Genetic Control of the Domestication Syndrome in Common Bean

Epimaki M. K. Koinange, Shree P. Singh, and Paul Gepts*

ABSTRACT

The marked phenotypic differences for morphological and physiological traits that distinguish wild progenitors and cultivated descendants ("the domestication syndrome") and the lack of information about their genetic control have limited the utilization of wild germplasm for crop involvement. This study was conducted to assess the genetic control of the domestication syndrome in common bean (*Phaseolus vulgaris* L.). A recombinant inbred population resulting from a cross between a wild and a cultivated common bean was subjected to molecular linkage mapping and evaluation in short-day and long-day environments. We show that the genetic control of this syndrome in common bean involves genes that can have a large effect (>25–30%) and account for a substantial part of the phenotypic variation observed (>40–50%). The distribution of domestication syndrome genes appears to be concentrations in three genomic regions with a major effect on the syndrome, one of which greatly affects growth habit and phenology, the other seed dispersal and dormancy, and a third, the size of fruit and seed, all of which are important traits in determining adaptation to a cultivated environment. Whereas the influence of genetic background and environment on the expression of some traits will have to be further analyzed, our results suggest, however, that domestication of common bean could have proceeded rapidly (provided that genetic diversity and selection intensity were high) and that evolution can proceed through changes involving a few genes with large effect rather than through a gradual accumulation of changes coded by changes with small effects. They also suggest that adaptation to rapidly changing environmental conditions may involve genes with large phenotypic effects. The information presented here should lead to marker-assisted selection experiments of introgression of additional genetic diversity into the cultivated common bean gene pool.

THE GENETIC BASIS of adaptation is a long-standing controversy in evolutionary biology, specifically with regard to the number of genes controlling adaptive traits and the magnitude of their phenotypic effect. According to the neo-Darwinian theory of evolution, adaptation is controlled by a large number of genes, each with a small effect (Fisher, 1958). An alternative view holds that adaptive changes are controlled at least in part by genes with large phenotypic effects (Orr and Coyne, 1992). Surprisingly, there is a dearth of evidence on this issue, which is due to the lack, until recently, of appropriate analytical tools. Biometrical analyses, used in studies of genetically complex traits, usually do not permit the identification of individual genes involved in genetically complex or quantitative traits. However, molecular linkage mapping (Paterson et al., 1991) can identify the minimum number of genes, their respective phenotypic effect, and their linkage relationships.

The study of evolution under cultivation as an experimental approach for the study of evolution presents several advantages. Both the wild ancestor (or its immediate descendant) and the cultivated descendant are often known and available. They generally belong to the same biological species and, hence, their progeny are usually devoid of viability and fertility problems. The time frame over which the changes occurred often is known (some 5000–8000 yr). In crop plants, genetic tools such as linkage maps are available to investigate not only the genetic control of simply inherited traits but also of quantitative traits and their linkage relationships.

Compared with their wild-growing progenitors, cultivated plants often show marked phenotypic differences although they belong to the same biological species (Hawkes, 1983; Harlan, 1992). These differences, collectively called the domestication syndrome (Hammer, 1984), result from selection during several thousands of years for adaptation to cultivated environments. Differences occur in traits such as seed dormancy, seed dispersal mechanisms, life history traits (e.g., earliness), growth habit, photoperiod sensitivity, photosynthate partitioning, and gigantism of the harvested parts (Table 1) (Schwanitz, 1966; Hawkes, 1983; Harlan, 1992). Investigations on the genetic control of the domestication syndrome have generally focused on individual traits. For example, the seed dispersal mechanism in cereals has often been found to be controlled by one to three major genes (e.g., Ladizinsky, 1985). Recently, however, a more comprehensive analysis has been made possible by the availability of molecular linkage maps. An analysis of the genetic control of the morphological differences between maize (*Zea mays* L. ssp. *mays*) and teosinte (*Zea mays* L. ssp. *mexicana*), one of the most likely ancestors of maize, showed that the control of several traits involved major genes and that most of these genes were located on a limited number of chromosome regions (Doebley et al., 1990; Doebley and Stec, 1991, 1993). Fatokun et al. (1992) were able to identify major factors for seed size distinguishing wild progenitor and cultivated descendant in cowpea [*Vigna unguiculata* (L.) Walp.] and mung bean [*Vigna radiata* (L.) Wilczek]. These results suggested that evolution of morphological traits could proceed by substitution of alleles with large effects. However, they raised the issue of the evolution of other traits such as physiological ones that are not accompanied by a distinctive morphological phenotype, which is potentially subject to conscious or unconscious

E.M.K. Koinange, Dep. of Agronomy and Range Science, Univ. of California, Davis, CA 95616-8515; present address: Ministry of Agriculture, Lyamungu Res. Stn, Moshi, Tanzania; S.P. Singh, Bean Program, Centro Internacional de Agricultura Tropical, Apartado Aéreo 6713, Cali, Colombia; P. Gepts, Dep. of Agronomy and Range Science, Univ. of California, Davis, CA 95616-8515; E.M.K. Koinange was the recipient of a fellowship from SADCC/CIAT. Research funded by the Agency for International Development, Washington, DC, under the PSTC and Bean/Cowpea CRSP programs. Received 19 Oct. 1995. *Corresponding author (plgepts@ucdavis.edu).

Published in Crop Sci. 36:1037–1045 (1996).

Abbreviations: cM, centimorgan; DF, days to flowering; DM, days to maturity; DO, seed dormancy; HI, harvest index; L5, length of the fifth internode; NM, number of nodes on the main stem; PL, pod length; NP, number of pods per plant; PD, photoperiod-induced delay in flowering; LOD, logarithm of the odds ratio; QTL, quantitative trait locus; RFLP, restriction fragment length polymorphism; SW, seed weight.

Table 1. The domestication syndrome of common-bean.

