDS/PAGE of 'B' phaseolin. a, 'B' phaseolin of cultivar Boyacá 22; b, mixture of phaseolins of wild accessions X636 and cultivar Boyacá 22.

TABLE 3. GEOGRAPHIC FREQUENCY DISTRIBUTIONS OF PHASEOLIN TYPES AMONG COMMON BEAN LANDRACES FROM COLOMBIA.

Departamento	Phaseolin type[a]			
	'S'	'T'	'C'	'B'
1. Northeast				
Atlántico	2			
Boyacá	9			
Magdalena	1	1		1
Santander del Norte	3			
	15 (88%)	1 (6%)	0 (0%)	1 (6%)
2. Southwest				
Antioquia	3	4		
Cauca	5	2		
Cundinamarca	2	3		
Huila	6	2		
Nariño	4	2	2	1
Tolima	1			
Valle	2	1	2	
	23 (55%)	14 (33%)	4 (10%)	1 (2%)

[a] Excluding accessions heterogeneous for phaseolin pattern.

area (Departamentos of Atlántico, Boyacá, Magdalena, and Santander del Norte), 15 of 17 cultivars (88%) had an 'S' phaseolin type, 1 (6%) a 'T' phaseolin type, and 1 (6%) a 'B' phaseolin type. In the southwestern part (Departamentos of Antioquia, Cauca, Cundinamarca, Huila, Nariño, Tolima, and Valle), 23 accessions of 42 (55%) showed an 'S' phaseolin type. However, the frequency of the 'T' type increased to around 30% and the 'C' type which was absent in the northeastern part, occurred at a frequency of 10%.

Relationship between seed size and phaseolin type

Previous analyses of seed size among Middle American and Andean cultivars showed that 'S' phaseolin genotypes generally had smaller seeds than 'T,' 'C,' 'H,' and 'A' cultivars. In Colombia, significant differences in seed dimensions were observed also among cultivars with different phaseolin types. 'T' and 'C' phaseolin cultivars had larger seeds than 'S' and 'B' cultivars (Table 4).

DISCUSSION

Two findings emerge from this study of phaseolin electrophoretic variability among Colombian wild and cultivated common bean lines.

First, the presence of the 'B' phaseolin type among both wild and cultivated genotypes from Colombia (and its absence elsewhere) suggests that this country (and more specifically the eastern slope of the Andes where wild-growing beans are distributed) may be a domestication center of the common bean in addition to Middle America and the southern part of the Andes (Gepts et al., 1986). Because of the low frequency of 'B' phaseolin types among cultivated genotypes, Colombia

