

Achievements and limitations of contemporary common bean breeding using conventional and molecular approaches

James S. Beaver · Juan M. Osorno

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Abstract Common bean (*Phaseolus vulgaris* L.) improvement programs have been successful using conventional breeding methods to accomplish a wide array of important objectives. Specific achievements include the extension of range of adaptation of the crop, the development of cultivars with enhanced levels of disease and pest resistance and breeding lines that possess greater tolerance to drought. The most effective breeding method depends on the expression and inheritance of the trait to be selected and the target environment. Many bean improvement programs use molecular markers to facilitate cultivar development. In fact, several recent germplasm releases have used molecular markers to introgress and/or pyramid major genes and QTL for disease resistance. Related species (*P. coccineus* and *P. acutifolius*) via interspecific hybridizations remain an important albeit long-term source for resistance to economically important diseases. Slow progress has been made in the improvement of traits such as adaptation to low soil fertility and tolerance to high levels of soluble Al in the soil using conventional breeding methods. The inability to

directly measure root traits and the importance of genotype × environment interaction complicate the selection of these traits. In addition, symbiotic relationships with *Rhizobium* and mycorrhiza need to be taken into consideration when selecting for enhanced biological N fixation and greater or more efficient acquisition of soil P. Genomic examination of complex traits such as these should help bean breeders devise more effective selection strategies. As integration of genomics in plant breeding advances, the challenge will be to develop molecular tools that also benefit breeding programs in developing countries. Transgenic breeding methods for bean improvement are not well defined, nor efficient, as beans are recalcitrant to regeneration from cell cultures. Moreover, if issues related to consumer acceptance of GMOs cannot be resolved, traits such as herbicide tolerance in transgenic bean cultivars which would help farmers reduce production costs and decrease soil erosion will remain unrealized.

Keywords Bean breeding methods · Bean breeding objectives · Marker-assisted selection · Conventional bean breeding achievements

J. S. Beaver (✉)
Department of Agronomy and Soils, University of Puerto Rico,
P.O. Box 9030, Mayaguez, PR 00681-9030, USA
e-mail: j_beaver@hotmail.com; jbeaver@uprm.edu

J. M. Osorno
Department of Plant Sciences, North Dakota State
University, NDSU Dept. 7670, P.O. Box 6050,
Fargo, ND 58108-6050, USA

Introduction

Common bean (*Phaseolus vulgaris* L.) breeders worldwide serve a diverse clientele ranging from

large-scale, mechanized producers to small-scale farmers in developing countries who produce beans on marginal land using few inputs (Hillocks et al. 2006; Broughton et al. 2003; Rosas et al. 2000a). Common beans are also produced in a wide range of climatic conditions ranging from the humid tropics in Latin America and Africa to the semi-arid highlands of Mexico and the High Plains of the U.S. and Canada. Each region has different production practices and a unique set of biotic and abiotic constraints. Consequently, breeding program objectives must be designed to address the needs of the farmers who will use the cultivars (Santalla et al. 2001; Singh 2001; Kelly 2001). Most public bean breeding programs are focused on dry bean improvement (Singh 2001), whereas snap bean breeding is conducted for the most part by the private sector for global markets (Myers and Baggett 1999). Disease resistance remains an important objective for most bean breeding programs. Selection for greater tolerance to abiotic stress such as drought, heat and low soil fertility is expected to gain importance in response to climate change and increased use of marginal land for bean production.

Bean breeders also need to be attuned to the needs of consumers (Kelly et al. 1998a; Santalla et al. 2004). Countries or regions within countries may differ in preferred seed type for dry edible beans (Voysest et al. 1994). Canning quality is an important trait in developed countries whereas cooking time is of greater importance in countries where beans are prepared using scarce or expensive fuel (Shellie-Dessert and Hosfield 1990). Myers and Baggett (1999) noted that some breeding objectives for fresh market and processing snap beans are distinct from dry beans. In some developing countries, consumers prefer to consume green-shelled beans or bean leaves (Singh 1999). Bean straw is a source of forage in some farming systems in Latin America (Funes-Monzote and Monzote 2001) and Africa (Ingratubun et al. 2000). In a global economy, the bean breeder needs to take in to consideration not only local preferences but the needs of the consumers where the beans are likely to be exported. Genome mapping and molecular breeding are additional tools that bean breeders may be able use to more effectively or more efficiently achieve the aforementioned objectives.

The purpose of this review is to document a few of the most important achievements of common bean

breeding utilizing conventional plant breeding methods. We also identified examples where molecular approaches such as marker-assisted selection have already contributed to the development of improved bean cultivars and germplasm. Finally, we discuss opportunities where molecular approaches may be used to address some of the more intractable bean breeding objectives.

Breeding objectives

Seed yield

Increased seed yield is a universal objective of common bean breeding programs. In addition to greater productivity, more stable yields can improve food security in developing countries. Moderate progress has been made using conventional plant breeding techniques in the development and release of dry bean cultivars with greater seed yield (Kelly et al. 1998a; Singh 1991). Market classes of beans differ significantly in seed yield potential. Smaller-seeded beans of Middle American origin generally have greater seed yield potential than larger-seeded Andean beans. Singh et al. (2007) reported that medium-seeded bean cultivars produced in the Western U.S. have reached a yield plateau and broadening the genetic base to increase seed yield potential will require an effective long-range strategy. This approach may involve several cycles of selection, large population sizes and intensive field evaluation for seed yield potential in diverse environments.

Kelly et al. (1998a) noted that ideotype breeding has been successful in the development of navy, pinto and great northern beans with improved architectural traits and greater seed yield potential. It should be kept in mind, however, that the ideotype may vary for different seed types or target environments. Cultivar development programs also may use different ideotypes based on the judgment of the plant breeder. Beaver and Kelly (1994) used inter-gene pool crosses and recurrent selection to develop indeterminate, large-seeded bean lines that had greater seed yield than determinate check cultivars.

An important challenge for dry bean breeders working with certain market classes is the negative association between seed size and seed yield potential

(Welsh et al. 1995; White and Gonzalez 1990). Myers and Baggett (1999) noted that breeding snap beans for small sieve size may also limit yield potential. In addition, Kelly et al. (1998a) noted that a lack of desirable alleles for seed yield in dry beans may limit breeding progress. Molecular plant breeding techniques may help to identify desirable alleles or permit the use of indirect selection to reduce negative associations between these economically important traits.

Selection for greater seed yield tends to increase harvest index to the point where biomass accumulation during the growing season becomes a limiting factor. Beebe et al. (2008) reported that bean lines selected for abiotic stress tolerance also had greater harvest indices and increased seed yield in favorable environments. Wallace et al. (1993) recommended that breeding for increased seed yield potential should include simultaneous selection for increased biomass accumulation and a greater rate of seed yield accumulation. However, the measurement of biomass production of a large number of bean breeding lines would be expensive and time-consuming. The availability of QTL associated with greater rates of biomass production might permit indirect selection for this trait.

Singh (2001) noted that most of the genetic variability in common bean has not yet been exploited by breeding programs. McClean et al. (1993) demonstrated by calculating coefficients of parentages that the genetic base of North American dry bean cultivars is narrow. Sorrells and Wilson (1997) noted that molecular plant breeding techniques can help to generate, characterize and utilize genetic variation. Sonnante et al. (1994) used DNA fingerprinting to demonstrate that the domestication of Middle American and Andean beans resulted in a loss of genetic diversity. Therefore, crosses with wild relatives could result in the identification of unique traits or greater genetic variability of existing traits such as seed yield (Acosta-Gallegos et al. 2007). The introgression of favorable alleles from wild beans and other close relatives to commercially acceptable bean cultivars will require a coordinated and sustained effort by bean breeding programs due to long time frame and large expense required. Bean research networks could help provide the interdisciplinary expertise, the exchange of information and long-term outlook needed to broaden the genetic base of bean cultivars.

The use of wild common beans as parents in breeding programs may help to overcome the founder effect, a genetic bottleneck caused by the domestication of the crop, and broaden the genetic base for the expression of seed yield (Blair et al. 2006b). However, Sorrells and Wilson (1997) noted the difficulty of identifying genotypes that combine all of the desirable alleles for a quantitative trait such as seed yield.

The availability of molecular markers for genes for photoperiod response and other traits associated with local adaptation would hasten the development of lines that could be evaluated in temperate regions for adaptation and seed yield potential. These markers would facilitate the use of unadapted parents by these breeding programs. Gu et al. (1998) identified RAPD markers linked to the recessive alleles of *Ppd* and *Hr* that confer photoperiod insensitivity. Unfortunately, these markers were only present in bean lines of Andean origin.

Resistance to biotic constraints

Disease and pests can cause significant losses to common bean production (Schwartz et al. 2005; Coyne et al. 2003; Wortman et al. 1998). Control of these biotic constraints using agrochemicals can increase production costs and create the potential for contamination of the environment. Resistance also represents a valuable disease and pest management tool for organic production of beans. Therefore, the development of cultivars with greater levels of disease and pest resistance is a primary objective of most bean breeding programs (Table 1).