General attribute	Trait	Wild (G12873)†	Domesticated (cv. Midas)†
Seed dispersal	Pod suture fibers	Present	Absent
	Pod wall fibers	Present	Absent
Seed dormancy	Germination	70.5%	100%
Growth habit	Determinacy	Indeterminate	Determinate
	Twining	Twining	Non-twining
	Number of nodes on the main stem	22.5	7.5
	Number of pods	43.2	13.9
	Internode length	1.6 cm	2.9 cm
Gigantism	Pod length	5.7 cm	9.8 cm
	One-hundred-seed weight	3.5 g	19.5 g
Earliness	Number of days to flowering under 12 h days	69	46
	Number of days to maturity	107	80
Photoperiod sensitivity	Delay in flowering under 16 h days	>60 days	0 days
Harvest index	Seed yield/biomass	0.42	0.62
Seed pigmentation	Presence vs. absence	Present	Absent

† Values or character states for the wild and cultivated genotypes were determined in the same way as in their progeny as described in Materials and Methods.

selection by humans. In addition, it has been suggested that linkage of genes controlling the domestication syndrome could be the consequence of a highly allogamous reproductive system (Pernès, 1983). In the initial stages of domestication when the wild ancestor and incipient crop were still sympatric, frequent outcrosses would have led to high proportions of progenies that were adapted neither to the cultivated nor the natural environment unless genes for adaptation traits were linked. This hypothesis suggests that in predominantly self-pollinated crops, genes controlling the domestication syndrome could have a more uniform distribution in the genome because autogamy maintains multilocus associations even among unliked loci (Hedrick et al., 1978).

The Domestication Syndrome in Common Bean

We have investigated the genetic control of both morphological and physiological traits constituting the domestication syndrome (Table 1) in common bean, *Phaseolus vulgaris* L., a predominantly autogamous species. The domestication history of the common bean is well known and its wild progenitor has been identified (Gepts, 1990, 1993; Gepts and Debouck, 1991). Crosses between the wild progenitor and cultivated descendant generally produce viable and fertile progeny (Koenig and Gepts, 1989). The two most important attributes of the domestication syndrome in common bean are the loss of seed dispersal ability and seed dormancy because they are crucial for adaptation to a cultivated environment. The former is conditioned by the presence of fibers in the pods, both in their sutures ("string") and their walls. Loss of these fibers leads to indehiscence of the pods and lack of seed dispersal at maturity. Cultivated beans have, thus, effectively come to depend upon human intervention for their continued survival. Cultivated beans also display a more compact growth habit compared with their wild progenitor. In its most evolved form under domestication, this growth habit is characterized by a combination of traits comprising determinacy, non-twining branches, few vegetative nodes, and long internodes. Less-evolved growth habits may show some or only one of these traits (Debouck, 1991). Determinacy, defined as the early transition from a vegetative terminal meristem to a reproductive one, has, by its very nature, multiple effects on growth habit and the life cycle as it causes the appearance of a terminal inflorescence, a reduction in the number of nodes and pods on the main stem and the branches, and a shortening of the life cycle. Selection by humans also has led to pods and seeds that are larger ("gigantism") and show different or no anthocyanin pigmentation. The dissemination of cultivated beans from their domestication centers in the tropics to new areas at higher latitudes has led to a selection of genotypes that are insensitive to daylength compared with the wild progenitor, which will only flower under short days. In concert with the changes in growth habit and photoperiod sensitivity, common bean cultivars flower and mature generally earlier than their wild ancestors.

The objective of this study was to gain a better understanding of the inheritance of morphological and physiological traits included in the domestication syndrome in common bean, by means of molecular linkage mapping in a recombinant inbred population resulting from a cross between a wild and a domesticated bean. Specifically, we tried to determine the minimum number of genes involved, the magnitude of their effect, the proportion of the variation for each trait that could be explained in genetic terms, and the linkage relationships among the genes involved.

MATERIALS AND METHODS

Our strategy to investigate the genetic control of the domestication syndrome in common bean was to first establish a cross between a wild and a cultivated bean that exhibited the broadest range of domestication syndrome traits. Secondly, we established a linkage map in this production by determining the segregation of molecular and biochemical markers that constituted a subset of the markers used in the development of the common bean linkage map (Nodari et al., 1993a; Gepts et al., 1993). Thirdly, the genetic control of the traits constituting the domestication syndrome was determined by linkage mapping.

Plant Material

Our analysis was conducted in an F_8 recombinant inbred population ($n = 65$), which resulted from single-seed-descent in insect-free conditions of an F_2 generation from the cross between cultivar Midas and wild bean accession G12873. As a wax snap bean, Midas exhibits the largest number of domestication traits among cultivars (Table 1). G12873, on the other hand, has the characteristic phenotype shown by wild *P. vulgaris* (Table 1). In addition, the two parents have been shown to exhibit a high level of RFLP making it faster to establish a molecular linkage map in a cross between them (Nodari et al., 1992). A recombinant inbred population was used because preliminary investigations from cultivated × cultivated crosses had shown that traits of the domestication syndrome could potentially be controlled either qualitatively

or quantitatively (Gepts, 1990). In addition, the evaluation of the segregating progeny had to be conducted in both a long-day environment to study the segregation of photoperiod sensitivity and in short-day environments to study the segregation of other traits in the absence of photoperiod sensitivity.

Molecular Linkage Map Construction

The segregation of 83 markers was analyzed in the 65 lines of the Midas × G12873 recombinant inbred population. These 83 markers represented a subset of approximately 220 markers distributed throughout the original common bean ($2n=2x=22$) genetic linkage map (Nodari et al., 1993a; Gepts et al., 1993). This original map covers an estimated 85% of the genome (Gepts et al. 1993) and currently has 13 linkage groups. For small linkage groups (D9 and D11), only one marker was sampled. The markers analyzed in this study represented one seed protein (phaseolin) locus, five isozyme loci, and 77 RFLP loci. The seed protein, isozyme, and RFLP procedures used to establish a molecular linkage map were described previously (Nodari et al., 1993a).

Gene order was determined by Mapmaker (Lander et al., 1987) as described previously (Nodari et al., 1993a) with threshold LOD (logarithm of the odds ratio) scores and recombination values of 3.0 and 30%, respectively. Map distances shown are Kosambi (1943) distances calculated after conversion of F_8 strain distribution patterns into F_2 recombination values (Haldane and Waddington, 1931).

Analysis of Segregation of Phenotypic Traits

Qualitative traits (determinacy vs. indeterminate; pigmented vs. white flowers and seeds; yellow ("wax") vs. green pods; presence or absence of pod fibers) were observed in a greenhouse during fall and winter in Davis, CA (38° N. Lat.; temperature range: 20–25°C). The presence of fibers in pod sutures and pod walls was determined by breaking the pod beak or pod wall, respectively, and examining the break surface for the presence of fibers. The genetic control and linkage map location of these qualitative traits was determined by a test of independence (χ^2) with each of the marker loci located on the linkage map, at a significance level of $P = 0.01$ to minimize type I errors.

