Prebreeding in Common Bean and Use of Genetic Diversity from Wild Germplasm

J.A. Acosta-Gallegos, Bean Program, CEBAJ-INIFAP, A.P. 310 Celaya, Gto., 38000 Mexico; J.D. Kelly, Crop and Soil Sciences Dep., Michigan State University, East Lansing, MI 48824; P. Gepts, Dep. of Plant Sciences, MS1, Section of Crop and Ecosystem Sciences, University of California, Davis, CA 95616-8780. Received 7 Apr. 2007.
*Corresponding author (jamk@prodigy.net.mx).

Published in Crop Sci. 47(S3) S44–S59 (2007).
doi: 10.2135/cropsci2007.04.0008IPBS
© Crop Science Society of America
677 S. Segoe Rd., Madison, WI 53711 USA
Common bean (*Phaseolus vulgaris* L.) is the most widely consumed grain legume in the world. This cultigen was domesticated from wild *P. vulgaris*, an indeterminate viny plant, distributed from Mexico to Argentina in midaltitude neotropical and subtropical regions. To colonize such diverse ecological niches, the species possesses many adaptation traits and a wealth of genetic diversity. However, breeding programs are limited by the under-utilization of the available genetic diversity because of the necessity of prebreeding exotic material. Due to partial reproductive isolation between the domesticated Andean and Mesoamerican gene pools, hybridizations between wild and domesticated types of *P. vulgaris* from the same gene pool offer greater potential to enhance the variation in the crop. Evaluations of wild *P. vulgaris* accessions have shown resistance to insects and diseases and higher N, Fe, and Ca content in seeds, which will ultimately contribute to improvements in nutritional quality and yield. Recurrent and inbred backcross methods are being used for the transfer of both qualitative and quantitative traits from wild into domesticated forms of *P. vulgaris*; specific data on yield and 100-seed weight are presented. The prebreeding efforts will be enhanced by (i) information on gene pool origins, domestication syndrome traits, molecular diversity, and mapping data of the wild forms; (ii) indirect screening for biotic and abiotic stresses; and (iii) marker-assisted selection.
The common bean (*Phaseolus vulgaris* L.) is the most widely distributed and consumed legume species of the genus *Phaseolus*, a genus comprised of some 70 species (Freytag and Debouck, 2002) that has contributed to human welfare with five cultivars domesticated in pre-Columbian times: the common bean (*P. vulgaris*), the year bean (*P. dumosus* Macf.), the runner bean (*P. coccineus* L.), the tepary bean (*P. acutifolius A. Gray*), and the lima bean (*P. lunatus* L.). The genus originated in the American continent and a large number of its species is found in Mesoamerica (Delgado-Salinas, 1985; Freytag and Debouck, 2002). Among the five domesticated species, *P. vulgaris* accounts for more than 90% of the cultivated crop worldwide and is by far the most widely consumed grain legume in the world (Singh, 2001). Common bean is a major food for rural and urban populations in Latin America and eastern Africa and is steadily gaining momentum in developed countries where the population is concerned with healthier diets. In Mexico, common bean constitutes the main source of vegetable protein, minerals (Ca, Cu, Fe, Mg, Mn, and Zn) and vitamins (folate). Its balance of essential amino acids in seeds is complementary to that in grains of cereals such as maize (*Zea mays* L.). It has been estimated that maize and beans should be consumed in a 2:1 ratio to achieve an optimum amino acid balance in the diet (Bressani, 1983). Recently, some bean seed properties have been shown to contribute positively to major health issues, such as the control of type II diabetes. In this regard, positive characteristics of bean seeds include the presence of essential minerals, such as Fe and Zn, and high fiber and polyphenolic content. Typically, consumption of bean seeds leads to lower glycemic and cholesterolomic indices and lower incidence of certain types of cancer (Andersen et al. 1984; Hangen and Bennink, 2003).

The common bean cultivar was domesticated from wild *P. vulgaris*, a viny plant with indeterminate growth from the midaltitude neotropics and subtropics that has a wide distribution range from northern Mexico to northwestern Argentina (Gepts and Debouck, 1991). In its range of distribution, *P. vulgaris* colonizes many and varied ecological niches, usually in disturbed habitats with secondary vegetation (Delgado-Salinas et al., 1988). The intraspecific genealogy and geographical origins of the common bean are now well understood (Gepts, 1998; Chacón et al., 2005); as is the phylogeny of the genus *Phaseolus* (Delgado-Salinas et al., 1999) and the centers of primary diversification in America (Debouck, 1986; Kram et al., 1995; Chacón et al., 2005). In Mexico, wild *P. vulgaris* is found from the northern state of Chihuahua to the southern state of Chiapas, along the western Sierra Madre, and in the Neovolcanic Axis of central Mexico. In its range of distribution, *P. vulgaris* grows in areas as diverse as the semiarid region of the state of Durango, which receives less than 350 mm of precipitation annually, and the subtropical region of Chiapas, with patterns of rainfall that exceed 2000 mm per annum. Wild *P. vulgaris* populations are mainly found in Mexico at altitudes ranging from 800 to 2200 masl (Miranda-Colin, 1967; Gentry, 1969; Delgado-Salinas et al., 1988; Torro et al., 1990). Adaptation to such different niches suggests that the wild form of *P. vulgaris* possesses many advantageous traits for adaptation and contains a wealth of genetic diversity.

Since wild progenitors are the foundation of landraces and landraces are the foundation of modern cultivars, it is important that breeders and conservationists define the sites of domestication (Chacón et al., 2005). Multiple domestications in time and space have been one of the key determinants in shaping the diversity observed in modern crops. In regard to the common bean, at least two domestication events occurred in the Americas (Gepts et al., 1986). In the case of Mesoamerica, Gepts (1988b) suggested an area bordering the states of Jalisco and Guanajuato as the area where Mesoamerican beans were domesticated. This suggestion was based on the similarity in phaseolin, a reserve protein found in the seed, between wild and domesticated beans from the area. Long before, this region has been recognized as an area of abundant genetic variation in both wild and landrace populations (Miranda-Colin, 1967; Gentry, 1969). Gepts et al. (1986), with phaseolin, and Chacón et al. (2005), with chloroplast sequences, have shown that domestication led to a reduction in genetic diversity. This suggests a founder effect probably due to a strong selection pressure practiced by humans during domestication and the fact that only few wild bean populations were included in the process. Therefore, a large amount of genetic variation is still untapped in the wild form of *P. vulgaris*, whose variation could be used to improve and enhance the diversity in the domesticated form. Chacón et al. (2005) also suggested that there were actually multiple domestications in the Mesoamerican gene pool based on the existence of four major cpDNA haplotypes. However, their data are inconsistent with phaseolin seed protein (Gepts et al., 1986; Gepts, 1988a) and amplified fragment length polymorphism (AFLP) data (Papa and Gepts, 2003). Instead, their data could be explained by postdomestication capture of chloroplast DNA caused by gene flow from domesticated to wild-types (Papa et al., 2005).

