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Evolution of genetic diversity during the domestication of common-bean (*Phaseolus vulgaris* L.)

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Abstract M13 DNA fingerprinting was used to determine evolutionary changes that occurred in Latin American germ plasm and USA cultivars of common-bean (*Phaseolus vulgaris* L.) during domestication. Linkage mapping experiments showed that M13-related sequences in the common-bean genome were either located at the distal ends of linkage groups or that they were unlinked to each other or to any previously mapped markers. Levels of polymorphism observed by hybridization with M13 (1 probe-enzyme combination) were comparable to those observed by hybridization with single-copy random *PstI* genomic probes (36 enzyme-probe combinations) but were higher than those observed for isozymes (10 loci). Results indicated that the wild ancestor had diverged into two taxa, one distributed in Middle America (Mexico, Central America, and Colombia) and the other in the Andes (Peru and Argentina); they also suggested separate domestications in the two areas leading to two cultivated gene pools. Domestication in both areas led to pronounced reductions in diversity in cultivated descendants in Middle America and the Andes. The marked lack of polymorphism within commercial classes of USA cultivars suggests that the dispersal of cultivars from the centers of origin and subsequent breeding of improved cultivars led to high levels of genetic uniformity. To our knowledge, this is the first crop for which this reduction in diversity has been documented with a single type of marker in lineages that span the evolution between wild ancestor and advanced cultivars.

Key words Crop evolution · M13 · Fingerprinting · Linkage map

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Introduction

Minisatellite sequences consist of tandem repeats of a core consensus sequence (Wyman and White 1980; Jeffreys et al. 1985). These sequences represent many loci dispersed in the genome, with many alleles at each locus. Consequently, hybridization of a minisatellite sequence to genomic DNA produces an individual-specific "DNA fingerprint". The occurrence of the different alleles is due to variation in the number of repeats in the minisatellite array, therefore these sequences are also called VNTRs (variable number of tandem repeats).

More recently, another source of hypervariable sequences was discovered in the protein III coding region of the *Escherichia coli* phage M13 DNA (Vassart et al. 1987). Both minisatellites and M13 hybridize to heterologous DNA from animals (Vassart et al. 1987; Jeffreys et al. 1987), plants (Rogstad et al. 1988; Dallas 1988), and fungi (Braithwaite and Manners 1989). Minisatellite markers have been applied to genetic studies for several purposes: forensics (Jeffreys et al. 1985), population genetics (Reeve et al. 1990; Balazs et al. 1992), linkage mapping (Donis-Keller et al. 1986), analysis of introgression (Hillel et al. 1990), estimating genetic variation (Nybom and Rogstad 1990; Kuhnlein et al. 1989), and cultivar identification (Dallas 1988; Nybom and Hall 1991).

Common-bean (*Phaseolus vulgaris* L., Fabaceae) is an annual, diploid ($2n = 2x = 22$) species derived from a wild ancestor distributed from northern Mexico to northwestern Argentina. Separate domestications in the Andes (Peru, Argentina) and in Middle America (Mexico, Central America, and Colombia) led to two distinct cultivated gene pools (Gepts 1993b). The existence of F_1 reproductive isolation barriers further sug-

gests substantial divergence between the two gene pools (Koinange and Gepts 1992). Both Andean and Middle American domesticates were introduced to the USA from their respective centers of origin; e.g., the kidney and cranberry beans were derived from Andean domesticates, whereas the navy, pinto, great northern, red Mexican, and pink beans originated from Middle American domesticates (Gepts et al. 1988).

In this paper, we report on the changes in levels of genetic diversity, as measured by M13 DNA fingerprinting, during domestication of the common-bean. Plant domestication involves genetic changes that adapt plants to cultivated environments. It is often associated with marked morphological changes such that fully domesticated plants cannot survive without the help of humans (Harlan 1992). Under this definition, domestication is an ongoing process that was initiated during the first stages of agriculture some 8,000–10,000 years ago (Harlan 1992) and continues to this day with the development of elite cultivars by plant breeders. In this study, we have analyzed two lineages, one originating in wild beans of the Middle American gene pool and the other in wild beans of the Andean gene pool. The former lineage led to the USA-bred pink-seeded cultivars via Middle American landraces, whereas the latter lineage led to the kidney-seeded cultivars through the Andean landraces. Previous results (Singh et al. 1991a; Stockton et al. 1992) suggested that only M13-related sequences provide sufficiently polymorphic markers to follow the evolution of genetic diversity from the wild ancestor to the highly bred USA cultivars.