Much remains to be achieved in order to improve disease resistance of common bean. Singh et al. (2007) reported that great northern, pinto, pink and small red beans produced in the Western U.S. are generally susceptible to diseases such as common bacterial blight caused by *Xanthomonas axonopodis* pv. *phaseoli*, halo blight caused by *Pseudomonas syringae* pv. *phaseolicola*, bacterial brown spot caused by *Pseudomonas syringae* pv. *syringae* van Hall, anthracnose caused by *Colletotrichum lindemuthianum* (Sacc. & Magnus), rust caused by *Uromyces appendiculatus* (Pers.) Unger, Fusarium wilt caused by *Fusarium oxysporum* f. sp. *phaseoli*, and white mold caused by *Sclerotinia sclerotiorum* (Lib.) de Bary. This lack of resistance limits the range of adaptation of these cultivars. Sources of resistance to

Table 1 Recent releases of bean cultivars and germplasm with unique or valuable combinations of traits that are the result of conventional plant breeding techniques

| Trait(s) | Description (seed type) | Reference |
|---|---|--|
| Angular leaf spot | | Mahuku et al. (2004) |
| Angular leaf spot and anthracnose resistance | | Singh et al. (2003a) |
| Anthracnose resistance | <i>Co-1</i> , <i>Co-2</i> (black bean) | Kelly et al. (2001) |
| | <i>Co-1</i> , <i>Co-2</i> (dark red kidney bean) | Kelly et al. (1998b) |
| | <i>Co-6</i> (small red bean) | Young and Kelly (1996) |
| | <i>CO-4²</i> (Pinto bean) | Miklas et al. (2003) |
| Bean common mosaic and bean common necrotic mosaic resistance | <i>I</i> , <i>bc3</i> (black bean) | Kelly et al. (1994) |
| | <i>I</i> , <i>bc3</i> (kidney bean) | Miklas et al. (2002) |
| | <i>I</i> , <i>bc-1²</i> (great northern) | Stewart-Williams et al. (2003) |
| | <i>bc-1²</i> (small red) | Hosfield et al. (2004) |
| | <i>bc-1²</i> (pinto) | Brick et al. (2001) and Grafton et al. (1999) |
| Bean golden yellow mosaic resistance | Pyramided genes producing high levels of resistance | Singh et al. (2000), Beaver and Miklas (1999), and Rosas et al. (1997) |
| | High levels of resistance derived from scarlet runner bean (<i>Phaseolus coccineus</i> L.) | Beaver et al. (2005) |
| Bruchid resistance | | Osborn et al. (2003) |
| Common bacterial blight | High levels of resistance derived from tepary bean (<i>Phaseolus acutifolius</i> L.) | Singh et al. (2001b) |
| | High levels of resistance derived from the scarlet runner bean (<i>Phaseolus coccineus</i> L.) | Zapata et al. (2004) and Miklas et al. (1999) |
| Drought tolerance | | Brick et al. (2008), Beebe et al. (2008), and Singh et al. (2001a) |
| Halo blight resistance | | Coyne et al. (2000) |
| Heat tolerance | | Beaver et al. (2008), Rosas et al. (2003a), and Rosas et al. (2000b) |
| | Heat tolerance derived from tepary beans | Rainey and Griffiths (2004). |
| Low soil fertility tolerance | Derived from germplasm accessions, landraces and improved lines | Singh et al. (2003a, b) |
| Low soil fertility and drought tolerance | | Beebe et al. (2008) |
| Multiple disease and pest resistance | Angular leaf spot, anthracnose, Common bacterial blight, bean Common mosaic virus, Bean golden mosaic virus and leafhopper resistance | Singh et al. (1998) |
| | Common bacterial blight, rust and Bean common mosaic virus resistance | Mutlu et al. (2005, 2008) |
| | Pyramided rust, Bean common mosaic virus and Bean common necrotic mosaic resistance genes producing high levels of resistance | Pastor-Corrales (2003) and Pastor-Corrales et al. (2007) |
| | Multiple virus resistance | Scully et al. (1995) |
| | Bean common mosaic virus, Beet curly top virus and root rot resistance | Silbernagel et al. (1998) |
| | | Smith et al. (2007) |

Table 1 continued

| Trait(s) | Description (seed type) | Reference |
|---|--|---|
| White mold | | Miklas (2007), Griffiths et al. (2004), and Miklas et al. (1998a) |
| | Resistance derived from scarlet runner bean (<i>Phaseolus coccineus</i> L.) | Schwartz et al. (2006) |
| Slow-darkening | SDIP-1 | Singh et al. (2006) |
| Tolerance to Zn deficiency in high pH soils | Single dominant gene (<i>Znd</i>) | Kelly et al. (1999) and Singh and Westermann (2002) |

many important bean diseases have been identified and used in cultivar development programs (Miklas et al. 2006b; Beaver et al. 2003). However, breeders also need information from plant pathologists concerning the virulence patterns of the pathogens in order to most effectively deploy disease resistance genes (Coyne et al. 2003).

Common bean production is often limited by more than one biotic constraint which poses a challenge for plant breeders who must develop cultivars having multiple disease or pest resistance. Kelly et al. (1998a) warned, however, that an over-emphasis on breeding for disease or pest resistance may reduce genetic variability and limit progress in breeding for increased seed yield.

Molecular markers have been developed for many disease resistance genes and these markers have been successfully used to develop improved common bean cultivars and germplasm (Miklas et al. 2006b; Kelly and Miklas 1998; Pedraza et al. 1997). Miklas et al. (2006b) noted that marker-assisted selection has been used more for breeding for disease resistance than for other traits of economic importance such as tolerance to abiotic stress. Molecular markers have also permitted the development of common bean lines that pyramid genes for disease resistance (Kelly and Miklas 1998). This strategy is designed to develop common bean lines with more durable resistance (McDonald and Linde 2002). Although many molecular markers linked to disease genes have been reported, only a handful of these markers are being used routinely by common bean breeding programs. Lack of repeatability in different genetic backgrounds, weak marker-gene linkages, overestimated QTL effects (due to small population sizes used to develop the marker), and lack of economic resources can limit the use of molecular markers in a breeding program (Bernardo 2008).

Tolerance to abiotic constraints

Bean production worldwide is threatened by an array of abiotic stresses such as drought, low soil fertility, soil acidity and temperatures unfavorable for the growth and development of the crop (Lynch 2007). The importance of abiotic stress may increase in developing countries as bean production shifts to more marginal environments. Global climate change may also produce more stressful environments for bean production that will require the development of bean cultivars with greater tolerance to high temperature and drought (Battisti and Naylor 2008; Porch et al. 2007).

Bean producers in the highlands of Mexico continually confront the threat of drought. The INIFAP breeding programs in Mexico has been successful in the development of bean cultivars better adapted to this semi-arid environment (Rosales-Serna et al. 2004).

In Brazil, bean production has expanded into regions where acidity or low soil fertility can limit seed yield (Adair 2003). Bean production in the U.S. has moved to more arid environments as soybean (*Glycine max* [L.] Merr.) and corn (*Zea mays* L.) production has expanded due to an increase in the prices of these commodities.

Greater tolerance to abiotic stress can help farmers to produce more stable bean yields in unfavorable environments (Miklas et al. 2006b). Edaphic constraints such as low soil fertility often have a great amount of spatial variability (Lynch 2007), whereas climatic constraints such as drought are unpredictable. This variability makes field screening for these traits more difficult to accomplish. Adding to the difficulty of evaluating beans for tolerance to abiotic stress is the importance of genotype \times environment interaction in the performance of beans under this type of stress.

Tolerance to abiotic stress tends to be a quantitatively inherited trait which requires that breeders work with larger populations and replicated field trials to be able to identify breeding lines with superior performance. Significant progress may require several cycles of selection and the use of multiple parents as sources of favorable alleles. Despite multi-genic inheritance, genotype \times environment interactions, and environmental variability associated with tolerance to abiotic stress, bean breeders have developed cultivars and breeding lines with enhanced tolerance to many important abiotic stresses such as drought (Brick et al. 2008; Muñoz-Perea et al. 2006; Frahm et al. 2004), low soil P (Beebe et al. 2008; Lynch 2007), and high temperature (Beaver et al. 2008; Rosas et al. 2000a).

Genomic studies leading to the development of molecular markers will provide bean breeders with new tools to identify traits associated with abiotic stress tolerance (Ishitani et al. 2004). The molecular markers should help breeders to combine specific traits related to abiotic stress tolerance (Miklas et al. 2006b). It should be noted, however, that the effectiveness of marker-assisted breeding will only be as effective as the association (linkage) of the markers with the different traits. Ideally, the markers should explain a large portion of the genetic variability associated with the abiotic stress tolerance and the expression of the trait should not be greatly affected by $G \times E$.

Enhanced nutrition and utilization

In addition to being an important source of protein and carbohydrates, common bean also supplies essential vitamins and micronutrients such as Zn and Fe (Welch et al. 2000). Enhancing the level of these micronutrients in common bean cultivars has the potential to improve human nutrition in developing countries (Guzmán-Maldonado et al. 2003; Frossard et al. 2000). Blair et al. (2005) found both Zn and Fe content in the seed of an Andean bean population to be inherited in a quantitative manner. Gelin et al. (2007) also found Zn and Fe content in the seed of a Middle American bean population to be quantitatively inherited. In both studies, Zn and Fe content were positively correlated although genotype \times environment interaction also affected the expression of the traits. Gelin et al. (2007) identified

a locus associated with seed Zn accumulation. Guzmán-Maldonado et al. 2003 identified a QTL that explained 15.2% of variability in seed Zn content in a population derived from a cross between a Middle American bean cultivar and a wild common bean accession. Cichy et al. (2005) reported a single dominant gene in a Middle American bean population that conferred higher seed Zn concentration in a navy bean population. Marker-assisted selection would be a useful tool to screen bean populations and tag new genes for enhanced levels of micronutrients in the seed.

The presence of oligosaccharides in common bean seed can result in gastrointestinal discomfort and can inhibit the absorption of nutrients (da Silva-Fialho et al. 2006). Significant differences in oligosaccharide concentrations were reported among a group of Andean and Middle American bean cultivars (da Silva-Fialho et al. 2006).

Reduced cooking time is an important breeding objective in developing countries where the fuel needed to prepare beans is scarce or expensive (Jacinto-Hernandez et al. 2003; Kelly and Miklas 1998; Shellie-Dessert and Hosfield 1990; Shellie and Hosfield 1991). Elia et al. (1997) reported a narrow sense heritability of 0.9 for cooking time in an Andean bean population whereas Jacinto-Hernandez et al. (2003) reported a narrow sense heritability of 0.74 in a Middle American bean population. Jacinto-Hernandez et al. (2003) reported that two dominant genes control cooking time in the Middle American bean population and cite the advantages of identifying molecular markers to select for this trait. Elia et al. (1997) reported a significant (>0.8) and negative phenotypic correlation between cooking time and water absorption of bean seed and suggested that water absorption might be useful for the indirect selection for cooking time.

