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Common bean (*Phaseolus vulgaris* L.)

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Abstract

This paper reviews the origins and general botany of *Phaseolus vulgaris*, the different cropping systems used for bean production, the agronomic and biological factors which most limit crop yield, and the strategies for improvement in this crop. While the common bean originated in the Americas, it is now grown widely in both the old- and the new world and in Africa, with the most suitable ideotype, and the disease and insect resistance factors needed for a particular production area, dependent on local conditions. Marked color and seed-type preferences further complicate the breeding and adoption of new varieties. The paper considers both conventional approaches and marker-assisted methods for breeding in this crop. The common bean is a crop with multiple disease and insect pests, and the ability to quickly and effectively select plants carrying multiple or different types of resistance gene is essential to an orderly and efficient processing of progeny. © 1997 Elsevier Science B.V.

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1. Introduction

The common bean (*Phaseolus vulgaris* L.) was originally a crop of the New World, but is now grown extensively in all major continental areas. Its production spans from 52° N to 32° S latitude (Schoonhoven and Voysest, 1991), and from near sea level in the continental USA and Europe, to elevations of more than 3000 m in Andean South America. It is a major source of dietary protein throughout both Latin America and Eastern Africa, but per capita consumption is declining as population increases outdistance production. The conditions under which this annual, predominantly self-pollinated legume is grown are extremely variable. While production tends to be centered on smaller holdings, the cropping system used can vary from the highly-mechanized, irrigated, and intensive production of monoculture bush beans, to complex associations of indeterminate or climbing beans with corn, other cereals, sugar cane, coffee or plantain. Technical inputs in such multiple-cropping systems are often limited, with the result that crop yields can range from less than 500 kg ha^{-1} in parts of Latin America and Africa to as much as 5000 kg ha^{-1} under experimental conditions. The diversity of conditions under which beans are grown, coupled with highly-specific local preferences for particular seed types or colors have complicated attempts at bean improvement. As a result, greatest progress has been in breeding for the resolution of disease, insect and

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nutritional constraints, with only limited — if any — improvement in yield potential. For earlier reviews that treat this important grain legume from a number of different perspectives, readers are referred to Graham (1978), Adams et al. (1985), Laing et al. (1985), Gepts (1988a), and Schoonhoven and Voysest (1991). The last-named publication includes a review of snap bean production for the tropics (Silbernagel et al., 1991). The present review considers the origins of *P. vulgaris*, the cropping systems used for bean production, the agronomic and biological factors which most limit crop yield, and the traits usually considered in bean improvement programs. It will also consider the impact of recent molecular advances to crop improvement on the prospects for the improved production of this important grain legume.

2. *Phaseolus vulgaris*: Origins and botanical description

2.1. Origins of *Phaseolus vulgaris* and current germplasm resources

The common bean (*Phaseolus vulgaris* L.) was domesticated in the upland regions of Latin America more than 7000 years ago (Kaplan, 1965; Kaplan and Kaplan, 1988; Gepts and Debouck, 1991). Two centers of origin for this crop have been identified, and their separation documented with archeological (Kaplan and Kaplan, 1988), morphological, agronomic and allozyme patterns Singh et al. (1991a,b) and seed protein (Gepts et al., 1986; Gepts and Bliss, 1986) evidence. The subject is reviewed by Gepts (1988b). Divisions between these two centers of origin are such that hybridization between representatives of the two groups of plants will often result in F_1 hybrid weakness (Singh and Guttierez, 1984; Gepts and Bliss, 1985). Following detailed studies of the wild ancestral bean forms found in the highland regions of Mexico and Andean South America it has been suggested that multiple domestication events occurred in each region (Gepts et al., 1986; Koenig et al., 1990; Koinange and Gepts, 1992), with genetic variability for seed size among Mesoamerican cultivars perhaps introduced through introgression from the larger-seeded *Phaseolus coccineus* (Miranda, 1967). Singh et al. (1991a,b) grouped 76 accessions of cultivated *Phaseolus vulgaris* from Mesoamerica and Andean Latin America into 9 clusters with characteristic allozyme and seed protein patterns. Most recently, Tohme et al. (1996) using AFLP, distinguished 16 groups in wild accessions from Mesoamerica, Colombia, Ecuador/Peru and the southern region of the Andes.

Dispersal from the Andean and Mesoamerican centers of origin appears to have followed different routes. Gepts (1988b) suggests that the smaller seeded Mesoamerican lines followed a route through Mexico and Central America, via the Caribbean and northern South America to Brazil. Common bean remains found in the southwestern USA are also likely to have been introduced from Mesoamerica (Kaplan, 1965), while Paredes and Gepts (1995) report extensive introgression of middle-American germplasm into Chile. By contrast, the majority of the cultivars found in Europe are of the larger-seeded Andean type, and were probably introduced into Europe via the Iberian peninsula, following discovery of the Americas. They are likely to have spread into Africa during the slave trade and colonial periods, and into the northeastern USA via immigration.

