Dissemination Pathways of Common Bean (*Phaseolus vulgaris*, Fabaceae) Deduced from Phaseolin Electrophoretic Variability. I. The Americas[1]

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*Dissemination pathways of common bean (*Phaseolus vulgaris*) cultivars from their areas of domestication to other parts of the Americas were determined using phaseolin type, as determined by 1-dimensional SDS/PAGE. Common bean cultivars of lowland South America exhibited approximately equal numbers of 'S' and 'T' phaseolin types. 'S' cultivars of that region may have been introduced along a route starting in Middle America and leading into Colombia, Venezuela, and eventually Brazil. 'T' phaseolin cultivars in lowland South America may have been introduced directly from the Andes or indirectly by European immigrants. In the southwestern U.S.A., most of the cultivars showed an 'S' phaseolin, confirming the Middle American origin of these cultivars, as suggested previously by the archaeological record. In northeastern U.S.A. and Canada, the 'T' and 'C' phaseolin types were more frequent than the 'S' phaseolin cultivars. While most of the former were possibly introduced into that region by European immigrants, most of the latter may have been introduced by the pre-Columbian Indian populations. Seed size analysis revealed that 'T' or 'C' phaseolin cultivars had significantly larger seeds than 'S' phaseolin cultivars, as had been observed previously in Middle America and the Andes. The phaseolin types of commercial seed types and of early northeastern U.S. cultivars are discussed.*

Botanical, archaeological, and seed protein data provide evidence for multiple domestications of the common bean (*Phaseolus vulgaris* L., Fabaceae) along the distribution area of its wild-growing relative. Wild common beans have been described from Mexico to Argentina (Berglund-Brücher and Brücher 1976; Brücher 1968, 1977; Burkart 1943; Burkart and Brücher 1953; Gentry 1969; MacBryde 1947; Miranda Colín 1967). Archaeological common-bean remains of similar age have been found in Mexico and in Peru (Kaplan 1965; Kaplan et al. 1973). Electrophoretic analysis of phaseolin—the major seed storage protein—has identified a wide range of electrophoretic patterns among wild beans—the 'B,' 'CH,' 'M,' 'S,' and 'T' patterns—and six patterns among Middle American and Andean landraces—'A,' 'B,' 'C,' 'H,' 'S,' and 'T' (Gepts and Bliss 1986; Gepts et al. 1986). Cultivars with a 'B' or 'S' phaseolin on the average had smaller seeds than 'A,' 'C,' 'H,' or 'T' phaseolin cultivars (Gepts and Bliss 1986; Gepts et al. 1986).

The geographic distribution of the different phaseolin types among wild and cultivated beans in Middle America and the Andes has led us to hypothesize several areas of domestication for the common bean: Middle America for small-seeded, 'S' phaseolin cultivars; Colombia for small-seeded, 'B' phaseolin cultivars;

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and the southern Andes (Peru and Argentina) for large-seeded, 'T' (and possible 'A,' 'C,' or 'H') phaseolin cultivars (Gepts 1984; Gepts and Bliss 1986; Gepts et al. 1986). In addition, Colombia appears to be a meeting place for the cultivars of Middle American and Andean origin, as evidenced by the high frequency of Colombian landraces heterogeneous for phaseolin type, the high frequency of 'S' and 'T' phaseolin types, and the geographical gradients exhibited by these phaseolin types (Gepts and Bliss 1986).

In this paper, we report on the electrophoretic analysis of phaseolin from cultivars of lowland South America, the Caribbean islands, the United States, and Canada. Phaseolin electrophoretic type was used as a marker to trace possible dissemination routes of the common bean from its centers of domestication to other regions of the Americas.

MATERIALS AND METHODS

The origin and identification of the common bean cultivars used in this study are indicated in Table 1. As for the preceding studies (Gepts and Bliss 1986; Gepts et al. 1986), all the cultivars examined here were actual landraces to the best of our knowledge.

One-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS/PAGE) was performed as described earlier (Brown et al. 1981; Ma and Bliss 1978).

Seed sizes of landraces homogeneous for seed and phaseolin types were determined as indicated in Gepts et al. (1986).

RESULTS

Phaseolin variability

The sample of cultivars from lowland South America comprised four accessions from Venezuela and 72 from Brazil. In addition, eight cultivars from the Caribbean (Haiti, Dominican Republic, and Jamaica) were examined (Table 1).