In developed countries, canning characteristics and culinary characteristics can be important criteria for selection in bean breeding programs. Kelly et al. (1998a) noted that bean breeders in North America dedicate a significant amount of time and resources to the evaluation and selection of lines for processing quality. These evaluations usually require large seed samples of advanced generation breeding lines (Ghaderi et al. 1984). Posa-Macalincag et al. (2002) identified QTLs linked to degree of splitting and overall appearance of kidney beans which are major

components of canning quality of this seed type. Marker-assisted selection could be used to screen breeding lines for canning quality in earlier generations. Although one of the parents used in the study was the principal source of canning quality, results from the QTL analysis and mapping suggested that both parents had alleles that contributed to canning quality. Walters et al. (1997), working with a navy bean population, identified RAPD markers linked to visual appearance, texture and washed drained weight of canned beans.

Health benefits

Annual per capita consumption of dry beans in the U.S. averaged 3.1 kg from 1998 to 2007, which was 7% lower than the period from 1988 to 1997 (USDA, ERS 2007). In developing countries, annual per capita consumption of beans can exceed 50 kg, especially in Africa and Latin America. Numerous health benefits from the consumption of beans have been documented. In addition to being a good source of protein, beans provide vitamins and minerals (Bennink and Rondini 2003), lower cholesterol (Anderson et al. 1999) and have preventive and curative faculties to terminal diseases such as cancer (Hangen and Bennink 2003). Antifungal peptides have been isolated from several *Phaseolus* species (Wang and Ng 2006; Patrick and Ng 2004). These peptides are able to inhibit the activity of reverse transcriptase, one of the key enzymes for virus replication. This may help extend the onset of symptoms of patients infected with HIV (Wong et al. 2006; Patrick and Ng 2004). Bean breeders need to ensure that new cultivars retain those characteristics that provide health benefits. Molecular plant breeding techniques should assist in the identification and facilitate the transfer of these desirable traits.

Bean breeding methods

Pedigree

Pedigree selection is a common method used by bean breeders to develop improved cultivars. An important limitation of pedigree selection is the amount of time needed to develop new cultivars (Fehr 1987). Bean breeders in the tropics can accelerate cultivar

development by planting irrigated nurseries during the dry season. Dry edible and snap bean breeding programs in North America have been able to speed up the process by growing an additional generation each year in winter nurseries planted in the Caribbean and locations in the Southern Hemisphere such as New Zealand and Chile. While the bean lines are growing in winter nurseries, plant breeders can screen breeding lines in the greenhouse in North America for resistance to diseases such as BCMNV and anthracnose. In recent years, common bean breeders have employed marker-assisted selection to identify breeding lines with specific genes for disease resistance (Miklas et al. 2006b). This allows the bean breeders to exclude susceptible lines when selections are made in the winter nursery. Beaver and Macchiavelli (1998) noted that screening bean breeding lines in F₄ or later generations would improve the probability of identifying lines with the desired genotype and would reduce the number of lines that need to be evaluated in earlier generations.

Backcross

In order to preserve horticultural and seed traits of snap and dry edible bean cultivars, plant breeders have often utilized backcross breeding to incorporate simply inherited traits. This selection method is also well suited for marker-assisted selection (Miklas 2007; Miklas et al. 2003). This breeding method is not useful, however, for the improvement of quantitatively inherited traits such as seed yield or tolerance to abiotic stress.

Michelmore (1995) also noted that backcrossing is inefficient in removing portions of the chromosome that are closely linked to the genes targeted for backcrossing. Reyes-Valdés (2000) noted that linkage drag can impede or delay efforts to use backcrossing to introgress desirable traits into a recurrent parent.

Bliss (1993) described the use of the Inbred Backcross Line (IBL) method to develop near homozygous lines that can be used for replicated testing for traits such as biological nitrogen fixation. One or two backcrosses are made after the initial cross. The backcrosses are followed by a few generations of single seed descent to produce the inbred backcross lines. The IBL method was used to identify quantitative trait loci conditioning resistance to Fusarium root rot (caused by *Fusarium solani* f. sp.

phaseoli) in common bean (Román-Avilés and Kelly 2005).

Tanksley and McCouch (1997) used advanced backcross QTL analysis and marker assisted selection to introgress QTL from the wild tomato species *Lycopersicon hirsutum* to produce breeding lines that were superior to the cultivated tomato (*Lycopersicon esculentum* Mill.) recurrent parent. Myers and Baggett (1999) suggested that advanced backcross QTL analysis and marker-assisted selection may be a useful approach to transfer traits from dry beans to snap beans. Myers and Baggett (1999) also noted that the availability of more dense molecular maps of the bean genome may permit Whole Genome Selection (Tanksley and Rick 1980). Selection of individual plants having the desired trait and the most complete set of markers of the recurrent parent would accelerate the transfer of traits into snap beans.

Urrea and Singh (1995) proposed the use of recurrent congruity backcrossing (crossing alternatively each generation to both parents) to maximize recombination and increase the retention of desirable alleles from parents of diverse origin. Singh et al. (2002) reported that congruity backcrossing was more effective than recurrent backcrossing (crossing each generation to the same parent) in the development of breeding lines with greater seed yield potential from an inter-gene pool (Andean \times Middle American) cross. Muñoz et al. (2004) reported that interspecific (*P. vulgaris* \times *P. acutifolius*) lines derived from congruity backcrossing had a higher level of introgression than lines derived from recurrent backcrossing.

Single seed descent (SSD)

Kelly et al. (1998a) recommended the use of SSD when working with crosses between elite lines within a market class. The procedure provides a way to maintain genetic variability while advanced-generation lines are produced. SSD can be conducted in the target environment or in winter nurseries or greenhouses where several generations of common beans can be produced each year. Macchiavelli and Beaver (2001) noted that grain legume breeders often bulk seed harvested from pods rather than single seeds. Although the bulking of multiple seed from each pod reduces genetic variability, they demonstrated that, on average, every third F_6 line would be derived from

a different F_2 plant. Although SSD is widely used by soybean breeders, its use by common bean breeding programs has been limited. Common bean breeders usually deal with a wide array of traits whereas soybean breeders generally focus on increased seed yield. Concentration on the improvement of a single trait would favor the use of SSD (JD Kelly, personal communication).

SSD is a rapid method to develop recombinant inbred lines for traits that cannot be phenotyped in earlier generations. Because the development of bean breeding lines by SSD and other breeding methods is costly, an important potential contribution of genome mapping and molecular plant breeding techniques would be the identification of parents for crosses that would improve the likelihood of producing desired genotypes. Since SSD is more difficult to manage on a large scale, breeders often use this technique for specific purposes such as genetic studies (Fehr 1987).

Gamete selection

Singh (1994) proposed the use of gamete selection to simultaneously select common beans for multiple traits. Gamete selection proved to be successful in the development of high-yielding, erect bean lines with resistance to leafhoppers and five diseases (Singh et al. 1998). Asensio-S.-Manzanera et al. (2006) also used gamete selection to develop breeding lines with resistance to common bacterial blight and halo blight. In breeding for multiple traits, gamete selection permits the early generation evaluation of the potential value of breeding populations. Populations that do not segregate for desired traits in early generations can be discarded, thus avoiding the loss of valuable time and resources. However, Singh et al. (1998) noted that labor-intensive nature of gamete selection permits the evaluation of only a few populations and that much care should be taken in the selection of parents that possess the desired traits. Gamete selection may be most effective in pyramiding simply inherited traits or traits that have QTLs with large effects. Molecular markers may facilitate gamete selection in the identification of early-generation populations that continue to possess the desired alleles (Singh et al. 1998). Liu et al. (2004) found in computer simulations that marker-assisted selection of self-fertilized crops was more advantageous in earlier generations. Marker-assisted selection in early

generations allows the elimination of breeding lines having inferior genotypes while maintaining sufficient variability to produce superior breeding lines in later generations. However, the evaluation of large populations for multiple markers would be expensive and time-consuming unless robotics were used (TG Porch, personal communication).

Bulk breeding

If multiple generations can be grown each year, bulk breeding can be used to rapidly advance bean populations. This approach would be most appropriate for crosses between elite lines within a market class where little segregation for seed type or adaptation would be expected. If the bulked populations are grown in the target environment, some natural selection may occur for traits of economic value. Renato Corte et al. (2002) evaluated the effect of natural selection on the seed yield of bulked bean populations evaluated each year in Brazil at three planting dates having diverse climatic conditions. They reported an average seed yield gain of 2.5% per generation over the mean yield of the parents.

Singh et al. (1990) conducted yield tests of early generation bulk populations. Using a selection intensity of 20%, gain in seed yield was reported to be >5% for the F_3 and F_4 generations. The higher-yielding populations could be used for individual plant selection in later generations.

Plant breeders would need to advance large samples of the bulked population to avoid the effects of genetic drift. Molecular plant breeding techniques might be used to monitor genetic variability in bulked populations to determine an adequate sample size for breeding common beans. Plant breeders must also avoid planting bulked populations in environments where natural selection would favor genotypes considered undesirable (Fehr 1987).