Observations on the number of nodes, length of the fifth internode, harvest index, and days to flowering and maturity were made in a replicated field trial under short-day conditions in Popayán in the cool highlands of Colombia (2° N. Lat.; photoperiod: approximately 12 h; average temperature: 18–20°C). This environment was chosen to avoid photoperiod sensitivity effects on growth and development. Sixty of the 65 recombinant inbred lines without apparent viability or fertility problems, together with the two parents and two cultivated local checks, were grown in single rows in a simple lattice with three replicates. Data were taken as described previously (Singh et al., 1991b). Biomass was the total above-ground dry matter yield. Harvest index was the ratio of seed yield to the total biomass.

To measure seed dormancy, 100 unscarified seeds from each recombinant inbred line were arranged in two replications, each of 50 seeds, in a petri dish on filter paper. The filter paper was soaked with distilled water and Bayleron 50 d to flowering (DF) fungicide added to prevent seed and seedling fungal rot diseases. To confirm that those seeds that did not germinate after 96 h were viable, seed scarification on those seeds was performed before repeating the germination test in different petri dishes. Observations on photoperiod sensitivity were made in two growth chambers with temperatures set at 25°C day/20°C night and daylengths of 16 and 12 h, respectively. Photoperiod sensitivity was measured as the delay in flowering expressed in number of days induced by the long-day regime in comparison with the short-day regime.

The location of quantitative trait loci were identified by univariate regression analysis (Edwards et al., 1987), which, in previous studies (Doebley and Stec, 1991; Nodari et al., 1993b), had given results comparable to interval mapping. Transformations of the original data to reduce skewness and kurtosis led to similar results in the experiments reported here. Significant differences at the $P = 0.01$ level were interpreted as indicating the presence of linkage of the marker locus to a quantitative trait locus (QTL) for the trait. When significant associations were identified with several adjacent markers linked by less than 30 cM, only one QTL was inferred, located near the molecular marker with the largest R^2 value. The proportion of the total phenotypic variation (multivariate R^2) explained by the various QTLs for a given trait was determined by multivariate regression analysis with markers significantly associated with the trait used as independent variables.

RESULTS

Establishment of a Linkage Map

Sixty-six of the 83 loci (80%) showed a non-distorted segregation. With the exception of four loci, the gene order in cross Midax × G12873 was conserved compared with cross BAT93 × Jalo EEP558 (Gepts et al., 1993) although an as yet unexplained map expansion was observed in certain intervals. Of the 56 RFLP probes, 38 probes detected a single locus but 18 probes detected more than one locus. This represents a minimum estimate of duplication of 32% in the common bean genome.

Segregation and Linkage Analysis of Domestication Syndrome Traits

The two single most important traits distinguishing wild and cultivated beans are seed dispersal, conditioned by the presence of fibers in the pods, and dormancy, conditioned by impermeability of the seed coat. The lack of pod suture fibers was conditioned by a single gene (*St*) on linkage group D2. Lack of pod wall fibers also was controlled by a single gene on linkage group D2 and was tightly linked or identical to the gene *St* controlling the presence of pod suture fibers (Fig. 1). Four unlinked QTLs were identified for seed dormancy (DO) that explained 69% (cumulative R^2 based on multiple regression) of the phenotypic variation for this trait (Table 2).

Among growth habit traits, determinacy was controlled by a single gene (*fin*) on linkage group D1 confirming previous results (Norton, 1915). Although control of twining has been attributed previously to the gene *Tor*, distinct from the *fin* locus (Norton, 1915), in our experiments twining was correlated with *fin* suggesting that either *fin* had a pleiotropic effect on twining or that *Tor* was tightly linked to *fin* in this population. Observations on the number of vegetative nodes on the main stem (NM) suggested three factors could explain 57% of the cumulative variation. The first was the *fin* gene as expected. The second one mapped near the *Ppd* gene for photoperiod sensitivity (see below). The third was un-