Materials and methods

Plant materials

Two groups of genotypes were analyzed in this study. Seeds of the first group of genotypes were provided by S.P. Singh, R. Hidalgo, and O. Toro (Centro Internacional de Agricultura Tropical, Cali, Colombia). This group included 54 Latin American cultivated and wild common-bean accessions (9 Middle American wild genotypes, 25 Middle American landraces, 6 Andean wild genotypes, and 14 Andean landraces). Landraces were defined as locally-adapted, cultivated genotypes that are selected by farmers (Harlan 1992). The Middle American wild genotypes originated in Mexico, Central America, and Colombia, whereas the Andean accessions originated principally in Argentina. The deficiency of wild accessions from Peru and Bolivia reflected their dearth in germ plasm collections at the time this study was initiated. Among Middle American landraces, races Jalisco, Durango, and Mesoamerica (Singh et al. 1991a) were represented by 10, 5 and 6 accessions; among Andean genotypes, races Peru, Chile, and Nueva Granada (Singh et al. 1991a) were represented by 3, 4, and 7 accessions. Seeds of the second group, which included 17 USA bean cultivars, were provided by D. Helms (Bean Breeding, Dept. of Agronomy and Range Science, University of California, Davis). In each gel, two standard genotypes were included, one from the Middle American group (ICA-Pijao) and the other from the Andean group (California Dark Red Kidney).

DNA analysis

DNA was extracted from leaves of greenhouse-grown plants according to published procedures (Stockton et al. 1992) and separate aliquots of 2.5 µg were digested with a restriction enzyme (*Taq*I, *Hin*fI, or *Hae*III). Digests were run on 1.4% or 0.8%, 22-cm-long agarose gel in 1 × TAE buffer at 25 V for about 24 h, or until the blue dye was 1.5 cm from the bottom of the gel. After denaturation and neutralization, DNA was transferred to a nylon membrane (Zetabind) using 20 × SSC (3 *M* NaCl, 0.3 *M* sodium citrate, pH 7.0). Membranes were prehybridized in 5 × SSPE (0.75 *M* NaCl, 0.05 *M* NaH_2PO4, 5 m*M* EDTA, pH 7.4), 7% SDS, 1% Bovine Serum Albumin (Fraction V), and 5 m*M* EDTA, at 56 °C for at least 1 h. A 781-bp fragment of bacteriophage M13, obtained by cutting the phage replicative form with *Cla*I and *Bsm*I (Sambrook et al. 1989) was labeled with [^{32}P] dCTP by the random primer method (Feinberg and Vogelstein 1984). It was then hybridized to the membranes in the same pre-hybridization solution at 56 °C for 16–24 h. Post-hybridization washes were performed at low stringency in 2 × SSC, 0.1% SDS at room temperature for four times, 15 min each. X-ray film were exposed to blots for 1–2 days without intensifying screens; avoiding the intensifying screens generated better and sharper bands (Stockton et al. 1992). This procedure gave reproducible fingerprinting patterns that were independent of environmental or experimental variation as individual extracts from 40 plants of a single genotype (cv 'Yolano') grown in four locations gave identical fingerprinting patterns (G. Sonnante, unpublished results).

Diversity and distance analyses

A phenetic analysis was conducted to examine relationships among accessions. In this analysis, the presence or absence of bands was scored without regard as to whether they represented ancestral or derived states. The diversity of fingerprinting patterns was determined using Nei's (1987) diversity parameters. Distances among accessions were calculated as $2m/(n+m)$ where m = number of matching bands, $n = u + m$ = total number of bands, and u = number of non-matching bands (Rohlf 1991). A UPGMA (unweighted paired group method) dendrogram (Sneath and Sokal 1973) was constructed using the program NTSYS (Rohlf 1991).