Recurrent selection

Recurrent selection permits the accumulation of favorable alleles as the result of recombination in each cycle of selection. Kelly and Adams (1987) used phenotypic recurrent selection to develop pinto bean lines having desired architectural traits and seed type. Because F_2 plants could be evaluated for plant type and seed traits, each cycle of selection

could be completed in shorter period of time than most recurrent selection schemes. Nevertheless, three cycles of selection were required to break up undesirable linkages and produce lines having the desired combination of traits. Singh et al. (1999) used recurrent selection based on S_1 evaluations to increase seed yield of inter-racial (Middle American) and inter-gene pool (Middle American \times Andean) bean populations. Patto Ramalho et al. (2005) evaluated S_2 and S_3 lines for seed yield in several environments to obtain more precise estimates of yield and to reduce the effects of genotype \times environment interaction. The mean annual gain for seed yield after four cycles of recurrent selection was 5.7%. Their recurrent selection scheme included new lines during each period of recombination to increase genetic variability and to introduce new traits. Ranalli (1996) used recurrent selection based on S_2 progeny testing to increase seed yield in a common bean population. Broad sense heritabilities for seed yield did not decrease after three cycles of selection suggesting that further progress could be made in the selection for this trait. García et al. (2003) used recurrent mass selection to select bean populations in Mexico with greater resistance to soil-borne diseases caused by *Pythium* spp., *Rhizoctonia solani*, *Macrophomina phaseolina*, and *Fusarium* spp. Breeding lines were developed that produced greater seed yield and higher survival rates than the parents and commercial varieties. Recurrent selection was used by Pereira et al. (1993) to increase nodule number and nodule weight of 21 to 28-day-old bean seedlings grown under controlled conditions. Seedlings with superior nodule number were replanted and used as parents in a crossing block. Seedlings of the F_1 plants with the greatest number of nodules were selected for use as parents for the next round of selection. This selection scheme permitted three periods of selection to be completed in a single year. Caixeta Franco et al. (2001) also recommended the use of recurrent selection to increase the frequency of alleles associated with enhanced biological nitrogen fixation. However, they suggested the evaluation of advanced lines in replicated trials would be needed to obtain more precise estimates of their performance.

Johnson and Gepts (2002) noted that cultivars in different gene pools have developed unique

combinations of genes for adaptation and the expression of seed yield. As a consequence, lines developed from inter-gene pool crosses usually have poor performance due to the breakup of these favorable gene complexes within each gene pool. Recurrent selection provides additional opportunities for recombination and the formation of new gene complexes that could lead to better adaptation or greater seed yield potential in lines from inter-gene pool crosses.

Participatory plant breeding

In many developing countries, participatory plant breeding techniques are being used to develop, multiply and distribute seed of improved bean cultivars (Danial et al. 2007). This de-centralized approach to plant breeding allows participation of farmers in the development, evaluation and selection of bean breeding lines (Mazón et al. 2007; Morris and Bellon 2004). New approaches need to be identified that permit knowledge from genomic mapping and molecular breeding to be used in participatory plant breeding (PPB) schemes (Machuka 2001).

The bean breeding program at the Escuela Agrícola Panamericana (EAP) in Honduras (Rosas et al. 2003b) and the grain legume research program of the Instituto Nacional Autónomo de Investigaciones Agropecuarias (INIAP) in Ecuador (Mazón et al. 2007) have successfully utilized PPB techniques to develop and release improved cultivars. Local research committees participate in the evaluation and selection of plants and bean breeding lines in the communities where the variety is expected to be released. Both the EAP and INIAP bean breeding programs assist farmers in the selection of parents for the PPB programs and utilize molecular markers to confirm the presence of specific genes for disease resistance before cultivars are released.

Most bean breeders seek input from stakeholders. Conventional plant breeding programs often conduct on-farm trials, host field days and meet with growers. In the U.S., bean growers and shippers use funds generated from the marketing of beans to support bean breeding activities at public universities (Michigan Bean Commission 2007). Bean breeders interested in using a more PPB approach should be prepared to adapt methods to the biophysical condi-

tions and the socioeconomic and cultural context in which they plan to work (Sperling et al. 2001). Morris and Bellon (2004) noted that PPB may be well suited for the development of a variety that needs to possess a unique combinations of traits, such as a specific bean type for a niche market. Breeding objectives for PPB programs need to be realistic (Sperling et al. 2001). For example, it should be recognized that there may be trade-offs between selection for traits such as earlier plant maturity and greater seed yield potential. Population size needs to be large enough to permit genetic progress for the traits under selection. Effective screening techniques also need to be employed. Finally, PPB programs need to be linked to effective seed multiplication and distribution systems to achieve results.

Research networks with international bean centers such as CIAT or universities may provide opportunities for bean research programs in small countries in the developing world to obtain access to molecular tools used for plant breeding (Ishitani et al. 2004). CIAT scientists and national research programs have used molecular techniques to study the genetic variability of bean breeding lines in Central America (Beebe et al. 2000; Beebe et al. 1995) and bean landraces from the Caribbean (Durán et al. 2005). International bean research centers or universities could assist national bean research programs in the use of molecular markers by local breeding programs. Selection for adaptation, agronomic traits, seed type and field screening for disease and pest resistance could be conducted by national bean research programs whereas the international bean research centers could assist national programs by screening advanced lines using molecular markers for resistance to specific bean diseases or pests or for micronutrient content.

Regional cooperative nurseries conducted by bean research networks provide valuable information concerning the range of adaptation of bean breeding lines. Results from regional performance trials could be used to obtain a better understanding of the importance of genotype \times environment ($G \times E$) interaction in the expression of seed yield and other traits of economic value. There may be opportunities for molecular scientists to gain a better understanding of the basis of $G \times E$ interaction by collaborating with bean research networks.

A few examples of conventional bean breeding achievements in common bean

Extending the range of adaptation of beans to non-traditional production regions and new production practices

Using conventional plant breeding techniques, bean breeders have been successful in extending the range of adaptation of dry edible beans. During the past 30 years, bean production in North America has expanded into North Dakota and the plains of Canada. This expansion would not have been possible without the development of bean cultivars that are adapted to these new environments. In traditional bean production regions such as Michigan, bean breeders have created new opportunities for producers by developing new market classes of beans that are locally adapted (Kelly 2001). In response to increased interest in direct mechanical harvest, as well as planting beans at narrower row widths, breeders have developed new cultivars with a more erect growth habit (Vandenberg and Nleya 1999; Kelly 2001; Kelly et al. 2008; Osorno et al. 2008).

Greater demand for beans in Central America generated interest in planting beans at lower altitudes using cultivars that possessed better heat tolerance (Rosas et al. 2000b). Bean lines from CIAT such as DOR 364, which were originally screened at lower altitudes in Guatemala for resistance to BGYM, expressed tolerance to higher temperatures (Beebe et al. 1995). The EAP bean breeding program in Honduras used DOR 364 and other sources of heat tolerance to develop small red bean cultivars such as ‘Amadeus 77’ that have permitted the expansion of bean production at lower altitudes throughout Central America (Rosas et al. 2004; Rosas et al. 2003a; Rosas et al. 2000b).

Myers and Baggett (1999) note that one of the greatest challenges facing snap bean breeders is the difficulty of incorporating novel traits without breaking up the desired complex of snap bean pod traits. Plant breeders in Oregon, however, were successful using conventional plant breeding techniques to develop determinate snap bean cultivars suitable for mechanized harvest that maintained the desirable horticultural characteristics of ‘Blue Lake’ pole beans (Kelly 2001).

The discovery, characterization of variability and deployment of genes for resistance to fungal bean diseases

Fungal diseases are major constraints to bean production throughout the world (de Jesus Junior et al. 2001; Schwartz et al. 1981). The relative importance of different fungal diseases varies among regions due to differences in soil, climate, crop management practices and degree of susceptibility of cultivars used by bean producers (Boland et al. 2004; Hall and Nasser 1996; Mmbaga et al. 1996b). The degree of virulence among isolates of some fungal pathogens can also vary between regions and over time. This has been observed for many bean pathogens such as rust (Araya et al. 2004; Sandlin et al. (1999); Mmbaga et al. 1996a), anthracnose (Ansari et al. 2004; Balardin et al. 1997), web blight caused by *Thanatephorus cucumeris* (Godoy-Lutz et al. 2003), angular leaf spot caused by *Phaeoisariopsis griseola* (Mahuku et al. 2002; Pastor-Corrales et al. 1998) and ashy stem blight caused by *Macrophomina phaseolina* (Tassi) Goid. (Reyes-Franco et al. 2006).

Plant breeders, pathologists and geneticists have made considerable progress in the identification of specific genes and QTL for resistance to anthracnose (Kelly and Vallejo 2004); angular leaf spot (Teixeira Caixeta et al. 2005); rust (Pastor-Corrales 2003); white mold (Maxwell et al. 2007; Schwartz et al. 2006; Ender and Kelly 2005; Kolkman and Kelly 2003; Miklas et al. 2001) and ashy stem blight (Mayek-Pérez et al. 2001). In addition, specific genes or QTL for resistance to many fungal diseases have been mapped, including rust (Kelly et al. 2003; Miklas et al. 2006b); ashy stem blight (Miklas et al. 2006b); anthracnose (Kelly and Vallejo 2004); white mold (Kolkman and Kelly 2003; Park et al. 2001; Miklas et al. 2001); and Fusarium wilt (Fall et al. 2001). Tar'an et al. (2003) noted, however, that the efficiency of marker-assisted selection depends on the number of markers available and the degree of linkage of the marker with the desired QTL. Because of this limitation, only few of the most reliable markers are being used routinely by bean breeding programs. Bernardo (2008) noted that only a very small portion of the thousands of marker-trait associations reported in different plant species (~10,000 QTLs) are currently being used by plant breeding programs. The author concluded that the development and use of

molecular markers by a plant breeding programs requires that: (i) the purpose of detecting the QTL be clearly defined before embarking on QTL mapping; (ii) the marker-based selection procedures be based on the number of QTL available for selection; (iii) gain per unit cost and time should be considered rather than gain per cycle and (iv) recognition that estimates of QTL effects for complex traits are often inconsistent.