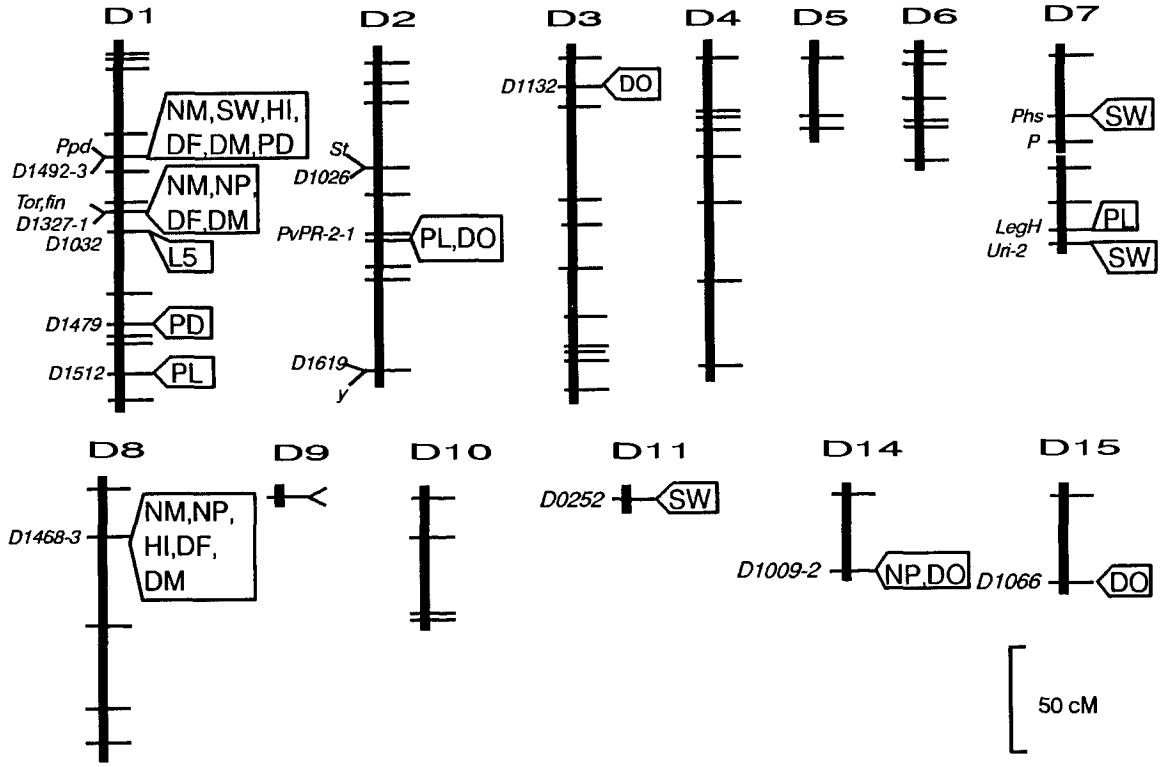

Fig. 1. Linkage map location of genes controlling the domestication syndrome in common bean. Symbols to the left of linkage groups are marker loci. Symbols of genes for phenotypic markers are as follow: *fin*, determinacy; *P*, anthocyanin pigmentation; *Ppd*, photoperiod-induced delay in flowering; *St*, pod string; *y*, yellow pod color. Symbols to the right of linkage groups are quantitative trait loci which are abbreviated as follow: DF, days to flowering; DM, days to maturity; DO, seed dormancy; HI, harvest index; L5, length of the fifth internode; NM, number of nodes on the main stem; PL, pod length; NP, number of pods per plant; PD, Photoperiod-induced delay in flowering; SW, seed weight. Map distances shown are Kosambi (1943) distances calculated after conversion of F_8 recombination values into F_2 recombination values (Haldane and Waddington 1931). Linkage groups D12 and D13 have since been joined with linkage groups D6 and D7, respectively.

linked to the first two and was located on linkage group D8 (Fig. 1). Three factors explained 51% of the variation in the number of pods (NP), a trait correlated with the number of vegetative nodes. Two of these factors mapped to the same location as QTLs for the number of vegetative nodes, one of them being the *fin* gene. One QTL was identified for the length of the fifth internode (L5), which mapped to linkage group D1 near the *fin* gene (Fig. 1). Two traits—pod length (PL) and seed weight (SW)—were analyzed as a measure of the increase in size of the harvested organs that characterizes common bean cultivars compared with their wild progenitor. Three unlinked factors explained 37% of the variation in pod length and four explained 57% of the variation in seed weight. One of the factors for seed size, located on linkage group D7 near the *P* locus for seed color, may actually correspond to one of the factors identified by Sax (1923) in his classic work on seed size inheritance.

Photoperiod sensitivity was influenced by at least two QTLs. The factor with the largest effect (*Ppd*; Wallace et al., 1993) was linked to the *fin* locus, confirming previous observations (Coyne, 1967; Gniffke, 1985; Gu et al., 1993). The number of days to flowering and maturity were each influenced by three, probably identical QTLs. The QTL with the largest effect was the *fin* gene. There was a second QTL for these traits linked to the *Ppd* gene. This was surprising because the number of days to flowering and to maturity had been observed in Colombia under short-day conditions in which the *Ppd* gene is supposedly not expressed. This observation suggests that the delay in flowering and maturity associated with the *Ppd* allele results from a residual effect of this allele under short days or from the expression of a gene closely linked to the *Ppd* locus. Two factors were identified that explained 18% of the variation for harvest index (HI). One factor mapped to the region marked by the *Ppd* locus and the other to the same region on linkage group D8 where QTLs were mapped for the number of nodes, pods, and days to flowering and maturity.

Pod color (wild-type green vs. mutant yellow) and seed color (wild-type agouti pigmentation vs. mutant white) were each controlled by a single gene, *y* on linkage group D2 and *P* on linkage group D7, respectively. These results confirm previous observations on the single-gene control of these traits and on their linkage relationships. Locus *y* is located on the same linkage group as *St*, the gene controlling the presence of pod suture fibers and locus *P* is linked to the *Phs* (phaseolin) locus on linkage group D7 (Bassett, 1991).

Our results, therefore, suggest that a sizable proportion (approx. 40–50% and over) of the phenotypic variation observed for most quantitative traits can be explained genetically (Table 2). These traits included seed dormancy (69%), number of nodes (57%), number of pods (51%), seed weight (56%), number of days to flowering (46%) and to maturity (40%), and photoperiod sensitivity

Table 2. Genetic factors influencing the domestication syndrome in common-bean.

General attribute	Trait	Loci					Phenotypes	
		Linkage group	Gene or linked marker	Significance	R^2 for locus (%)†	R^2 for trait (%)†	Wild bean allele (G12873)	Domesticated bean allele (cv. Midas)
Seed dispersal	Pod suture fibers	D2	*St*	***			Present	Absent
	Pod wall fibers	D2	*St*(?)‡	***			Present	Absent
Seed dormancy	Germination	D2	*PvPR-2-1*	***	18		54%	84%
		D3	*D1132*	***	52		47%	98%
		D14	*D1009-2*	***	19		85%	54%
		D15	*D1066*	**	12	69	50%	77%
Growth habit	Determinacy	D1	*fin*	***			Indeterminate	Determinate
	Twining	D1	*Tor* or *fin*	***			Twining	Non-twining
	Number of nodes on the main stem	D1	*fin*	***	53		15	8
		D1	*D1492-3*	***	20		13	9
		D8	*D1468-3*	**	16	57	12	9
	Number of pods	D1	*fin*	***	32		29	17
		D8	*D1468-3*	**	21		25	15
		D14	*D1009-2*	**	14	51	24	16
	Internode length	D1	*D1032*	***	19	19	2.7 cm	4.0 cm
Gigantism	Pod length	D1	*D1512*	***	23		6.4 cm	7.5 cm
		D2	*PvPR-2-1*	**	20		6.7 cm	7.6 cm
		D7	*LegH*	**	16	37	7.5 cm	6.5 cm
	100-seed weight	D1	*D1492-3*	***	18		14.0 g	17.2 g
		D7	*Phs*	***	27		13.6 g	17.5 g
		D7	*Uri-2*	**	16		14.1 g	17.0 g
		D11	*D0252*	**	15	57	16.8 g	14.0 g
Earliness	Number of days to flowering	D1	*fin*	***	38		56	47
		D1	*Ppd*(?)‡	**	19		54	47
		D8	*D1468-3*	**	12	46	52	47
	Number of days to maturity	D1	*fin*	***	30		89	83
		D1	*Ppd*(?)‡	***	18		87	83
		D8	*D1468-3*	**	14	40	87	84
Photoperiod sensitivity	Delay in flowering under 16 h days	D1	*Ppd*	***	44		20	3
		D1	*D1479*	**	17	52	17	8
Harvest index	Seed yield/biomass	D1	*Ppd*(?)‡	***	28		42%	58%
		D8	*D1468-3*	**	15	18	45%	58%
Seed pigmentation	Presence vs. absence	D7	*P*	***			Present (agouti)	Absent (white)

***, ** Significant at the 0.001 and 0.01 probability levels, respectively.
† The magnitude of the effects for individual loci, determined by univariate regression analysis, and the magnitude of all loci combined, determined by multivariate regression analysis, are indicated only for quantitative traits.
‡ The question mark indicates that pleiotropy and tight linkage cannot be distinguished at this stage.