Linkage mapping

Polymorphisms revealed by M13 were mapped in the F_2 population BAT93 × Jalo EEP556, the same population used to develop a restriction fragment length polymorphism (RFLP)-based genetic linkage map (Nodari et al. 1992; Gepts 1993a; Gepts et al. 1993). DNA was extracted from 75 individuals as described (Nodari et al. 1993). After digestion with *Taq*I, DNA was separated by electrophoresis on 1.5% agarose gels and transferred to nylon membranes by Southern blotting (Stockton et al. 1992). Hybridization with the M13 protein III tandem repeat that had been labeled by the random primer method was then performed (Stockton et al. 1992; Feinberg et al. 1984). Segregations were scored for presence or absence of individual fragments. Mapping of the loci was performed with Mapmaker (Lander et al. 1987; Nodari et al. 1993). Loci were considered to be linked if their LOD score was larger than 3.0 and their recombination frequency less than 0.30.

Results

Linkage mapping of M13-related sequences

Segregation of individual fragments in the fingerprinting patterns was examined in an F_2 population of cross BAT93 × Jalo EEP556, the same F_2 population used to generate an RFLP-based linkage map of the common-bean genome (Nodari et al. 1992; Gepts 1993a; Gepts et al. 1993). *Taq*I-digested total genomic DNA of the F_2 plants was hybridized with the M13 *Bsm*I/*Cla*I frag-

ment. Map positions were obtained for three markers (Fig. 1). Marker M13a was located at 14 cM from marker M13 m at the end of linkage group D10. Marker M13 m was located 4 cM from a rRNA locus. The other mapped marker (M13b), located at one end of linkage group D3, was linked to the locus *D1388-1*. These 2 loci were separated by 11 cM. No statistically significant linkages were found for the 6 other markers. Overall these results suggest that a majority of the bands observed by fingerprinting represent individual, unlinked loci.

Comparison of levels of diversity detected by isozymes, RFLPs for low-copy-number sequences, and RFLPs for M13-related sequences

To compare levels of polymorphism detected by these three categories of molecular markers, gene diversities were calculated from information obtained with each marker class for 54 Latin American accessions distributed in eight gene pools. These included three Middle American and three Andean cultivated races in addition to the Middle American and Andean wild beans. Data on variation at 20 isozyme loci, of which 10 were polymorphic, had been obtained previously (Koenig and Gepts 1989). RFLP data for low-copy-number sequences were provided by Becerra and Gepts (1994). Twelve probes were used to analyze genomic DNA digested with three restriction enzymes (*Eco*RI, *Eco*RV, and *Hin*dIII) for a total of 36 probe-enzyme combinations. These data were then compared with the fingerprinting data obtained by hybridization with M13 of *Taq*I-digested genomic DNA, i.e., 1 probe-enzyme combination. Gene diversities were comparable between RFLPs for low-copy-number sequences and for sequences hybridizing to M13 (henceforth M13-related sequences). In turn, they were 3–7 times higher on average than those observed for isozymes (Table 1).

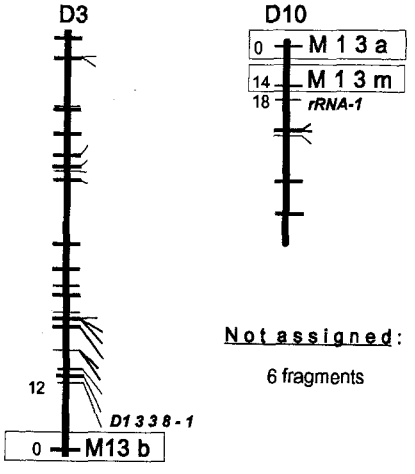

Fig. 1 Map location of M13-related sequences in common-bean. Only linkage groups D3 and D10, on which linked fragments were mapped, are shown. Locus names and distances are omitted except for the loci of M13-related sequences, which are *boxed* and the adjacent loci. Genetic distances measured from the most distal locus are Kosambi distances (cM). For a full description of this map, see Nodari et al. (1993), Gepts (1993a, b), and Gepts et al. (1993)

M13 fingerprinting patterns in the Latin American common-bean germ plasm

Patterns and levels of diversity for M13-related sequences were investigated in a sample of 54 accessions from Latin America, the center of origin of common-bean. This sample included 15 wild and 39 cultivated accessions belonging to either the Middle American or Andean gene pools. These same accessions had been previously characterized for their phaseolin type (Gepts et al. 1986; Gepts and Bliss 1986; Koenig et al. 1990), isozyme variants (Koenig and Gepts 1989; Singh et al. 1991b), and restriction fragment length polymorphisms (Becerra Velásquez and Gepts 1994). A numerical taxonomy analysis based on the presence or absence of bands between 2.5 and 7.5 kb was conducted.

