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ORIGINAL PAPER

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Domestication patterns in common bean (*Phaseolus vulgaris* L.) and the origin of the Mesoamerican and Andean cultivated races

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Abstract Chloroplast DNA polymorphisms were studied by PCR sequencing and PCR-restriction fragment length polymorphism in 165 accessions of domesticated landraces of common bean from Latin America and the USA, 23 accessions of weedy beans, and 134 accessions of wild beans covering the entire geographic range of wild *Phaseolus vulgaris*. Fourteen chloroplast haplotypes were identified in wild beans, only five of which occur also in domesticated beans. The chloroplast data agree with those obtained from analyses based on morphology and isozymes and with other DNA polymorphisms in supporting independent domestications of common bean in Mesoamerica and the Andean region and in demonstrating a founder effect associated with domestication in each region. Andean landraces have been classified into three different racial groups, but all share the same chloroplast haplotype. This suggests that common bean was domesticated once only in South America and that the races diverged post-domestication. The haplotype found in Andean domesticated beans is confined to the southern part of the range of wild beans, so Andean beans were probably domesticated somewhere within this area. Mesoamerican landraces have been classified into four racial groups. Our limited samples of Races Jalisco and Guatemala differ from the more widespread and commercially important Races Mesoamerica and Durango in types and/or frequencies of haplotypes. All four Mesoamerican races share their haplotypes with local wild beans in parts of their ranges. Independent domestications of at least some of the races in Mesoamerica and/or conversion of some locally adapted wild beans to cultigens by hybridization with introduced domesticated beans, followed by introgression of the "domestication syndrome" seem the most plausible explanations of the chloroplast and other molecular data.

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Introduction

The domestication of plants is the human-driven process by which cultivars or landraces emerge from wild progenitors. Wild progenitors are the genetic foundation of landraces, and landraces are the genetic foundation of our modern crop cultivars. Although it is generally understood that crop domestication is a dynamic and ongoing process (Diamond 1997; Harlan 1992; Zohary 1999), pinpointing the sites of original domestication is of interest to crop evolutionists and of practical importance for breeders and conservationists. Multiple domestications in time and/or space may have been one of the key determinants in structuring the genetic diversity present in our modern crops. Well-documented examples of multiple domestications of distinct but related species exist in the Americas for chili peppers (*Capsicum*) (Pickersgill 1989), *Cucurbita* (Andres 1990; Sanjur et al. 2002; Smith 1997), cotton (Brubaker and Wendel 1994; Wendel et al. 1992), and *Phaseolus* beans (Gepts 1988a). Multiple domestications of different populations of the same species are rare but have also occurred. Common bean (*Phaseolus vulgaris* L.) and Lima bean (*Phaseolus lunatus* L.) provide the best-known examples (Chacón et al. 1996; Gepts and

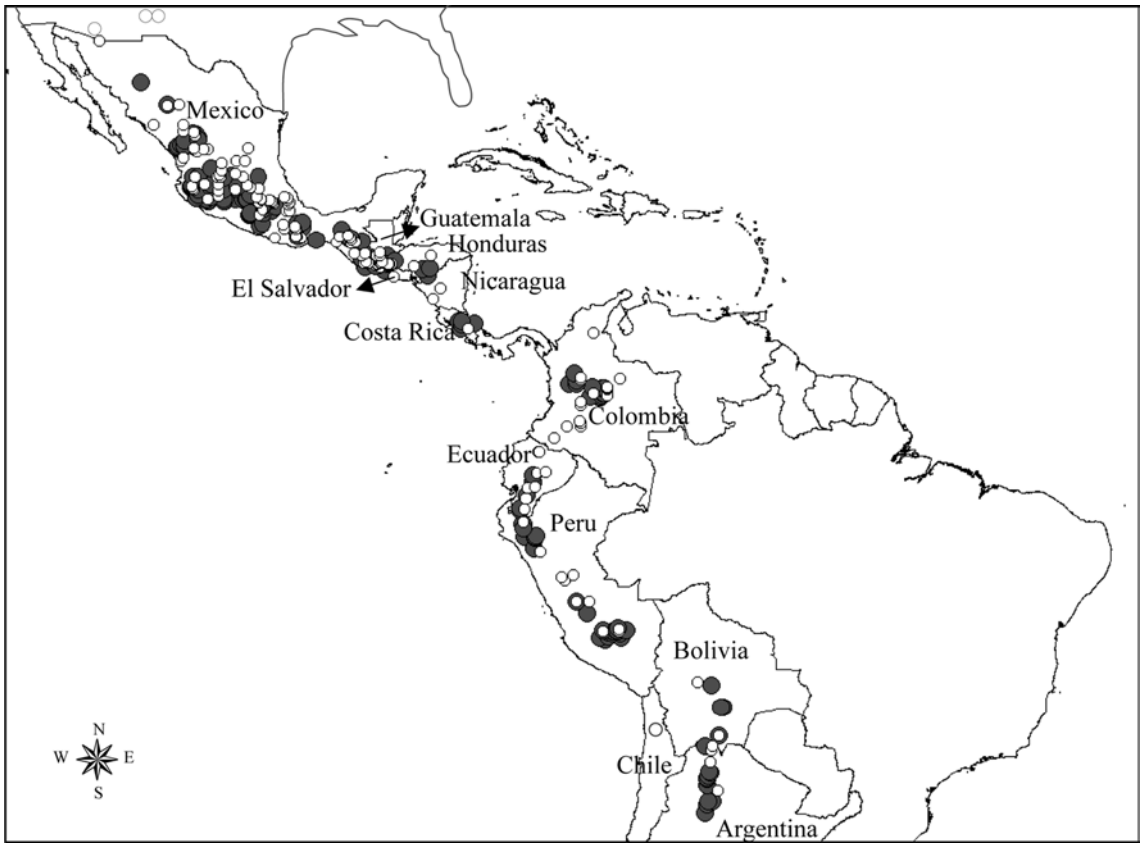


Fig. 1 Geographic distribution (Meso- and South America) of wild (*solid circles*) and cultivated (*open circles*) accessions of common bean (*Phaseolus vulgaris* L.) used in this study. *Names* Countries

Debouck 1991; Gepts et al. 1986; Gutiérrez Salgado et al. 1995; Khairallah et al. 1992; Sonnante et al. 1994).