(52%). Pod length showed an intermediate value (37%) whereas internode length (19%) and harvest index (18%) showed a low value. The latter two traits are known to be strongly influenced by environmental conditions (Singh, 1991). Alternatively, they could be influenced by a larger number of genes, most of which have an effect that was too small to be detected in this experiment. Factors with large effects were identified for many traits, in particular number of nodes on the main stem (53%), number of days to flowering (38%), seed dormancy (52%), and photoperiod sensitivity (44%).

For most traits, the associations between marker and QTL alleles in the recombinant inbred population were as expected based on the parental phenotypes. Three exceptions concerned dormancy, pod length, and seed weight. The Midas allele at locus *D1009-2* was associated with higher levels of dormancy than the G12873 allele at that locus. The G12873 allele at the *LegH* and *D0252* loci were associated with longer pods and larger seeds, respectively.

Inspection of the linkage map location of the factors controlling the various component traits of the domestication syndrome showed them to be distributed on eight of the 13 linkage groups (Fig. 1). To test the randomness of the genomic distribution of factors identified in this study, χ^2 tests were calculated under the assumptions of independent gene action or pleiotropy on other traits of the *fin*, *Ppd*, and *St* genes and the QTL for number of nodes on the main stem on linkage group D8 (see above, Fig. 1, and Table 3). Assuming independent gene action, we identified 31 quantitative or qualitative factors; assuming pleiotropy at all loci, we identified 21 factors. Expected numbers of factors on each linkage group were calculated on the basis of the genetic length of each linkage group. The χ^2 values were 44.2 and 23.3, respectively, each with 12 degrees of freedom (Table 3). The former value was significant at the $P = 0.001$ level and the later at the $P = 0.05$ level suggesting a departure from random distribution across the common bean genome. Three linkage groups appeared to play an important role in the domestication syndrome (Fig. 1 and Table 3). In addition to the *fin* gene for determinacy, linkage group D1 carried factors influencing all the quantitative traits analyzed, except dormancy. This linkage group appeared to have a major effect on growth habit and phenology (Fig. 1). Linkage group D2 appeared to play an important role in seed dispersal (*St*) and dormancy (DO) and linkage group D7 in harvested organ size, i.e., pod length (PL) and seed size (SW) (Fig. 1).

DISCUSSION

Several observations suggest that a high degree of confidence can be associated with our linkage results for

Table 3. Linkage group distribution of genes for domestication under hypotheses of pleiotropy or independent gene action.

Linkage group		Pleiotropy			Independent gene action		
Number	Length (cM)	Factors†	Expected number	χ^2	Factors†	Expected number	χ^2
D1	150	D1492-3 (PD, SW), D1327-1 (*fin*), D1032 (L5), D1479 (PD), D1512 (PL)	2.8	6.12	D1492-3 (NM, DF, DM, PD, SW, HI), D1327-1 (*fin*, *Tor*, NM, NP, DF, DM), D1032 (L5), D1479 (PD), D1512 (PL)	4.2	27.95
D2	130	D1026 (*St*), *PvPr-2-1* (PL, DO)	2.5	0.97	D1026 (*St*, pod wall fiber), *PvPr-2-1* (PL, DO)	4.1	0.04
D3	160	D1132 (DO)	3.0	1.36	D1132 (DO)	4.5	2.69
D4	150	None detected	2.8	2.84	None detected	4.2	4.19
D5	33	None detected	0.7	0.62	None detected	1.0	0.92
D6	50	None detected	1.0	0.95	None detected	1.5	1.40
D7	90	*Phs* (SW), *LegH* (PL), *Uri-2* (SW), *P*	1.8	3.25	*Phs* (SW), *LegH* (PL), *Uri-2* (SW), *P*	2.6	0.88
D8	130	D1468 (NM)	2.6	0.86	D1468 (NM, NP, HI, DF, DM)	3.5	0.52
D9	40	None detected	0.8	0.76	None detected	0.6	1.11
D10	58	None detected	1.1	1.10	None detected	1.7	1.62
D11	40	D0252 (SW)	0.4	0.08	D0252 (SW)	0.6	0.01
D14	38	D1009-2 (NP, DO)	0.7	2.29	D1009-2 (NP, DO)	1.1	0.83
D15	42	D1066 (DO)	0.8	0.05	D1066 (DO)	1.2	0.03
Totals	1111		21	23.3*		31	44.2***

***, * Significant at the 0.001 and 0.05 probability levels, respectively.
† Nearest molecular marker (major genes or QTLs).

the major genes identified here. First, several linkages identified in previous linkage studies between phenotypic markers have been confirmed in our study. These linkages include the linkage between *fin* and *Ppd* on linkage group D1 (Coyne, 1970), between *Ppd* and another photoperiod sensitivity locus on linkage group D1 (N. Weeden, 1994, personal communication), between the *St* and *I-B* genes on linkage group D2 (Bassett, 1991), and between the *Phs* and *P* genes on linkage group D7 (Vallejos et al. 1992). Second, whereas determinacy and the number of nodes were determined independently in Davis and in Colombia, respectively, one of the QTLs for number of nodes mapped to the same genomic region as *fin*. This was expected given the phenotypic effect of *fin* on terminal meristem identity. A caveat needs to be introduced, however, regarding our results. It remains to be determined to what extent the specific map location and magnitude of individual factors, especially those of smaller magnitude, depends on the genetic background and environment in which these factors are expressed.