Overall, in lowland South America, 60% of the investigated cultivars had an 'S' phaseolin type and 40% a 'T' phaseolin (Table 2). In Venezuela, the four cultivars exhibited an 'S' phaseolin type. In Brazil, the 'S' and 'T' phaseolin were found each in about half of the accessions. The 'S' phaseolin cultivars were distributed over all the bean-growing regions of Brazil, including the western state of Rondonia, close to the Andes. The 'T' phaseolin cultivars were found predominantly in Minas Gerais (eastern Brazil) and Santa Catarina (southern Brazil). In the Caribbean islands, the majority of the landraces had an 'S' phaseolin type, with some cultivars showing a 'T' phaseolin type (Table 2).

Consideration of the seed type (color, shape, and size) allowed a few additional observations to be made. The four Venezuelan cultivars—all with an 'S' phaseolin type—had small, black seeds, which is the typical commercial common bean type of that country (the so-called caraota type). In Brazil, the mulatinho, rosinha, roxão, preto, chumbinho, 'Carioca,' 'Bico de Ouro,' and 'Banha de Galinha' seed types—all small seeded—showed 'S' phaseolin patterns. 'T' phaseolin cultivars included the medium-seeded cultivar 'Goiano Precoce,' the large-seeded cultivar 'Jalo,' the manteigão and bolinha types, and cultivars whose seeds had a cream or pink background covered with dark streaks (e.g., G5129, G5167, and G13765). The enxofre and vermelho types exhibited either an 'S' or a 'T' phaseolin type.

In the Caribbean, the large, red-mottled seed type (e.g., Azael 266 and 'Pompadour Mocana') had a 'T' phaseolin type, while the small, black- or brown-seeded types (e.g., HS1 and HS11) had an 'S' phaseolin type. 'Miss Kelly'—a popular small-seeded cultivar in Jamaica—also exhibited an 'S' phaseolin pattern.

Our sample of landraces from North America (north of Mexico) consisted of 66 accessions from southwestern United States (Arizona, New Mexico, and Utah) and 40 accessions from northeastern United States (remainder of the United States, toward the northeast) and Canada (Table 1). Seventy-two percent of these cultivars had an 'S' phaseolin type, 23% a 'T' type, and 5% a 'C' type.

A geographical pattern in the phaseolin type distribution was observed (Table 2). In the southwestern United States, all the 65 accessions homogeneous for phaseolin type showed an 'S' phaseolin pattern except NS/S7 (from Utah), which showed a 'T' pattern. A heterogeneous accession (PI353584) showed both 'S' and 'C' phaseolins. In the northeastern part of the United States and in Canada, out of 40 accessions homogeneous for phaseolin type, 60% had a 'T' phaseolin type, 30% an 'S' phaseolin type, and 10% a 'C' phaseolin type.

In the sample from the southwestern United States, several seed types were represented. In addition to the better-known types such as the pintos (e.g., PI353572, PI353581, and PI353626), bayos (e.g., NS/S18, PI313587, PI353604, and PI353621), and ojo de cabra (e.g., PI353577 and PI353601), our sample contained several other seed types: white (e.g., NS/S14 and PI353623); dark red (e.g., PI353570, PI353573, and PI353592); purple with black speckles and stripes (e.g., NS/S2, NS/S13, and PI353568); light brown with yellow stripes (e.g., PI353572 and PI353574); cream with dark speckles and stripes (e.g., PI353593 and PI353594); orange or brown (e.g., NS/S15, PI353568, PI353583, and PI353614); and cream covered with red speckles (NS/S8). The latter seed type resembles closely the 'Cutshort' type (Hedrick 1931). Several accessions had seeds exhibiting white sectors (e.g., PI353569, PI353571, PI353576, and PI353578). All these types had an 'S' phaseolin type. The only accession with a 'T' phaseolin type in the southwestern United States sample (NS/S7) had elongated, white seeds.

Several seed types from the northeastern United States were represented in our sample. Seed types of cultivars with an 'S' phaseolin type included the navy or pea beans (e.g., BN510 and BN799); the great northern types ('Great Northern' U.I. 31 and BN683); a 'Sulphur' bean (BN142); a 'Cutshort' type (BN570); the cultivar 'Lightning' (BN745); and a type resembling the 'Carioca' seed type of Brazil (BN85). Cultivars with a 'T' or a 'C' phaseolin pattern also exhibited several seed types among which were the red kidney type (G6592 and BN433); the soldier beans (BN13, BN39, BN143, BN352, and BN422); the trout beans (BN23, BN26, and BN30); the eye beans (BN66 and BN446); the horticultural and cranberry beans (BN3, BN211, BN220, BN357, and BN533); a turkey bean (BN673); and a white-seeded bean (BN209). The phaseolin types of the most frequent seed types in our sample of the northeastern United States are summarized in Table 3.

