

When gene flow counteracts domestication: the case of common bean (*Phaseolus vulgaris* L.)



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Introduction

Domestication is the human-driven process by which our crop plants originated. During domestication, wild plants transform and adapt to human-made environments through a series of genetic changes and become dependent on humans for survival. The three main evolutionary forces that act during domestication are unconscious and/or conscious selection, founder events and gene flow between crop and wild relatives. The first two forces promote genetic differentiation between crop and wild relatives and reduce crop genetic diversity. In contrast, the third force narrow the genetic gap between crop and wild relatives and increase crop genetic diversity. Domestication of a wild species may occur one or several times in space and or time. Given enough time and geographic isolation, domesticated races (which differentiate in their allelic frequencies, geographic distributions and ecological adaptations) may evolve in a pre or post-domestication context. In the first one, races evolve from multiple domestications of wild populations already genetically divergent and locally adapted, and in the second one, races evolve from a unique domestication event followed by geographic diffusion and “secondary domestications”. Secondary domestications are conversions of local wild beans to cultigens through hybridization with introduced domesticated types. Here we report recent evidence for multiple and secondary domestications in wild common bean, gene flow between the crop and its wild relative (1,2) and document the opposite effects of these two forces on the genetic diversity in this crop.

Gene flow in wild-weedy-cultivated complexes

Although common bean has long been considered as an autogamous plant, it can outcross naturally with its wild relative or even with sister species leading to the formation of complexes “wild-weedy-cultivated” (6). These complexes have been phenotypically observed in Oaxaca (México), El Progreso (Guatemala), San José (Costa Rica), Boyacá (Colombia), Azuay (Ecuador), Apurimac (Perú) and Tarija (Bolivia). We applied molecular markers using cpDNA (SNPs) and nuclear DNA (SSRs) to individuals putatively resulting from gene flow events under natural conditions (2, 7) from this geographic range.

The results shown in Table 1 display the diversity of chloroplast haplotypes in elements of the complexes and the direction of the flow. The wild and cultivated populations were characterized with such markers allowing then to infer about weedy individuals. The main direction was that of wild pollen towards cultivated materials, although the other direction was also evidenced at lower frequency in many places.

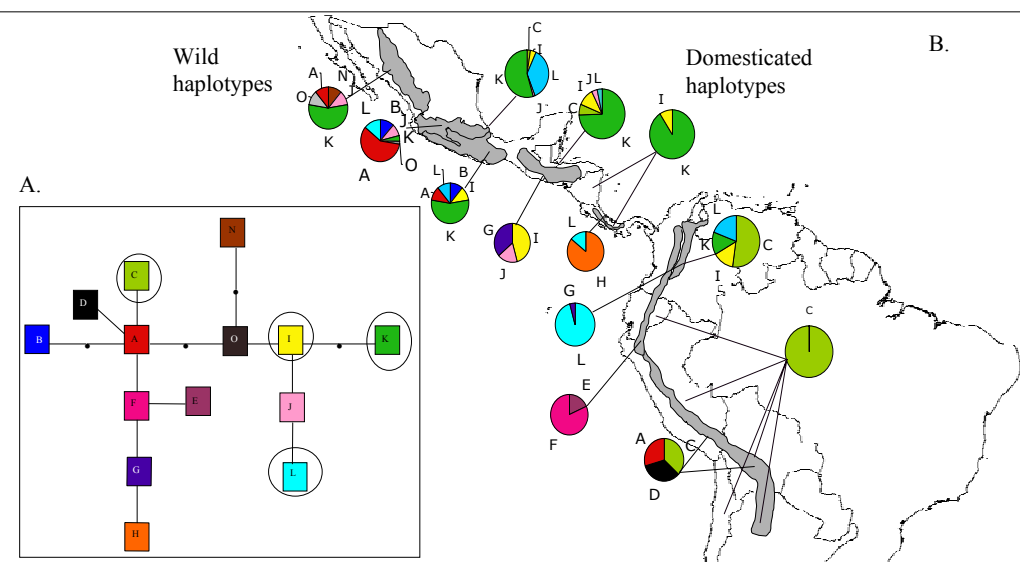


Fig 1. Domestication patterns in common bean. A. Network showing the phylogenetic relationships between wild and domesticated chloroplast haplotypes. Haplotypes enclosed in a circle were observed in wild beans and domesticated races. B. Map showing the frequency distribution of haplotypes in wild (left) and domesticated (right) beans in Latin America.

