Origin and Evolution of Common Bean: Past Events and Recent Trends

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Common bean (*Phaseolus vulgaris* L.; 2n = 2x = 22) is grown on all continents except Antarctica. The principal products are dry beans (seeds harvested at complete maturity), shell beans (seeds harvested at physiological maturity, i.e. before the desiccation associated with complete maturity sets in), and green or snap beans (pods harvested before the seed development phase).

According to data published by the Food and Agriculture Organization (FAO) for dry bean production, world production was estimated at 18,639,095 t in 1996 (Food and Agricultural Organization, 1997). This number is an overestimate because FAO does not report data for *Phaseolus* and non-*Phaseolus* species separately. Production in the United States in 1994 was 1,323,922 t (U.S. Department of Agriculture, 1995). Among the major dry bean producers were (in decreasing order) Brazil, Mexico, the United States, Ethiopia, Uganda, Burundi, Tanzania, Turkey, Argentina, Rwanda, Angola, and Colombia (Food and Agricultural Organization, 1997).

World production of snap beans in 1996 was 3,620,187 t. The same caveat about FAO's data applies to snap beans. Among the leading producers were (in decreasing order) Turkey, Spain, Italy, the United States, France, the Netherlands, Belgium, Greece, Chile, and Mexico (Food and Agricultural Organization, 1997).

Dry beans are grown in Latin America in regions where the average mean temperature ranges between 17.5 and 25 °C. Most of the production takes place in areas with mean temperature during the growing season of around 21 °C. This corresponds to an average altitude of 1,250 m in the tropics (Laing et al., 1984). During its evolution under domestication, common bean has experienced a widening of its ecological range, principally by adaptation to warmer temperatures and long-day photoperiods. For example, dry beans are grown in parts of the Central Valley of California, where average temperatures during the growing season reach 27 °C. Dry beans are also grown at latitudes as high as 60 °N, such as in northern Europe.

Wild beans were first described in Argentina (Burkart, 1941; Burkart and Brücher, 1953) and Guatemala (McBryde, 1947). Since then, several additional findings have been made (reviewed in Gepts and Debouck, 1991). In spite of these numerous findings, our knowledge of the distribution of wild beans continues to increase. Recently, Debouck et al. (1993) and Freyre et al. (1996) have provided more detailed descriptions of the habitat and genetic relationships of wild beans in Ecuador–Colombia and Bolivia, respectively.

Based on our current knowledge, wild beans grow in a wide arc stretching from northern Mexico (approx. 30 °N.) to northwestern Argentina (approx. 35 °S.) at altitudes ranging from 500 to 2000 m and rainfall from 500 to 1800 mm. Two taxonomic subdivisions have been described, *P. vulgaris* var. *aborigineus* and *P. vulgaris* var. *mexicanus* (Delgado Salinas, 1985). They can be distinguished at both the morphological and molecular levels (see below).

The very broad distribution of wild beans has raised several questions about the number of domestication events, the levels of genetic diversity in wild and cultivated forms, and the genetic divergence between wild and cultivated beans. More recently, studies of the role of gene flow between wild and cultivated beans have gained prominence, as have studies on patterns of genetic diversity and pathogenicity of related organisms.

In this article, I review some of the salient features recently uncovered in the study of common bean evolution, and I speculate about possible future orientations of bean breeding based on our results.

EVOLUTIONARY EVENTS AND TRENDS

Wild and cultivated gene pools in common bean. The current organization of genetic diversity in the cultivated gene pool of common bean is the result of evolution under both natural conditions (i.e., prior to domestication) and cultivation. Before domestication, wild *P. vulgaris* had already diverged into two major gene pools, each with its characteristic geographic distribution, in Mesoamerica and the Andes (Fig. 1). In addition to these two major gene pools, recently discovered wild bean populations constitute a third, distinct germplasm segment of particular significance for the evolutionary history of common bean (Debouck et al., 1993).

The southern part of Central America, together with Colombia and Venezuela, are not included in the traditional definition of Mesoamerica, which encompasses roughly the southern half of Mexico and the northern half on Central America. Nevertheless, analyses with biochemical and molecular markers (see below) show that wild bean populations in these areas are closely related to those of the actual Mesoamerican area. For lack of a better word to designate the areas mentioned, the word Mesoamerica is now being used. (Some of our earlier publications have used the designation Middle America, which can also be confusing.) Likewise, the Andean gene pool comprises wild bean populations from southern Peru, Bolivia, and Argentina. For the sake of brevity, the word Andean is used to designate this group, with the understanding that they are actually distributed in the countries just mentioned.