Several of the accessions included in our sample of the northeastern United States were first described in the first half of the 19th century (Hedrick 1931; Tracy 1907; Wing 1882). The 'T,' 'C,' and 'S' phaseolins were represented in approximately equal proportions among these earlier cultivars (Table 4).

TABLE 1. IDENTIFICATION, PHASEOLIN TYPE, AND SEED SIZE OF COMMON BEAN CULTIVARS FROM THE CARIBBEAN ISLANDS, LOWLAND S. AMERICA, U.S., AND CANADA.

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a] and/or name			Length	Height	Width
1. Caribbean Islands					
	Dominican Republic				
	'Pompadour Mocana'	T	12.4	7.7	6.8
	Haiti				
	Azael 266	T	14.1	7.3	5.5
	HS11	S	8.6	6.2	4.6
	HS1 = B789	S	9.7	6.9	4.9
	NIC2	S	8.7	6.0	4.7
	NIC3	S	7.3	5.6	3.6
	PSCl 9	T	11.8	6.2	4.8
	Jamaica				
	'Miss Kelly'	S	9.8	6.9	4.6
2. Lowland S. America					
	Brazil				
GF3049	'Baetão'	S	11.1	6.7	4.1
GF0017	'Bico de Ouro'	S	10.8	7.1	5.3
GF3054	'Caetezinho'	S	10.2	6.3	4.6
	'Carioca'	S	10.7	7.0	5.4
	'Flor Roxa de Cacho'	S	9.8	6.4	5.1
G4826	'Pintado'	T	13.1	8.0	6.6
G5066	'BZL-374'	T	13.2	8.3	6.7
G5129	'Sacavém 597'	T	15.3	8.1	5.5
G5132	'Tubarão Cruzado'	T	13.1	8.1	6.2
G5147	'Cavalho Amarelo'	T	14.0	7.7	5.6
G5164	'Amendoím'	T	12.0	7.8	5.5
G5167	'Manteigão Rajado'	T	12.2	7.9	6.0
G5169		T	12.2	7.6	5.9
G6499	'Fogo na Serra'	T	12.5	8.1	6.6
G6515	'Faveta'	T	12.7	8.3	7.0
G7077	'Mulungu'	T	12.0	7.7	5.7
G7148	211-95/50 P.S.	S	9.9	6.1	4.5
G13763	'Amendoím'	T	12.7	8.1	6.1
G13765	'Anadoran'	T	12.7	8.1	6.5
	'Goiano Precoce'	T	10.2	6.7	5.1
	'H6 Mulatinho'	S	10.4	6.8	4.4
	'Jalo'	T	12.5	6.9	5.2
	'Mulatinho'	S	8.8	6.1	4.7
	'Rico 23'	S	9.6	6.4	4.9
	'Rím de Porco'	S	10.4	6.2	4.0
	'Rio Tibagí'	S	8.8	6.6	5.0
	'Rosinha 6-1'	S	8.6	5.9	3.7
	'Roxão'	S	9.6	6.5	5.2
	'Sacavém'	S	9.7	6.4	4.2
GF3043	'Salta Corrego'	S	11.9	7.1	5.4
	'Vagem Roxa'	S	9.3	6.4	3.8
GF810487	'Chumbinho'	S			
GF810057	'Chumbinho'	S			
GF830026	'Manteiguinha Miudo'	S			

TABLE 1. CONTINUED.