Consideration of segregation and linkage map data for both qualitative and quantitative traits leads us to propose that the genetic control of the domestication syndrome in common bean is relatively simple compared with that of other complex traits, based on four parameters provided by this approach. These parameters are the minimum numbers of genes involved, the magnitude of their individual phenotypic effect, the proportion of the phenotypic variation that could be explained in genetic terms, and their linkage relationships (Tables 2 and 3). An average of 2.3 factors per quantitative trait was identified, representing a range of one to four factors for each trait. These factors accounted for an average of 44% of the phenotypic variation with a range of 18 to 69%. For a majority of the traits, therefore, few genes with major effects explained most of the phenotypic variation observed in this cross. In addition to those genes with a qualitative effect (i.e., presence or absence of a trait), several major genes controlling quantitative traits were identified. Particularly striking were genes for photoperiod sensitivity (44%) and seed dormancy (52%) (Table 2).

In some cases, the large effect of individual genes was further magnified by pleiotropic effects. The *fin* gene, which conditions the early transformation of terminal meristems from a vegetative to a reproductive state, also has, by its very nature, pleiotropic effects on the number of nodes on the main stem, the number of pods, and the number of days to flowering and maturity (Table 2). Identification and selection of the *fin* mutation will have led to genotypes with a markedly more compact growth habit and earlier phenology compared with the wild progenitor. The *fin* allele occurs at high frequency in the Andean cultivated gene pool of common bean compared with the Mesoamerican gene pool (Singh et al. 1991a). In contrast with the Mesoamerican domestication center where maize provides physical support to climbing beans grown in association, the absence of maize in the early domestication phases in the Andean center of origin, would have favored common bean genotypes with a bush growth habit, which do not require physical support.

Our results extend earlier observations about the genetic control of morphological traits in plants to that of physiological traits, which have no direct morphological effect. Knight (1948), Hilu (1983), and Gottlieb (1984) concluded that many morphological traits in cultivated plants are controlled by genes with a major phenotypic effect. Doebley and Stec (1991, 1993) and Dorweiler et al. (1993) showed that several of the morphological differences between maize and its wild ancestor teosinte were controlled by major genes and that only a few genomic regions were involved. In our study, the genetic control of physiological traits, including photoperiod sensitivity or seed dormancy, also involved major genes. This suggests that evolution for a broad range of traits can involve major gene mutations in addition to minor gene mutations.

Traditional neo-Darwinian evolutionary genetic theory holds that evolutionary change proceeds by substitutions of alleles at a large number of loci each with small phneotypic effects. This theory is predicated on the hypothesis that mutations with large effects are in most cases deleterious (Lande, 1981, 1983). While this may be true in fairly stable and homogeneous environments, it may not hold in environments that are spatially heterogeneous or highly variable in time. Mutations with large

effects may in those situations provide opportunities for adaptation by selection to markedly different environments leading to the appearance of distinctive "adaptive peaks" sensu S. Wright (Dobzhansky et al., 1977). The cultivated environment is markedly different compared with the natural environment. Whereas mutations in common bean such as determinacy, lack of pod fibers, or permeable seedcoats, would reduce fitness in natural environments, they would have conferred a selective advantage in cultivated environments. Genotypes adapted to cultivated environments would have represented a distinctive adaptive peak compared with wild genotypes.

Selection intensity for adaptation to a cultivated environment could have been quite intense given the contrast between natural and cultivated environments. Under those circumstances, mutations with a major phenotypic effect would have had a relative advantage over the mutations with a small phenotypic effect because they contributed more towards the expression of a trait. To what extent are situations with strong selective effects common in natural environments? A recent survey concluded that strong selection pressures are not unusual in natural populations (Endler, 1986). Situations that potentially involve strong selection pressures include colonization of novel habitats, rapid climate change, and sudden modifications of the biotic environment. Although there is a dearth of information on the genetic control of adaptive traits in natural populations, a recent report shows that bill size in the African finch *Pyrenestes* was subject to disruptive selection and appeared to be controlled by a single gene (Smith, 1993). Twenty to 30% of bristle number in *Drosophila melanogaster* was correlated with molecular variation at the *scabrous* locus (Lai et al., 1994). A corollary to this observation is that major morphological changes can apparently be correlated with small changes at the molecular level as observed previously in fungi (Bruns et al., 1989) and fishes (Sturmbauer and Meyer, 1992). Whether small changes at the molecular level can also lead to major changes in adaptation in natural populations can now be investigated with molecular linkage mapping and a concomitant quantitative trait analysis as precursors to the eventual cloning of the genes involved (e.g., Bradshaw et al., 1995).

The high proportion of phenotypic variation for most traits in the F_8 recombinant inbred population that could be explained in genetic terms suggests that these traits have a high heritability in agreement with previous results based on classical, biometric analyses. For example, Motto et al. (1978) found that seed size in a wild × cultivated cross had a narrow-sense heritability of 0.85. Both the major phenotypic effect of individual factors and the high heritability of individual traits may reflect the domestication process. Mutations with a major effect would have had a higher likelihood of being selected, whether consciously or unconsciously. The high heritability would have increased the likelihood of recovery in the progeny. Provided genetic diversity and a sufficient selection pressure were present, there would have been no genetic impediment for a rapid change during domestication. The potentially rapid selection of a domesticated phenotype may explain why sequences encompassing the wild ancestors, their cultivated descendants, and forms intermediate between them have not been identified so far in the archaeological record of common bean (Kaplan and Kaplan, 1988). It also may explain why only a few species have been domesticated. Only those plants in which domestication syndrome traits were controlled by few genes with a major phenotypic effect would have quickly responded to selection taking place during the transition from hunting-gathering to agrarian societies.

Linkage data show that linkage group D1, and to a lesser extent linkage groups D2 and D7, had an effect on the domestication syndrome that was disproportionately large when considering their genetic length. Of the 16 qualitative or quantitative traits of the domestication syndrome analyzed in this study, 11 were controlled partially by factors on linkage group D1 (principally growth habit and phenology), four on linkage group D2 (principally seed dispersal and dormancy), and two on linkage group D7 (size of the harvested organs). The results of the χ^2 tests suggest that the factors involved in the domestication syndrome are not distributed proportionately to the genetic length of the linkage groups.