These two wild gene pools can be distinguished at the morphological (Gepts and Debouck, 1991) and molecular levels (Becerra Velásquez and Gepts, 1994; Freyre et al., 1996; Gepts et al., 1986; Koenig and Gepts, 1989; Tohme et al., 1996). They are also separated by incomplete reproductive isolation, which leads to F_1 lethality in some, but not all, crosses (Koinange and Gepts, 1992). The existence of this reproductive isolation and the level of divergence at the molecular level suggest that these two gene pools may actually represent two subspecies. Over an evolutionary time scale, *P. vulgaris* could eventually split into two geographically isolated species.

Separate domestications in the Andean and Mesoamerican gene pools have led to two cultivated gene pools, which can also be distinguished at the morphological (Singh et al. 1991b) and molecular (Becerra Velásquez and Gepts, 1994; Gepts et al., 1986; Singh et al., 1991c) levels, and display partial reproductive isolation (F_1 lethality in some crosses) similar to that observed for wild beans (Gepts and Bliss, 1985; Singh and Gutiérrez, 1984). Shii et al. (1980) determined that the F_1 lethality is controlled by two semi-dominant, complementary genes, *Dl-1* and *Dl-2*. Singh and Molina (1996) have recently characterized the genetic basis of crippled trifoliolate leaves. A recessive gene, *lcr*, interacts with either *Dl-1* or *Dl-2* to cause leaf crippling.

With few exceptions, no successful recombinations have occurred between the two major gene pools. A first exception is provided by Chilean landraces (Paredes and Gepts, 1995). In this study, a majority of Chilean landraces showed signs of introgression from the Mesoamerican gene pools, based on phaseolin seed protein and allozyme data. This introgression may have taken place between genotypes of race Chile, from the Andean gene pool, and race Durango, from the

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Mesoamerican gene pool. These two races present similar morphologies and adaptations to drier environments (Singh et al., 1991a). (For a contrasting view on introgression in Chilean landraces, however, see Johns et al., 1997). The second exception is constituted by snap bean cultivars. Although they originated in the Andean gene pool, many varieties are actually intermediate between the two gene pools as shown by RAPD data of Skroch and Nienhuis (1995). This intermediate position may be attributed to recent breeding efforts aimed at introducing disease resistance from the Mesoamerican gene pool into the snap bean background.

The existence of the two major geographic gene pools presents both a challenge and an opportunity for bean breeders. Recombination between these two pools may provide new gene combinations, provided that the reproductive isolation and reduced performance in the progeny can be overcome (see below). Associated organisms, such as pathogens, also exhibit the Andean-Mesoamerican divergence, with Andean strains being generally more pathogenic to Andean beans and vice versa for Mesoamerican strains (Guzmán et al., 1995). Hence, resistance to pathogens in the Andean group can be identified in the Mesoamerican gene pool and vice versa (Young and Kelly, 1996).

The evolution of genetic diversity in common bean. Many crops have been marked by a progressive reduction in genetic diversity at the molecular level (Doebley, 1989, 1992; Ladizinsky, 1985), and common bean is no exception. Sonnante et al. (1994) used M13 fingerprinting to assess the diversity in two evolutionary lineages. The Andean lineage included wild beans from the southern Andes, landraces from the same region, and kidney bean cultivars from the United States, the latter having originated from Andean domesticates (Brown et al., 1982; Gepts et al., 1986). The Mesoamerican lineage included wild beans from Mexico, Central America, and Colombia, landraces from the same region, and pink-seeded cultivars from the United States, the latter being of Mesoamerican origin (Brown et al., 1982; Gepts et al., 1986).

Both lineages showed a marked reduction in genetic diversity, not only between the landraces and their respective U.S. counterparts, but also between the ancestral, wild materials and their landrace descendants (Fig. 2). Reductions in genetic diversity between landraces and U.S. cultivars result from the effects of long-range dispersal of cultivars from their centers of origin to, among other countries, the United States (Gepts and Bliss, 1988; Gepts et al. 1988) and of plant breeding. Reductions in genetic diversity between wild ancestors and landraces result from selection during and after domestication. Dispersal within the regions of domestication (in the Americas) led to further reductions in diversity because of genetic drift and selection for adaptation to new environments and consumer preferences. In addition, continued cultivation under subsistence conditions may have led to multiple rounds of genetic drift or extinction because of crop failures.