Wild common bean is widely but discontinuously distributed throughout the highlands of Mesoamerica (the region extending from Mexico to Panama) and South America (the region extending from northeastern Colombia to Argentina) (Fig. 1). Its range is naturally fragmented by areas of unsuitable habitat such as wet lowland areas in Central America and areas of high altitude (more than 3,000 m) in the Andes. Its range has also been fragmented more recently by human activities such as agriculture, urbanization, and deforestation (Debouck et al. 1993; Jones et al. 1997). Wild *P. vulgaris* may have reached its current wide distribution by at least three range expansion events, two from Mesoamerica to northern South America and one from the northern Andes to Central America (Chacón 2001). Relatively recently in the history of the species (probably little more than 4,000 years ago; Kaplan and Lynch 1999), humans started its domestication independently in Mesoamerica and South America (Gepts et al. 1986). Following domestication, common beans spread between Mesoamerica and South America and, after European discovery of the Americas, to Europe and Africa (Gepts and Bliss 1986, 1988; Gepts et al. 1986, 1988). They were cultivated under diverse environments and farmer preferences.

Currently, the domesticated gene pool of the species seems to be organized into four Mesoamerican and three Andean races (Beebe et al. 2000, 2001; Singh et al. 1991). The origin of these races is still controversial. It is not known if they are the results of multiple independent domestications within each region or the result of a single domestication in each region followed by diversification under cultivation. The fact that the four Mesoamerican races Durango, Jalisco, Mesoamerica, and Guatemala differ in ecological adaptation, geographic range, morpho-agronomic traits, allozyme alleles, and random amplification of polymorphic DNA (RAPD) markers (Beebe et al. 2000; Singh et al. 1991) supports multiple domestications. However, the presence of one predominant phaseolin electrophoretic type, S, and similar amplification fragment length polymorphism (AFLP) patterns among Mesoamerican races suggest a single domestication (Gepts et al. 1986; Papa and Gepts 2003). The three Andean races, Nueva Granada, Peru, and Chile, also differ in morpho-agronomic characters, allozymes, and phaseolin types (Singh et al. 1991), which supports multiple domestications. However, their geographic ranges overlap, and they seem to be similar in AFLP patterns (Beebe et al. 2001), which supports a single origin.

Studies of domestication have recently benefitted from the application of molecular markers to comparative

analyses of crops and their wild progenitors. Nuclear DNA markers have been used to study domestication in several crops (Becerra Velásquez and Gepts 1994; Buckler and Holtsford 1996; Heun et al. 1997; Hilton and Gaut 1998). Chloroplast (cp)DNA polymorphisms have also been useful (Anderson et al. 1996; Clegg et al. 1984; Hosaka and Hanneman 1988; Palmer et al. 1983).

We have used data from cpDNA to complement data obtained from previous studies in which nuclear DNA markers were used to investigate domestication in common bean. First, cpDNA sequence variation was examined in wild *P. vulgaris*, and a minimum spanning network relating the chloroplast haplotypes was built. Then, chloroplast haplotypes were identified in domesticated beans and mapped onto the network. The number of haplotypes found in domesticated beans, and the phylogenetic relationships among these haplotypes, may suggest how many times common bean was domesticated, while the geographic distribution of the haplotypes in wild and domesticated beans may suggest where the domestication(s) occurred. However, the data must be interpreted cautiously for two reasons. Firstly, present-day distributions of haplotypes do not necessarily correspond to their distributions 4,000 years ago, when common bean was apparently first domesticated. Secondly, hybridization may result in chloroplast introgression (chloroplast capture; Doebley 1992) from domesticated to wild beans and/or vice versa. The resulting local convergences in haplotypes could obscure the independent histories of the crop versus wild elements of these hybrid complexes.

Materials and methods

Plant materials

A sample consisting of 134 wild, 23 weedy, and 165 domesticated accessions of common bean (*Phaseolus vulgaris* L.) was analyzed (Table 1). The wild and weedy accessions were obtained from the Wild Bean Core Collection at CIAT (International Center for Tropical Agriculture, Cali, Colombia) (see Table 1 in Tohme et al. 1996) supplemented by accessions recently collected from Central America and also held at CIAT. These accessions cover the geographic range, variation in phaseolin types, and AFLP and mitochondrial (mt)DNA polymorphisms (Khairallah et al. 1992; Tohme et al. 1996). The distinction between wild and weedy beans was made at CIAT according to the criteria outlined by Beebe et al. (1997). The domesticated accessions were obtained from the *P. vulgaris* collection held at CIAT (http://www.ciat.cgiar.org/pgr/beans.htm) and consist of traditional landraces with complete passport data. These accessions were chosen to represent the diverse races defined on morpho-agronomic, biochemical, and molecular characters (Beebe et al. 2000; Singh et al. 1991) and cover the range of traditional bean-growing areas in the Americas. Some are sympatric and some allopatric with wild beans. The geographic distribution of the wild and domesticated accessions studied is shown in Fig. 1. A complete list of the accessions used is available as online supplementary material.

Table 1 Geographic distribution from North America to South America of the wild, weedy and cultivated common bean (*Phaseolus vulgaris* L.) accessions used in this study

Country	Wild	Weedy	Cultivated
United States	–	–	4
Mexico	57	8	71
Guatemala	19	2	25
El Salvador	1	–	3
Honduras	4	–	2
Nicaragua	–	–	4
Costa Rica	6	1	3
Colombia	16	6	20
Ecuador	6	1	9
Peru	9	5	10
Bolivia	5	–	4
Chile	–	–	5
Argentina	11	–	5
Total	134	23	165

cpDNA analyses

Genomic DNA was isolated using the CTAB method of Doyle and Doyle (1987). Ten non-coding regions of cpDNA were amplified by PCR (Table 2). PCR reactions consisted of 10 ng genomic DNA, 0.2 m *M* each dATP, dCTP, dGTPm, and dTTP (GibcoBRL, Gaithersburg, Md.), 0.5 μM each primer (GibcoBRL) (Table 2), 1× *Taq* polymerase buffer, and 0.5 U *Taq* polymerase (both from Amersham Pharmacia Biotech, Piscataway, N.J.). The thermal profiles consisted of one cycle of 1 min at 94°C; 30 cycles of 1 min at 94°C, 1 min at the specific annealing temperature (Table 2), and 2 min at 72°C; one cycle at 72°C for 10 min. These conditions were varied as follows: the concentrations of primers for the *rps*14-*psa*B intergenic spacer and the *ndh*A intron were optimized at 0.005 μM; the dNTP concentration for the *rps*14–*psa*B intergenic spacer was optimized at 0.05 m *M*; the extension temperature for the *rpl*16 intron was 65°C; the numbers of cycles used for the *rps*14–*psa*B and *acc*D–*psa*I intergenic spacers were 45 and 35, respectively.