**Genetic Diversity in P. vulgaris**

*Phaseolus vulgaris* is considered a noncentric crop with at least two centers of domestication (Harlan, 1971) and

**Abbreviations:** AFLP, amplified fragment length polymorphism; APA, arcelin, phytohemagglutinin, and α-amylase inhibitors; BC, backcross; IB, inbred backcross; QTL, quantitative trait loci; RI, recombinant inbred; SCAR, sequence characterized amplified region; STS, sequence tagged site.
a wide geographical distribution of its wild relatives in Middle and South America. The wild and domesticated forms of common bean display higher variation in Mesoamerica as compared to Andean populations (Gepts et al., 1988; Chacón et al., 2005). Most of the variation originated probably during the process of dispersal from the ancestral form still extant in an area encompassing southern Ecuador and northern Peru. Support for this assertion is based on DNA sequence at the Phaseolin locus (Kami et al., 1995). Previously, an area comprising the south of Mexico and Guatemala was considered the area where common bean had originated, based on observation of the high diversity present in wild and landrace populations from that region (Miranda-Colin, 1967; Gentry, 1969) (Table 1).

Genetic variation is essential for the development of improved cultivars. Knowledge, access, and use of the available diversity in domesticated and wild relatives are essential for broadening the genetic base of cultivars to sustain improvement (Singh, 2001). The process of domestication inherently reduces genetic variation (Ladizinsky, 1985) and the intensive modern breeding practiced in industrial countries has further diminished their available variability.

In the case of domesticated *P. vulgaris*, two large gene pools that pre-existed domestications are recognized in Mesoamerica and the Andes, respectively (Koinange and Gepts, 1992). Within the two domesticated gene pools, several ecogeographic races have been identified within each gene pool based on plant morphology, geographic and ecological distribution, and isozyme and molecular information (Table 1; Singh et al., 1991a, 1991b, 1991c). Within the Mesoamerican pool, races Mesoamerica (tropical black and red Central American beans; carioca beans in Brazil) and Durango (pinto, bayos, small red, and great northern beans) are probably the most widely grown. Climbers from the Jalisco and Guatemala races have received little attention from breeders and constitute an untapped resource within the domesticated form of the species. Beebe et al. (2000) indicated that the races Durango and Mesoamerica could be further subdivided in two subraces, and a distinct race was separated from the Jalisco race, namely race Guatemala that includes the climbers found in the highlands of Guatemala and Chiapas, Mexico (Chacón et al., 2005).

More recently, several investigations along the distribution area of wild *P. vulgaris* have shown the existence of gene flow between wild and domesticated beans in spite of the fact that common bean is a predominantly self-pollinated species (Acosta-Gallegos et al., 1994; Beebe et al., 1997; Papa and Gepts, 2003; Papa et al., 2005; Payró de la Cruz et al., 2005; Zizumbo-Villarreal et al., 2005). These investigations have shown that gene flow is widespread and has altered the distribution of genetic diversity among wild and domesticated populations. Gene flow takes place predominantly from domesticated to wild-types (Papa and Gepts, 2003) over short distances (<100m; Payró de la Cruz et al., 2005). As a consequence of this gene flow, genetic diversity in wild populations tends to be displaced by that in cultivars, potentially leading to a reduction in genetic diversity (Papa et al., 2005).

Since the 1980s, intergene pool reproductive barriers have been described that cause difficulties in crossing between gene pools; that is, reduced viability and fertility (Singh and Gutierrez, 1984; Gepts and Bliss, 1985; Koinange and Gepts, 1992), a situation that suggests that the gene pools have reached the subspecies level (Becerra-Velásquez and Gepts, 1994). In contrast, crosses between wild and domesticated common bean within each gene pool are compatible (Koinange and Gepts, 1992). The crossing of distinct cultivars from different gene pools is pursued to widen the reduced variation observed in the domesticated form (Voysest et al., 1994; Singh, 2001), particularly in those cases where breeders have used a limited

---

**Table 1. Gene pools, races, and popular cultivars within each domesticated race of *Phaseolus vulgaris***

<table>
<thead>
<tr>
<th>Gene pool and race</th>
<th>Phaseolin†</th>
<th>cpDNA haplotype‡</th>
<th>Characteristic cultivars</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andean</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nueva Granada</td>
<td>T</td>
<td>C</td>
<td>Jalo EEP558, California Dark Red Kidney</td>
</tr>
<tr>
<td>Chile</td>
<td>C, H</td>
<td>C</td>
<td>Coscorrón, Blanco Español, Frutilla</td>
</tr>
<tr>
<td>Peru</td>
<td>T, C, H</td>
<td>C, K</td>
<td>Cargamanto, Bolón Bayo, Núňa Coneja</td>
</tr>
<tr>
<td>Mesoamerican</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesoamerica</td>
<td>S, Sb, B</td>
<td>K, L, I, J</td>
<td>Jamapa, ICA Pijao, Carioca, Black Turtle Soup, Vista, Tío Canela</td>
</tr>
<tr>
<td>Durango</td>
<td>S, Sd</td>
<td>K, L, J</td>
<td>Maverick, Sierra, Pinto Villa, Bayo Blanco</td>
</tr>
<tr>
<td>Jalisco</td>
<td>S</td>
<td>L, K</td>
<td>Garbancillo Zarcó, Rosa de Castilla, Flor de Junio Marcela, Negro San Luís</td>
</tr>
<tr>
<td>Guatemala</td>
<td>S, ?</td>
<td>I</td>
<td>Colorado de Teopisca, Bolonillo</td>
</tr>
</tbody>
</table>

†Phaseolin seed protein electrophoretic type (Gepts et al., 1986, 1988; Gepts and Bliss, 1986; Koenig et al., 1990; Singh et al., 1991b, 1991c).

‡Frequency of haplotypes in descending order from left to right; distribution of haplotypes based on the survey of 127 Mesoamerican and Andean landraces (Chacón et al., 2005).
set of related elite parents within the same seed commercial class. Within a commercial class, genetic variation is narrow and inadequate levels of resistance to stresses are the norm (Sonnante et al., 1994; Singh, 2001). Crosses within the commercial class allow for the rapid recovery of progenies with commercial seed value, but variation within the class is highly diminished. An example of this is the reduced variation observed in the Azufraido-Peruano yellow bean seed class in the coastal areas of northwestern Mexico (Pallotini et al., 2004) where the pressure to recover the commercial seed type is high (Rosales-Serna et al., 2005).