A world collection comprising somewhat more than 40 000 accessions is maintained at the Centro Internacional de Agricultura Tropical (CIAT) in Cali, Colombia, and includes indigenous wild and weedy specimens, unimproved landraces, and pure lines of *Phaseolus vulgaris*, as well as numerous related species. Included are accessions collected earlier by private individuals, the United States Department of Agriculture (USDA), Cambridge University and a number of national programs, as well as newer collections made in collaboration with the International Board for Plant Genetic Resources (IBPGR). The accessions are maintained both as short-to-medium term working stocks stored at +5°C, and as longer term stocks sealed in laminated plastic bags at 5–8% moisture content, and stored at −20°C (Hidalgo, 1991).

The germplasm is characterized on the basis of 25 plant and 6 seed descriptors (Hidalgo, 1991) and by additional disease and insect resistance information. A principal component analysis of the descriptor values for a subset of about 1000 accessions (CIAT, 1979) showed that three components explained 83%

of the variability. Component 1 included growth habit, plant height, nodes at flowering, racemes plant^{-1}, nodes at maturity, seeds pod^{-1} and 100-seed weight; component 2 included leaflet width and length, stem thickness, biological and grain yield; and component 3, length of hypocotyl, days to flowering, racemes with pods, pods plant^{-1}, and duration of flowering.

2.2. General botany

Phaseolus vulgaris L is a member of the Leguminosae, tribe Phaseoleae, subfamily Papilionoideae. Cultivated forms are herbaceous annuals, which are determinate or indeterminate in growth habit. On germination, the plant is initially tap-rooted, but adventitious roots emerge soon thereafter, and dominate the tap root which remains 10–15 cm in length (Duke, 1981). Papilionaceous flowers are borne in axillary and terminal racemes. Racemes may be one to many flowered. Flowers are zygomorphic with a bi-petalled keel, two lateral wing petals and a large outwardly-displayed standard petal. Flower color is genetically independent of seed color, but association between particular flower and seed colors is common. Flowers may be white, pink or purple (also red in *P. coccineus*). The flower contains ten stamens and a single multi-ovuled ovary, is predominantly self-fertilized, and develops into a straight or slightly curved fruit or pod. Seeds may be round, elliptical, somewhat flattened or rounded elongate in shape, and a rich assortment of coat colors and patterns exists. Seed size ranges from 50 mg seed^{-1} in wild accessions collected in Mexico, to more than 2000 mg seed^{-1} in some large-seeded Colombian varieties. A more detailed description is provided by Debouck (1991).

Determinate plants of common bean (Growth habit I) may have 3 to 7 trifoliate leaves on the main stem before the terminal double raceme (as found in 'bush' or 'dwarf' cultivars selected for earliness in Europe and the USA), or may be many noded with 7–15 (Middle American) or 15–25 (Andean) trifoliate leaves on the main stem (Debouck, 1991). Three indeterminate growth habits are distinguished (Schoonhoven and Pastor-Corrales, 1987):

- Growth habit II: upright habit, with an erect stem and branches, and often without a guide.
- Growth habit III: bush habit with weak and prostrate stem and numerous branches; having a short or long guide and with variable ability to climb.
- Growth habit IV: climbing if supported on a suitable tutor, with a weak, long and twisted stem and reduced branching.

Germination in *P. vulgaris* is epigeal, and requires 5–7 days at a soil temperature of 16°F. Time to flowering varies with cultivar, temperature and photoperiod. Flowering is usually initiated 28–42 days after planting, but amongst climbing varieties grown at high elevation, can be significantly later. Flowering in cultivars of growth habit I is concentrated over a very short period of time (usually 5–6 days), with drought or other stresses imposed at this time having a marked effect on yield. Indeterminate cultivars produce additional nodes after initial flowering, with flower formation thereby extended to 15–30 days. As many as two-thirds of all the flowers produced may abscise, and under temperature or water stress young fruits and /or developing seeds may also abort. Abscission is greatest among flowers formed on the upper nodes and branches, and within a raceme is greatest among the later flowers to form (CIAT, 1975). Seed filling periods may extend from as few as 23 days in the case of the determinate cultivars to nearly 50 days in indeterminate and climbing varieties. Physiological maturity, the stage beyond which no further increase in seed dry matter takes place, may occur only 60–65 days after planting amongst those early varieties used in areas where the growing season is very short, or extend to 200 days after planting amongst climbing varieties used in cooler upland elevations.

2.3. Reproductive biology

With the exception of specific tropical locations where outcrossing can be significant (G. Freytag, personal communication), *P. vulgaris* is normally self-fertilized. Accordingly, interpecific crossing is rare in nature, though hybridization between *P. vulgaris* and *P. coccineus* does occur.