High levels of polymorphism were observed in this sample of Latin American germ plasm after Southern hybridization of *Taq*I-digested genomic DNA with M13 (Fig. 2). Total genetic diversity for M13-related sequences was $H_t = 0.28$; within-gene pool diversity was $H_s = 0.17$ and between-gene pool diversity was $D_{st} = 0.11$. Genetic distances based on M13-related sequences

Table 1 Gene diversities among gene pools and races of *Phaseolus vulgaris* in its centers of domestication in Latin America

		n	Isozymes[a]	RFLPs for low-copy-number nuclear DNA[b]	RFLPs for sequences hybridizing to M13
Middle America	Wild	9	0.13	0.37	0.24
	Cultivated	25	0.09	0.31	0.20
	All Middle American	34	0.11	0.32	0.22
Andes	Wild	6	0.05	0.23	0.20
	All cultivated	14	0.01	0.28	0.16
	All Andean	20	0.03	0.25	0.21

[a] From Koenig and Gepts 1989; Singh et al. 1991b
[b] From Becerra Velásquez and Gepts 1994

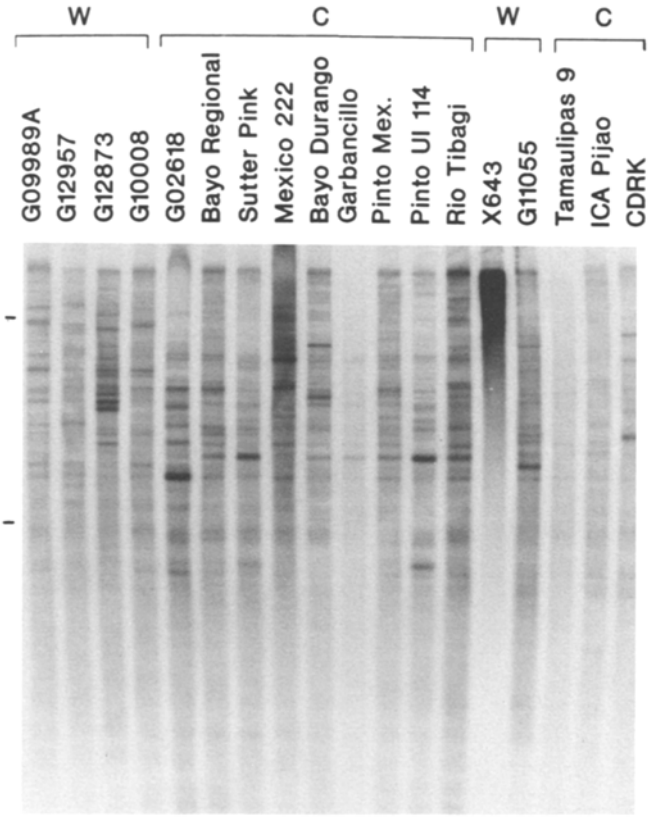

Fig. 2 M13 fingerprinting pattern, after *Taq*I digestion of genomic DNA, of wild (*W*) and cultivated (*C*) accessions of Latin American germ plasm of common-bean. *Tick marks* to the *left* correspond to fragment sizes of 7,500 bp (*top*) and 2,500 bp (*bottom*)

among Middle American gene pools and among the Andean gene pools, respectively, were in the 0.05–0.10 range, whereas those between Middle American and Andean gene pools were in the 0.20–0.30 range (Table 2). These values were comparable to those obtained in other crop plants for intra- and inter-subspecific comparisons, respectively (Doebley 1989, 1992).

UPGMA dendrograms based on the distance parameter $2m/(2n+m)$ (see Materials and methods) were calculated for individual accessions (not shown) and for