The divergence between the Middle American and the Andean gene pools suggests that germplasm of both areas should be simultaneously used in breeding. Because of the divergence in those two gene pools, novel gene combinations could be obtained provided gene transfer and recombination can take place freely (Becerra-Velasquez and Gepts, 1994). In Mexico, from the 1960s onward, intergene pool crosses have been made mainly between the race Nueva Granada [as a source of resistance to rust [caused by Uromyces appendiculatus Pers.:Pers (Unger)] and rust-susceptible cultivars from the Durango and Jalisco races (Rosales-Serna et al., 2005). These intergene pool crosses have been possible since most of the genotypes in the Durango and Jalisco races do not carry the complementary DL./DL. alleles that cause F1 lethality (Singh and Gutierrez, 1984). Nevertheless, even in the majority of the crosses in which lethality factors are absent, the recovery of superior progenies is much more difficult than in intragene pool crosses. The large number of epistatic relationships broken up by the cross may be to blame for the poor performance (Johnson and Gepts, 1999; 2002). Re-establishment of these extensive epistatic networks requires different breeding methods than the ones used in intragene pool crosses (Beaver and Kelly, 1994). However, the potential of intergene pool crosses is based on the co-evolution of host and rust pathogen that has led to specialized isolates (pathotypes), which attack beans primarily from the same gene pool (Miklas et al., 2006). Isolates of Central America origin attack beans primarily from the Meso-American gene pool and similar compatible reactions occur in the Andean gene pool. Co-evolution has also been observed between the bean gene pool and pathogen virulence for angular leaf spot [caused by Phaeoisariopsis griseola (Sacc.) Ferraris] (Guzman et al., 1995), anthracnose [caused by Colletotrichum linde-muthianum (Sacc. & Magnus) Lambs.-Scrib.] (Balardin and Kelly, 1998), and common bacterial blight [caused by Xanthomonas axonopodis pv. phaseoli (Smith) Vauterin et al.] (Mkandawire et al., 2004). The co-evolution of pathogen virulence within each gene pool influences resistance gene deployment strategies. The development of lines with resistance from both gene pools is a recognized strategy for developing improved, broad-base, long-lasting resistance in common bean (Miklas et al., 2006).

In addition to the diversity available within the species, interspecific hybrids can readily be produced between the common bean and P. coccineus, P. costaricensis Freytag and Debouck, and P. dumosus, three related species, but the recovery of useful progenies from such crosses is low due to reduced viability and fertility (Singh et al., 1997; Gepts et al., 2007). With the aid of embryo rescue, progenies can also be recovered from crosses with P. acutifolius, a species in the tertiary pool of P. vulgaris (sensu Harlan and de Wet, 1971). Phaseolus acutifolius has been used as a source of resistance to common bacterial blight (Singh and Muñoz, 1999), and it is well known for its tolerance to drought and high temperatures.

**Useful Traits from Wild Species**

Some traits present in wild populations are either absent or underrepresented in the domesticated form of P. vulgaris. A few of these are shown in Tables 2 and 3. Since wild beans have coexisted with pests and pathogens on an evolutionary time scale, they have developed pest and pathogen resistances, although at low frequency in their wild habitat, as known from the case of arcelin seed protein where only a few individuals in a population carry the resistant allele (Acosta-Gallegos et al., 1998). Wild common bean extends across many ecological niches including semi-arid areas to moist tropical environments. To be able to colonize such diverse niches, wild common bean must possess a wide array of adaptive traits, some of which may be missing in cultivars because of the genetic bottleneck induced by domestication.

**Efforts to Transfer Useful Traits from Wild Species into Common Bean**

Breeders recognize that a vast amount of genetic diversity within crop plants exists untapped in wild germplasm as a result of domestication (Frey 1975; Frey et al., 1984; Tanksley and McCouch, 1997). These wild relatives are a potential source of novel alleles that can be exploited for the improvement of yield and other quantitative traits in domesticated bean. Following are some examples from wild common bean.

**APA Seed Proteins**

The APA proteins consist of three related seed proteins: arcelin, phytohemagglutinin, and α-amilase inhibitors. These proteins are coded by a small multigene family, each protein being coded by a different subfamily. Most of the genes are located in tandem at a complex locus on linkage group B4. One or more of these proteins has functional insecticidal properties against storage weevils known as bruchids (Goossens et al., 2000). This protein was first described by Romero-Andreas et al. (1986) in
the United States at the same time that some wild bean accessions were discovered to be resistant against bean weevil [Acanthoscelides obtectus (Say)] (Vanderboorth, 1983; Schoonhoven et al., 1983). The transfer of the resistance from wild accessions into elite tropical material has been enhanced by serological bioassays and replicated insect feeding tests (Cardona et al., 1990; Kornegay et al., 1993). More recently, the entire APA locus has been cloned and sequenced in the accession G02771, a wild bean from Mexico that harbors the three gene subfamilies (Kami et al., 2006). The results show that the locus consists of, in the following order, two arcelin genes, three phytohemagglutinin genes, and one α-amylase inhibitor gene. Each subfamily is separated by retrotransposons, but it is not known at this stage to what extent each gene is expressed, nor what the mechanisms are that generated this structural complexity at the APA locus (Kami et al., 2006). Further information on the structure of the locus may help identify other proteins in the APA family with different insect specificities.

**Resistance to Apion spp.**

In the highlands of Mexico and Central America, two species of the Mexican bean pod weevil, Apion godmani Wagner and A. aurichalceum Wagner, attack domesticated common bean. Both species cause substantial damage in wild stands not only in common bean but also in related species. In beans grown under rainfed conditions in Durango, A. godmani caused yield losses of 60% (Acosta-Gallegos et al., 1992). Some resistance sources have been described in the cultigens and among wild accessions. Since wild beans are constantly exposed to the attack of this insect, sources of resistance should exist among wild accessions. The resistance seems to be effective since young pods are always exposed to the insects during the reproductive stage as a result of the climbing growth habit of the wild accessions. In the case of domesticated beans, pods are partially hidden under the canopy due to the prostrate growth habit of many cultivated types. Acosta-Gallegos et al. (1992) evaluated 123 accessions from the range of distribution of wild P. vulgaris under the natural insect pressure in the field and found that only accessions from Mexico and Guatemala were resistant to A. godmani, with the highest frequency of resistant accessions from the states of Jalisco and Michoacán. In a later study conducted in Central Mexico, two independent dominant genes Agr and Agm conferred resistance in the Mesoamerican (Jalisco race) landrace J-117 (Garza et al., 1996). These genes have been mapped to linkage groups B1 and B11, respectively (Blair et al., 2006c). In this last study, sequence tagged site (STS) markers were developed from nine random amplified polymorphic DNA (RAPD) bands associated with Apion resistance. One of the markers was dominant and may find immediate utility in marker-assisted selection.