For PCR-restriction fragment length polymorphism (RFLP) analyses, genomic DNA from five seedlings per accession was pooled and then amplified by PCR. Ten-microliter aliquots of unpurified PCR product were subjected to restriction digestion by adding 2 U restriction enzyme (GibcoBRL) and the buffer to a final concentration of 1×. This mixture was incubated overnight at the recommended temperature and the resulting restriction fragments run on 1.5% agarose gels.

For sequencing, genomic DNA from one seedling was amplified by PCR, then cleaned with the Qiaquick

Table 2 cpDNA regions used in this study and primers for their PCR amplification

cpDNA region	Primer sequence (5′-3′) for PCR	Direction	Annealing temperature (°C)	Size (bp)[a]	Reference
Large single copy					
*trn*T-*trn*L spacer	CAT TAC AAA TGC GAT GCT CT	Forward	52	800	Taberlet et al. (1991)
	TCT ACC GAT TTC GCC ATA TC	Reverse			
*trn*L intron	CGA AAT CGG TAG ACG CTA CG	Forward	52	630	Taberlet et al. (1991)
	GGG GAT AGA GGG ACT TGA AC	Reverse			
*trn*L-*trn*F spacer	GGT TCA AGT CCC TCT ATC CC	Forward	52	530	Taberlet et al. (1991)
	ATT TGA ACT GGT GAC ACG AG	Reverse			
*rpl*16 intron	CCA ACA CAT CAC TTC GGA TT	Forward	52	1210	Redesigned from Jordan et al. (1996)
	GCT CCT CGC GAA TGA AGT AA	Reverse			
*rpo*C1-*rpo*C2 spacer	GAA GTT CAC TAT GAA TCT TTN GGT ACC	Forward	52	1700	Asmussen and Liston (1998)
	TAG ACA TCG GTA CTC CAG TGC	Reverse			
atpβ-*rbc*L spacer	GAA GTA GTA GGA TTG ATT CTC	Forward	50	950	Manen et al. (1994)
	TAC AGT TGT CCA TGT ACC AG	Reverse			
*rps*14-*psa*B spacer	CAT TTC ACG AAG TAT GTG TCC G	Forward	55	600	Fofana et al. (1997)
	TGG CGT GGA TAT TGG CAG GA	Reverse			
*pet*A-*psb*E region	GCA TCT GTT ATT TTG GCA CA	Forward	53	1200	Fofana et al. (1997)
	TAC CTT CCC TAT TCA TTG CG	Reverse			
*acc*D-*psa*I spacer	GGA AGT TTG AGC TTT ATG CAA ATG G	Forward	55	700	Small et al. (1998)
	AGA AGC CAT TGC AAT TGC CGG AAA	Reverse			
Small single copy[b]					
*ndh*A intron	GGW CTT CTY ATG KCR GGA TAT RGM TC	Forward	42	1500	Small et al. (1998)
	CTG YGC TTC MAC TAT ATC AAC TGT AC	Reverse			

[a]Size of amplified fragment in common bean
[b]K = G or T, M = A or C, R = A or G, W = A or T, Y = C or T

PCR Purification kit (Qiagen, Valencia, Calif.) and used as template in a sequencing reaction using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction kit (Perkin Elmer, Foster City, Calif.). Extension products were run on an ABI 373XL automated sequencer (Applied Biosystems, Foster City, Calif.).

Chloroplast haplotypes and haplotype tree

The ten chloroplast regions shown in Table 2 were PCR-sequenced in a limited sample of wild beans and the sequences aligned using the LASERGENE software (DNAStar 1994), which revealed polymorphisms in seven regions. The polymorphisms were of three sorts: point mutations resulting in the gain or loss of a restriction site, point mutations not detectable by any restriction enzyme, and insertion/deletion events (indels). Accessions differing by one or more changes were assigned different haplotypes (Table 3). All of the wild accessions were then screened for all characters detectable by restriction digestion. Additional combinations of restriction characters (i.e., further haplotypes) were thereby detected, and all seven polymorphic regions were then sequenced in these haplotypes. Altogether, 19 wild accessions were sequenced and 16 haplotypes (A–P) identified. Sequences of the seven polymorphic regions in each of these 16 haplotypes were deposited in GenBank under accession numbers AY077850 to AY077961. In total, 32 point mutations and two indels (one 28-bp tandem duplication and one 1-bp indel) were detected. Of the 32 point mutations, 16 were detectable by restriction digestion using the appropriate set of enzymes (Table 3). The 28-bp tandem duplication can be detected after restriction of the *trn*T–*trn*L spacer with the enzyme *Rsa*I followed by electrophoresis on 1.5% agarose. Two fragments are generated, one of 500 bp and another one of 300 bp, if the duplication is present, or of 273 bp if the duplication is absent. Of the 16 haplotypes, 14 can thus be detected by the appropriate restriction digestions (Table 3). Haplotype P can be distinguished from haplotype A only by sequencing the *rpl*16 intron to assess which base is present at position 758 (T in haplotypes A and G in haplotype P). Haplotype M can be distinguished from haplotype L only by sequencing the *trn*T-*trn*L spacer to assess which base is present at position 445 (T in haplotypes L and G in haplotype M). We did not sequence all 134 wild accessions for these regions, so throughout the rest of this paper, haplotype A includes also haplotype P and haplotype L includes also haplotype M. The accessions of domesticated beans were screened by PCR-RFLP only.

The phylogenetic relationships of the haplotypes found in wild and domesticated beans were investigated by building a minimum spanning network using the population genetic program ARLEQUIN V2.000 (Excoffier and Smousse 1994; Schneider et al. 2000). This network encompasses all of the minimum spanning trees from a matrix of RFLP pairwise distances between haplotypes. The haplotype diversity index or gene diversity (Nei 1987), defined as the probability that two randomly chosen haplotypes are different in the sample, was calculated for wild and domesticated beans within