The results of Sonnante et al. (1994) confirm the results of McClean et al. (1993), who showed, based on pedigree analysis, that most bean cultivars have resulted from crosses between closely related cultivars. Table 1 shows the percentage of genes shared by cultivars belonging to three cultivated races (Durango, Mesoamerica, and Nueva Granada) with four "founding" (i.e., now obsolete) cultivars (Pinto UI 111 of race Durango, Michelite of race Mesoamerica, and Dark Red Kidney and California Light Red Kidney, both of race Nueva Granada). Ninety-three percent of cultivars belonging to race Durango shared genes with Pinto UI 111, but only 17% and 11% of these cultivars shared genes with members of races Mesoamerica and Nueva Granada, respectively. The lower levels of gene sharing for the two kidney cultivars can be attributed to more modest breeding activities in this commercial class. In spite of the high level of gene sharing within races, bean breeders have used a wider range of sources of diversity on occasion, especially more recently (e.g., Burke et al., 1995; Coyne and Schuster, 1969; Kelly et al., 1990; Myers et al., 1991; Singh et al., 1993).

The limited diversity in the commercial bean classes from the United States has serious consequences for bean breeding, and suggests that an important goal of bean breeding programs should be to broaden the cultivated gene pool, particularly the genetic diversity of specific commercial classes.

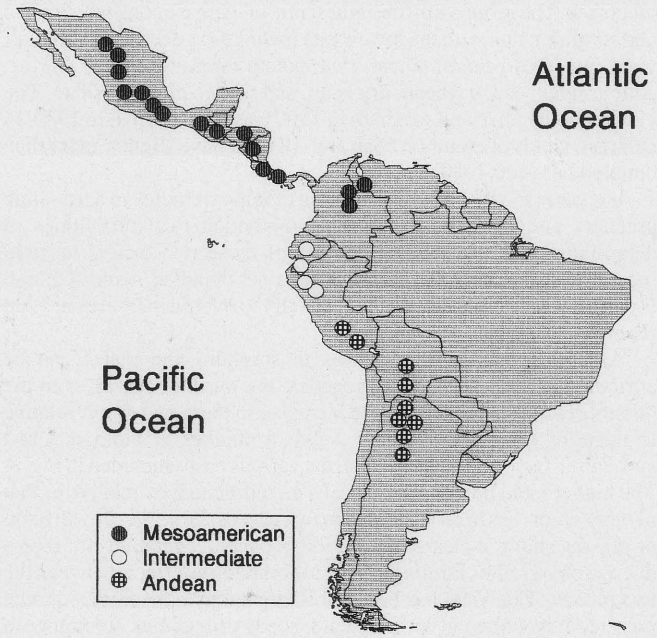

Fig. 1. Distribution of wild *Phaseolus vulgaris* in Latin America.

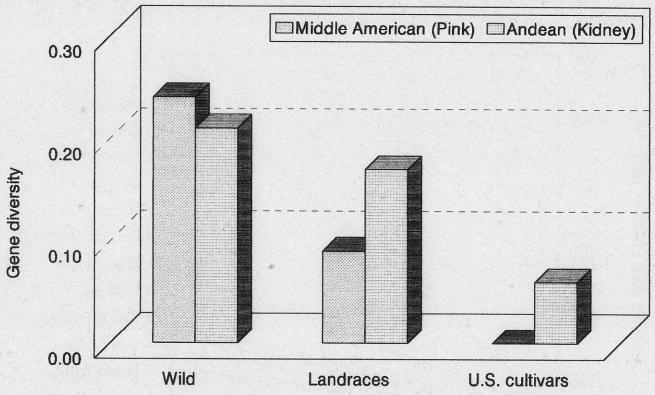

Fig. 2. Gradual reduction in genetic diversity during and after domestication in two common bean evolutionary lineages (modified from Sonnante et al., 1994).

Table 1. Proportion of genes shared among U.S. bean cultivars (modified from McClean et al., 1993).