**Protein and Mineral Content**

It has been estimated that three billion people in developing countries are deficient in Fe (Bouis, 2000), a problem that is more acute for women and children because of their greater physiological need for Fe. In poor countries, more than half

<table>
<thead>
<tr>
<th>Trait</th>
<th>Comments</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insect resistance</td>
<td>Resistance to Mexican bean weevil</td>
<td>Acosta-Gallegos et al., 1992</td>
</tr>
<tr>
<td>Mineral content</td>
<td>Higher Ca, N, Fe, and Zn in wild populations than in domesticated form</td>
<td>Guzmán-Maldonado et al., 2000; Díaz-Batalla et al., 2006; Espinosa-Alonso et al., 2006; Vázquez and Cardenas, 1992</td>
</tr>
<tr>
<td>Amino acid balance</td>
<td>The balance of essential amino acids</td>
<td>Sotelo et al., 1995</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Trait</th>
<th>Species</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthracnose resistance</td>
<td>P. coccineus and P. dumosus</td>
<td>Mahuku et al., 2003</td>
</tr>
<tr>
<td>Root rots resistance</td>
<td>P. coccineus</td>
<td>Mahuku et al., 2002</td>
</tr>
<tr>
<td>Freezing tolerance</td>
<td>P. angustissimus A. Gray</td>
<td>Balasubramanian et al., 2004</td>
</tr>
<tr>
<td>Bean golden yellow mosaic virus</td>
<td>P. coccineus</td>
<td>Osorno et al., 2003</td>
</tr>
<tr>
<td>Salt tolerance</td>
<td>P. macvagui Delgado, P. micranthus Hook. and Arn, P. filiformis Benth.</td>
<td>Bayuelo-Jimenez et al., 2002</td>
</tr>
<tr>
<td>Drought tolerance</td>
<td>P. acutifolius</td>
<td>Parsons and Howe, 1984; Markhart, 1985; Federici et al., 1990</td>
</tr>
<tr>
<td>Heat tolerance</td>
<td>P. acutifolius</td>
<td>Federici et al., 1990</td>
</tr>
</tbody>
</table>

Table 2. Some cases of superiority in traits in the wild form of common bean compared to the domesticated P. vulgaris.

Table 3. Important traits found in domesticated and wild Phaseolus species.
of pregnant women and more than 40% of nonpregnant women and preschool children are anemic. An interdisciplinary, international effort (Harvest Plus Challenge Program of the CGIAR, www.harvestplus.org) is under way to breed mineral- and vitamin-dense varieties of rice (Oryza sativa L.), wheat (Triticum aestivum L.), maize, beans, and cassava (Manihot esculenta Crantz) for release to farmers in developing countries. In the particular case of beans, this effort is called “Agrosalud” and is supported by the Canadian International Development Agency. We have been searching for mineral-dense bean _P. vulgaris_ genotypes and, to date, higher Fe and Ca content has been detected in seeds of wild beans as compared to those of domesticated landraces and bred cultivars (Espinosa-Alonso et al., 2006). Using a segregating population derived from a domesticated × wild population, a few putative quantitative trait loci (QTL) associated with some of those compounds in the seeds were detected (Guzmán-Maldonado et al., 2003). Crossing between those high, mineral-dense wild bean genotypes with elite cultivars will be pursued in our local breeding program following the inbred backcross method or the recurrent backcross method (Wehrhahn and Allard, 1965). The inbred backcross method is useful for transferring polygenic traits such as N fixation capacity from exotic domesticated beans into bred temperate cultivars (Bliss, 1993), and root rot [caused by _Fusarium solani_ (Mart.) Sacc. f. sp. _phascoli_ (Burr.) W.C. Snyder and H.N. Hans] resistance between gene pools (Román-Avilés and Kelly, 2005). Since these traits are polygenic, the method might also be useful for the transfer of other complex traits such as mineral content.

**Seed Yield**

In contrast to pest resistance, which in the case of the arcelin gene is considered qualitative, yield-related traits are genetically much more complex and under the control of many genes that are also substantially influenced by environmental factors. Collectively, these genes are referred to as QTL. The use of wild germplasm for the improvement of yield in bean has been limited because the highly heritable, qualitative, morphological traits (domestication syndrome) that distinguish wild from domesticated germplasm, mask any alleles or QTL that might contribute positively to yield. A genotype, regardless of its inherent yield potential, will not reproduce if it does not flower. Thus, typically photoperiod-sensitive and viny wild germplasm does not appear to possess any desirable traits for the improvement of yield when grown in temperate production zones.

Given similar limitations in other crops, Tanksley and Nelson (1996) and Xiao et al. (1997) proposed shifting the paradigm away from phenotypic and toward genotypic selection. Their approach called advanced backcross-QTL is a modification of the inbred backcross breeding system proposed by Bliss (1993) for use in beans. The most common type of population structure used for genetic analysis of quantitative traits in self-pollinating crops is the recombinant inbred (RI) population. Recombinant inbred populations are developed from a single cross between contrasting genotypes that results in maximum genetic variation. Each parent of an RI population contributes 50% to its progeny. While maximum genetic variation is desirable when studying populations derived from genetically related parents, it becomes problematic when working with crosses between wild and domesticated genotypes. Most of the observed variation present in these populations can be explained by a few major loci, those involved in the domestication syndrome; QTL with smaller effects are effectively unidentifiable. It follows then that eliminating the variation attributed to these major loci will expose QTL of lesser effect and potentially those novel alleles that would contribute positively to yield performance. To reduce the amount of undesirable genetic variation the contribution made by the wild parent must be reduced and this can be achieved through the inbred backcross method.

Scientists at the Centro Internacional de Agricultura Tropical (CIAT, Cali, Colombia) have used the inbred backcross method to introgress wild _P. vulgaris_ from one gene pool into the domesticated germplasm of the other gene pool. One such example is the development of an inbred backcross population between an elite black bean cultivar Negro Tacaná from Mexico and a wild bean accession G24423 from Colombia (López Salinas et al., 1997). The original cross and two backcrosses were made at CIAT and the inbred progenies were evaluated through the Bean/Cowpea Collaborative Research Support Program (B/C CRSP) network in Mexico and the United States. One BC$_2$F$_{4}$ line produced the highest recorded bean yield in a Michigan State University yield trial (5790 kg ha$^{-1}$) and outperformed the recurrent parent, Negro Tacaná, by 27% (Kelly, 2004). The line has continued to outperform commercial checks in National Cooperative Dry Bean Nurseries from 2002 to 2005. The most striking observations in these inbred backcross populations derived from wild _P. vulgaris_ is the similarity after two backcrosses of the progeny to the domesticated recurrent parent, despite the obvious undesirable characteristics of the wild parent. From 2003 to 2005, five lines derived from the above-mentioned population were tested in uniform yield trials in Central Mexico and compared to cultivars derived from crosses between elite parents. In terms of seed yield, the average of the five backcross lines in eight trials was 11% higher than the recurrent parent Negro Tacana (1861 vs. 1656 kg ha$^{-1}$). The best backcross line, UG-21141-102(F$_{1}$)-1-1-M, out-yielded the recurrent parent by 17% and the best improved cultivar in the trial, Negro 8025, by 6%. In six out of the eight trials, a backcross line was the top yielder.
In general, progenies derived from crosses between wild and domesticated common bean do not show problems related to viability and fertility, which theoretically should allow for the transfer of useful traits from the wild into the domesticated form. Singh et al. (1995) crossed 39 accessions of wild and weedy beans from both regions, Andean and Mesoamerican, with an improved high-yielding tropical cultivar, ICA Pijao. Derived populations were evaluated for seed yield, days to maturity, and 100-seed weight in the F1, F2, F3, and F4 generations. In the F3, 30 random selections were made and evaluated for seed yield from the F1 to F4. In general, yield was higher in the F2 and F3, since in later generations a marked reduction was observed, which was due to inbreeding depression. Average yield was higher in populations derived from Mesoamerican wild-types compared to those derived from Andean wild-types.