Table 3 Restriction sites defining 14 chloroplast haplotypes in *P. vulgaris*

cp region	Base number	Enzyme	Chloroplast haplotype[a]													
			A+P	B	C	D	E	F	G	H	I	J	K	L+M	N	O
*acc*D–*psa*I spacer	379	*Dde*I	+	–	+	+	+	+	+	+	+	+	+	+	+	+
*ndh*A intron	984	*Dra*I	+	+	+	+	+	+	+	–	+	+	+	+	+	+
*rps*14–*psa*B spacer	150	*Tsp*509I	–	–	–	–	–	–	+	+	–	–	–	–	–	–
	425	*Alu*I	–	–	+	–	–	–	–	–	–	–	–	–	–	–
*trn*L-*trn*F spacer	16	*Dra*I	–	–	–	–	–	–	–	–	–	–	–	–	+	–
	171	*Tsp*509I	+	+	+	+	+	+	+	+	–	–	–	–	+	+
	199	*Vsp*I	+	+	+	+	+	+	+	+	+	+	–	+	+	+
	205	*Ssp*I	–	–	–	+	–	–	–	–	–	–	–	–	–	–
*trn*L intron	202	*Hph*I	–	–	–	–	–	–	–	–	–	–	+	–	–	–
	283	*Mse*I	+	+	+	+	+	+	+	+	+	+	+	–	+	+
*trn*T–*trn*L spacer	427	*Dra*I	–	–	–	–	–	–	–	–	–	–	–	–	+	–
	624	*Rsa*I	0	0	0	0	0	0	0	0	0	1	0	1	0	0
*rpl*16 intron	182	*Dra*I	–	+	–	–	–	–	–	–	–	–	–	–	–	–
	379	*Dra*I	–	–	–	–	+	–	–	–	–	–	–	–	–	–
	449	*Pac*I	–	–	–	–	+	+	+	+	–	–	–	–	–	–
	585	*Rsa*I	–	–	–	–	–	–	–	–	+	+	+	+	+	+
	778	*Dra*I	+	+	+	+	+	+	+	+	–	–	–	–	–	–

[a] + or –, Presence or absence, respectively of restriction site; 1 or 0, presence or absence of the 28-bp duplication

Mesoamerica and the Andes with the computer program ARLEQUIN V2.000 (Excoffier and Smousse 1994; Schneider et al. 2000).

Results

Chloroplast haplotypes in wild beans and weedy beans

Fourteen chloroplast haplotypes were found among wild common beans. The geographic distribution of these haplotypes is shown in Table 4. Some haplotypes (B, H, J, K, N, and O) are restricted to Mesoamerica, while others (C, D, E, and F) are restricted to South America; a few (A, G, I, and L) occur in both areas. Eight haplotypes were found among weedy beans from Mesoamerica and South America (A, C, F, H, I, J, K, and L), all of which were also found in sympatric wild beans. Figure 2 shows the network relating the haplotypes.

Reduction of chloroplast haplotype diversity in domesticated common bean

Only five chloroplast haplotypes (C, I, J, K, and L) out of the 14 present in wild common beans have been found

Table 4 Geographic distribution of RFLP chloroplast haplotypes in wild, weedy, and domesticated common beans

Country	Chloroplast haplotypes															
	Wild beans															
	A	B	C	D	E	F	G	H	I	J	K	L	N	O	Total	
North America																
United States	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Mesoamerica																
Mexico	26	5	–	–	–	–	–	–	6	5	9	4	1	1	57	
Guatemala	–	–	–	–	–	–	7	–	6	5	–	1	–	–	19	
Nicaragua	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Honduras	–	–	–	–	–	–	4	–	1	–	–	–	–	–	5	
El Salvador	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	
Costa Rica	–	–	–	–	–	–	–	5	–	–	–	1	–	–	6	
South America																
Colombia	–	–	–	–	–	–	1	–	1	–	–	14	–	–	16	
Ecuador	–	–	–	–	–	6	–	–	–	–	–	–	–	–	6	
Peru	1	–	6	–	2	2	–	–	–	–	–	–	–	–	11	
Bolivia	5	–	–	–	–	–	–	–	–	–	–	–	–	–	5	
Chile	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Argentina	1	–	1	9	–	–	–	–	–	–	–	–	–	–	11	
Total	33	5	7	9	2	8	13	5	14	10	9	20	1	1	137[a]	

Country	Chloroplast haplotypes									
	Weedy beans									
	A	C	F	H	I	J	K	L	Total	
North America										
United States	–	–	–	–	–	–	–	–	–	
Mesoamerica										
Mexico	–	–	–	–	3	–	2	3	8	
Guatemala	–	–	–	–	1	1	–	–	2	
Nicaragua	–	–	–	–	–	–	–	–	–	
Honduras	–	–	–	–	–	–	–	–	–	
El Salvador	–	–	–	–	–	–	–	–	–	
Costa Rica	–	–	–	1	–	–	–	–	1	
South America										
Colombia	–	–	–	–	–	–	–	6	6	
Ecuador	–	–	1	–	–	–	–	–	1	
Peru	1	4	–	–	–	–	–	–	5	
Bolivia	–	–	–	–	–	–	–	–	–	
Chile	–	–	–	–	–	–	–	–	–	
Argentina	–	–	–	–	–	–	–	–	–	
Total	1	4	1	1	4	1	2	9	23	

Country	Chloroplast haplotypes					
	Domesticated beans					
	C	I	J	K	L	Total
North America						
United States	–	–	–	4	–	4
Mesoamerica						
Mexico	2	3	1	40	27	73
Guatemala	2	3	1	20	1	27
Nicaragua	–	–	–	4	–	4
Honduras	–	–	–	2	–	2
El Salvador	–	–	–	3	–	3
Costa Rica	–	1	–	2	–	3
South America						
Colombia	11	3	–	3	4	21
Ecuador	8	–	–	1	–	9
Peru	10	–	–	–	–	10
Bolivia	4	–	–	–	–	4
Chile	3	–	–	–	–	3
Argentina	5	–	–	–	–	5
Total	45	10	2	79	32	168[a]

[a] This total is greater than the number of accessions analyzed due to intra-accession polymorphisms

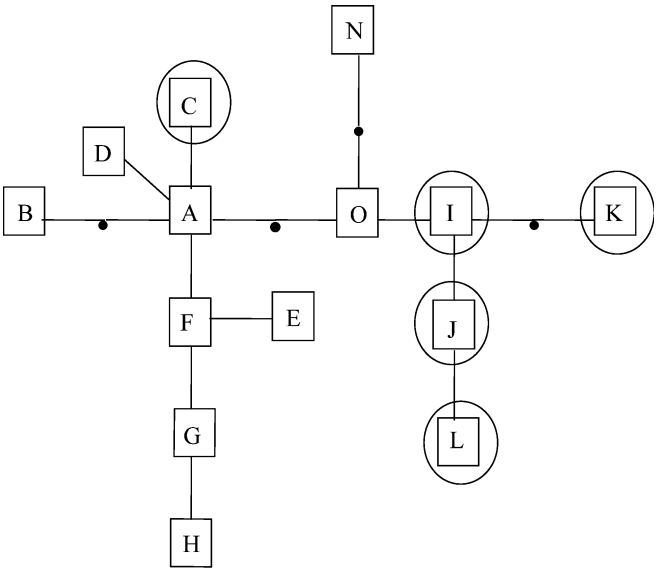


Fig. 2 Unrooted minimum spanning network estimated for the wild and domesticated *P. vulgaris* chloroplast haplotypes using the computer program ARLEQUIN. Observed haplotypes are indicated by *capital letters enclosed in a box only* for haplotypes present in wild beans only and in a *box enclosed in a circle* for haplotypes present in both wild and domesticated beans. Missing intermediate haplotypes are indicated by a *black dot*