Identification		Phaseolin	Seed sizes (mm)[c]		
Number[a] and/or name		type[b]	Length	Height	Width
GF830374	'Feijão Chumbinho'	S			
GF830156	'Chumbinho'	S			
GF830036	'Vermelhinho'	S			
GF830392	'Vermelho de Minas'	T			
GF830427	'Vermelho 132'	S			
GF830096	'Feijão Vermelho'	S			
GF810494	'Feijão Mineiro'	S			
GF830448	'Manteigão Fosco'	T			
GF830447	'Manteigão'	T			
GF810014	'Jalo'	T			
GF830497	'Jalão'	T			
GF830322	'Enxofrão/Rosinha'	T			
GF800098	'Enxofre'	S			
GF810066	'Banha de Galinha/Enxofre'	S			
GF800351	'Feijão Canario'	S			
GF800271	'Bolinha Comprido'	T			
GF810064	'Banha de Galinha'	S			
GF830138	'Feijão Taquara'	T			
GF830110	'Feijão Criolo'	S			
GF830177	'Preto Commúm'	S			
GF830219	'Feijão Pintado'	T			
GF830223	'Iguaçu Gigante'	T			
GF830129	'Feijão Lustroso'	S			
GF830168	'Feijão Mourinho'	S			
GF830147	'Feijão Enxofre'	T			
GF830144	'Feijão Cavalo'	T			
GF810023	'Preto Vagem Roxa'	S			
GF1029	'Roxão' or 'Fogo na Rampa'	S			
GF1047	'Rosinha de Cipo'	S			
GF1036	'Roxao' or 'Fogo na Rampa'	S			
GF1030	'Bolinha Precoce'	T			
GF0938	'Lustrosa'	S			
GF0937	'Rajado'	S			
GF1542	'Carnaval'	T			
	Venezuela				
PI313879		S	10.4	6.5	4.4
PI313888		S	9.5	6.5	4.8
	Venz. 36	S	11.4	6.8	4.9
	Venz. 54	S	7.3	5.4	3.5
3. Northeastern U.S. and Canada					
BN3	'King Horticultural'	T, C			
BN13	'Bumble Bee'	C	15.7	9.9	7.6
BN23	'Big Light Red Trout'	T	15.4	7.1	5.4
BN26	'Durham Trout'	T	16.5	8.3	6.2
BN30	'Mammoth Trout'	T	18.4	9.0	7.3
BN39	'Mammoth Soldier'	T	17.2	8.2	6.6
BN66	'Yelloweye'	T	12.2	8.6	7.5
BN85	'Old Homestead'	S	10.3	6.8	5.2
BN100	'Appaloosa'	T	14.2	8.2	6.3
BN142	'Sulphur'	S	10.0	7.7	6.6
BN143	'Highmoor Yelloweye'	T	12.0	8.0	6.5

TABLE 1. CONTINUED.

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a] and/or name			Length	Height	Width
BN146	'Shelleasy'	T	16.5	9.6	7.9
BN209	'Lazy Wife'	C	11.4	9.0	6.8
BN211	'Ruby Dwarf Horticultural'	T	13.4	9.4	6.8
BN220	'Mohawk'	T	20.0	9.0	8.3
BN229	'Black Valentine'	C	13.0	6.8	5.7
BN284	'Crimson Beauty'	T	13.1	8.0	7.2
BN320	'Palomino'	T	14.4	7.9	6.1
BN336	'Goose Cranberry'	T	13.4	8.7	7.5
BN345	'Brown Kidney'	T	13.0	6.9	6.1
BN352	'New Hampshire Yellow'	T	13.2	8.3	7.4
BN357	'Cranberry'	C	15.9	10.8	8.7
BN373	'Canadian Wild Goose'	S	10.0	6.9	6.3
BN421	'Canadian Doteye'	S	12.3	8.1	6.6
BN422	'Pinkeye Soldier'	T	14.9	8.1	6.2
BN433	'Loitokitok'	T	13.9	6.8	6.2
BN446	'Squaw Bean'	T, C			
BN447	'Michigan Indian Bean'	T	14.0	9.6	8.1
BN476	'Goddard'	T	20.0	9.1	8.0
BN510	'Creaseback Bunch'	S	9.6	5.9	4.5
BN526	'Fat Goose'	S	16.4	9.6	5.9
BN533	'Arlington Red Cranberry'	C	14.6	10.3	9.1
BN570	'Cutshort'	S	9.2	6.8	5.4
BN593	'Bird Egg'	T, C			
BN673	'Tennessee Turkey'	T	12.5	9.3	5.9
BN683	'Fat Horse'	S	12.7	7.6	5.1
BN745	'Lightning'	S	12.7	8.2	6.0
BN758	'Grannie Patrick Bunch'	S	10.5	6.8	5.1
BN799	'Potato Patch'	S	9.6	6.2	5.6
BN1084	'Old Time Baking Bean'	T	13.5	8.1	6.4
	'Bush Blue Lake 274'	T	12.8	5.8	5.6
G6592	'Canadian Wonder'	T	15.3	7.7	5.9
	'Stockbridge'	T	17.0	9.1	8.1
	'Great Northern Nebraska No. 1'	S	12.3	7.6	5.2
G7564	'Maestro'	T	13.1	5.7	4.8
	'Spartan Arrow'	C	14.4	6.2	4.7
U.I.31	'Great Northern'	S	12.1	7.4	5.1
4. Southwestern U.S.					
NS/S1		S	13.5	7.8	5.5
NS/S2		S	14.2	7.6	6.2
NS/S3		S	14.1	7.6	6.1
NS/S4		S	13.3	7.9	5.8
NS/S5		S	13.2	7.7	5.8
NS/S6		S	13.0	7.8	5.2
NS/S7		T	13.4	6.7	4.5
NS/S8		S	9.4	6.6	5.3
NS/S11		S	10.8	6.8	4.5
NS/S12		S	14.4	7.4	5.7
NS/S13		S	14.1	8.2	5.7
NS/S14		S	13.4	7.6	5.5
NS/S15		S	13.4	8.4	5.6
NS/S16		S	15.0	8.6	5.0
NS/S17		S	11.2	7.1	4.9
NS/S18		S	10.2	8.2	4.6