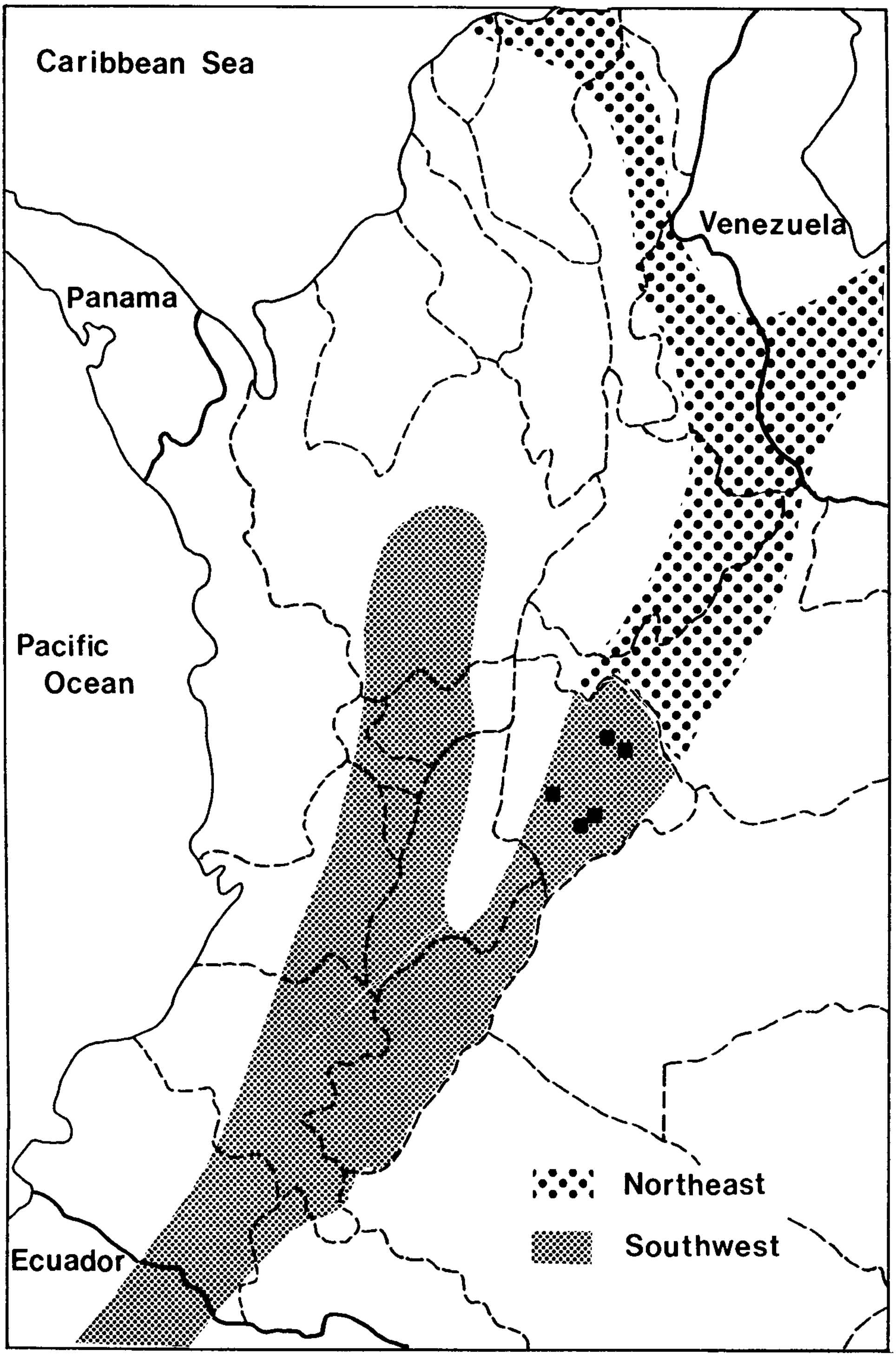


Fig. 5. Northeastern and southwestern parts of the bean-growing area of Colombia as defined by phaseolin electrophoretic variability. The filled squares indicate the location of origin of the wild common bean accessions included in this study.

TABLE 4. STATISTICAL ANALYSIS OF SEED DIMENSIONS IN RELATION TO PHASEOLIN TYPE FOR COMMON BEAN LANDRACES OF COLOMBIA.

1. Analysis of variance[a]

	F value[c]		
df[b]	Length	Height	Width
H_0: No differences in seed size among cultivars with different phaseolin types.			
3,42	37.08***	28.14****	46.36***

2. Duncan's multiple range test[a]

	Seed sizes (mm)[d]		
Phaseolin type	Length	Height	Width
'T'	14.0a	8.3a	6.1 b
'C'	11.7 b	7.8a	6.7a
'S'	10.3 bc	6.5 b	4.7 c
'B'	10.0 c	6.4 b	4.8 c

[a] Excluding accessions heterogeneous for phaseolin or seed type.
[b] df, degrees of freedom of the numerator and denominator, respectively.
[c] ***, significant differences at the $P = 0.001$ level; ns, absence of significant differences at the $P = 0.05$ level.
[d] Within columns, values followed by the same letter are not significantly different at the $P = 0.05$ level, according to Duncan's multiple range test.

is probably only a minor domestication center compared to Middle America and the Andes. It appears, nevertheless, that the common bean was domesticated repeatedly along the distribution area of its wild relative, which extends from Mexico to northern Argentina. This domestication pattern does not conform to the model of Vavilov (1951), but fits rather that of a noncentric crop (Harlan, 1975). The noncentric crop domestication pattern is characteristic of crops whose wild relatives are widely distributed. Other examples of noncentric crops include the lima bean (*Phaseolus lunatus*), sorghum (*Sorghum bicolor*), radish (*Raphanus sativus*), colza (*Brassica campestris*), and Asian rice (*Oryza sativa*) (Allard, 1960; Harlan, 1975; Shechter and de Wet, 1975; Second, 1982).

Second, Colombia also appears to be a meeting place for the Middle American and Andean cultivated forms as evidenced by the high frequencies of the 'S' and 'T' phaseolin types, the high proportion of heterogeneous accessions with 'T' and 'S' phaseolin types, as well as by the geographical gradients of the 'S' and 'T' phaseolin types in that country. Common beans in Colombia should, therefore, be very diverse as illustrated by the many different seed types observed in the collection we have analyzed. Possibly, this diversity is increased even further by natural outcrosses between wild and cultivated beans. Accessions PI313578 (Antioquia 63), PI313589 (Boyacá 21), PI212590 (Boyacá 22), and PI313593 (Boyacá 104) have brown seeds covered with black speckles and stripes, somewhat similar to the seeds of wild-growing beans. It may be significant that most of these accessions come from the Departamento of Boyacá, which is located in the distribution area of wild common beans. Outcrosses between wild and cultivated common beans may also account for the presence of an 'S'phaseolin type in wild common bean accessions NI926. Seeds of this accession were larger than seeds of the other wild accessions.

The phaseolin data confirm the findings of the Colombian archaeologist Reichel-

Dolmatoff (1965), who observed that Colombia was located at one of the major crossroads of cultural exchange in the Americas. In addition, Bernal and Reichel-Dolmatoff (1953) observed that the 2 maritime coasts of Colombia, its large Andean rivers, and the rivers and plains of the Amazon basin in the eastern part of its territory constitute natural ways of penetration and contact.

The presence of wild common beans and the diversity of cultivated common beans make Colombia a prime objective for future germplasm collection activities.

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