"Founding" cultivar (race)	Cultivated race (number of cultivars)		
	Durango (n = 71)	Mesoamerica (n = 40)	Nueva Granada (n = 19)
Pinto UI 111 (Durango)	93	17	11
Michelite (Mesoamerica)	7	55	0
Dark Red Kidney (Nueva Granada)	18	0	37
California Light Red Kidney (Nueva Granada)	0	0	26

RECENT TRENDS

Crop evolution not only consists of events in the remote past, such as domestication and dissemination from centers of domestication, but, in a broader sense, also includes recent events, those in the last century in particular. In this respect, U.S. Department of Agriculture production data for several field crops were compared for the period 1930–1990 (except for soybean where the period 1935–1990 was covered). For each crop, a linear regression line of yield data at 5-year intervals was plotted against time. Yield in 1930 was set at 100 to allow comparison among yield trends of all crops. A wide disparity in yield trends was observed among crops (Fig. 3). Two major groups can be

identified. The group with the highest rate of increase consists of maize and sorghum; that with the lowest rate includes (in decreasing order of yield increase) peanut, wheat, rice, potato (spring-planted), barley, cotton, snap bean, soybean, dry bean, and winter-planted potato. The yield of both maize and sorghum in 1990 was 11 times that in 1930. In contrast, yields of common bean and soybean have slightly more than doubled between 1930 and 1990.

Increases in yield can be attributed to improvements in agronomic practices and cultivars. In spite of methodological difficulties in determining the relative contribution of these two factors to yield increases and the rather broad range of values obtained, a rule of thumb is that they have contributed about equally to overall increases in yield (Fehr, 1984).

Assuming that yield increases in sorghum and maize can be attributed at least partially to genetics, the question arises as to the possible causes of the large yield increases in these two crops, relative to those of other crops. Table 2 lists a number of biological and agronomic factors that distinguish the various crops included in Fig. 3. The higher yield potential of cereals, including maize, relative to that of other crops, has been attributed to two causes. First, the growth habit of grasses shows a clearer separation between vegetative and reproductive phases, thus limiting potential competitive effects between the two phases. This view has been substantiated by a theoretical model presented by Cohen (1966). Second, seeds of legumes are higher in proteins and, in some cases, lipids, both of which are metabolically more costly to synthesize than carbohydrates, the main component of cereal grains. In addition, nitrogen fixation also carries a metabolic cost. The presence of cereals such as wheat and barley in the group with lower increases in yield suggests, however, that growth habit and metabolism may not be the only factors explaining the advantage of sorghum and maize.

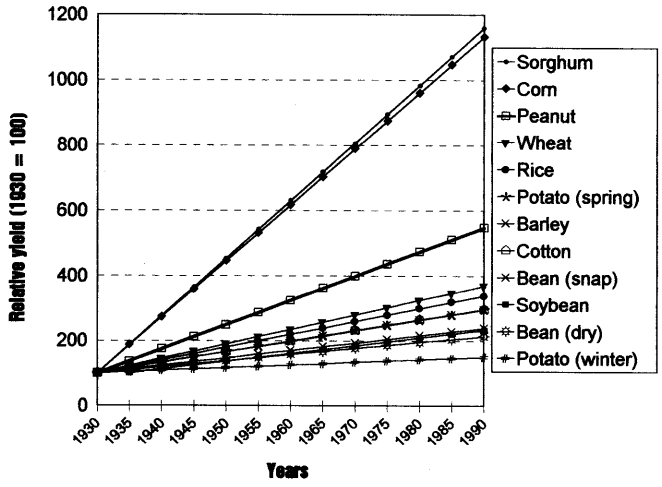

Fig. 3. Relative increase in average U.S. yield of selected field crops in the 1930–90 period (U.S. Dept. of Agriculture Agricultural Statistics). Crops in the legend are listed in decreasing order of relative yield increases.

Nor does ploidy seem to provide a satisfactory explanation. Although both maize and sorghum are diploid, maize is a diploidized ancient tetraploid (Ahn and Tanksley, 1993). Conversely, at the lower end, soybean is also believed to be a diploidized tetraploid (Shoemaker et al., 1992). Polyploidization is thought to improve the accumulation of intralocus interactions favoring hybrid vigor (e.g., in potato: Ortiz et al., 1991; Watanabe and Peloquin, 1991; Werner and Peloquin, 1991). On the other hand, the added complexity resulting from the presence of multiple genomes may make breeding more difficult, particularly in attempts to identify rare, superior progenies. In this regard, the size of the breeding force (meant to include individuals involved not only in varietal release, but also in breeding studies and germplasm enhancement) appears to be unrelated to overall progress in yield; witness the ten-fold difference in staffing between maize and sorghum (Frey, 1996; Table 2).