TABLE 1. CONTINUED.

Identification	Phaseolin	Seed sizes (mm)[c]		
Number[a] and/or name	type[b]	Length	Height	Width
NS/S19	S	10.7	7.0	4.7
PI353568*	S			
PI353569	S	12.8	8.8	5.7
PI353570	S	10.3	6.8	4.3
PI353571	S	11.6	7.3	4.7
PI353572*	S			
PI353573	S	12.8	8.1	5.0
PI353574	S	12.6	8.1	4.8
PI353575*	S			
PI353576*	S			
PI353577	S	11.5	7.4	5.2
PI353578*	S			
PI353579	S	11.8	7.7	5.2
PI353580*	S			
PI353581	S	12.0	7.6	4.9
PI353582	S	12.0	7.1	4.9
PI353583	S	13.3	7.7	5.3
PI353584*	S, C			
PI353585	S	12.2	7.8	5.2
PI353587	S	11.9	9.1	6.1
PI353588	S	11.7	8.3	5.3
PI353589	S	13.6	8.7	5.9
PI353591	S	12.1	7.5	5.1
PI353592*	S			
PI353593*	S			
PI353594*	S			
PI353596*	S			
PI353601	S	12.3	8.3	5.4
PI353602	S	11.8	6.8	5.1
PI353603	S	12.4	8.3	4.9
PI353604	S	12.1	7.6	5.5
PI353605*	S			
PI353606*	S			
PI353609*	S			
PI353610	S	12.8	7.1	5.3
PI353611	S	12.4	7.4	4.6
PI353612	S	13.3	7.9	4.8
PI353613	S	13.3	8.1	4.9
PI353614*	S			
PI353615	S	10.5	6.9	5.2
PI353616	S	11.6	7.9	5.1
PI353617	S	11.0	7.8	5.3
PI353620*	S			
PI353621*	S			
PI353622*	S			
PI353623	S	11.1	6.9	4.3
PI353624*	S			
PI353625*	S			
PI353626	S	10.6	7.4	5.1
PI353627*	S			

[a] The asterisk indicates accessions heterogeneous for seed type.
[b] C = 'Contender'; S = 'Sanilac'; T = 'Tendergreen' phaseolin types.
[c] Only seed sizes of accessions homogeneous for seed and phaseolin types were included.

TABLE 2. FREQUENCY DISTRIBUTIONS OF PHASEOLIN TYPES AMONG COMMON BEAN CULTIVARS FROM DIFFERENT BEAN-GROWING REGIONS OF THE AMERICAS.[a]

Region	n	Phaseolin type		
		'S'	'T'	'C'
Lowland South America	35	20 (57)[b]	15 (43)	
Caribbean islands	8	5 (62)	3 (38)	
Southwestern U.S.	65	64 (98)	1 (2)	
Northeastern U.S.	40	12 (30)	23 (57)	5 (13)

[a] Excluding accessions heterogeneous for phaseolin type.
[b] Values represent frequencies and, between parentheses, percentages.