In another study, the improved cultivar Negro Tacaná was crossed with three different wild bean accessions. For each of these three crosses, three different populations were established: (i) simple cross, (ii) double recombinants (the crossing of different F1 plants within a simple cross), and (iii) first backcross. A field trial was established in the summer of 1998 at the Valle de Mexico Experiment Station, near Texcoco, Mexico, which included the domesticated parent Negro Tacaná and the nine segregating populations, all of which were in the F4 generation (Table 4). The three backcrosses and double recombinant populations showed a phenology similar to that of the domesticated parent (Table 4). In the case of the segregating populations, maturity was determined on tagged individual plants when they exhibited at least one dry pod since in the simple and double recombinants many plants exhibited wild traits such as ripe pods in the lower nodes and flowers on the tips of the branches and aggressive vegetative growth. In all segregating populations, there were individual plants that produced higher yields than the plants of the domesticated parent. In the case of seed yield per hectare, all three backcross derived populations and the one derived from the simple cross of Negro Tacaná × G24429 showed a yield similar to that of the bred parental line.

The three backcross populations showed a seed size similar to that of the domesticated parental line, while all the populations derived from simple crosses and double recombinants showed an intermediate seed size. The seed size of the wild populations ranged from 5 g per 100 seeds in G12947 to 9.5 g per 100 seeds in the Hidalgo population, a typical weedy type. In this study, a single backcross allowed the recovery of the average seed yield and seed size displayed in the domesticated parent. In addition, most plants in the backcross populations resembled the type III growth habit of landraces and cultivars widely grown in the Mexican highlands (Table 4).

In a second trial, 41 F6.8 lines derived from F4 individual plants, chosen in different numbers from each cross on the basis of seed size, were grown in two consecutive years at the same location as the previous trial (Table 5). Families derived from double recombination produced the lowest yields, while families from the single crosses and backcrosses produced yields comparable to that of the domesticated bred cultivar. Among the single crosses, those with the weedy parent had at least a line with yields exceeding 4 Mg ha⁻¹, while the single cross and backcross with the wild parent G24429, produced lines yielding 3.5 Mg ha⁻¹. These lines were significantly (P > 0.01) superior in seed yield to the cultivated parent Negro Tacaná. Only a few lines from the backcross plants were observed with type II growth habit similar to those of Negro Tacaná; most of the plants in all the populations had a type III growth habit. In synthesis, the backcross method resulted in lines with most of traits recovered from the domesticated parent, such as phenology, seed size, and yield. Those traits were also recovered but in smaller proportions from single crosses, particularly with the weedy parent Negro Hidalgo. These results also support the use of weedy populations in the improvement of the domesticated common bean as previously suggested by Beebe et al. (1997) (Table 5).

### Table 4. Agronomic traits of nine segregating F4 populations resulting from wild × cultivated crosses and the bred cultivated parent Negro Tacaná, grown in Texcoco, Mexico, 1998.

<table>
<thead>
<tr>
<th>Population or cultivar</th>
<th>Days to flowering</th>
<th>Days to maturity</th>
<th>Yield (n = 27)</th>
<th>100 seed weight</th>
<th>Yield</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>g plant⁻¹</td>
<td>g</td>
<td>kg ha⁻¹</td>
</tr>
<tr>
<td>Negro Tacaná (NT)</td>
<td>1565</td>
<td>1563</td>
<td>67.0</td>
<td>16.7</td>
<td>1688</td>
</tr>
<tr>
<td>Negro Tacaná × G24429</td>
<td>1561</td>
<td>1563</td>
<td>62.4</td>
<td>15.8</td>
<td>1651</td>
</tr>
<tr>
<td>Negro Tacaná × Hidalgo</td>
<td>1474</td>
<td>1563</td>
<td>71.1</td>
<td>17.0</td>
<td>1563</td>
</tr>
<tr>
<td>Negro Tacaná × G12947</td>
<td>1474</td>
<td>1563</td>
<td>73.1</td>
<td>13.3</td>
<td>1378</td>
</tr>
<tr>
<td>Average double cross</td>
<td>1474</td>
<td>1563</td>
<td>73.1</td>
<td>13.3</td>
<td>1378</td>
</tr>
<tr>
<td>NT (NT × G12947)</td>
<td>81</td>
<td>1378</td>
<td>63.1</td>
<td>19.3</td>
<td>1474</td>
</tr>
<tr>
<td>NT (NT × G24429)</td>
<td>81</td>
<td>1378</td>
<td>60.4</td>
<td>13.2</td>
<td>1166</td>
</tr>
<tr>
<td>NT (NT × Hidalgo)</td>
<td>81</td>
<td>1378</td>
<td>59</td>
<td>10.9</td>
<td>1378</td>
</tr>
<tr>
<td>NT (NT × G12947)</td>
<td>81</td>
<td>1378</td>
<td>58.4</td>
<td>13.2</td>
<td>1166</td>
</tr>
<tr>
<td>Average simple cross</td>
<td>81</td>
<td>1378</td>
<td>57.1</td>
<td>17.0</td>
<td>1563</td>
</tr>
<tr>
<td>Average backcross one</td>
<td>81</td>
<td>1378</td>
<td>50.4</td>
<td>13.2</td>
<td>1166</td>
</tr>
<tr>
<td>(NT × G12947) (NT × G12947)</td>
<td>81</td>
<td>1378</td>
<td>47.1</td>
<td>13.2</td>
<td>1166</td>
</tr>
<tr>
<td>(NT × Hidalgo) (NT × Hidalgo)</td>
<td>81</td>
<td>1378</td>
<td>47.1</td>
<td>13.2</td>
<td>1166</td>
</tr>
<tr>
<td>(NT × G24429) (NT × G24429)</td>
<td>81</td>
<td>1378</td>
<td>47.1</td>
<td>13.2</td>
<td>1166</td>
</tr>
<tr>
<td>LSD0.05</td>
<td>8</td>
<td>12</td>
<td>38</td>
<td>6</td>
<td>597</td>
</tr>
</tbody>
</table>
In 2000, four yield trials were performed at the same location, this time two of the trials included families derived through the inbred backcross (IB) method. Seed yields in these two trials with IB families were substantially higher than those observed in previous years, mainly due to a favorable rainfall pattern (Table 6). The parental weedy Hidalgo genotype displayed the highest average yield from the two trials it was included in; however, high-yielding families were also observed in the IB population with G12947 as donor parent.

Recently, the advanced backcross QTL analysis (Tanksley and Nelson, 1996) was used to identify QTL loci for agronomic performance including seed yield in a BC2 population from the cross of a large-seeded Andean cultivar, ICA Cerinza, and a wild common bean accession from Colombia G24404 (Blair et al., 2006b). One hundred fifty-seven lines were evaluated in replicated trials at three locations in Colombia and genotyped with microsatellites, sequence characterized amplified region (SCAR), and phaseolin markers that were used to construct a genetic map. Segregation distortion was most significant in regions orthologous for a seed coat color locus (C-R) on linkage group B8 and two domestication syndrome genes, the determinate locus (fin) on B1 and the pod shattering locus (st) on B2. Forty-one significant QTL for eight traits were identified. These included five for seed weight, two for flowering time, and one for yield, which were consistent across environments. Segregation distortion was a significant feature of the advanced backcross population. Regions of segregation distortion probably reflected the presence of genes in these regions from the wild parent that had a negative phenotypic effect and that were selected against as a result of linkage drag around these loci. The wild accession contributed positive alleles for yield and other traits to the introgression lines showing the advantages that advanced backcrossing has in common bean improvement (Blair et al., 2006b) (Table 6). Thus, in addition to the recurrent backcross method, the advanced backcross QTL analysis can be successful at transferring genes from wild populations into cultivars with commercial seed types.