Two additional factors that appear to be more promising for explaining the divergence in yield trends are the level of molecular diversity and the type of cultivar used in the various crops. Analyses of genetic diversity with molecular markers have been conducted on a number of crops. Whereas they cannot always be compared directly because of differences in the markers used, sample sizes, and methods of statistical analysis, they do shed some light on levels of molecular diversity within major crop species.

Maize is highly polymorphic at the molecular level (Helentjaris et al., 1985). The major heterotic combination used in the development of U.S. hybrid cultivars (Smith, 1995) involves two quite distinct groups (Lancaster Sure Crop and Reid's Yellow Dent derivatives) (Doebley et al., 1988). Sorghum diversity at the molecular level is high, especially among the five races. There is also evidence for gene flow between domesticated and wild populations in Africa (Aldrich and Doebley, 1992; Aldrich et al., 1992; Deu et al., 1994). In addition, an active conversion program has attempted to introduce more genetic diversity into the U.S. sorghum gene pool (Maunder, 1992). Over 1500 lines of sorghum have thus been converted since 1963 (Smith, 1995).

Among the other crops, genetic diversity levels are generally low for a variety of reasons. The number of initial introductions into the United States has been limited (e.g., soybean: Keim et al., 1992; Maughan et al., 1995, 1996). The material introduced into the United States may have been fairly diverse, but most breeding has involved closely related materials until recently (e.g., common bean: Nodari et al., 1992). The material introduced was already genetically depauperate because polyploidization had caused a genetic bottleneck, as in the case of peanut (Halward et al., 1991, 1992; Kochert et al., 1991), wheat (Plaschke et al., 1995), and cotton (Brubaker and Wendel, 1994; Wendel et al., 1992).

Some crops with low rates of increase in yield may have higher than expected diversity. The existence of 2n gametes in potato provides a

Table 2. Comparison of some biological, agronomic, and research features of selected field crops.

Crop	Yield trend[z] Annualized compound rate	Yield trend[z] Ratio 1990/1930	Family	Ploidy	SY[y] devoted to breeding	Molecular diversity	Cultivar type
Sorghum	4.1	11.6	Poaceae	Diploid	55	High	Hybrid
Maize	4.1	11.3	Poaceae	Diploid (diploidized tetraploid)	545	High	Hybrid
Peanut	2.9	5.5	Fabaceae	Allotetraploid	20	Low	Pure line
Wheat	2.1	3.7	Poaceae	Allohexaploid	130	Low	Pure line
Rice	2.1	3.4	Poaceae	Diploid	42	Medium	Pure line (hybrid)
Potato (spring)	1.9	3.1	Solanaceae	Autotetraploid	50[x]	Medium	Clone
Barley	1.8	3.0	Poaceae	Diploid	32	Medium	Pure line
Cotton	1.8	3.0	Malvaceae	Allotetraploid	134	Low	Pure line
Common bean (snap)	1.5	2.5	Fabaceae	Diploid	10	Medium	Pure line
Soybean	1.4	2.3	Fabaceae	Diploid (diploidized tetraploid)	156	Low	Pure line
Common bean (dry)	1.3	2.1	Fabaceae	Diploid	24	Medium	Pure line
Potato (winter)	0.7	1.5	Solanaceae	Autotetraploid	50[x]	Medium	Clone

[z]U.S. Dept. of Agriculture Agricultural Statistics for 1930–90 (1935–90 for soybean).
[y]SY, scientist year; data of Frey (1996): includes breeding research, germplasm enhancement, and cultivar development.
[x]Potato SY are grouped for winter and spring-planted crops.

way for additional diversity to be introduced from diploid to cultivated, tetraploid potatoes (Barone et al., 1995; Watanabe and Peloquin, 1991; Werner and Peloquin, 1991). Rice and common bean show a similar organization of genetic diversity in two geographic gene pools (indica vs. japonica; Mesoamerican vs. Andean). In both crops, individuals from the two gene pools can be crossed and traits transferred, although with some difficulty (rice: Mackill et al., 1996; Second, 1982; Yu and Nguyen, 1994; for beans see below). The gene pool of cultivated barley is less diverse than that of wild barley (Clegg et al., 1984; Saghai-Maroof et al., 1984, 1995), although Jana and Pietrzak (1988) reported no decrease in diversity between wild and landrace barley populations in the center of origin.