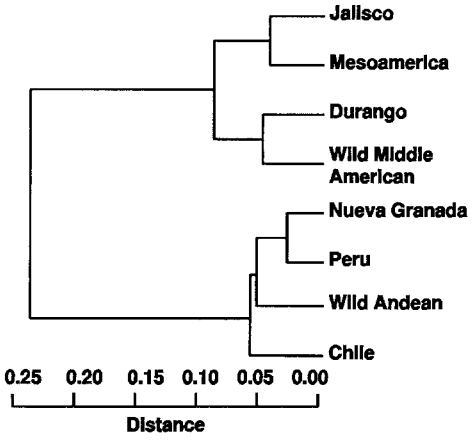

Fig. 3 Dendrogram of phenetic distances based on M13 fingerprinting patterns of Latin American germ plasm of common-bean. The distance parameter is $2m/(2n+m)$ (see Materials and methods)

accessions grouped according to their race membership (for cultivated materials) and geographic origin (i.e, Middle American and Andean, for wild materials) (Fig. 3). Both dendrograms exhibited two major branches. One branch represented the Middle American gene pool and included Middle American wild beans as well as cultivated races Durango, Jalisco, and Mesoamerica. The other branch included Andean wild beans and cultivated races Chile, Nueva Granada and Peru. This parallel geographic variation between the wild ancestor and cultivated progenitor supports earlier evidence of divergence between the two gene pools (e.g., Koinange and Gepts 1992) and multiple domestications in this species (Gepts 1990).

In this analysis, the wild Andean beans seemingly exhibited a closer relationship to cultivated materials of race Chile than to cultivated materials of the two other Andean races, Nueva Granada and Peru. This may be due to the fact that most wild Andean materials included in this study originated in Argentina. The dearth of wild beans from southern Peru and Bolivia should be remedied by additional explorations in these two countries.

Table 2 Nei distances for RFLPs of sequences hybridizing to M13 among races and gene pools of *Phaseolus vulgaris* in its centers of domestication

		Middle America origin				Andean origin		
		Jalisco	Durango	Mesoamerica	Wild	Nueva Granada	Chile	Peru
Middle America	Wild	0.06	0.05	0.08	0.16	0.21	0.27	0.16
	Jalisco		0.11	0.04	0.23	0.28	0.36	0.32
	Durango			0.12	0.15	0.23	0.29	0.25
	Mesoamerica				0.17	0.20	0.27	0.24
Andes	Wild					0.05	0.07	0.06
	Nueva Granada						0.06	0.03
	Chile							0.06

Table 3 Levels of gene diversity in USA commercial common-bean germ plasm classes and Latin American germ plasm from which they were derived

Gene pool	Wild ancestor	Landrace group	US commercial class
Middle American	0.24	Durango: 0.09 Nueva Granada:	Pink: 0.00 Kidney:
Andean	0.20	0.17	0.06

M13 fingerprinting patterns in USA common-bean cultivars

A similar analysis was conducted for USA common-bean cultivars belonging to four different commercial classes: kidney, cranberry, small-seeded whites or blacks, and pink beans. Monomorphism or low levels of polymorphism were observed within commerical classes after Southern hybridization of *Taq*I-digested genomic DNA with M13 (not shown). A phenetic analysis of banding patterns was conducted as described for the Latin American germ plasm. Total gene diversity was $H_t = 0.32$; within-commercial class diversity was $H_s = 0.05$; and between commercial class diversity was 0.27.

A UPGMA dendrogram confirmed the divergence between commercial classes of Andean (kidney, cranberry) and Middle American (small-seeded whites or blacks, pink) origins (not shown). Gene diversities in those cultivar classes containing more than 1 cultivar were low compared to those observed in the Latin American races and the wild ancestral materials from which they were derived (Table 3).

Discussion

Attributes of M13-related sequences as genetic markers

Sequences hybridizing to M13 in common-bean showed the following characteristics as genetic markers. First, these sequences appeared to characterize unlinked regions of the common-bean genome, as suggested by the mapping results. The three restriction fragments that were linked mapped at the end of linkage groups. This suggested that the polymorphic sequences may be located preferentially at the end of chromosomes. While more definitive data are needed to confirm these observations, in situ hybridization and mapping experiments in humans have shown that the most variable minisatellite arrays are located preferentially near the telomeres (Nakamura et al. 1987; Royle et al. 1988; O'Connell et al. 1989; Wells et al. 1989). Although M13-related sequences may not represent all regions of the genome, they can form multilocus associations and behave as if they were linked with other loci in the genome because of the predominantly autogamous reproductive system of common-bean. In addition, they can be subject to hitchhiking, particularly because they might be located at ends of chromosomes (Golding et al. 1986).

Second, the level of polymorphism detected by the M13-related sequences was higher than that observed with other markers. It was approximately 3–7 times higher than that observed in isozymes and was comparable to that observed for RFLPs of low-copy-number sequences. However, the latter were observed with 36 enzyme-probe combinations, whereas the M13 polymorphism was observed with a single enzyme-probe combination. The high levels of polymorphism revealed by M13 result from the ability to analyze many loci in a single hybridization compared to low-copy-number RFLP analyses.