Breeding beans for virus resistance

Bean common mosaic virus (BCMV) and Bean common mosaic necrosis virus (BCMNV) are seed-transmitted potyviruses that pose a serious threat to bean production throughout the world (Miklas et al. 2006b). Bean breeders and geneticists have identified and deployed several different genes for resistance to these important viral diseases. Staveland et al. (1989) released BelNeb RR-1 and BelNeb RR-2 germplasm with the *bc-1²* and *bc-2²* genes that provide resistance to BCMV and BCMNV. The dominant *I* gene provides broad protection against many strains of BCMV and other potyviruses but is vulnerable to the necrotic strains of BCMNV (Miklas et al. 2006b; Kelly et al. 1995). Melotto et al. (1996) developed the SCAR marker SW13 which has been widely used to screen both Andean and Mesoamerican bean breeding lines for the presence of the *I* gene. Pyramiding the dominant *I* gene with the recessive gene *bc-3* provided resistance to all known strains of BCMV and BCMNV (Kelly et al. 2003). Plant breeders have screened lines with the SCAR marker SW13 and with a virulent strain of BCMNV (NL-3) to develop cultivars such as ‘Raven’ (Kelly et al. 1994) and Middle American and Andean bean germplasm (Pastor-Corrales 2003; Miklas and Kelly 2002; Beaver et al. 1998) that combine the dominant *I* gene and the recessive *bc-3* gene. Mukeshimana et al. (2005) identified a RAPD marker (OG6₅₉₅), and a codominant AFLP marker (E_{ACA}M_{CGG}-169/172) that was converted to the STS marker (SE_{ACA}M_{CGG}-134/137) which were linked to the *bc-3* resistance gene. These markers may permit indirect selection for resistance to BCMNV.

The whitefly (*Bemisia tabaci* Genn.) transmitted geminivirus Bean golden yellow mosaic virus (BGYMV) can significantly reduce bean yields in Mexico, Central America and the Caribbean (Blair

et al. 2007b). Initial sources of resistance to BGYM were identified in bean germplasm screened in Guatemala by CIAT and ICTA scientists. Adequate levels of resistance to BGYMV were not achieved until different genes for resistance were pyramided into bean breeding lines (Singh et al. 2000). The most BGYMV resistant cultivars such as ‘Don Silvio’ (DOR 482) and ‘Morales’ (Beaver and Miklas 1999) combine the recessive gene *bgm* for resistance to leaf chlorosis (Blair et al. 2007b; Velez et al. 1998), the dominant gene *Bgp* for resistance to pod deformation in the presence of BGYMV (Acevedo-Román et al. 2004) and the QTL SW12 that is associated with delayed symptom expression (Miklas et al. 1996). The SCAR marker SR-2 has facilitated the deployment of the recessive gene *bgm* into snap beans and different seed types of dry edible beans (Blair et al. 2007b). The SW-12 and SR-2 SCAR markers also permit breeding programs at locations where BGYMV is not present to incorporate resistance to this important disease without the need to initially inoculate plants with the virus. Results from a survey conducted in 2001 found 41–46% of bean farmers in two principal bean-producing regions of Honduras to have adopted BGYMV resistant bean varieties (Mather et al. 2003). The incidence of BGYMV in Puerto Rico decreased drastically after the release of resistant cultivars (Osorno et al. 2007).

In Brazil, another whitefly-transmitted geminivirus, Bean golden mosaic virus (BGMV), is a serious threat to bean production (Blair et al. 2007b; Morales 2006). Bean researchers in Brazil used pedigree and bulk breeding methods combined with field screening under natural conditions to develop and release bean cultivars, IAPAR 57 (MD 806) and IAPAR 65 (MD 821), that have high levels of resistance to BGYM (Bianchini 1999). Recently, a transgenic approach using RNAi was used successfully to engineer BGMV virus resistance in Brazil (Bonfim et al. 2007).

In the semi-arid regions of Northwestern U.S., the beet leafhopper (*Circulifer tenellus*) transmitted geminivirus Beet curly top virus (BCTV) is an endemic disease that can cause yield loss in beans, sugar beets (*Beta vulgaris* L.), and certain vegetable crops (Larsen and Miklas 2004). The dominant gene *Bct* in bean has provided durable resistance to BCTV. Unfortunately, field screening for the disease has proven to be difficult because disease infection is

sporadic and greenhouse evaluations are complex because the virus cannot be transmitted mechanically. Larsen and Miklas (2004) developed a SCAR marker (SAS8.1550) directly linked to the *Bct* gene that has been outsourced by snap bean breeding companies through a commercial marker laboratory (PN Miklas, personal communication) for marker-assisted selection of snap beans and Andean dry beans for BCTV resistance. The SCAR was mapped on linkage group B7 of the core map within a cluster of disease resistance genes.

Plant breeders, plant pathologists and geneticists have identified resistance genes for several other viruses that can infect the common bean; *Bcm* for resistance to Blackeye cowpea mosaic virus, *Bpm* for resistance to Bean pod mottle virus resistance, *Bsm* for Bean southern mosaic virus, *By-1* and *By-2* for Bean yellow mosaic virus, *Bdm* for Bean dwarf mosaic virus, *Cam* for Cowpea aphid mosaic virus and *Mrf* and *Mrf²* for Bean rugose mosaic virus (Porch 2008; Jahn 2008). At present, many of these resistance genes have not been mapped onto the common bean genome (Bean Improvement Cooperative 2008). Mapping would help determine if some of these dominant resistance genes are present in clusters with other resistance genes.

The use of interspecific crosses to develop cultivars and improved bean germplasm

Interspecific hybridizations between the common bean and the scarlet runner bean (*Phaseolus coccineus* L.) and the tepary bean (*Phaseolus acutifolius* L.) have been conducted since the middle of the nineteenth century (Debouck 1991). The scarlet runner bean was originally considered to be a variety of common bean which may have encouraged scientists to make hybridizations (Debouck 1999). Many pollinations are required to produce interspecific F_1 seed and this seed may require special treatment to produce plants (Freitag and Debouck 2002; Debouck 1991, 1999). Embryo rescue techniques are often needed to ensure the survival of interspecific F_1 hybrids (Mejía-Jiménez et al. 1994). In addition, the choice of the common bean parent can affect the rate of success of the interspecific crosses. Cultivars such as ‘ICA Pijao’ that are double recessive for the *dl₁* and *dl₂* dwarf lethal genes (Singh and Gutiérrez 1984) have proven to be most useful for interspecific

crosses. Broughton et al. (2003) suggested that molecular markers could be used to help reduce or remove barriers to inter-specific hybridization. Mejía-Jiménez et al. (1994) reported that recurrent and congruity backcrossing improved the rate of success of interspecific crosses between common and tepary beans.

Bean researchers have successfully used conventional plant breeding techniques to introgress traits of economic value from the tepary bean and the scarlet runner bean into common bean. Breeding objectives include the development of beans as an ornamental plant (Lamprecht 1945), the transfer of disease resistance (Abawi et al. 1978; Baggett, 1956; Hubbeling, 1957; Singh and Muñoz 1999; Beaver et al. 2005; Schwartz et al. 2006), the improvement of abiotic stress tolerance (Bannerot 1979) and the enhancement of seed yield potential (Wilkinson 1983).

Common bacterial blight (CBB) caused by *Xanthomonas axonopodis* pv. *phaseoli* (Smith) Dye is an important seed-borne disease in common bean. Bean breeders have been able to identify only moderate levels of resistance to CBB in common bean (Coyne and Schuster 1973; Yoshii et al. 1978) whereas high levels of resistance has been identified in some tepary bean lines (Urrea et al. 1999; Singh and Muñoz 1999). Results from inheritance studies suggested that common bacterial blight resistance in tepary bean lines was controlled by few genes (McElroy 1985; Urrea et al. 1999). In 1989 CIAT scientists initiated an effort to introgress tepary bean resistance into common bean (Singh and Muñoz 1999). After the interspecific (*P. vulgaris* × *P. acutifolius*) populations were developed, breeding lines were screened in the field in Colombia for several generations during a five-year period in order to identify breeding lines with high levels of resistance to common bacterial blight. Some of the lines with the highest levels of CBB resistance such as VAX 3, VAX 4, and VAX 6 pyramid resistance genes from tepary and common beans (Singh and Muñoz 1999). These authors noted that one of the biggest problems with breeding for CBB resistance derived from tepary beans is the instability of the expression of resistance. The SU-91 SCAR marker is currently being used in the transfer of the tepary-derived common bacterial blight resistance into different market classes of beans (Kelly et al. 2003; Miklas et al. 2006c). The use

of the SAP-6 SCAR marker to screen for CBB resistance is limited to bean lines of Andean origin because many susceptible Middle American bean lines have the SAP-6 marker (Kelly et al. 2003).

Researchers in France and Canada have identified *P. angustissimus* as a potential source of cold tolerance (Buhrow 1980; Balasubramanian et al. 2004). Interspecific crosses have been made to initiate the transfer of this trait to common beans, but success has been very limited (Belivanis and Doré 1986; Schryer et al. 2005; Gurusamy et al. 2007).

Koinange et al. (1996) reported that many of the genes associated with the domestication of common bean were concentrated in three genomic regions. The simple genetic control of most traits related to the domestication of beans should facilitate the introgression of genes from wild beans to cultivated lines. Papa and Gepts (2003) noted that greater knowledge of the location of genes related to the domestication of common bean is needed to be able to exploit the genetic variability linked to the domestication loci.

Tanksley and McCouch (1997) noted that the genetic potential available in crop germplasm collections can be made more readily available to plant breeders by the identification of superior genes and the utilization of information in genetic linkage maps. Tanksley and McCouch (1997) also suggested that unadapted lines may possess desirable alleles for quantitative traits that may not be present in elite lines. Phenotypic selection cannot identify these desirable alleles in unadapted lines.

New genes for resistance to important bean diseases such as BGYM (Osorno et al. 2007) and white mold (Schwartz et al. 2006) have been recently identified in scarlet runner bean. Interspecific crosses between common and scarlet runner bean have been used to develop bean germplasm lines with a novel source of resistance to BGYM (Beaver et al. 2005), BGM (Bianchini 1999) and common bacterial blight (Freytag et al. 1982; Miklas et al. 1999; Zapata et al. 1985).

Drought tolerance

Drought is a widespread and important constraint to bean production (Beebe et al. 2008; Terán and Singh 2002; Ramirez-Vallejo and Kelly 1998). Broughton et al. (2003) reported that 74% of the beans in Latin

American and 40% of beans produced in Africa suffer from moderate to severe drought stress sometime during the growing season. Greater drought tolerance and improved water use efficiency is expected to gain importance as a trait for selection by plant breeding programs because of increased production of beans and other grain legumes on drought-prone land (Graham and Vance 2003). The potential for water stress will also increase as global temperatures continue to rise (Battisti and Naylor 2008; Rosenzweig et al. 2000). The timing and duration of the water stress are critical in determining potential yield loss and the possible response of bean plants to drought.