Table 1. Chloroplast haplotypes found in the complex “wild-weedy-cultivated” and their frequency. Countries are organised from north to south.

Country	Chloroplast haplotypes found			Pollen flow direction and frequency
	Wild	Weedy	Cultivated	
Costa Rica	H (540/540)	G (3/481) H (179/481) J (98/481) K (1/481) L (199/481) F (1/481)	J (18/56) K (23/56) L (15/56)	Wild to Cultivated (98+1+199/481)
Guatemala	I (6/16) J (10/16)	C (1/32) J (31/32)	K (16/16)	Cultivated to Wild (31/32)
Colombia	J (50/68) L (18/68)	L (64/96) J (28/96) A (2/96) C (2/96)	L (14/158) C (3/158) J (140/158)	Wild to Cultivated Or Cultivated to Wild
Ecuador	F (28/28)	F (47/51) A (3/51) J (1/51)	C (15/15)	Cultivated to Wild (47/49)
Perú	C (51/51)	C (126/181) I (1/181) J (38/181) L (11/181) F (4/181) A (1/181)	C (70/105) J (18/105) L (17/105)	Wild to Cultivated Or Cultivated to Wild
Bolivia	A (6/6)	A (1/20) C (2/20) I (1/20) J (16/20)	C (6/12) J (6/12)	Wild to Cultivated (16+2/20)
Argentina	D (6/6)	C (40/40)	C (51/51)	Wild to Cultivated (40/40)

Origin of domesticated races

Wild common bean is widely distributed from northern Mexico to northern Argentina (Fig. 1). Previous studies reported the existence of four Mesoamerican races: Mesoamerica (M), Durango (D), Jalisco (J) and Guatemala (G), and three Andean races: Nueva Granada (N), Peru (P) and Chile (C) (3,4). Chloroplast haplotypes (cpHps) were studied in wild and domesticated common beans by means of PCR-RFLP and sequencing. The phylogenetic relationships among wild and domesticated cpHps and their frequency and geographic distributions are shown in Fig. 1. cpHp diversity indexes (S) are not significantly different among Mesoamerican and Andean wild beans ($H=0.8442 \pm 0.0206$ and $H=0.8298 \pm 0.0250$ respectively) but they do differ significantly from their Mesoamerican and Andean domesticated counterparts ($H=0.5231 \pm 0.0429$ and 0.3703 ± 0.0815 respectively). The data then support a founder effect due to domestication. cpHps are not randomly distributed among races. Andean races carry only Hp C, races M and D carry mainly Hp K, race J carry mainly Hp L and race G carry only Hp I. The phylogenetic relationships among wild and domesticated cpHps, their geographic distribution and association with races suggest multiple domestications of beans. Andean races share their Hp C with wild beans from southern Peru, which suggests a single origin of races in this area followed by post-domestication differentiation. In contrast, the scenario in Mesoamerica seems more complex. All Mesoamerican races share their Hps with local wild beans in parts of their ranges. These results, along with previous data, suggest independent domestications of at least some of the races in Mesoamerica, diffusion of the initial domesticates to other regions followed by “secondary domestications” of some locally adapted wild beans.

We were also interested in examining gene flow events over time by sampling materials at the same localities in different years (1987, 1998, 2003, 2004, and 2006), in San José and Cartago, Costa Rica. We evaluated 9 nuclear SSR *loci* in a total of 520 weedy individuals to evidence the gene transfer and its quantification. We determined characteristic alleles for each population belonging to the complex and these were detected in the weedy populations suggesting that the evaluated hybrids are real cases of gene flow. The weedy individuals were confirmed by morphoagronomic and biochemical markers found in wild or cultivated populations. Table 2 shows the number of real hybrids revealed for each year screened in Quircot and Jerico populations in Costa Rica.

Table 2. Hybrid individuals resulting from gene flow found in populations of Costa Rica over time.

Year	1987	1998	2003	2004
Population				
Cartago (Quircot)	29	40	123	50
San José (Jerico)	--	9	50	40

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Conclusions

The chloroplast analysis provided evidence on the effects of the evolutionary forces of domestication and gene flow on the levels of genetic diversity in this crop. On the one side, the few domestication events induced a strong founder effect, thus reducing crop genetic diversity. On the other side, the gene flow events have worked against this consequence, over millennia and across the range of the wild relative, contributing to the richness of the common bean gene pools (nuclear and chloroplast genomes). These two forces, among others, have taken part in the formation of domesticated races (3, 4), an unexpected result in a reported autogamous (!) crop.

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