Relationship between phaseolin type and seed size

In Middle American and in the Andes, the following relationship between seed size and phaseolin type had been observed: the 'S' and 'B' phaseolin-type cultivars had smaller seeds than the 'T,' 'C,' 'H,' and 'A' phaseolin cultivars (Gepts and Bliss 1986; Gepts et al. 1986). The same type of analysis was performed for the other bean-growing areas in the Americas. In all areas, with the exception of the southwestern United States, significant differences were observed between phaseolin types with regard to seed length, height, and width (Table 5). In the southwestern United States, the absence of significant differences may be due to the fact that the 'T' phaseolin type was observed in only one cultivar. Multiple comparisons of means by Duncan's multiple range test (Dagnelie 1969) revealed that the 'T,' 'C,' and 'H' phaseolin cultivars had larger seeds than the 'S' phaseolin cultivars, as had been observed previously for Latin American cultivars (Table 6).

DISCUSSION

The existence of both small-seeded, 'S' phaseolin-type cultivars and large-seeded, 'T' phaseolin cultivars in Brazil allows the postulation that the common bean was introduced by at least two routes into that country. A first route—leading to the introduction of several seed types from the Middle American center—would have started from Mexico and could have followed the Caribbean coast into

TABLE 3. RELATIONSHIP BETWEEN SEED TYPE AND PHASEOLIN PATTERN AMONG COMMON BEAN LANDRACES OF THE NORTHEASTERN U.S.

Seed type	Phaseolin pattern[a]
1. Dry beans	
Navy	'S'
Great northern	'S'
Pinto	'S'
Red kidney	'T'
Eye	'T'
Trout	'T'
Soldier	'T'
Cranberry	'T', 'C'
2. Snap beans	'T', 'C'

[a] From Brown et al. (1982) and present results.

TABLE 4. PHASEOLIN TYPE OF EARLY COMMON BEAN CULTIVARS OF THE NORTHEASTERN U.S. AND CANADA.

Cultivar			
Name	Identification	Year first described[a]	Phaseolin type
'Great Northern'	U.I. 31	before 1800	'S'
'Fat Horse'	BN683	before 1800	'S'
'Lazy Wife'	BN209	1810	'C'
'Mohawk'	BN220	1820	'T'
'Yelloweye'	BN66	1822	'T'
'Cranberry'	BN357	1825	'C'
'Sulphur'	BN142	1828	'S'
'Arlington Red Cranberry'	BN533	1828	'C'
'Ruby Dwarf Horticultural'	BN211	1830	'T'
'Black Turtle Soup'		1832	'S'[b]
'Cutshort'	BN570	1835	'S'
'Black Valentine'	BN229	1850	'C'
'Lightning'	BN745	1850	'S'
'Navy Pea'		1832	'S'[b]
'Canadian Wonder'	G6592	1873	'T'

[a] From Hedrick (1931), Tracy (1907), and Wing (1882).
[b] Phaseolin pattern determined by Brown et al. (1982) and Ma (1977).

Colombia and Venezuela and eventually into Brazil. Alternatively, the route could have left Mexico for the Caribbean islands and from there to Venezuela, Colombia, and Brazil.

Seed types transported along the first route include the small black beans (e.g., Mexico: Chis. 4A1 and 'Veracruz Negro'; Colombia: PI3133593 and PI313636; Venezuela: PI313789; and Brazil: pretos) and the small, light-brown beans (e.g., Mexico: Jal. 132; Colombia: PI313635; Brazil: mulatinhos: G7148, 'Flor Roxa de Cacho,' and 'Rim de Porco'). Voysest (1983) has already suggested that the small-seeded cultivars of Central America, the Caribbean coast of Mexico, the Caribbean islands, Venezuela, and Brazil are related.

The second route may have led to the introduction of large-seeded, 'T' phaseolin types from the Andes. The cultivar 'Jalo' has yellow-brown seeds, which can also be observed in Colombia (PI313598) and Ecuador (PI299019). The other large-seeded, 'T' phaseolin cultivars included in the Brazilian sample also could have been introduced from the Andes. Alternatively, some of these cultivars may have been introduced by immigrants from Europe where large-seeded, 'T' phaseolin

TABLE 5. ANALYSES OF VARIANCE OF SEED DIMENSIONS IN RELATION TO PHASEOLIN TYPE FOR COMMON-BEAN CULTIVARS FROM DIFFERENT BEAN-GROWING REGIONS OF THE AMERICAS.[a]

Region	df[b]	F value[c] Length	Height	Width
Lowland South America	1,33	57.02***	83.89***	51.70***
Southwestern U.S.	1,43	0.74^{ns}	2.83^{ns}	2.27^{ns}
Northeastern U.S. and Canada	2,37	10.96***	8.68***	11.60***

[a] Excluding accessions heterogeneous for phaseolin or seed type.
[b] df = degrees of freedom of the numerator and denominator, respectively.
[c] *** = significant differences between phaseolin types at the $P = 0.001$ level; ns = no significant differences at the $P = 0.05$ level.