Pernès (1983) predicted that, in cross-pollinated species, the genes controlling the domestication syndrome would have a tendency to be linked in order to facilitate the recovery of parental, cultivated types following frequent outcrosses between the wild ancestor and the cultivated descendant. This prediction was borne out by the results of Doebley and Stec (1991, 1993) in maize, a highly allogamous species. In predominantly self-pollinated species such as the common bean, on the other hand, the disruption of established cultivated genotypes by hybridization with wild genotypes would be less frequent but the recovery of parental, cultivated types in the progeny of the outcrosses would occur at a similarly low probability compared with cross-pollinated species if the domestication syndrome genes were distributed throughout the genome. Our observation that a majority of the major genes controlling the domestication syndrome in common bean also were concentrated on few (three) of the 11 linkage groups of the genome (Table 3; Fig. 1) can be tentatively explained by a number of non-mutually exclusive hypotheses. First, it is possible that the limiting factor in the recovery of cultivated genotypes in the progeny of wild × cultivated common bean crosses is not the frequency of outcrossing but the genome distribution of domestication syndrome genes. Even low levels of gene flow, and the concomitant recombination, could prevent the establishment of a cultivated phenotype combining essential elements of the domestication syndrome. Second, although common bean is considered to be a predominantly self-pollinated species with outcrossing rates below 5% (Bliss, 1981; Triana et al., 1993), another report suggests outcrossing in the presence of insect pollinators can reach 20–30% or more (Wells et al., 1988). All published estimates of outcrossing levels in common bean have been obtained outside the distribution area of wild common bean. Outcrossing levels within the distribution area could be higher because of the presence of native insect pollinators. Third, the linkage relationships identified here may be due to chance rather than as a result of selection pressures. Similar studies on other, self- or cross-pollinated, species would allow us to address these hypotheses.

Finally, the simple genetic control of the phenotypic differences between wild and cultivated beans shows that introgression of diversity from the wild gene pool into the

cultivated gene pool should present no special difficulties, except for occasional linkages. For example, the successful transfer of the arcelin, a seed protein conferring resistance against certain seed weevils (Osborn et al., 1988), from the wild common bean gene pool into the cultivated one (Kornegay et al., 1993) is consistent with the absence of linkage between major genes for domestication and the arcelin locus on linkage group D4 (Tables 2 and 3; Nodari et al., 1993; Gepts et al., 1993). The introgression of additional genetic diversity into the cultivated gene pool may acquire added importance in light of genetic bottlenecks induced by domestication in common bean and other crops (Ladizinsky, 1985; Sonnante et al., 1994).

ACKNOWLEDGMENTS

We thank S. Jain, H.A. Orr, K. Rice, and D. St. Clair for their valuable comments on this manuscript.

REFERENCES

Bassett, M.J. 1991. A revised linkage map of common bean. HortScience 26:834–836.

Bliss, F.A. 1981. Common bean. p. 273–284. *In* W.R. Fehr and H.H. Hadley (ed.) Hybridization of crop plants. ASA, Madison, WI.

Bradshaw, H.D., S.M. Gilbert, K.G. Otto, and D.W. Schemske. 1995. Genetic mapping of floral traits associated with reproductive isolation in monkeyflower. Nature 376:762–765.

Bruns, T.D., R. Fogel, T.J. White, and J.D. Palmer. 1989. Accelerated evolution of false-truffle from a mushroom ancestor. Nature 339:140–142.

Coyne, D.P. 1967. Photoperiodism: Inheritance and linkage studies in *Phaseolus vulgaris*. J. Hered. 58:313–314.

Coyne, D.P. 1970. Genetic control of a photoperiod-temperature response for time of flowering in beans (*Phaseolus vulgaris*). Crop Sci. 19:246–248.

Debouck, D.G. 1991. Systematics and morphology. p. 55–118. *In* A. Van Schoonhoven and O. Voysest (ed.) Common beans: Research for crop improvement. CAB, Wallingford, Oxon, UK.

Dobzhansky, T., F.J. Ayala, G.L. Stebbins, and J.W. Valentine. 1977. Evolution. Freeman, San Francisco.

Doebley, J., and A. Stec. 1991. Genetic analysis of the morphological differences between maize and teosinte. Genetics 129:285–295.

Doebley, J., and A. Stec. 1993. Inheritance of the morphological differences between maize and teosinte: Comparison of results for two F_2 populations. Genetics 134:559–570.

Doebley, J., A. Stec, J. Wendel, and M. Edwards. 1990. Genetic and morphological analysis of a maize-teosinte F_2 population: implications for the origin of maize. Proc. Natl. Acad. Sci. USA 87: 9888–9892.

Dorweiler, J., A. Stec, J. Kermicle, and J. Doebley. 1993. *Teosinte glume architecture 1*: a genetic locus controlling a key step in maize evolution. Science 262:233–235.

Edwards, M.D., C.W. Stuber, and J.F. Wendel. 1987. Molecular-marker facilitated investigations of quantitative-trait loci in maize. I. Numbers, genomic distribution and types of gene action. Genetics 116:113–125.

Endler, J.A. 1986. Natural selection in the wild. Princeton University Press, Princeton, NJ.

Fatokun, C.A., D.I. Menancio-Hautea, D. Danesh, and N.D. Young. 1992. Evidence for orthologous seed weight genes in cowpea and mung bean based on RFLP mapping. Genetics 132:841–846.

Fisher, R.A. 1958. The genetical theory of natural selection. Dover, New York.

Gepts, P. 1990. Biochemical evidence bearing on the domestication of *Phaseolus* beans. Econ. Bot. 44(3S):28–38.

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

Gepts, P., and D.G. Debouck. 1991. Origin, domestication, and evolution of the common bean, *Phaseolus vulgaris*. p. 7–53. *In* O. Voysest and A. Van Schoonhoven (ed.) Common beans: Research for crop improvement. CAB, Oxon, UK.

Gepts, P., R. Nodari, R. Tsai, E.M.K. Koinange, V. Llaca, R. Gilbertson, and P. Guzmán. 1993. Linkage mapping in common bean. Annu. Rept. Bean Improv. Coop. 36:xxiv–xxxviii.

Gniffke, P. 1985. Studies of phenological variation in the common bean (*Phaseolus vulgaris* L.) as modulated by mean temperature and photoperiod. PhD diss. Cornell Univ., Ithaca, NY (Diss. Abstr. 46:2698B).