A possible factor accounting for the higher yield increases observed in maize and sorghum may be the higher level of genetic diversity in the respective U.S. germplasm. An additional difference appears to be the extent to which heterosis has been exploited. The standard cultivars in maize (since before World War II) and sorghum (since the 1950s) are hybrids. Crops of the low-yield-increase group consisted of either pure line or clonal cultivars. The only exception is rice, for which hybrid cultivars have been developed in China (Zhang et al., 1995). Because this development is fairly recent, it has not yet had a major effect on overall rice yields in China.

What are the prospects of increasing diversity and developing hybrid cultivars in common bean?

Broadening the cultivated gene pool in common bean. The magnitude of the divergence between the Andean and Mesoamerican gene pools has implications for bean breeding that have not yet been fully explored. Despite their partial reproductive isolation, the two gene pools still belong to the same biological species. In most crosses, viable and fertile progeny can be obtained, and, therefore, genes can be transferred between the two pools. This has been achieved for individual genes, such as the *I* gene for resistance to Bean Common Mosaic Virus and the *Co-2* gene for resistance to anthracnose [caused by *Colletotrichum lindemuthianum* (Sacc. & Magnus) Lams.-Scrib.]. These two genes are of Mesoamerican origin (Johnson et al., 1997; Mastenbroek, 1960), yet they have been introduced into numerous cultivars of the Andean gene pool.

The transfer of quantitative traits between the Mesoamerican and Andean gene pools appears to be more problematic. Attempts by breeders to recombine traits between the two gene pools, such as the large seed size of the Andean gene pool with the yield potential of the Mesoamerican gene pool, have generally failed (e.g., Nienhuis and Singh, 1986; Singh et al., 1989) although there are notable exceptions (Beaver and Kelly, 1994; F. Bliss, pers. comm). The average performance of the progeny from inter-gene pool crosses is usually below that of the parents (Singh et al., 1989; Welsh et al., 1995). The cause of this apparent outbreeding depression is not yet known, although it is worth discussing because of the potential benefits to be derived from these crosses.

Divergence between the two gene pools may have led to different, independent suites of genes controlling overall performance (e.g., yield, phenology, etc.) in the Mesoamerican and Andean gene pools. Hybridization between the two pools breaks up these suites, which are then difficult to reconstitute in the progeny because of recombination and lack of adaptation. Evidence that the two gene pools affect yield in different ways is recent. González et al. (1995) showed that photosynthetic characteristics of Mesoamerican and Andean beans (wild or cultivated) are quite distinct. As a group, Mesoamerican accessions (both wild and landraces) had higher specific leaf mass, more chlorophyll, a higher CO_2 exchange rate (CER), higher stomatal conductance, a higher stomatal density, and lower N content than did Andean accessions. The Andean landraces had the lowest CER, and the Mesoamerican landraces had the highest. Sexton et al. (1994) observed higher partitioning, seed growth rate, and yield at warmer sites (but not at cooler sites) in Mesoamerican than in Andean varieties. This differential adaptation was attributed to the greater ability of Mesoamerican cultivars to accumulate nitrogen. Welsh et al. (1995) reported a positive association between days to maturity and biomass, pod number, and seed yield, but a negative association between days to maturity and 100-seed mass and harvest index in the progenies of three interracial and one intraracial cross. According to the authors, these correlations suggested that Andean, large-seeded beans achieve higher yield by maturing earlier and by producing fewer pods with larger seeds. Mesoamerican beans, in contrast, achieve higher yield by maturing later, but producing more pods and a higher biomass.

The exceptions just mentioned may be illustrative of the problems involved in recombining the two gene pools, as well as approaches to solving them. Beaver and Kelly (1994) wished to recombine the medium-large seed type characteristic of Andean genotypes with the indeterminate growth habit of Mesoamerican genotypes. This change in growth habit is expected to increase the yield potential and stability of Andean, large-seeded genotypes (Beaver et al., 1985; Kelly et al., 1987). Recurrent selection with both early-generation (F_2) and late-generation (F_5) testing was attempted to recombine the two traits. Both selection methods were effective in obtaining the desired recombinants, although late-generation testing identified a larger proportion of higher-yielding, indeterminate populations. The most productive populations yielded as much as 30% more than did the determinate parent.