in domesticated common beans (Table 4). The values calculated for the Haplotype Diversity Index (Nei 1987) show that this reduction in chloroplast diversity in domesticated beans has occurred in both Mesoamerica and the Andes (Table 5). In Mesoamerica, four haplotypes, I, J, K, and L, out of the ten found in Mesoamerican wild beans occur in domesticated beans. However, two haplotypes, K and L, predominate, while haplotype I is present at a lower frequency (Table 4). Haplotype J was found in only two domesticated accessions and in only one individual of the five analyzed in each accession. The other four individuals carried the predominant Mesoamerican haplotypes, K and L. One of these polymorphic accessions originates from Sacatepequez, Guatemala where haplotype J is present in local wild beans. Therefore, the presence of haplotype J in this accession may be explained by chloroplast capture from local wild beans. The other polymorphic accession comes from the state of Durango, Mexico. In this state, haplotype J is absent in local wild, weedy, and domesticated beans, which carry mostly haplotype K. With the data available to date it is not obvious how this accession captured haplotype J. In the Andes, one haplotype, C, is dominant in domesticated beans even though eight haplotypes occur in Andean wild beans.

Table 5 Haplotype diversity index (H) for wild and domesticated beans from Mesoamerica and the Andes

Population	H
Mesoamerican-wild	0.8442 ± 0.0206
Mesosmerican-domesticated	0.5231 ± 0.0429
Andean-wild	0.8298 ± 0.0250
Andean-domesticated	0.3703 ± 0.0815

Chloroplast haplotypes and races of common bean

Only 127 landraces of the 165 studied here have been classified by race at CIAT. Haplotype K, the most abundant haplotype among Mesoamerican landraces, occurs in South America only in a few landraces from Colombia and Ecuador not yet classified by race, hence not included in Table 6. This haplotype is associated with Races Mesoamerica and Durango. Haplotype L also occurs in these two races, but at a lower frequency, and a third haplotype, I, is present at a similar low frequency in Race Mesoamerica (Table 6). Haplotype L predominates in Race Jalisco (Table 6) and occurs also in other accessions not classified by race. It is found in domesticated beans from the central Mexican states of Jalisco, Michoacán, Puebla, and Guanajuato, and also in a few landraces from Colombia. Haplotype I is the only haplotype found in Race Guatemala (Table 6). It occurs mainly in accessions from the southern Mexican state of Chiapas and from Guatemala but is also found in one accession of Race Guatemala from Costa Rica and three accessions from Colombia not classified by race. Haplotype C is virtually the only haplotype found in the Andean Races Nueva Granada, Peru, and Chile (Table 6). It is also present in two accessions from Mexico and two from Guatemala. As the two Guatemalan accessions have been classified as Race Nueva Granada at CIAT, they were probably introduced from the Andes. The two Mexican accessions have not yet been classified by race.

The association among races and chloroplast haplotypes is not perfect. There are several discrepancies that suggest introgression (Table 6). For example, the pres-

Table 6 Distribution of chloroplast haplotypes among 127 accessions of Mesoamerican and Andean landraces of common bean classified into the racial groups of Singh et al. (1991) and Beebe et al. (2000)

Races[a]	Chloroplast haplotypes					Total
	C	I	J	K	L	
Mesoamerican races						
Mesoamerica (M)	0	4	1	45	5	55
Durango (D)	0	0	1	18	7	26
Jalisco (J)	0	0	0	1	8	9
Guatemala (G)	0	3	0	0	0	3
Andean races						
Nueva Granada (N)	7	0	0	0	0	7
Peru (P)	23	0	0	1	0	24
Chile (C)	3	0	0	0	0	3
Total	33	7	2	65	20	127

[a]Associations between races and haplotypes were evaluated by Fisher's exact test. P (Mesoamerican races vs. Andean races) = 0.000; P (M vs. D) = 0.073; P (M vs. J) = 0.000; P (M vs. G) = 0.000; P (D vs. J) = 0.006; P (J vs. G) = 0.005

Fig. 3 **a** Geographic distribution of wild and weedy *P. vulgaris* accessions carrying haplotypes I, K, and L in Mesoamerica. *Names* States within Mexico and Central American countries. **b** Geographic distribution of domesticated *P. vulgaris* accessions carrying haplotypes K, L, I, and C. *Names* States within Mexico and Central American countries

ence of haplotype K in one accession of Race Jalisco may be the result of chloroplast capture from local wild beans in Jalisco, where haplotype K is present, or from domesticated beans belonging to Races Mesoamerica and/or Durango. The presence of haplotype K in Race Peru from Ecuador is very likely the result of chloroplast capture from landraces introduced from Mesoamerica.

Sites of domestication and the origin of races

Further details of the geographic distribution of haplotypes I, K, and L in wild and weedy beans and domesticated landraces in Mesoamerica are shown in Fig. 3a, b. Haplotype L is the most frequent haplotype in wild beans from Colombia (with only one wild accession showing haplotype I) (Table 4), but otherwise the three haplotypes characteristic of Mesoamerican landraces do not occur in truly wild (i.e., non-weedy) beans in South America. Figure 4 shows that haplotype C, characteristic of Andean domesticated beans, occurs in wild beans only in the southern part of their South American range. The network relating the haplotypes (Fig. 2) shows that the Andean haplotype C is only distantly related to the haplotypes I, J, K, and L characteristic of Mesoamerican domesticated and wild beans. All this suggests that at least two domestication events have occurred in common bean: one in southern Peru or Argentina for the Andean races and at least one event in Mexico for the Mesoamerican races. The single chloroplast haplotype found among the Andean races (Table 6) suggests that these three races diverged after domestication. Conversely, the number of chloroplast haplotypes among the Mesoamerican races (Table 6) suggests that their origin may have been more complex. As discussed below, possible explanations for the distribution of chloroplast haplotypes among the Mesoamerican races are a single domestication from a polymorphic wild population followed by lineage sorting; multiple domestications from different wild populations, each carrying a different chloroplast haplotype; or hybridization between wild and domesticated beans in different parts of their Mesoamerican range followed by chloroplast capture.