Third, the pattern of genetic relationships, principally the divergence between Middle American and Andean gene pools, observed with the M13-related sequences matches that observed with other markers such as isozymes (Koenig and Gepts 1989; Singh et al. 1991b) and RFLPs for low-copy-number nuclear sequences (Becerra Velásquez and Gepts 1994).

Reduction in genetic diversity upon domestication

The most significant finding of our research was a marked reduction in genetic diversity for M13-related sequences during domestication in the Middle American lineage leading to the USA pink-seeded cultivars and the Andean lineage leading to the USA kidney-seeded cultivars. This reduction characterizes two major phases in the domestication process, namely that of selection for adaptation to cultivated environments in the center of origin and that of selection for adaptation to areas outside these centers. Molecular markers do not usually have a major effect on the phenotype, although specific data for M13-related sequences are lacking at this stage. Because of hitchhiking and autogamy, however, selection acting on loci elsewhere could affect the genetic diversity patterns of M13-related sequences. Selection has played a significant role during domestication. Indeed, the cultivated environments both within and beyond the centers of domestication differ from the environment in which the wild ancestor grows for several biotic (e.g., pathogens and pests) and abiotic variables (such as temperature, plant competition for light and water, and photoperiod). Divergent selection may have acted both for beneficial variants conferring adaptation to cultivated environments and consumer acceptance (e.g., seed color) or against variants with unfavorable effects in cultivated environments. In addition, the dissemination of common-bean likely involved small quantities of seeds increasing the probability of genetic drift.

Such reduction in diversity during domestication has been posited before in other crops on theoretical and

experimental grounds (Ladizinsky 1985; Doebley 1989, 1992; Gepts 1993b). To our knowledge, however, this is the first crop for which this reduction has been documented with a single type of marker in lineages that span the evolution between wild ancestor and advanced cultivars. This reduction contrasts with the increase in diversity observed for morphological traits such as seed type and growth habit. This discrepancy derives from the phenotypic nature of the morphological traits, that could be subjected to selection. The broad range of morphological variability that characterizes the cultivated gene pool results from selection during the domestication of new variants that may have appeared by mutation or recombination. In contrast, RFLP markers usually lack any phenotypic effect, although exceptions may exist. Unless a mutation had a pronounced favorable phenotypic effect, its probability of survival would be very low (Haldane 1927; Fisher 1930). The relative lack of variability at the molecular level among common-bean cultivars reflects the time span that has elapsed since the initiation of domestication (8,000–10,000 years BP), which is quite short on an evolutionary time-scale. There has probably been insufficient opportunity to replenish the diversity at the molecular level of the cultivated gene pool. Furthermore, pedigree analyses of USA cultivars showed that most cultivars resulted from crosses between genotypes belonging to the same commercial class (McClean et al. 1993). Hybridizations among related genotypes would have further reduced genetic diversity, which is consistent with our data.

Consequences for genetic conservation and plant breeding

Our findings indicate additional emphasis should be put on the conservation of wild ancestors and relatives, whether by in situ or ex situ methods. The representation of these wild relatives in germ plasm repositories is usually limited to less than 5% of the entire collection (Hoyt 1988) and their habitat is severely threatened in many regions of the world. The utilization of wild ancestral germ plasm should be encouraged because these wild ancestors and relatives represent an infrequently used source of genetic diversity that is conspecific with the cultivated gene pool and they generally do not exhibit reproductive isolation barriers when crossed to cultivars (Simmonds 1976). As an example, insect resistance present only in wild common-bean but not in cultivars has already been identified and transferred to common-bean cultivars (Kornegay et al. 1993).