The success of Beaver and Kelly (1994) may be attributed to the need to recombine a relatively large number of genes distributed over most or all of the bean chromosomes. Seed mass quantiative trait loci (QTLs) have so far been identified on linkage groups D1, D3, D4, D7 (2 different ones), and D11 (Johnson et al., 1996; Koinange et al., 1996). Seed color loci have been identified so far on linkage groups D2 (*B*), D6 (*V*), and D7 (*P*). Other loci show independent inheritance from loci *B*, *V*, and *P*, and should therefore be located in unlinked regions, on the same or other linkage groups (Gepts et al., 1993). Growth habit factors have been located on D1 for determinacy (*fin*), D1 (*fin* and another factor) and D8 for number of nodes on the main stem, and D1 (different locus from the preceding ones) for internode length (Koinange et al., 1996). Although no QTLs for yield have been mapped in beans, they are likely to be widely distributed in the genome, given the quantitative nature of the traits. In attempting to obtain recombinants for these complex traits, opportunities for recombination must be provided, such as intermating during cycles of recurrent selection, similar to the breeding method used by Beaver and Kelly (1994). Traditional genealogical or pedigree selection, which relies on selfing in a predominantly self-pollinated species such as common bean, would be insufficient in this respect unless extremely large, unwieldy population sizes were used to identify the rare recombinant.

The cross 'Sanilac' (Michigan cultivar of Mesoamerican origin) x Cargamanto (Colombian landrace of Andean origin) was made by F. Bliss (pers. comm.) to transfer high levels of nitrogen fixation and yield from the male to the female parent. The nitrogen fixation capability was transferred successfully into the adapted background of 'Sanilac' using the inbred backcross procedure (Wehrhahn and Allard, 1965). This procedure may be particularly appropriate when introducing a trait from an unadapted genetic background. Traits may be identified in the adapted progeny that would normally not be expressed because of the lack of adaptation of the donor parent. Note that Beaver and Kelly (1994) included local parents among the progenitors of their recurrent selection experiment, thus ensuring that improved traits or combinations thereof could be obtained against an adapted genetic background. Because the inbred backcross transfers relatively large segments of genome, further intermating will be necessary to obtain full expression of the trait in the genetic background of the recipient genotype, as shown by St. Clair and Bliss (1991) for nitrogen fixation in common bean.

Hence, the transfer of genetically complex traits across the gene pool divide requires attention to two major factors: 1) recovery of adapted progenies; and 2) sufficient opportunities for recombination among the traits of interest. Mating and selection designs will have to be devised accordingly.

A largely unexplored strategy is to exploit diversity from wild common bean. The extreme phenotypic distinctness of wild common bean, compared with cultivated common bean, and their lack of adaptation to long-day environments, make them unlikely sources of additional diversity. Their potential as a source of genetic diversity can be illustrated by the arcelin seed protein, which is responsible for resistance of common bean to the weevil *Zabrotes subfasciatus* (Boheman). Several expressed allelic variants of the arcelin locus (*Arl*) have been identified among wild common bean populations from

various places in Mexico. No expressed allelic variant has been identified among cultivated common bean (Osborn et al., 1988), vividly attesting to the genetic bottleneck induced by domestication in common bean. The *Arl* gene has been transferred successfully into a cultivated background (Kornegay et al., 1993a). Singh et al. (1995) identified a number of crosses between wild beans and cultivar 'ICA-Pijao' that had F_2 and F_3 yields comparable to that of the cultivated parent, suggesting that lines can be extracted from these segregating populations with yields significantly higher than that of 'ICA-Pijao'.

Many of the concerns raised about the introgression between the Mesoamerican and Andean cultivated gene pools are also valid for the introgression between the wild and cultivated gene pools. There are some additional concerns, however, resulting from the two-fold lack of adaptation of wild beans and evaluation of their breeding potential. Wild beans are clearly not adapted to temperate environments, principally because of their photoperiod × temperature requirements, and to field cultivation, given the lack of domestication syndrome traits (Koinange et al., 1996).

Sensitivity to photoperiod in common bean is controlled by two genes, *Ppd* and *Hr*, both of which have been tagged and mapped (Kornegay et al., 1993b; Gu et al., 1995; Koinange et al., 1996). The inheritance of sensitivity to the temperature interaction with photoperiod has not yet been determined. Among the domestication syndrome traits, growth habit stands out, because most wild beans sprawl or climb. Among growth habit genes, the *fin* gene coding for determinacy plays an important role not only in its own right, but also because it is linked in coupling to the allele for photoperiod insensitivity at the *Ppd* locus (Coyne, 1967; Koinange et al., 1996) and may also be linked to other genes affecting the degree of climbing ability.