Gottlieb, L.D. 1984. Genetics and morphological evolution in plants. Am. Nat. 123:681–709.

Gu, W.K., N.F. Weeden, D.H. Wallace, and S. Singh. 1993. A DNA marker for *ppd*, a gene conferring insensitivity to photoperiod in common bean. Annu. Rept. Bean Improv. Coop. 36:1–2.

Haldane, J.B.S., and C.H. Waddington. 1931. Inbreeding and linkage. Genetics 16:357–374.

Hammer, K. 1984. The domestication syndrome (In German.) Kulturpflanze 32:11–34.

Harlan, J.R. 1992. Crops and man. ASA, Madison, WI.

Hawkes, J.G. 1983. The diversity of crop plants. Harvard Univ. Press, Cambridge, MA.

Hedrick, P., S. Jain, and L. Holden. 1978. Multilocus systems in evolution. Evol. Biol. 11:101–182.

Hilu, K. 1983. The role of single-gene mutation in the evolution of flowering plants. p. 97–128. *In* M.K. Hecht et al. (ed.) Evolutionary biology. Plenum, New York.

Kaplan, L., and L.N. Kaplan. 1988. *Phaseolus* in archaeology. p. 125–142. *In* P. Gepts (ed.) Genetic resources of *Phaseolus* beans. Kluwer, Dordrecht, the Netherlands.

Knight, R.L. 1948. The role of major genes in the evolution of economic characters. J. Genet. 48:370–387.

Koenig, R., and P. Gepts. 1989. Segregation and linkage of genes for seed proteins, isozymes, and morphological traits in common bean (*Phaseolus vulgaris*). J. Hered. 80:455–459.

Kornegay, J., C. Cardona, and C.E. Posso. 1993. Inheritance of resistance to Mexican bean weevil in common bean, determined by bioassay and biochemical tests. Crop Sci. 33:589–594.

Kosambi, D.D. 1943. The estimation of map distances from recombination values. Ann. Eugenics 12:172–175.

Ladizinsky, G. 1985. Founder effect in crop-plant evolution. Econ. Bot. 39:191–198.

Lai, C., R.F. Lyman, A.D. Long, C.H. Langley, and T.F.C. Mackay. 1994. Naturally occurring variation in bristle number and DNA polymorphisms at the *scabrous* locus of *Drosophila melanogaster*. Science 266:1697–1702.

Lande, R. 1981. The minimum number of genes contributing to quantitative variation between and within populations. Genetics 99:541–553.

Lande, R. 1983. The response to selection on major and minor mutations affecting a metrical trait. Heredity 50:47–65.

Lander, E.S., P. Green, J. Abrahamson, A. Barlow, M. Daly, S.E. Lincoln, and L. Newburg. 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181.

Motto, M., G.P. Soressi, and F. Salamini. 1978. Seed size inheritance in a cross between wild and cultivated common beans (*Phaseolus vulgaris* L.). Genetica 49:31–36.

Nodari, R.O., E.M.K. Koinange, J.D. Kelly, and P. Gepts. 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, R.O., S.M. Tsai, R.L. Gilbertson, and P. Gepts. 1993a. Towards an integrated linkage map of common bean. II. Development of an RFLP-based linkage map. Theor. Appl. Genet. 85: 513–520.

Nodari, R.O., S.M. Tsai, P. Guzmán, R.L. Gilbertson, and P. Gepts. 1993b. Towards an integrated linkage map of common bean. 3. Mapping genetic factors controlling host-bacteria interactions. Genetics 134:341–350.

Norton, J.B. 1915. Inheritance of habit in the common bean. Am. Nat. 49:547–561.

Orr, H.A., and J.A. Coyne. 1992. The genetics of adaptation: a reassessment. Am. Nat. 140:725–742.

Osborn, T.C., D.C. Alexander, S.S.M. Sun, C. Cardona, and F.A. Bliss. 1988. Insecticidal activity and lectin homology of arcelin seed protein. Science 240:207–210.

Paterson, A.H., S.D. Tanksley, and M.E. Sorrells. 1991. DNA markers in plant improvement. Adv. Agron. 46:39–90.

Pernès, J. 1983. The genetics of domestication in cereals. (In French.) La Recherche 14:910–919.

Sax, K. 1923. The association of size differences with seed coat

pattern and pigmentation in *Phaseolus vulgaris*. Genetics 8:552–560.

Schwanitz, F. 1966. The origin of cultivated plants. Harvard University Press, Cambridge, MA.

Singh, S.P. 1991. Bean genetics. p. 199–286. *In* A. van Schoonhoven and O. Voysest (ed.) Common beans: research for crop improvement. C.A.B., Wallingford, Oxon, UK.

Singh, S.P., P. Gepts, and D.G. Debouck. 1991a. Races of common bean (*Phaseolus vulgaris* L., Fabaceae). Econ. Bot. 45:379–396.

Singh, S.P., J.A. Gutiérrez, A. Molina, C. Urrea, and P. Gepts. 1991b. Genetic diversity in cultivated common bean: II. Marker-based analysis of morphological and agronomic traits. Crop Sci. 31:23–29.

Smith, T.B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. Nature 363: 618–620.

Sonnante, G., T. Stockton, R.O. Nodari, V.L. Becerra Velásquez, and P. Gepts. 1994. Evolution of genetic diversity during the domestication of common-bean (*Phaseolus vulgaris* L.). Theor. Appl. Genet. 89:629–635.

Sturmbauer, C., and A. Meyer. 1992. Genetic divergence, speciation and morphological stasis in a lineage of african cichlic fishes. Nature 358:578–581.

Triana, B., M. Iwanaga, H. Rubiano, and M. Andrade. 1993. A study of allogamy in wild *Phaseolus vulgaris*. Annu. Rept. Bean Improv. Coop. 36:21.

Vallejos, C.E., and C.D. Chase. 1991. Extended map for the phaseolin linkage group of *Phaseolus vulgaris* L. Theor. Appl. Genet. 82: 353–357.

Wallace, D.H., K.S. Yourstone, P.N. Masaya, and R.W. Zobel. 1993. Photoperiod gene control over partitioning between reproductive and vegetative growth. Theor. Appl. Genet. 86:6–16.

Wells, W.C., W.H. Isom, and J.G. Waines. 1988. Outcrossing rates of six common bean lines. Crop Sci. 28:177–178.