Discussion

Reduction of chloroplast diversity in common bean landraces

Our chloroplast data suggest a founder effect due to domestication in Mesoamerica and in the Andes, in that only a subset of the wild haplotypes is present in landraces (Table 5). This result agrees with those of previous studies where a reduction in genetic diversity in the gene pool of the domesticate was observed with respect to phaseolin types and molecular polymorphisms (Beebe et al. 2001; Gepts et al. 1986; Papa and Gepts 2003; Sonnante et al. 1994). The reduction in chloroplast haplotype diversity seems to have been stronger in the Andes (55%) than in Mesoamerica (38%) (Table 5). This difference may mainly reflect the history of domestication within each region.

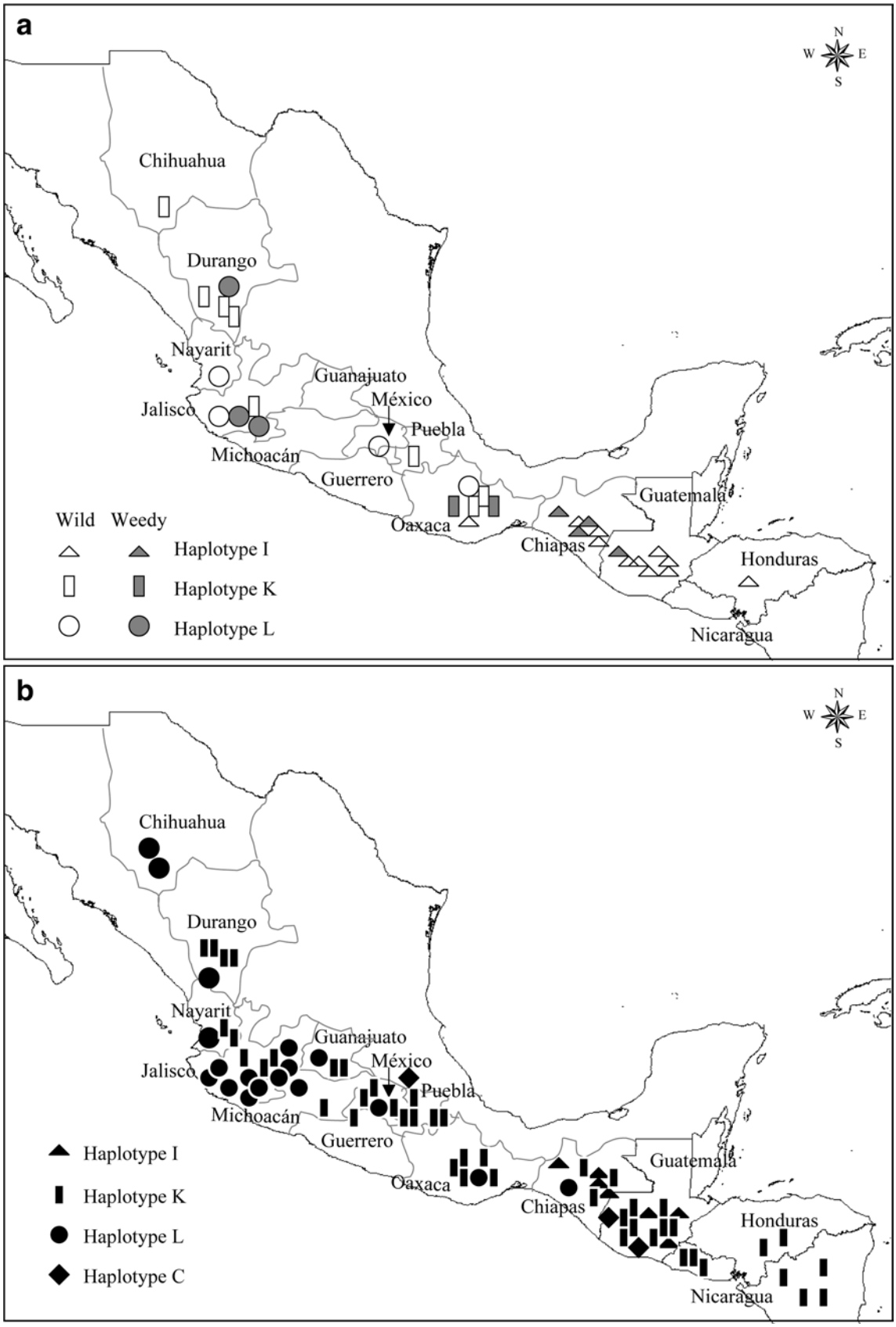
Domestication of common bean in the Andes

Gepts et al. (1986) suggested that the diversity of phaseolins in Andean landraces indicates multiple domestications of Andean wild beans. However, Cattan-Toupance et al. (1998) found that 8 out of 21 wild bean populations from Argentina were polymorphic for phaseolin type. A single domestication from a polymorphic wild population could therefore explain the diversity of phaseolins in Andean domesticated beans. Beebe et al. (2001) studied AFLPs in Andean landraces of common bean and found that they formed a relatively compact group with no subdivisions corresponding to the Races Nueva Granada, Peru, and Chile. They concluded from this that the three races have a common origin and have diverged as a result of human selection.

Our data likewise suggest a single domestication of Andean beans. We found that 33 out of 34 landrace accessions, representing all three Andean races, carried a single chloroplast haplotype, C, whereas we found eight different haplotypes in Andean wild beans. Haplotype C is the most frequent haplotype in wild beans from central-southern Peru (Fig. 4). Elsewhere among wild beans, we have found this haplotype only in one of 11 accessions from Argentina. This may indicate that Andean common bean was domesticated in central-southern Peru.

Southern Peru, central Bolivia, or Argentina have been suggested as areas for domestication of Andean beans on the basis of a mtDNA study of a limited sample of wild beans (Khairallah et al. 1992). However, according to our data, Bolivian wild beans are not likely to be the ancestors of domesticated beans because they carry haplotype A, not C. In contrast to the chloroplast data, a study of AFLPs in Andean wild beans and landraces showed that wild beans from southern Peru cluster clearly apart from the Andean landraces, while wild beans from eastern Bolivia and northern Argentina group very closely with Andean domesticated beans (Beebe et al. 2001).

Recent studies on AFLPs, mtDNA, and chloroplast haplotypes thus all suggest that common bean was domesticated only once in South America and that this domestication took place in the southern part of the


a
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Chiapas
Honduras
Nicaragua
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Durango
Nayarit
Guanajuato
México
Jalisco
Puebla
Michoacán
Guerrero
Oaxaca
Guatemala
Chiapas
Honduras
Nicaragua
Haplotype I
Haplotype K
Haplotype L
Haplotype C

Fig. 4 Geographic distribution of wild *P. vulgaris* accessions carrying haplotype C in southern Peru, a possible area of domestication in the Andes. *Names* Peruvian departments

range of wild beans. To pinpoint the center of domestication more precisely, and reconcile differences between the different sets of data, more collections of wild beans from southern Peru, Bolivia and Argentina are needed, together with more studies of natural populations rather than gene bank accessions. This would establish to what extent wild populations are polymorphic for the various molecular markers and which polymorphisms coexist in different wild populations.