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References

Balazs I, Neuweiler J, Gunn P, Kidd J, Kidd KK, Kuhl J, Mingjun L (1992) Human population genetic studies using hypervariable loci. I. Analysis of Assamese, Australian, Cambodian, Caucasian, Chinese and Melanesian populations. Genetics 131: 191–198

Becerra Velásquez VL, Gepts P (1994) RFLP diversity in common bean (*Phaseolus vulgaris* L.). Genome 94:256–263

Braithwaite KS, Manners JM (1989) Human hypervariable minisatellite probes detect DNA polymorphisms in the fungus *Colletotrichum gloeosporioides*. Curr Genet 16:473–475

Dallas JF (1988) Detection of DNA "fingerprints" of cultivated rice by hybridization with a human minisatellite DNA probe. Proc Natl Acad Sci USA 85:6831–6835

Doebley J (1989) Isozymic evidence and the evolution of crop plants. In: Soltis DE, Soltis PS (eds) Isozymes in plant biology. Dioscorides, Portland, Ore. pp 165–191

Doebley J (1992) Molecular systematics and crop evolution. In: Soltis PS, Soltis DE, Doyle JJ (eds) Molecular systematics of plants. Chapman Hall, New York, pp 202–222

Donis-Keller H, Barker DF, Knowlton RG, Schumm JW, Braman JC, Green P (1986) Highly polymorphic RFLP probes as diagnostic tools. Cold Spring Harbor Symp Quant Biol 51: 317–324

Feinberg AP, Vogelstein B (1984) Addendum: a technique for radiolabelling DNA restriction endonuclease fragments to high specific activity. Anal Biochem 137:266–267

Fisher RA (1930) The genetic theory of natural selection. Dover, New York

Gepts P (1988) A Middle American and Andean gene pool. In: Gepts P (ed) Genetic resources of *Phaseolus* beans. Kluwer, Dordrecht, the Netherlands, pp 375–390

Gepts P (1990) Biochemical evidence bearing on the domestication of *Phaseolus* beans. Econ Bot 44:28–38

Gepts P (1993a) Linkage map of common bean (*Phaseolus vulgaris* L.). In: O'Brien SJ (ed) Genetic maps. Cold Spring Harbor Laboratory, Cold Spring Harbor, N.Y. pp 6.101–6.109

Gepts P (1993b) The use of molecular and biochemical markers in crop evolution studies. Evol Biol 27:51–94

Gepts P, Bliss FA (1986) Phaseolin variability among wild and cultivated common beans (*Phaseolus vulgaris*) from Colombia. Econ Bot 40:469–478

Gepts P, Osborn TC, Rashka K, Bliss FA (1986) Phaseolin-protein variability in wild forms and landraces of the common bean (*Phaseolus vulgaris*): evidence for multiple centers of domestication. Econ Bot 40:451–468

Gepts P, Kmiecik K, Pereira P, Bliss FA (1988) Dissemination pathways of common bean (*Phaseolus vulgaris*, Fabaceae) deduced from phaseolin electrophoretic variability. I. The Americas. Econ Bot 42:73–85

Gepts P, Nodari R, Tsai R, Koinange EMK, Llaca V, Gilbertson R, Guzmán P (1993) Linkage mapping in common bean. Annu Rep Bean Improv Coop 36:xxiv–xviii

Golding GB, Aquadro CF, Langley CH (1986) Sequence evolution within populations under multiple types of mutation. Proc Natl Acad Sci USA 83:427–431

Haldane JBS (1927) A mathematical theory of natural and artificial selection, part V. Selection and mutation. Proc Camb Philos Soc 23:838–844

Harlan JR (1992) Crops and man. American Society of Agronomy, Madison, Wis.

Hillel J, Schaap T, Haberfeld A, Jeffreys AJ, Plotzky Y, Cahaner A, Lavi U (1990) DNA fingerprints applied to gene introgression in breeding programs. Genetics 124:783–789

Hoyt E (1988) Conserving the wild relatives of crops. International Board for Plant Genetic Resources, Rome

Jeffreys AJ, Wilson V, Thein SL (1985) Hypervariable 'minisatellite' regions in human DNA. Nature 314:67–73

Jeffreys AJ, Wilson V, Kelly R, Taylor BA, Bulfield G (1987) Mouse DNA 'fingerprints': analysis of chromosome localization and germ-line stability of hypervariable loci in recombinant inbred strains. Nucleic Acids Res 15:2823–2836