TABLE 6. SEED-SIZE DIFFERENCES BETWEEN COMMON BEAN CULTIVARS HAVING DIFFERENT PHASEOLIN TYPES IN VARIOUS BEAN-GROWING AREAS OF THE AMERICAS.[a]

Area	Phaseolin type	Mean seed sizes (mm)[b]		
		Length	Height	Width
Lowland South America	'T'	12.7a	7.8a	6.0a
	'S'	9.9b	6.5b	4.6b
Southwestern U.S.	'T'	13.4a	7.7a	5.2a
	'S'	12.3a	6.7a	4.5a
Northeastern U.S. and Canada	'T'	15.0a	9.4a	6.9a
	'C'	14.1a	8.4b	7.6a
	'S'	11.3b	7.3c	5.6b

[a] Excluding accessions heterogeneous for phaseolin or seed type.
[b] For each region, within each column, values followed by the same letter are not significantly different at the $P = 0.05$ level.

cultivars are prevalent (Gepts and Bliss 1988). The population of southern Brazil is characterized by a high proportion of immigrants of European ancestry. It may, therefore, be significant that a high proportion of the common bean cultivars from that region exhibited a 'T' phaseolin type.

In more recent times, Brazilian breeders have been introducing materials from other countries, especially those in Middle America. The small, black-seeded 'S' phaseolin cultivars included in this study ('Rio Tibagí' and 'Rico 23') were introduced from Costa Rica (C. Vieira, R. Guazzelli, and A. Pompeu, pers. comm.).

The Caribbean islands also received their common-bean cultivars from both the Middle American and Andean centers. The cultivars with a 'T' phaseolin and large, red-mottled seeds (e.g., Haiti: Azael 266, PSC1 9; Dominican Republic: 'Pompadour Mocana') were introduced from the Andes where cultivars with the same seed and phaseolin types can also be found (e.g., Colombia: PI313618 and PI313641; Ecuador: PI299022; Peru: PI290993). The 'S' phaseolin, small, brown- and red-seeded cultivars were introduced from Middle America, either directly or indirectly via Colombia and Venezuela.

Observations on the size and distribution of chromosome knobs among maize races (McClintock et al. 1981) have revealed dissemination routes for maize that show some parallels with the ones just described for the common bean. Based on the presence of the abnormal chromosome 10, of B chromosomes, and of large chromosome knobs 7S and 9L, McClintock et al. (1981) were able to identify a route starting from Mexico and Guatemala into Central America, Colombia, Venezuela, and eventually into the Caribbean islands and the eastern coast of South America. The 'Entrelazado' (Interlocked) race in the Mato Grosso state of Brazil showed some influence of the Andean maize complex as evidenced by the presence of the 6L3 and 7L small chromosome knobs.

For both the common bean and maize, the South American continent can be divided into two areas: lowland South American (Brazil, Venezuela, and northern Colombia) and the Andes (from the southern part of Colombia to Chile and Argentina). The correspondence between maize and beans does not extend, however, to the domestication pattern of the two crop species, as maize was domesticated in Middle America and introduced later in the Andes. For the common bean, the Andean region represents an area of domestication and lowland South America an area of introduction of mostly Middle American domesticates.

Archaeological, historical, and linguistic data indicate that the common bean was cultivated in North America (north of Mexico) before the arrival of the Europeans. In particular, archaeological data point to a dispersal movement that introduced the common bean from Mexico into southwestern United States at least 2,300 yr ago and from there to the northeastern United States some 1,000 yr ago (Ford 1981; Kaplan 1971, 1981).

The phaseolin data confirm this dispersal route. All the common-bean cultivars from the southwestern United States had an 'S' phaseolin type with the exception of one cultivar with a 'T' phaseolin type. However, all the cultivars of that region may not have been introduced from Middle America at the same time. Kaplan (1956, 1971) pointed to the difference between the archaeological and contemporary seed types. For example, the 'pinto' type was rare in archaeological findings, but appears much more frequently nowadays.