The near-uniform chloroplast haplotype in all three Andean races of domesticated common bean supports the suggestion of Beebe et al. (2001) that these races differentiated mainly through human selection. Isolation among early agriculturalists and diffusion to other Andean regions with different ecological conditions would also have promoted differentiation among domesticated beans. The hypothesis of Diamond (1997) of a slow diffusion of Native American crops along a north-south axis does not appear to apply to common bean. The archaeological record, though still very incomplete, suggests that common bean was domesticated in the Andes about 2,000 years before it was domesticated in Mesoamerica (Kaplan and Lynch 1999). Andean domesticated beans then diffused north to Colombia and, eventually, to Mesoamerica (Gepts et al. 1988).

Domestication of common bean in Mesoamerica

The distribution of chloroplast haplotypes among Mesoamerican races of domesticated common bean suggests that the origin of these races has been more complicated than the origin of the Andean races. Haplotype K predominates in races Mesoamerica and Durango, although haplotypes L, I, and J also occur. Haplotype I is the only haplotype that we have found in Race Guatemala, while haplotype L is the most frequent haplotype in Race Jalisco. All of these haplotypes also occur in Mesoamerican wild and weedy beans, with different, though overlapping, geographic ranges (Fig. 3a).

Gepts (1988b) argued that the limited diversity of phaseolins in Mesoamerican domesticated beans suggests a single domestication. Papa and Gepts (2003) studied AFLP markers and found that the different Mesoamerican races grouped together in a single large cluster, which they regarded as support for the conclusions from the phaseolin data. They considered that the races had differentiated after domestication as a result of farmers' selection.

If our data on chloroplast haplotypes are to be explained on the hypothesis of a single domestication, one or more of the following must have occurred: the ancestral wild population must have been polymorphic

for at least three chloroplast haplotypes; and/or mutations must have occurred post-domestication, replicating in the domesticate some of the haplotypes already present in wild beans; and/or domesticated beans must have captured chloroplasts from (or donated chloroplasts to) local populations of wild beans as domesticated beans extended their range in cultivation.

In our study of 134 wild accessions, only three were polymorphic for chloroplast haplotype and only one (from Oaxaca, Mexico) was polymorphic for the two haplotypes (K and L) predominant in Mesoamerican domesticates. We studied gene bank accessions, which may under-represent the diversity present in natural wild populations. However, a study of wild populations in Costa Rica showed that most are monomorphic for chloroplast haplotype and that a single haplotype may be dominant on a regional scale (González and Debouck 2004; CIAT, unpublished data). We therefore consider it unlikely that a single wild population would contain the three haplotypes characteristic of the Mesoamerican landraces in sufficient frequency that none was lost by founder effect or drift in the initial stages of domestication. However, more studies of natural populations, especially in the Mesoamerican center of diversity, are needed to establish whether, or to what extent, these populations are polymorphic for chloroplast haplotype.

The chloroplast haplotypes I, J, K, and L found in Mesoamerican domesticated beans are closely related (Fig. 2). Some of these haplotypes might therefore have arisen independently in the landraces after common bean was domesticated. This would then be a case of convergent evolution, not an indication of either multiple domestication or introgression between wild and domesticated beans. However, we consider independent occurrence of the same mutation unlikely. Proponents of a single domestication of common bean in Mesoamerica have located this in west-central Mexico (Gepts and Debouck 1991). Wild beans in this area carry haplotypes K and L (see Fig. 3a), so the earliest Mesoamerican domesticated beans would probably also carry these haplotypes. Derivation (post-domestication) of haplotype I (characteristic of Race Guatemala) from either K or L would require two independent mutations in different non-coding regions within the part of the chloroplast molecule, bounded by the *trnT-trnL* and *trnL-trnF* spacers (see Table 3). These regions comprise a total of nearly 2,000 bp (Table 2). It seems unlikely that mutations occurring post-domestication in this length of DNA should exactly replicate the gains or losses of restriction sites and/or the 28-bp tandem duplication that distinguish haplotypes K, L, and I in wild beans. A similar argument applies if Race Jalisco, characterized by haplotype L, was the earliest Mesoamerican domesticate. Furthermore, construction of the haplotype network shown in Fig. 2 required no instance of repeated occurrence of any given mutation, even though the time involved in the evolution of the geographical and molecular differences found within wild common bean (Papa and Gepts 2003; Tohme et al. 1996) is presumably much longer than the approximately 2,000 years that have elapsed since Mesoamerican common beans were domesticated (Kaplan and Lynch 1999).

Another possible explanation of the chloroplast haplotype data is that common bean was domesticated more than once in Mesoamerica, from different wild populations. Beebe et al. (2000) argued that, if the various Mesoamerican races had diverged simply through farmers' selection post-domestication, they should have very similar genomes. However, the RAPD data showed sufficient differences between the warm lowland Race Mesoamerica and the highland Races Durango and Jalisco to suggest to Beebe et al. (2000) that these two groups were domesticated independently. Our chloroplast haplotype data, on the other hand, separate Race Jalisco (predominantly haplotype L) from Races Mesoamerica and Durango (both polymorphic, with similar frequencies of K, as the predominant haplotype, and L). Race Jalisco might perhaps have been domesticated in the region of Jalisco where wild beans with phaseolin S and chloroplast haplotype L occur. The lowland Race Mesoamerica could then have been domesticated in Oaxaca, where haplotype K is frequent among local wild beans. The highland Race Durango might have been domesticated further north, possibly in Durango, where haplotype K is the only haplotype among local wild beans. Beebe et al. (2000) also recognized a fourth Mesoamerican race, Guatemala, from the highlands of southern Mexico and Guatemala. They considered that the geographical isolation of these highlands could have led to the evolution of distinct populations of both domesticated and wild beans. Chloroplast haplotype I occurs in wild beans only in southern Mexico, Guatemala, and Honduras and is the only haplotype we found in our three accessions of Race Guatemala (haplotype I occurs also in three further landrace accessions from southern Mexico and Guatemala that have not yet been classified but may also belong to Race Guatemala). Chloroplast and RAPD data could therefore support the independent domestication of Race Guatemala in the highlands of southern Mexico or Guatemala.