Kimura M (1983) The neutral theory of molecular evolution. Cambridge University Press, Cambridge, UK
Koenig R, Gepts P (1989) Allozyme diversity in wild *Phaseolus vulgaris*: further evidence for two major centers of diversity. Theor Appl Genet 78:809–817
Koenig R, Singh SP, Gepts P (1990) Novel phaseolin types in wild and cultivated common bean (*Phaseolus vulgaris*, Fabaceae). Econ Bot 44:50–60
Koinange EMK, Gepts P (1992) Hybrid weakness in wild *Phaseolus vulgaris* L. J Hered 83:135–139
Kornegay J, Cardona C, Posso CE (1993) Inheritance of resistance to Mexican bean weevil in common bean, determined by bioassay and biochemical tests. Crop Sci 33:589–594
Kuhnlein U, Dawe Y, Zadworny D, Gavora JS (1989) DNA fingerprinting: a tool for determining genetic distances between strains of poultry. Theor Appl Genet 77:669–672
Ladizinsky G (1985) Founder effect in crop-plant evolution. Econ Bot 39:191–198
Lander ES, Green P, Abrahamson J, Barlow A, Daly M, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linakge maps of experimental and natural populations. Genomics 1:174–181
McClean PE, Myers JR, Hammond JJ (1993) Coefficient of parentage and cluster analysis of North American dry bean cultivars. Crop Sci 33:190–197
Nakamura Y, Leppert M, O'Connell P, Wolff R, Holm T, Culver M, Martin C, Fujimoto E, Hoff M, Kumlin E, White R (1987) Variable number of tandem repeat (VNTR) markers for human gene mapping. Science 235:1616–1622
Nei M (1987) Molecular evolutionary genetics. Columbia University Press, New York
Nodari RO, Koinange EMK, Kelly JS, Gepts P (1992). Towards an integrated linkage map of common bean I. Development of genomic DNA probes and levels of restriction fragment length polymorphism. Theor Appl Genet 84:186–192
Nodari RO, Tsai SM, Gilbertson RL, Gepts P (1993) Towards an integrated linkage map of common bean. II. Development of an RFLP-based linkage map. Theor Appl Genet 85:513–520
Nybom H, Hall HK (1991) Minisatellite DNA 'fingerprints' can distinguish *Rubus* and estimate their degree of relatedness. Euphytica 53:107–114
Nybom H, Rogstad SH (1990) DNA "fingerprints" detect genetic variation in *Acer negundo* (Aceraceae). Plant Syst Evol 173:49–56
O'Connell P, Lathrop GM, Nakamura Y, Leppert ML, Ardinger RH, Murray JC, Lalouel J-M, White R (1989) Twenty-eight loci form a continuous linkage map of markers for human chromosome 1. Genomics 4:352–360
Reeve HK, Westneat DF, Noon WA, Sherman PW, Aquadro CF (1990) DNA "fingerprinting" reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. Proc Natl Acad Sci USA 87:2496–2500
Rogstad SH, Patton JC II, Schaal BA (1988) M13 repeat probe detects DNA minisatellite-like sequences in gymnosperms and angiosperms. Proc Natl Acad Sci USA 85:9176–9178
Rohlf FJ (1991) NTSYS-pc. Exeter Software, Setauket, N.Y.
Royle NJ, Clarkson RE, Wong Z, Jeffreys AJ (1988) Clustering of hypervariable minisatellites in the proterminal regions of human autosomes. Genomics 3:352–360
Sambrook J, Fritsch E, Maniatis T (1989) Molecular cloning. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, N.Y.
Simmonds NW (1976) Evolution of crop plants. Longman, London
Singh SP, Gepts P, Debouck DG (1991a) Races of common bean (*Phaseolus vulgaris* L., Fabaceae). Econ Bot 45:379–396
Singh SP, Nodari R, Gepts P (1991b) Genetic diversity in cultivated common bean. I. Allozymes. Crop Sci 31:19–23
Sneath PHA, Sokal R (1973) Numerical taxonomy. Freeman, San Francisco, Calif.
Stockton T, Sonnante G, Gepts P (1992) Detection of minisatellite sequences in *Phaseolus vulgaris*. Plant Mol Biol Rep 10:47–59
Vassart G, Georges M, Monsieur R, Brocas H, Lequarre AS, Christophe D (1987) A sequence of M13 phage detects hypervariable minisatellites in human and animal DNA. Science 235:683–684
Wells RA, Green P, Reeders ST (1989) Simultaneous genetic mapping of multiple human minisatellite sequences using DNA fingerprinting. Genomics 5:761–772
Wyman AR, White R (1980) A highly polymorphic locus in human DNA. Proc Natl Acad Sci USA 77:6754–6758