The presence of 'S' phaseolin patterns among northeastern United States cultivars, the existence of specific words to designate the common bean in several Indian languages, and the mention of the common bean by 16th and 17th century discoverers, indicate that common-bean cultivars were introduced eventually into that region from Middle America. Hedrick (1931) mentioned several common-bean cultivars grown by the Indians living near the Missouri River (e.g., 'Creaseback' or 'Fat Horse', 'Hidatsa Red', 'Arikara Yellow', and 'Great Northern') and by the Indians of the state of New York (e.g., 'Ground Bird', 'Navy Pea', and 'Robust'). The cultivars 'Fat Horse', 'Great Northern', and 'Navy Pea' have an 'S' phaseolin type (Brown et al. 1982; Ma 1977; and present results).

There could be other sources of 'S' phaseolin cultivars in the northeastern United States. The cultivar 'Black Turtle Soup', also called 'Venezuelan' or 'Brazilian Runner Bean' (Hedrick 1931), has small, black seeds and an 'S' phaseolin type. It may have been introduced from lowland South America where cultivars with the same phaseolin and seed types have been identified. Hedrick (1931) also reported on the introduction of common bean cultivars from Europe (see below), some of which have an 'S' phaseolin type: e.g., 'Prédome Nain'.

The majority of the cultivars of the northeastern United States have a 'T' phaseolin type and, therefore, should represent introductions from regions other than Middle America. Some of these cultivars may have been introduced directly from the Andes. Hedrick (1931) mentioned that 'Red Kidney,' which was grown for the export market to the Caribbean islands, was also called 'Chilean' initially. The introduction and establishment of this material, compared to other Latin American common bean cultivars, may have been facilitated because of more adequate environmental requirements (e.g., photoperiod and temperature).

Most of the 'T' and 'C' phaseolin type cultivars of the northeastern United States, however, came probably from Europe, where 'T' and 'C' phaseolin cultivars are prevalent (Gepts and Bliss 1988). Immigrants or seed companies may have introduced some of the following cultivars: e.g., 'Swedish Brown' from Sweden, 'Lazy Wife' ('Sophienbohne' in Germany and 'Coco Blanc' in France), 'Emperor of Russia' ('Empereur de Russie' in France), 'Flageolet' and 'Soissons' from France, 'Trout' ('Forellen') beans from Germany, and 'London Horticultural' ('Haricot de Prague Marbré' in France) from the United Kingdom and continental Europe (Hedrick 1931; Martens 1869).

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Book Review

Corn: Chemistry and Technology. Standley A. Watson and Paul E. Ranstad (eds.). American Association of Cereal Chemists Inc., 3340 Pilot Knob Rd., St. Paul, MN 55121. 1987. 605 pp. $74.00 (nonmembers $87.00).

Corn, or better maize, is one of the 10 plants that feed the world and one of the three major cereals. As a consequence there has been much research from many points of view devoted to this crop plant. Recent discoveries in botanical, nutritional, agricultural, and other aspects have greatly advanced our knowledge of this cereal inherited from the Amerindians.

It is, consequently, very appropriate that these two specialists have collaborated to pull together and edit in one encyclopedic volume an up-to-date summary of the chemistry and technology of maize. The present volume is the synthesis of material divided into 20 chapters and written by an impressive roster of experts. The scope of the book can be appreciated by the titles of the chapters: 1) Corn perspective and culture; 2) Breeding, genetics and seed production; 3) Structure and composition; 4) Harvesting and post-harvesting management; 5) Measurement and maintenance of quality; 6) Insect pests—control and effect; 7) Production, marketing and utilisation; 8) Kernel carbohydrates; 9) Kernel proteins; 10) Kernel lipids; 11) Dry milling; 12) Wet milling; 13) Food uses of whole corn and dry-milled fractions; 14) Sweet corn; 15) Nutritional values of corn and its by-products; 16) Modification and uses of corn starch; 17) Corn sweeteners; 18) Corn oil; 19) Fermentation processes and products; and 20) Biomass use and conversions. There follows a comprehensive index to the mass of material within the two covers. Each chapter has its extended list of literature cited.

Many specialists in the plant industries and in economic botany will welcome a volume of this calibre. The editors and contributing authors are to be congratulated.

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