Plant breeders have been able to exploit different mechanisms to cope with drought stress (Chaves et al. 2003). Early maturity can be used to avoid terminal drought although earliness and seed yield are often negatively associated. Rosales-Serna et al. (2004) noted that in the semi-arid highlands of Mexico the bean cultivar ‘Pinto Villa’ was able to reduce the impact of drought on seed yield by accelerating maturity while simultaneously maintaining a high rate of seed fill. Beebe et al. (2008) identified bean lines with greater yield potential in both drought and non-stress environments. They hypothesized that certain phenotypic traits expressed under drought stress such as delayed flowering may limit seed yield potential and that the elimination of this drought response may increase yield potential in both stress and non-stress environments.

Deep roots improve the ability of bean plants to absorb soil moisture under drought conditions (Lynch 2007). However, the evaluation of root systems poses a challenge for plant breeders. Traditional methods for the evaluation of roots is labor-intensive and expensive (Lynch 1995). Moreover, the development of the root system is influenced by biotic factors such as root rots and abiotic factors such as soil compaction, and constraints in soil moisture, pH and fertility (Rao 2001). A better understanding of the genetics of the expression of root traits would permit the development of molecular markers that might permit indirect selection for improved tolerance to drought and other traits associated with roots (Lynch 2007). Schneider et al. (1997) used marker-assisted selection (5 RAPD’s) to identify lines with superior performance under drought stress whereas phenotypic selection based on seed yield performance was not successful.

Greater resistance to root rots associated with drought such as ashy stem blight or *Fusarium* root rot would promote root systems that are more efficient in the absorption of the moisture available in the soil (Singh et al. 2001a; Miklas et al. 1998b). Román-Avilés and Kelly (2005) reported a QTL associated with *Fusarium* root rot resistance in bean which should also contribute to drought resistance. Román-Avilés et al. (2003) noted that the identification of genetic differences in growth patterns of roots may provide criteria for selection for root rot resistance under drought stress. Greater resistance to pests, such as leafhoppers (*Empoasca* spp.), may also help to protect a drought-stressed leaf canopy (Schaafsma et al. 1998).

Limitations of traditional breeding and a rationale for molecular breeding

Adaptation to low soil fertility and Al tolerance

Deficiencies and toxicities of minerals in soils are common seed yield constraints for bean producers (Singh et al. 2003b). Broughton et al. (2003) reported that 50% of the beans in Latin America and almost 75% of the beans in Africa are planted in soils deficient in P. In addition, tropical soils often have low pH, that can result in Al and/or Mn toxicity (Gonzalez and Lynch 1999). Lynch (2007) cites several factors that can limit the success of field screening for adaptation to low soil fertility, including spatial variability in the level of fertility, pH, compaction of the soil and confounding effects caused the presence of other abiotic, biotic or environmental constraints. The development of beans with greater tolerance to these soil-related constraints would help to reduce production costs and permit farmers to produce beans on more marginal land. Singh et al. (2003b) noted that farmers often encounter deficiencies or toxicities to more than one soil-related constraint which may require the development of cultivars that have more general adaptation to acid or low fertility soils. Due to the importance of genotype \times environment interaction in the expression of seed yield in low soil fertility environments, Singh et al. (2003b) advocated the evaluation of advanced lines in multiple environments. Because plant scientists cannot directly observe root traits,

molecular breeding may prove to be a particularly useful tool.

Low soil P is an important constraint to bean production in Africa and Latin America (Lynch 2007; Wortman et al. 1998; Lynch and Beebe 1995). The application of fertilizers is not an economically viable option for many small-scale bean producers in developing countries (Kimani et al. 2007). In addition, the recovery of P from fertilizers applied to tropical soils is often low (Araújo et al. 2005). Adaptation of beans to low P soils is associated with mycorrhizal symbiosis, the abundance of root hairs and the exudation of organic acids (Lynch and Brown 2001). Yan et al. (1995) reported significant genetic variability in P efficiency among common bean cultivars and lines. Kimani et al. (2007) studied the inheritance of tolerance of beans to low P soils in Kenya using an 8×8 half diallel of Andean bean lines. Significant general combining ability (GCA) was reported for agronomic and root traits associated with greater P tolerance. Araújo et al. (2005) studied the inheritance of root traits and P uptake of beans of Middle American origin in a low P soil in Brazil. They reported intermediate ($0.4 \leq 0.6$) broad sense heritabilities for root area, root length, root weight and total P content and significant and positive genotypic correlations between shoot weight and root weight and shoot weight and total P uptake. Therefore, selection for greater bean shoot weight in a low P soil should result in greater P efficiency. Selection for drought resistance in Colombia produced bean lines that also had greater plant efficiency (seed yield day^{-1}) and superior performance in a low P soil (Beebe et al. 2008). Beebe et al. (2006) and Liao et al. (2001) identified QTL for root architecture traits associated with P acquisition in common bean.

Lynch and Brown (2001) noted that an ideal root architecture should optimize soil nutrient acquisition at the lowest possible metabolic cost. Beans use topsoil foraging as a means to adapt to low P soils (Lynch and Brown 2001). However, selection for topsoil foraging may be negatively associated with the ability of bean plants to mine water at lower soil depths to tolerate drought stress (Lynch and Brown 2001). Yan et al. (2004) identified multiple QTLs for greater total acid exudation and longer and more dense basal root hairs; traits that were associated with greater P efficiency in the field.

Tesfaye et al. (2001) reported that over-expression of malate dehydrogenase in transgenic alfalfa (*Medicago sativa* L.) resulted in enhanced exudation of organic acids in root tips which should lead to greater tolerance to aluminum. A similar approach might be used to develop transgenic common beans with enhanced tolerance to Al.

Biological nitrogen fixation (BNF)

Low soil N limits bean production throughout the world (Hungria et al. 2003). The application of N increases production costs and, in some intensive bean production systems, can contribute to groundwater contamination (Graham and Vance 2003). Although a legume, the common bean is not considered an efficient fixer of N (Caixeta Franco et al. 2001; Vadez et al. 1999). This may be due, in part, to the short growing season (<90 days) of common bean compared with other grain legumes such as soybeans (~120 days) and to the promiscuous nodulation with native rhizobia (Caixeta Franco et al. 2001). In addition, biological nitrogen fixation in common bean is sensitive to abiotic stresses such as drought and high temperatures (Hungria and Vargas 2000). Hungria et al. (2003) reported a synergistic effect between low levels of N fertilizer application (15 kg ha⁻¹ at planting and early flowering) and biological nitrogen fixation. Greater N fixation would help to reduce production cost for farmers, increase seed yield in marginal environments, and reduce groundwater contamination where irrigated beans are produced using high levels of N fertilizer.

Pereira et al. (1993) reported that three cycles of recurrent selection of beans of Middle American origin for increased nodule number in a controlled environment resulted in greater biological nitrogen fixation in the field. They noted that direct selection in the field for nodule number and other root traits associated with BNF is not practical due to the difficulty of extracting the root system from the soil. Indirect selection for enhanced BNF can be conducted in the field on low-N soils that receive little or no fertilizer. Miranda and Bliss (1991) recommended the evaluation of bean lines in replicated trials in low N environments using total seed nitrogen as a criteria for selection. Araújo and Grandi Teixeira (2003) reported large and positive phenotypic correlations between seed yield and total seed nitrogen and total

seed phosphorous. They also found indeterminate bean lines with floppy (Type III) growth habits to have greater N and P harvest indices than erect (Type II) bean lines. Caixeta Franco et al. (2001) identified bean lines of Andean origin that had significant positive GCA for nodule number/plant and mean nodule weight. They recommended the use of a recurrent selection program using a large base population and the evaluation in more advanced generations as a strategy to increase the frequency of favorable alleles for BNF. Vadez et al. (1999) identified significant variability in the tolerance for biological nitrogen fixation to low levels of P. The most tolerant indeterminate lines were BAT 271, ICA Pijao and 'San Cristobal 83' (G17722).

Vásquez-Arroyo et al. (1998) encountered a large amount of variability in nitrogen fixation efficiency among native strains of *Rhizobium etli* in Mexico although nodules on the bean roots were mostly occupied by inefficient strains. *Rhizobium tropici*, which is more adapted to acid soils and higher temperatures than other species of *Rhizobium* (Hungria et al. 1993), increased BNF in oxisols in southern Brazil when used as an inoculum on common bean (Hungria et al. 2003).

Giongo et al. (2007) reported that in a greenhouse trial conducted in Brazil, 'Mexico 309' selected the most efficient rhizobia strains which resulted in the greatest dry weight and nitrogen content. Rosas et al. (1998) described a screening technique that was used to identify lines that preferentially nodulated with an efficient strain of *Rhizobium etli*. The availability of molecular markers associated with preferential nodulation would facilitate the selection for this trait. Graham and Vance (2003) noted that the formation of root nodules for biological nitrogen fixation requires signaling between the host and the microsymbiont and that this process involves the expression of numerous genes. Molecular breeding and genomic approaches may permit the manipulation of both the host plant and the bacteria to enhance BNF (Tsai et al. 1998; Werner 2005).

A better understanding of the expression of seed yield and $G \times E$

$G \times E$ affects the range of adaptation of bean breeding lines and cultivars (Singh et al. 2007). Hoogenboom and White (2003) noted that the use of

crop models by plant breeding programs has been limited due to an inability to simulate genetic differences in yield among bean cultivars and breeding lines. White and Hoogenboom (1996) developed the simulation model for common bean, GeneGro, to estimate differences among bean genotypes based on the effects of seven genes. In a subsequent study, Hoogenboom et al. (1997) found the GenGro model to be a good predictor of phenological traits such as days to flowering and maturity in common bean but a poor predictor for the quantitatively inherited trait seed yield. Hoogenboom and White (2003) noted that a better understanding of the expression of quantitatively inherited traits would help to improve the predictive ability of simulation models.