### Table 5. Seed yield of 41 F_{6.8} lines derived from crosses between the bred cultivar Negro Tacaná and three wild genotypes grown under rainfed condition at the Valley of Mexico Experimental Station during 1998 and 1999.

<table>
<thead>
<tr>
<th>Genotype or population</th>
<th>No. of families</th>
<th>Average seed yield</th>
<th>Yield range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Negro Tacaná (NT)</td>
<td>1</td>
<td>2570</td>
<td>--</td>
</tr>
<tr>
<td>NT/G12947</td>
<td>2</td>
<td>2790</td>
<td>2420–3160</td>
</tr>
<tr>
<td>NT/Hidalgo</td>
<td>10</td>
<td>2390</td>
<td>1070–4280</td>
</tr>
<tr>
<td>NT/G24429</td>
<td>6</td>
<td>3000</td>
<td>2610–3640</td>
</tr>
<tr>
<td>(NT/G12947)(NT/G12947)</td>
<td>5</td>
<td>1820</td>
<td>1020–2230</td>
</tr>
<tr>
<td>(NT/Hidalgo)(NT/Hidalgo)</td>
<td>2</td>
<td>1520</td>
<td>1290–1760</td>
</tr>
<tr>
<td>(NT/G24429)(NT/G24429)</td>
<td>7</td>
<td>2170</td>
<td>1400–2770</td>
</tr>
<tr>
<td>NT/NT/Hidalgo</td>
<td>2</td>
<td>3440</td>
<td>3380–3510</td>
</tr>
<tr>
<td>NT/NT/Hidalgo</td>
<td>4</td>
<td>2980</td>
<td>2630–3260</td>
</tr>
<tr>
<td>NT/NT/G24429</td>
<td>3</td>
<td>2960</td>
<td>2130–3720</td>
</tr>
<tr>
<td>LSD_{0.05}</td>
<td></td>
<td>467</td>
<td></td>
</tr>
</tbody>
</table>

In 2000, four yield trials were performed at the same location, this time two of the trials included families derived through the inbred backcross (IB) method. Seed yields in these two trials with IB families were substantially higher than those observed in previous years, mainly due to a favorable rainfall pattern (Table 6). The parental weedy Hidalgo genotype displayed the highest average yield from the two trials it was included in; however, high-yielding families were also observed in the IB population with G12947 as donor parent.

Recently, the advanced backcross QTL analysis (Tanksley and Nelson, 1996) was used to identify QTL loci for agronomic performance including seed yield in a BC2 population from the cross of a large-seeded Andean cultivar, ICA Cerinza, and a wild common bean accession from Colombia G24404 (Blair et al., 2006b). One hundred fifty-seven lines were evaluated in replicated trials at three locations in Colombia and genotyped with microsatellites, sequence characterized amplified region (SCAR), and phaseolin markers that were used to construct a genetic map. Segregation distortion was most significant in regions orthologous for a seed coat color locus (C-R) on linkage group B8 and two domestication syndrome genes, the determinate locus (fin) on B1 and the pod shattering locus (st) on B2. Forty-one significant QTL for eight traits were identified. These included five for seed weight, two for flowering time, and one for yield, which were consistent across environments. Segregation distortion was a significant feature of the advanced backcross population. Regions of segregation distortion probably reflected the presence of genes in these regions from the wild parent that had a negative phenotypic effect and that were selected against as a result of linkage drag around these loci. The wild accession contributed positive alleles for yield and other traits to the introgression lines showing the advantages that advanced backcrossing has in common bean improvement (Blair et al., 2006b) (Table 6). Thus, in addition to the recurrent backcross method, the advanced backcross QTL analysis can be successful at transferring genes from wild populations into cultivars with commercial seed types.

### Other Traits

Traditionally, wild germplasm has been used for the introgression of easily identifiable qualitative traits like pest resistance. The transfer of the arcelin gene, which confers resistance to the storage weevil [Zabrotes subfasciatus (Boheman)], from wild germplasm into domesticated bean exemplifies the extent to which wild germplasm has contributed to the improvement of current bean cultivars (Kornegay et al., 1993). Other traits from wild beans that might be useful include root rot resistance. For example, during the advance of generation in the greenhouse of 150 F1 plants from two backcross populations with Negro Tacaná as the recurrent parent, around 100 plants from the population resulting from the cross with the weedy W10 parent were killed by Fusarium spp., while those F1 derived from G12947, a wild-type from Jalisco, Mexico, were resistant. The resistance of G12947 was further tested and verified in field and greenhouse trials (Navarrete-Mayo and Acosta-Gallegos, 1999). In another example, a BC2F2 population of 200 inbred lines developed using the widely adapted, drought and root rot resistant Durango race cultivar Pinto Villa (Acosta-Gallegos et al., 1995) crossed to a wild parent from Jalisco, was evaluated under severe moisture and root rot stress in Durango, Mexico, in 1999. All the lines survived the severe root rot similar to the recurrent parent, whereas over 90% of other lines planted adjacent to the trial.
had succumbed to root rot. This underscores the fact that the potential value of the wild species is unknown before crossing in contrast to the traditional selection of parents before crossing. The potential, however, to exploit novel variability not previously available in the domesticated species is exciting and needs to be actively pursued in common bean.

Germplasm Conversion

The ability to use wild accessions in crop improvement has become less formidable as breeders become more familiar with the basis for the domestication syndrome in beans (Koinange et al., 1996). To effectively utilize the variability present in nonadapted exotic domesticated beans, photoperiod reaction and growth habit must be considered. Certain growth habits interfere with the breeder’s ability to recognize potential attributes in the nondomesticated species. The unadapted Type IV climbing growth habit as well as photoperiod sensitivity prevents bean breeders in temperate zones from growing and effectively evaluating such materials. Valuable traits, novel to domesticated beans, may be masked in these climbing genotypes. Such materials must first be converted to a more manageable growth habit to permit evaluation in temperate regions. The process of germplasm conversion is not new, but one that could be approached much more efficiently using the newer molecular tools that are increasingly available to breeders (Paterson, 1998). Molecular markers linked to growth habit traits such as the \textit{fin} gene have been placed on the integrated bean map (Freyre et al., 1998) and these maps are revealing some very interesting linkages. The \textit{fin} gene, for example, on linkage group B1 is linked to the photoperiod \textit{Ppd} gene, which controls flowering response. Changes from dominant to recessive alleles at these two loci would produce a genotype with at least the fundamental adaptation traits to permit its evaluation in higher latitude regions. Selection for traits such as the \textit{fin} gene, although not difficult phenotypically under long-day field conditions, could be substantially hastened by selecting for tightly linked molecular markers, freeing up efforts to evaluate the material for other, more useful agronomic or novel traits. Alternatively, markers could be used to select for, or against, major linkage groups of adapted or donor materials. These tools are being integrated into marker-aided breeding and germplasm conversion programs to assist in reducing the interference from undesirable growth habit and photoperiod sensitivity.