Selection of determinacy and insensitivity to photoperiod, either directly by phenotypic means or indirectly by molecular markers, could accelerate introgression from wild beans into an adapted genetic background. Actually, these two traits may be prime targets of a germplasm conversion program, if such a program were to be established to broaden the genetic basis of cultivated common bean.

Development of hybrid bean cultivars. Bannerot (1989) has proposed that hybrid cultivars could be developed in common bean. Some conditions have been met toward this development while several others remain to be satisfied. Hybrids appear to be most promising in snap bean cultivars. Snap beans have a higher commercial value, and therefore the added cost of hybrid seed may be integrated more easily into the cost structure of the crop. In addition, improving snap beans only involves one major yield component (number of pods), thus decreasing potential problems with yield component compensation observed in dry beans (Adams, 1967).

Various researchers have investigated the magnitude of heterosis in common bean. As reviewed by Lestienne (1986), yield averages above the best parent ranged from 20% to 170%. In particular, Nienhuis and Singh (1986) observed average heterotic effects of 30% above the best parent, with the best crosses yielding up to 100% above the best parent. Heterosis is, therefore, present and its magnitude seems to warrant further investigations.

The single most important problem from an economic standpoint is the production of hybrid seeds. These have to be produced both abundantly and reliably. Difficulties in achieving this goal should not be underestimated, as common bean is a predominantly self-pollinated species. In most environments, levels of outcrossing are very low (well below 5%) (Brunner and Beaver, 1989; Park et al., 1996). Higher levels of outcrossing have been noted, however, by Wells et al. (1988) and Ibarra-Pérez et al. (1996). The factors involved in these differences can be surmised but their precise determination will require additional information. Bannerot (1989) reported that selection conducted in a *P. vulgaris* x *P. coccineus* progeny increased outcrossing rates from 3% to 20%–30%.

Differences in insect pollinator populations can account for part of the contrasting outcrossing rates. This suggests that additional studies should be conducted on the attractiveness of bean flowers to pollinators and its genetic control. In alfalfa, Henning et al. (1992) identified both attractant and repellent compounds among floral volatiles. Breeding for increased attractant levels could assure higher frequencies of pollinator visits.

To ensure high levels of fertilization, especially in snap beans, by the limited number of pollen grains transported and deposited by insect pollinators, pollen of male parents should be vigorous, an attribute that is under genetic control (e.g., Hormaza and Herrero, 1994; Robert et al., 1991; Rosellini et al., 1994; Sari-Gorla et al., 1992). The inheritance of pollen tube growth vigor remains to be determined. Nevertheless, one can speculate that in the experiments conducted by Wells et al. (1988) the high outcrossing levels shown by the white-seeded female parent, FM53, can be attributed in part to the relatively low vigor of its pollen or, conversely, to the high vigor of the black-seeded male parents used.

In order to guarantee a high level of hybridity, seed production systems will probably require cytoplasmic sterility. Five sterile cytoplasms have been identified in common bean, all of which are functionally similar, i.e., they are maintained with the same set of maintainer lines, although their mtDNA show different restriction digestion patterns after digestion with *Sal*I (Bannerot, 1990; Hervieu et al., 1994). Maintainer lines are rare in common bean but they represent a fairly diverse group, as they include contrasting growth habits, seed colors, and dry vs. snap beans (Bannerot, 1989). Dominant restoration is also rare. However, Bannerot (1989) was able to identify some genotypes with high levels of restoration (above 80 % stainability) and lack of tetrad aggregation.

Finally, restoration of an acceptable phenotype in the F_1 generation is important to satisfy preferences of farmers and consumers. In addition to growth habit and phenology, pod and seed type are important considerations. Achieving such an acceptable phenotype will require additional studies on the genetic control of the various traits mentioned and the interactions among them. These studies will undoubtedly be helped by molecular marker technology, both to elucidate the genetic control and to assist in marker-directed selection during the development of the inbred parents.

In summary, molecular marker analyses have greatly helped us in clarifying genetic relationships and levels of genetic diversity in common bean germplasm. In turn, this information is being utilized by bean breeders in devising new strategies to obtain improved bean cultivars with higher yields and broader disease and pest resistance.

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