Kelly et al. (1998a) noted that the expression of seed yield may vary among beans of diverse origin. White and Hoogenboom (2003) suggested that an increased availability of molecular markers and genomic maps associated with the expression of physiological traits would help to characterize genetic differences and should lead to improvements in the crop model. However, the generation of information useful for further refinement of the crop model will require collaboration from a wide range of disciplines.

Singular value decomposition analyses such as GGE biplots (Gabriel 1971; Yan et al. 2000), Additive Main Effects and Multiplicative Interaction (AMMI) (Gauch 1992), and Principal Component Analysis (PCA), are often used to better understand $G \times E$ interaction (Gauch 2006). Many of these approaches permit a graphic representation of multi-environment data collected from field trials (Yan et al. 2000). The GGE biplot provides a useful tool for data analysis and allows the visual appraisal of the structure of large data matrices (Laffont et al. 2007; Yan 2001). However, a drawback of these approaches is the lack of appropriate methods to measure statistical significance (JJ Hammond, personal communication). Kang et al. (2006) used the GGE biplots approach to evaluate and enhance the efficiency of bean breeding/testing locations in Africa. The authors used bean data from multi-environment trials made between 1995 and 2002. GGE biplot methodology helped to identify redundant and/or non-informative locations, as well as locations that showed greater differentiation among cultivars. This suggested that the number of testing locations could be reduced,

hence making a more efficient use of the program resources and allocations. A better understanding of the genetic and physiological basis of genotype \times environment interaction is needed to more effectively map and utilize genetic markers for traits such as seed yield that are influenced by environmental conditions.

Molecular markers

Marker-assisted selection has become a common tool used in many common bean breeding programs (Miklas et al. 2006b; Kelly et al. 2003). Marker-assisted selection permits the indirect selection of traits in the absence of selection pressure for the trait. For example, bean breeders can screen for genes for a disease resistance without running the risk of introducing the disease agent. Because disease resistance genes are often present in clusters, bean breeders should be aware of the risk of introducing susceptibility to a different disease if the target gene and a gene for susceptibility are linked (Michelmore 1995).

Many recent bean germplasm and cultivar releases have used molecular markers for trait selection or for confirmation of the presence of a specific gene (Table 1). Pastor-Corrales et al. (2007) used the SW-13 SCAR to confirm the presence of the *I* gene for BCMV resistance in the development of great northern bean germplasm with multiple disease resistance. Miklas et al. (2006c) used marker-assisted selection to identify plants with the SCAR markers SU-91 and SAP-6 in the development of the common bacterial blight resistant dark red kidney germplasm USDK-CBB-15. Miklas et al. (2003) used the SCAR marker SAS-13 to develop pinto bean germplasm having the *Co-4²* gene for anthracnose resistance. Blair et al. (2006a) used the SCAR marker SR-2 to confirm the presence of the recessive gene *bgm* for resistance to BGYMV in red mottled bean germplasm after results from screening with the SCAR marker SW-12 suggested that the red mottled germplasm lines did not have a QTL associated with BGYMV resistance. Miklas (2007) used marker-assisted backcrossing of two QTL to introgress partial resistance to white mold into pinto and great northern breeding lines. In this case, marker-assisted selection permitted the selection for physiological resistance to white mold without the confounding effects of traits related to disease avoidance. This approach may be useful

for breeding for resistance to other bean diseases such as web blight.

Miklas et al. (2006b) and Kelly et al. (2003) provide numerous examples of the effectiveness of molecular markers in the selection of bean lines with enhanced resistance to disease and pests and greater tolerance to abiotic stress. Problems with current molecular markers include the specificity of some markers to only one gene pool (Miklas et al. 2006b). As more genes are cloned and sequenced, Michelmore (1995) noted that it should be possible to design specific molecular markers for specific alleles. The rapid evolution in technology makes it difficult for bean breeding programs in many developing countries to adopt the most current techniques. Ideally, a marker for routine screening in a plant breeding program should be reliable, rapid and inexpensive (Michelmore 1995). Broughton et al. (2003) noted that molecular plant breeding techniques are an additional set of tools available to plant breeders. The most appropriate combination of conventional and molecular tools will depend upon the specific agricultural problem that needs to be addressed and the resources available (Bernardo 2008).

Utilization of information from the bean genome map

Classical mapping efforts

The common bean is diploid ($2n = 22$) with a genome size ranging from 450 to 650 Mbp/haploid genome [Bennett and Leitch (1995) cited in Broughton et al. (2003)].

The common bean is an autogamous plant species with a low percentage of natural outcrossing (Brunner and Beaver 1989) although environmental factors can influence the rate of outcrossing (Ibarra-Pérez et al. 1997). Genetic recombination in common bean breeding programs is achieved through manual pollinations conducted in the field or greenhouse.

Many specific genes for seed, morphological and phenological traits, and resistance to diseases have been identified by plant breeders, plant pathologists and geneticists (Porch 2008). Bassett (2007) published a comprehensive review of the genetics of seed coat color in common bean. There are, however, fewer specific genes identified for pest resistance,

tolerance to abiotic stress, nutritional quality and cooking characteristics of common bean.

Bassett (1991) used classical genetic techniques to develop a linkage map for common bean that contained 13 linkage groups with 46 marker genes. Different morphological and molecular markers (RFLP, RAPD, and SCAR) have been used to develop genetic maps for the common bean (Vallejos et al. 1992; Nodari et al. 1993).

An integrated linkage map was developed to line up the markers used in the different maps (Freyre et al. 2004). Blair et al. (2003) incorporated micro-satellite markers into the integrated linkage map. Pedrosa et al. (2003) integrated the information in the common bean linkage and chromosomal maps.

Michelmore and Meyers (1998) noted that clusters of genes for resistance to different pathogens or different races of the same pathogen are common in plants. Kelly et al. (2003) reported that genes for disease resistance are also concentrated in different regions of the common bean genome. Miklas et al. (2006b) noted the increased importance to bean breeders of understanding the physical arrangement of sequence diversity of these gene clusters. For example, Méndez-Vigo et al. (2005) found genes for resistance to anthracnose (*Co-3/Co-9*), rust (*Ur-5*) and the SW-12 QTL for resistance to BGYM to be linked. Rodríguez-Suárez et al. (2007) reported that the anthracnose resistance genes *Co-3/Co-9* and *Co-2* were organized in two clusters. They concluded that most anthracnose resistance genes could be organized in clusters of genes that confer race-specific resistance. The authors suggest that previously reported alleles could be haplotypes having different combinations of race-specific resistance genes.

Gaitán-Solís et al. (2002) noted that microsatellites or simple sequence repeats (SSR) are valuable genetic markers for studying genetic diversity and molecular mapping. Because the sequences flanking the repeat regions are highly conserved, polymerase chain reaction (PCR) oligonucleotide primers can be designed for the amplification of the repeat loci. Miklas et al. (2006a) noted that resistance gene analogs (RGA) can be cloned and targeted region amplified polymorphisms (TRAPs) can be developed and used as molecular markers or used to dissect gene clusters. Bioinformatics will help to aggregate and organize information from evolutionary genetics, structural and functional genomics and advances in

the biochemical, and the genetic and physiological basis of the expression of traits of economic importance (Broughton et al. 2003).

DNA fingerprinting to preserve the purity or protect the identity of cultivars

Private and public bean breeding programs will likely increase their use of utility patents and Plant Variety Protection certificates for bean cultivars to protect intellectual property rights. Nybom (1994) noted that DNA fingerprinting techniques can help plant breeders identify cultivars, estimate genetic relatedness of lines and conduct pedigree analysis. Recently, the same techniques were used to provide evidence of the lack of novelty of a bean cultivar that had received a U.S. utility patent (Pallottini et al. 2004).

Transgenic beans

Although genetic transformation has been reported for all major pulse crops, transgenic cultivars have not yet been commercially released (Eapen 2008). Factors that have contributed to the lack of progress in developing transgenic pulse crops include the difficulty in obtaining reproducible and repeatable results due to the lack of competent totipotent cells for transformation, the long period of time required to develop transgenics, lack of long-term funding, the absence of a coordinated research by the scientific community and, in some cases, an unfavorable public perception toward the use of transgenic crops (Dita et al. 2006; Eapen 2008).

Broughton et al. (2003) reported that efforts to transform common beans have had only limited success. At present, a rapid and efficient protocol to transform common beans does not exist. The first reports of transformed beans were made in the 1990's, by using particle bombardment (Russell et al. 1993; Aragao et al. 1996; Aragao et al. 2002). In Brazil, researchers used particle bombardment techniques to produce transgenic common bean lines with resistance to BGMV (Bonfim et al. 2007; Faria et al. 2006), however the rate of transformation efficiency was reported to be low (<0.7%). Zambre et al. (2005) reported the development of a reproducible *Agrobacterium tumefaciens*-mediated genetic transformation method for tepary bean. Interspecific crosses could be used to transfer traits from a

transformed tepary bean to common bean although this approach would be cumbersome, costly and time-consuming. Liu et al. (2005) reported successful transformation of kidney beans using Sonication assisted *Agrobacterium*-mediated transformation (SAAT). The authors reported that obtained transgenic kidney beans were more tolerant to soils with high salt content and drought conditions.

Because weed competition can significantly reduce seed yield, the development of transgenic beans with tolerance to herbicide would be a desirable characteristic for some bean production systems. Herbicide tolerance would also facilitate no-till bean production resulting in less soil erosion (Wolfenbarger and Phifer 2000). No-till bean production may be beneficial for bean production in the humid tropics by providing a mulch on the soil surface that would reduce the spread of web blight disease.

An important consideration for the development and release of transgenic beans in Latin America is the potential for contamination of wild bean populations with transgenes. Papa and Gepts (2003) reported that domesticated beans had measurable amounts of gene flow to wild beans. In the presence of transgenic beans, this gene flow may adversely affect the genetic diversity of landraces and wild relatives in centers of bean domestication. Acceptance of transgenic common beans will depend on public perception that the technology provides clear and lasting benefits to society without causing unnecessary risk to the environment or the health of the consumers.