Prebreeding

The term prebreeding refers to the transfer or introgression of genes and gene combinations from nonadapted sources into breeding materials (FAO, 1996). There are two distinct approaches for using wild species, exotic, and landrace germplasm in plant breeding: introgression and incorporation (Simmonds, 1993). Introgression indicates the transfer of one or few alleles from exotic genotypes to adapted bred cultivars that lack the allele(s) controlling a specific trait. Incorporation refers to a large-scale effort aiming to develop locally adapted genotypes using exotic germplasm, which will broaden the genetic base of new breeding materials. The broadening of the genetic base will contribute to increased crop stability and performance (Ortiz, 2002; Singh, 2001).

Traits to Consider During Prebreeding of Common Bean

In common bean, pod shattering, seed dormancy, seed size, lateness, and photoperiod sensitivity are all determined by few loci with effects of large magnitude (Koinange et al., 1996), and they could be eliminated in a conversion program. Therefore, in choosing a recurrent domesticated parent for introgression of wild \textit{P. vulgaris} germplasm, the traits discussed above must be taken into consideration.

Photoperiod Response

The conversion needed is from sensitive to neutral. At intermediate latitudes, such as those in the bean growing areas encountered in the Mexican highlands, where wild beans are grown, the photoperiodic sensitivity is not a problem when beans are grown during the rainy season since the reproductive stage occurs under short days in August or September. However, it is a problem when beans are sown earlier under irrigation in March and April, and the bean plants at the preflowering stage are exposed to longer and hotter days in April and May. The photoperiod gene is strongly expressed above 19°C (Wallace et al., 1993). Photoperiod sensitivity is also a problem at higher latitudes such as those encountered in Europe, the United States, and Canada.

Most wild \textit{P. vulgaris} genotypes are photoperiod sensitive; the trait is more accentuated in late maturity accessions such as those from Chiapas and Costa Rica in Mesoamerica. During the seed increase performed under rainfed conditions at the Valley of Mexico (19°20’ N), a set of wild and companion landraces from the range of distribution of wild \textit{P. vulgaris} from Northern Mexico to Argentina followed a gradient in days to flowering. Those accessions from the state of Chihuahua in the north of Mexico to Chiapas in the South, flowered from 55 to 110 d after planting, and even some accessions from Costa Rica never flowered before being killed by frost in early December. Accessions from Colombia, Ecuador, and Peru displayed a response similar to those from Costa Rica. It is likely that during the process of adaptation to latitudes within Mexico, wild population from the states of Chihuahua and Durango, where the environment is semiarid with a short rainy season from July to September, alleles for earliness have accumulated in local materials. The segregation of photoperiod response in crosses between a
neutral, indeterminate domesticated Mesoamerican genotype with two wild genotypes displayed under greenhouse conditions a normal segregation for a single gene (Table 7); while the populations of two intergene pool crosses segregating for two linked traits where a large proportion of the recombinants displayed the genotype of the parental classes (Table 8). Based on these results, it might be better to use recurrent domesticated parent cultivars from the Mesoamerican races, unless breeders really need to improve cultivars from the Nueva Granada race (Table 7).

Maturity and Growth Habit
The conversion is needed from late maturity and climbing growth habit in the wild to early to mid season and bush growth habit (determinate or indeterminate) in the domesticated form. Usually lateness is related to growth habit, as domesticated beans climbers are later to flower and mature than bush types. Thus early bush types would be preferred as recurrent parents in a prebreeding program. Earliness exists in many cultivars from the Durango race, cultivars that also display good general combining ability for seed yield (Singh et al., 1991b), and from the Mesoamerican race such as the Desarrural cultivar (Beaver and Rosas, 1998) (Table 8).

Pod Shattering
Shattering is the natural mechanism for seed dispersal in wild *P. vulgaris* (Delgado-Salinas et al., 1988). Nonshattering in legumes constitute one of the earliest and most consistent differences between domesticates and their wild relatives (Evans, 1993). Even in the domesticated form there are some problems of dehiscence; that is, when beans originated in a humid tropical environment are grown in a semiarid area where low moisture and cool night conditions prevail near physiological maturity. Some cultivars from the Nueva Granada race such as Michigan Dark Red Kidney, Cacahuate Bola, and Montcalm display higher rates of pod shattering in dry environments, thus they are not suited as recurrent parents in a conversion program. Cultivars from the Durango and Jalisco races usually do not show problems of pod shattering in dry environments such as those encountered in the Mexican semiarid highlands. Cultivars that are shattering-resistant include Negro San Luis, Flor de Junio Marcela, Flor de Mayo Bajío, and Pinto Villa.

Seed Dormancy
There is no true dormancy in common bean, but hard seed coat or hard shell that inhibits water uptake is not uncommon. Seed scarification overcomes this negative trait allowing germination and subsequent growth. Water uptake or germination speed can be used to score for this trait and discard those families with low water uptake. In the field, the planting of large segregating populations without seed scarification allows for the self-elimination of individual with hard shell seeds. Koinange et al. (1996) identified four QTL for seed dormancy, one of which—on linkage group B3—accounted for half of the phenotypic variation in the RI population Midas (domesticated) × G12873 (wild). This QTL would be a prime candidate for conversion.

Molecular Markers, Genome Mapping and Genomics as an Adjunct to Breeding
At several points in this article, reference has been made, directly or indirectly, to the use of molecular markers and genome mapping. Our knowledge of the pattern of genetic diversity and the genetics of important traits would be much more limited had these tools not been available and effectively used (Gepts, 1993). The analysis of genetic diversity has benefited from information obtained with seed proteins, mainly phaseolin (e.g., Gepts et al., 1986; Koenig et al., 1990; Brown et al., 1982), isozymes (Koenig and Gepts, 1989; Singh et al., 1991b; Santalla et al., 2002), RFLP (nuclear: Becerra-Vélásquez and Gepts, 1994; disease resistance gene cluster: de Meaux et al., 2003); mtDNA and DNA: Khairal-lah et al., 1990, 1992), RAPD (Haley et al., 1994; Skroch and Nienhuis 1995; Freyre et al., 1996; Beebe et al., 2000; Galván et al., 2001, 2006; Franco et al., 2001), AFLP (Tohme et al., 1996; Maciel et al., 2001; Papa and Gepts, 2003; Rosales-Serna et al., 2005), inter simple sequence repeat (Galván et al., 2003; González et al., 2005), DNA sequence (phaseolin: Kami et al., 1995; dihydroflavonol 4-reductase intron 1: McClean et al., 2004), microsatellites (Yu et al., 1999; Guo et al., 2000; Métais et al., 2002; Gaïtan-Solis et al., 2002; Masi et al., 2003; Blair et al., 2003, 2006a), and STS (Murray et al., 2002).