A cogent objection to the hypothesis of multiple domestications is that common bean seems to have been domesticated relatively late in Mesoamerica (little more than 2,000 years ago) and then spread rapidly (Kaplan and Lynch 1999). Archaeological specimens of domesticated common bean from central Mexico and the southwest of the USA are approximately contemporaneous (Kaplan and Lynch 1999). It is unlikely that several different groups of farmers, who were already growing maize and squash, would independently start domesticating their local wild beans. It is easier to envisage the new crop spreading as a curiosity from one agricultural community to another.

Although common bean is a predominantly autogamous species, significant amounts of outcrossing occur (e.g., Ibarra-Perez et al. 1997 for domesticated beans; Tohme et al. 1996 for wild beans). Farmers in both Mesoamerica and the Andes traditionally grow mixtures

of bean landraces in their fields (Beebe et al. 1997; Kaplan 1981), although in commercial cultivation in Mexico landraces or cultivars are increasingly grown singly (Andrade-Aguilar and Hernandez-Xolocotzi 1991). Singh et al. (1991) considered that races of beans in Mesoamerica and the Andes have independently evolved similar agroecological adaptations. Landraces from similar races from the different continents would thus be better adapted to co-cultivation than landraces from the different Mesoamerican races, which are each adapted to rather different growing conditions. Beebe et al. (1997) noted that, in Colombia, some bean mixtures combine landraces of Mesoamerican and Andean origin. Recombinants with Mesoamerican seed morphology but Andean phaseolin, and vice versa, were present, showing that hybridization between the components of the mixture was occurring. Andean landraces have also been introduced to Mesoamerica (Gepts et al. 1988). RAPD bands characteristic of Andean beans are present in some Mesoamerican landraces, and this has again been attributed to introgression (Beebe et al. 2000). We found some examples of the Andean chloroplast haplotype C in Mesoamerican landraces and of the Mesoamerican haplotype K in an Andean landrace (Table 4) and attribute these to inter-racial outcrossing.

Intentional hybridization has been used to improve common beans in Latin America, predominantly those belonging to Race Mesoamerica (Voysest et al. 1994). Deliberate hybridization between domesticated races could result in the transfer of chloroplasts, but our study was confined to landraces and did not include improved cultivars. We therefore consider that transfer of chloroplast haplotypes between landraces and cultivars through accidental or deliberate hybridization is possible and may account for the polymorphism in haplotypes displayed by widespread races such as Race Mesoamerica. However, hybridization among domesticated beans does not explain how these beans became polymorphic for chloroplast haplotypes in the first place.

Hybridization and gene flow may also occur between sympatric domesticated and wild beans. This has been used to explain the presence of morphological, RAPD, or AFLP markers characteristic of domesticated beans in populations of wild beans (see examples in Beebe et al. 1997, 2000; Papa and Gepts 2003; Tohme et al. 1996). Gene flow seems to be predominantly from domesticated to wild beans, although some gene flow in the reverse direction does occur (Papa and Gepts 2003). The capture of chloroplasts from wild beans by sympatric domesticated beans is, however, potentially more difficult than the introgression of nuclear traits. The maternal inheritance of chloroplasts has not been rigorously demonstrated in *P. vulgaris*, but Corriveau and Coleman (1988) found no evidence of plastid DNA in sperm cells of pollen of common bean, and Schmit et al. (1993), in a study of cpDNA polymorphisms, found that a natural hybrid of *P. coccineus* × *P. polyanthus* resembled *P. coccineus* in differing from *P. polyanthus* by two RFLPs. We therefore consider that common bean probably resembles the majority of angiosperms in having maternally inherited chloroplasts.

If bean chloroplasts are indeed maternally inherited, weedy beans resulting from pollen flow from domesticated to wild beans will have the chloroplast haplotype of their wild parent. Papa and Gepts (2003) suggested that the vigor of these hybrids would give them a selective advantage in the wild. However, these hybrids will also have the dehiscent pods and small seeds of their wild parent (Koinange et al. 1996). Farmers would therefore select against these hybrids when establishing their seed stocks for the next season's planting. Nevertheless, at least in Colombia, farmers tolerate weedy beans—growing from naturally dispersed seed—in their fields and may harvest them for grain (Beebe et al. 1997). Repeated selfing or backcrossing of these weedy beans with pollen of the sympatric landrace could produce segregates with the characteristic traits of the domesticate but the chloroplast haplotype of the local wild population. Such plants would initially be present at a very low frequency in the landrace population, so the original chloroplast haplotype of the landrace is unlikely to be displaced unless these late-generation hybrids have some selective advantage in cultivation. This advantage could be an adaptation to local conditions inherited from their wild parent. In this study we observed that weedy beans contain all of the haplotypes that have been detected in landraces (C, I, J, K, and L), thereby supporting the view that weedy beans may be an intermediate stage in chloroplast introgression from wild to domesticate.

The hypothesis outlined above is based on a suggestion by Beebe et al. (2000). In considering possible alternatives to multiple domestications to explain their RAPD data, they reasoned that beans with the S-type phaseolin predominant in Mesoamerican landraces might have been domesticated once, then spread in cultivation to other regions where they hybridized with local wild beans. The phaseolin locus is very close to one of the factors influencing seed size, so selection among the wild × domesticated hybrids for large seed would favor the linked S-type phaseolin. Beebe et al. (2000) suggested that this process might have occurred repeatedly, producing different populations of domesticated beans that derive most of their genome from diverse populations of wild bean but derive traits of the domestication syndrome from the original domesticate and hence share its S-type phaseolin. Such a scenario could explain our finding that some of the different Mesoamerican races, with their different agroecological adaptations, differ also in chloroplast haplotype. It could also explain the finding of González and Debouck (2004; CIAT, unpublished data) that chloroplast introgression seems to occur predominantly from wild to domesticate, whereas the introgression of nuclear genes is predominantly from domesticate to wild (Papa and Gepts 2003).

It is not easy to devise tests to discriminate conclusively between the two hypotheses that we consider the most plausible explanations of our chloroplast haplotype data: multiple domestications versus single domestication followed by "secondary domestication", through introgression and chloroplast capture, of different locally adapted wild populations. One possible test is a modification of a method mentioned by Papa and Gepts (2003). Koinange et al. (1996) found that genes controlling the various components of the domestication syndrome are concentrated in just three linkage groups. Papa and Gepts (2003) used AFLP markers to study relative amounts of diversity in these regions of the genome. We would expect geographically isolated populations of wild common bean in Mexico, and more specifically those in Mesoamerica versus the Andes, which have evolved independently for a long time, to differ among themselves with respect to markers in these regions. Races derived by independent domestications should share the differences of their progenitor wild populations. On the other hand, races resulting from "secondary domestication" of wild populations by introgression of the domestication syndrome from introduced domesticated beans should be very similar in those regions of the genome associated with the domestication syndrome.

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