Studies of diversity of landrace varieties, core collections and identification of germplasm most likely to have the desired traits

Amirul Islam et al. (2004) used molecular markers to demonstrate that there was a low degree of introgression from the Middle American gene pool in most Andean bean germplasm accessions from South America. On the other hand, Durán et al. (2005) used similar molecular techniques to demonstrate introgression between the Andean and Middle American gene pools in bean landraces from the Caribbean. Rosales-Serna et al. (2005) used AFLP markers to study the genetic relationship of Mexican bean cultivars and Blair et al. (2007a) used SSR markers to characterize Andean races of common bean. Their

results suggested that the morphological classification of all climbing beans as Peru race genotypes and all bush beans as Nueva Granada race genotypes is erroneous and that growth habit traits have been mixed in both races, requiring a re-adjustment in the concept of morphological races in Andean beans.

Molecular breeding (MAS) may be useful for the selection of the most effective alleles for disease resistance

Miklas et al. (2006b) noted that greater resistance to biotic factors and enhanced tolerance to abiotic constraints can benefit farmers using a wide range of production practices. Hillocks et al. (2006) also observed that as many as three diseases can simultaneously threaten a bean crop planted in Tanzania. Therefore, beans in the tropics, and in many temperate production regions, often need to be bred for resistance to multiple diseases or pests. Sorrells and Wilson (1997) noted that linkage between a marker and a trait may not be maintained in distantly related germplasm. This has been the case for common bean where the utility of many molecular markers is limited to either the Andean or Middle American gene pool (Miklas et al. 2006b). Yu et al. (2004) noted that plant breeders using marker-assisted selection need molecular markers that are stable, reproducible and easy to use. Verification of the magnitude of the effect of the QTL and an accurate chromosome map location are also needed to fully realize the potential of a marker for a breeding program (Liu et al. 2004).

Marker-assisted selection has already proven to be a valuable tool to screen for disease resistance. Breeding for specific disease resistance genes often requires artificial inoculations using specific isolates of pathogens. Artificial inoculations and the maintenance of pathogen populations are time-consuming and expensive. Yu et al. (2000) reported that screening bean lines for common blight resistance using the SCAR marker BC420 was about 1/3 less than the cost of screening beans for common blight reaction using conventional techniques. Moreover, marker-assisted selection using BC420₉₀₀ produced results in much less time than conventional screening techniques. The ability to obtain results before flowering may be critical when backcrossing traits. Yu et al. (2004) recently identified an SSR marker closely linked to

the BC420₉₀₀ marker. This co-dominant marker was more efficient than BC420₉₀₀ because lines heterozygous for common bacterial blight resistance could be identified in early generations.

Common bean breeders should be aware of the existence of multiple alleles for disease resistance genes. Melotto and Kelly (2000) reported that the *Co-1* locus for anthracnose resistance has multiple alleles (*Co-1*² and *Co-1*³). In addition, Young et al. (1998) identified multiple alleles for other anthracnose resistance genes (*Co-3* and *Co-3*²; *Co-4* and *Co-4*², respectively). Teixeira Caixeta et al. (2005) reported that four dominant genes for resistance to angular leaf spot (*Phg-2*, *Phg-3*, *Phg-4* and *Phg-5*), have multiple alleles (*Phg-2*², *Phg-3*², *Phg-4*² and *Phg-5*²). Once specific genes have been cloned, Michelmores (1995) suggested the different disease resistance genes could be pyramided and introduced as cassettes into transgenic plants. Different alleles of the same resistance gene could be incorporated into a cassette, thus producing genotypes not found in nature that may provide resistance to a wider range of pathotypes.

McDonald and Linde (2002) noted that the choice of a breeding strategy for disease resistance depends on the evolutionary potential of the pathogen population. The deployment of a single gene for resistance may be an appropriate strategy for a pathogen population with asexual reproduction, low mutation rates and gene flow and small effective population size. Pyramiding major genes for resistance may be an effective strategy for pathogen populations that pose a moderate risk of evolving virulent pathotypes. Pyramiding disease resistance genes of Middle American and Andean origin has been used to develop bean germplasm lines with broad and more durable resistance to rust (Pastor-Corrales 2003). Pyramiding genes for disease resistance requires that virulence patterns of pathogens be monitored and new resistance genes be introgressed into commercial bean cultivars to provide resistance to emerging virulent pathotypes (Young and Kelly 1996). McDonald and Linde (2002) note that genetic engineering may permit the development of unique pyramids of disease resistance genes that could be incorporated into plants as a cassette of linked genes. However, plant pathogen populations with mixed reproduction systems, a greater potential for gene flow, high mutation rates and large effective population sizes

may be capable of overcoming pyramided genes for disease resistance (McDonald and Linde 2002). In this case, plant breeders should focus on breeding for quantitative resistance which would require a sustained effort to keep ahead of the evolution of the pathogen. Parleviet and Zadoks (1977) recommend the accumulation of resistance genes from diverse sources of origin. Molecular plant breeding tools such as marker-assisted selection could aid in this effort. Regional or temporal deployment of major genes for resistance or the use of cultivar mixtures or multilines are other strategies that can be used to deal with pathogens with a greater capacity to develop virulent pathotypes (McDonald and Linde 2002). Molecular techniques to monitor the virulence patterns of pathogen populations would be valuable tools in the management of plant pathogen populations.

Co-evolution of the host and pathogen has produced pathotypes of some bean diseases that are more virulent to either the Andean or the Middle American bean gene pool (Miklas et al. 2006b; Pastor-Corrales 2004). However, pathotypes of rust (Sandlin et al. 1999) and anthracnose (Balardin et al. 1997) have been identified that are virulent to both Andean and Middle American sources of resistance. Consequently, plant breeders should be aware of the virulence patterns of bean pathogens in the regions where lines under development are expected to be released as cultivars. Monitoring the virulence patterns of pathogens can be achieved by obtaining samples of the pathogen from the field and screening in the greenhouse for disease reaction using a group of bean lines (differentials) known to possess different genes or different combinations of genes for resistance to the pathogen. Because virulence patterns can vary over time, pathogen populations need to be constantly monitored, which is both expensive and time-consuming. Steadman et al. (1998) proposed for bean rust the use of mobile nurseries to take differentials to the field for a short period of time to permit natural infection. The mobile nurseries are returned to the greenhouse where the disease reactions are noted after infection has developed.

Molecular techniques have been used successfully to describe the genetic variability of pathogen populations of many bean diseases (Balardin et al. 1997; Ansari et al. 2004; Pastor-Corrales et al. 1998; Mahuku et al. 2002; Godoy-Lutz et al. 2003; Araya et al. 2004). However, more research needs to be

conducted in the development of molecular markers to detect specific virulence patterns in plant pathogens. The existence of molecular markers for specific virulence patterns would provide a rapid diagnostic tool to detect the emergence of new pathotypes and aid the plant breeder identifying the most effective combination of resistance genes. In addition, the movement of DNA samples of potential new races of bean pathogens across borders for research would pose less phytosanitary risk than the importation of living organisms.

Pyramiding genes of Mesoamerican and Andean origin may provide the highest and most durable resistance to bean diseases such as rust, angular leaf spot and anthracnose (Miklas et al. 2006b). On the other hand, pyramided resistance genes from only one gene pool, usually Middle American, has provided good levels of resistance to certain diseases such as BGYM and BCMNV.

Publications that describe new molecular markers for traits of economic value should include the sequence of the primer(s) and the protocols needed to repeat the procedures. In addition, researchers developing molecular markers should test the potential usefulness of the marker by screening bean lines of diverse origin that have and do not have the trait of interest. Seed of lines having the trait of economic value should be made available to the bean research community. These steps will help to insure that bean breeders utilize the molecular markers in their bean breeding program.

The development of biomarkers as the result of advances in proteomics may permit marker-assisted selection to be conducted by monitoring the presence or absence of gene products rather than genetic markers (Service 2008). Monoclonal antibody test strips are already commercially available to detect the presence or absence of specific Bt toxins in leaves and seed of transgenic plants (<http://www.agdia.com/gmo.html>).

Conclusion

Conventional plant breeding techniques have proven to be effective for the improvement of many traits of economic importance in common bean, especially disease resistance (Table 1). Plant breeders have extended the range of adaptation of the crop,

improved agronomic traits and developed and released cultivars with resistance to many important diseases and some pests. Limited progress has been made in the improvement of biological nitrogen fixation and tolerance to abiotic stresses such as drought and low soil fertility. Progress in increasing the seed yield potential of common bean has also been slow, but moderately successful. Molecular plant breeding techniques may prove to be valuable tools for the improvement of quantitatively inherited traits such as seed yield, characteristics related to the nutritional content of bean seed or traits related to the root that do not easily allow phenotypic selection. Some have already proven to be effective for MAS of disease related traits.

Bean breeders in developed countries have been early adopters of molecular plant breeding techniques. Marker-assisted selection for certain disease resistance genes has become a routine activity for some bean breeding programs and many recent cultivar and germplasm releases provide evidence of the effectiveness of the technique. The use of marker-assisted selection for more complex traits such as seed yield and abiotic stress tolerance will require a much better understanding of the genetic basis of the expression of these traits. Genomic mapping of these traits should help bean breeders devise more effective selection strategies for these complex traits. Incorporation of genomic information into a crop model may provide an appropriate platform to study the expression of seed yield, adaptation and other traits of economic importance. It may also help breeders better understand the basis of genotype \times environment interactions.

A reliable and efficient transformation system needs to be developed for common bean. Traits such as herbicide tolerance have the potential to lower the cost of bean production and reduce soil erosion. However, the issue of consumer acceptance should be taken into consideration before the development and release of transgenic common beans.

It should be kept in mind that most common beans are produced and consumed in developing countries. Bean breeding programs in these countries need access to knowledge and technology that will enable them to make use of molecular plant breeding techniques. This may require the out-sourcing of molecular analyses or the development of new technologies that permit the identification of genes

of economic importance without the need to have direct access to a molecular biology laboratory.

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