What has been gained from these analyses is an understanding of the hierarchical structure of genetic diversity in the primary gene pool of common bean. Molecular markers have been used to (i) identify and confirm the existence of the two major Andean

---

**Table 7. Photoperiod response measured as the onset of flowering of two segregating populations of 62 F$_{2.4}$ families each derived from the cross of cv. Negro Tacaná by two wild Phaseolus vulgaris genotypes. Plants were grown under extended photoperiod (>14 h) in the greenhouse.**

<table>
<thead>
<tr>
<th>Population</th>
<th>Photoperiod phenotypic class</th>
<th>Observed</th>
<th>Expected</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Negro Tacaná × G12947</td>
<td>Sensitive$^1$</td>
<td>45</td>
<td>46.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Neutral</td>
<td>17</td>
<td>15.5</td>
<td>0.193</td>
</tr>
<tr>
<td>Negro Tacaná × G24324</td>
<td>Sensitive</td>
<td>47</td>
<td>46.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Neutral</td>
<td>15</td>
<td>15.5</td>
<td>0.0214</td>
</tr>
</tbody>
</table>

$^1$Sensitive plants did not flower at 100 d after planting, time when the trial was stopped. Day/night temperatures in the greenhouse were 30/20°C.
and Mesoamerican gene pools of common bean; (ii) identify and confirm the existence of ecoregographic races among domesticated beans in each of the two gene pools; (iii) the reduction of molecular genetic diversity during and after domestication in each of the two gene pools (Sonante et al., 1994); (iv) assess the relative levels of genetic diversity in the Andean and Mesoamerican gene pools; and (v) document the importance of gene flow from domesticated to wild populations (Papa and Gepts, 2003; Payró de la Cruz et al., 2005; Zizumbo-Villarreal et al., 2005).

Furthermore, molecular markers have laid the foundation for extensive molecular mapping and QTL analyses in common bean. In addition to the core mapping population established as a RI population in the cross BAT93 × Jalo EEP558 (Freyre et al., 1998), more than 20 mapping populations have been established to investigate the inheritance of specific traits as disease resistances (common bacterial blight: Nodari et al., 1993; white mold [caused by Sclerotinia sclerotiorum (Lib.) de Bary]: Miklas et al., 2001), product quality (canning quality: Posa-Macalincag et al., 2002), and abiotic stress (Yan et al., 2004). It is beyond the scope of this article to enter in detail of the extensive work on common bean molecular mapping and its application to marker-assisted selection. The topic has been reviewed in Kelly et al. (2003) and Miklas et al. (2006). Furthermore, a list of SCAR markers is available from Miklas (2005).

The limiting factor for further molecular studies and their applications to bean breeding is clearly the lack of availability of more markers that are (i) PCR-based, highly polymorphic, and reproducible; and (ii) located in specific regions of the genome harboring genes of agronomic interest to take advantage of the extensive molecular mapping conducted already. Clearly, genomics can represent a significant source of markers. To achieve this, however, serious investment in genomics of Phaseolus itself will have to be pursued instead of relying solely on progress in other legumes (Gepts et al., 2005). Additional, physically or genetically anchored markers can be obtained either through physical mapping (e.g., end sequencing of BAC clones anchored to the genetic map), expressed sequence tag mapping, and whole-genome sequencing. The current status of bean genomics has been reviewed by McClean et al. (2004, 2007) and Gepts et al. (2007).

**Perspectives**

To maximize and sustain bean production, high-yielding, superior quality cultivars that are less dependent on water, fertilizer, pesticides, and manual labor should be developed. Breeders need to accumulate available alleles present in domesticated and wild relatives in superior cultivars to meet these objectives. A tiered breeding approach involving: (i) gene introgression from exotic germplasm, (ii) pyramiding favorable alleles from different sources, and (iii) simultaneous improvement of multiple traits for common bean cultivars would be the most appropriate strategy to accomplish these goals (Singh, 2001). A pyramiding scheme previously proposed by Kelly et al. (1998) integrated these objectives by utilizing cyclic intermating and different breeding systems and germplasm at separate levels of the pyramid. Base populations developed by intermating parents from related species, exotic and wild germplasm are advanced to the mid part of the pyramid followed by crosses between germplasm from different gene pools and races. Only elite lines are advanced to the top of the pyramid where genetic diversity is maintained through selective intermingling. Improved materials at each level are advanced to the next tier in the pyramid. Such a structured approach would facilitate the introgression of wild germplasm and provide breeders with enhanced germplasm to adapt to their local conditions and needs. A similar approach named recurrent introgressive population enrichment was utilized in barley (Hordeum vulgare L.) to add new gene complexes into elite cultivars (Kannenberg and Falk, 1995). In this scheme male sterility was used to facilitate recurrent selection and four sequential steps with distinct hierarchical levels (base, intermediate, high, and elite) were used following the introduction of exotic germplasm into the system. This system reduces unfavorable linkages at each step through genetic recombination, while promoting at the same time attractive recombinants to the elite level.

Although backcross followed by selection has been the most common method for gene introgression from wild germplasm into elite genotypes, new methods should be

<table>
<thead>
<tr>
<th>Class†</th>
<th>Cacahuate 72 × Flor de Junio Marcela</th>
<th>Canario 60 × Pinto Villa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>Sensitive (Ppd_ <em>) and indeterminate (Fin</em>)</td>
<td>89</td>
<td>73.8</td>
</tr>
<tr>
<td>Sensitive (Ppd_ _) and determine (finfin)</td>
<td>5</td>
<td>24.6</td>
</tr>
<tr>
<td>Neutral (ppdpdp) and indeterminate (Fin_)</td>
<td>6</td>
<td>24.6</td>
</tr>
<tr>
<td>Neutral (ppdpdp) and determine (finfin)</td>
<td>31</td>
<td>8.2</td>
</tr>
</tbody>
</table>

†Sensitive plants did not flower at 100 d after planting, time when the trial was stopped. Day/night temperatures in the greenhouse were 30/20°C.
attempted to assess the breeding value of exotic germplasm since parental phenotypes are poor predictors of progeny performance (Vetelainen et al., 1996). Recent advances in gene technology provide a mean to broaden the genetic basis of crops, and to monitor the introgression of new alleles into breeding stocks. Molecular markers are being increasingly used to tag specific DNA segments encoding desired traits to be transferred into elite breeding materials. Combining molecular tools and information with traditional breeding methods should help bean breeding programs exploit the genetic diversity available within Phaseolus to solve production constraints and enhance the value of the bean commodity among consumers.

Acknowledgments
We gratefully acknowledge the help of M.M. Khairallah in the review of this manuscript. We express our gratitude to the McKnight Foundation, the Bean-Cowpea CRSP, the Fundación Guanajuato Produce, INIFAP (Mexico), and SINAREFI-SNICS-SAGARPA (Mexico) for partial funding of the fieldwork. Thanks also to G. Esquivel-Exquivel and B. Aguilar-Garzón for help in the conduct of field trials.

References
Frey, K.J. 1975. Plant breeding in the seventies: Useful genes from wild