Several species of *Phaseolus* (all $2n = 22$) can be hybridized to common bean (Smartt, 1976), though the hybrid seeds are only likely to survive when embryo-cultured on synthetic media. Honma (1956)

succeeded in crossing tepary with common bean, and the resulting cultivar Great Northern Nebraska 1 selection 27 carries resistance to common blight incited by *Xanthomonas campestris* pv *phaseoli*. Unfortunately, this selection is poorly adapted to tropical conditions, a trait commonly manifest in its progeny (Beebe and Pastor-Corrales, 1991). Anderson et al. (1996) suggest congruity backcrossing between *P. vulgaris* and *P. acutifolius* as a way to maintain exotic germplasm in immediately useful forms. *Phaseolus coccineus* has been more commonly used in wide-crosses with *P. vulgaris* especially for traits such as cold temperature tolerance and resistance to root rot and bean yellow mosaic virus. Mok et al. (1978) have studied some of the barriers to interspecific hybridization.

3. Cropping systems for bean production

Wooley et al. (1991) describe 5 broad classes of cropping system for the common bean:

- Sole crops of bush or (occasionally) climbing beans.
- Relay intercropping of bush, indeterminate or climbing beans with maize. In such systems the beans are usually planted when the maize is physiologically mature, with the maize serving basically as an inanimate support.
- Row intercropping of bush or indeterminate beans with corn. Planting is often simultaneous, but differences of up to 30 days in planting date of maize and beans occur in some areas.
- Mixed intercropping of maize and beans of growth habit III or IV. In these systems planting is often simultaneous, with maize and beans planted into the same hill.
- Intercropping of beans with other cereals, or with bananas, cassava, coffee or sugarcane. The purpose of such intercropping is often to provide a source of revenue when the principal crop takes time to mature.

In North America, Europe and in limited areas of other production regions, much of the bean production is highly commercialized. The beans are grown on level lands with mechanization, fertilizer and pesticide inputs, and sometimes with irrigation. In these areas plants of growth habit I or II predominate since they are the best suited to intensive cultivation, including semi-mechanized harvest. In a few areas, for example Southern Brazil and Argentina, monoculture beans are grown with only modest inputs, and are commonly rainfed, with accordingly smaller yields. Most monoculture beans, however, are grown as high-input crops with yield potential ranging from 1000 to 3000 kg ha^{-1}. A highly-specialized variant of the monoculture system is the growth of climbing beans on trellises under plastic, with drip irrigation and fertilization. This system is used in Egypt for the production of snap beans for the European winter market.

Phaseolus vulgaris is most commonly grown intercropped with maize. Intercropping minimizes risk by having more than one crop in the ground at a time; it can contribute to weed control and reduce the spread of pathogens; and it provides for more effective use of time and land area usually resulting in improved profitability. An economic analysis of 20 experiments in which climbing beans and corn were either grown in association or as monocultures (Adams et al., 1985) showed that monoculture beans were only more profitable when a very inexpensive system was available to support the climbing bean.

Rainfall pattern, temperature and the optimum planting densities for beans of different growth habit, all influence the cropping system that is used. In parts of Central America where the growing season is about 6-months in duration, beans planted at the beginning of the rainy season would mature at a time of significant rainfall, complicating harvest and predisposing the seed to disease. Here, the predominant system is of relay intercropping, with beans planted into the almost mature maize. By contrast, where there are two distinct growing seasons of shorter duration, as occurs in some intermediate elevations in Colombia, maize and beans are planted simultaneously in both seasons. Optimum planting densities for bean cultivars vary from only 6 plants m^{-2} (growth habit III) to around 48 plants m^{-2} (growth habit I: CIAT, 1976; Graham and Rosas, 1978). For climbing beans in monoculture the optimum planting density is about 12 plants m^{-2}. When grown in association both maize and beans densities are somewhat greater than would be suggested by these figures. Thus, Davis et al. (1987) obtained optimum results with 9 climbing bean and 4 maize plants

m^{-2}. Even where plant densities are held constant, the spatial arrangement of maize and beans can affect yield (Raposo et al., 1995).

Management of the intercropping system requires a good understanding of maize and bean physiology and nutrient needs. Maize plants that are too vigorous shade the beans, while aggressive climbing beans may need to be planted some time after the maize to prevent the latter from being smothered. Planting in hills allows fertilizers to be efficiently applied, and reduces phosphate fixation in some soils, but can create competition for nutrients. Given the differing rates of growth and nutrient requirements of the two plant species it can also affect efficient nutrient utilization. Fertilization of the maize plant with N has the potential to inhibit early nodulation and N_2 fixation by the bean (Graham, 1981), but several studies have now shown that maize grown in association with beans can actually benefit from bean N_2 fixation (Pineda, 1992).

4. Limitations to yield

Constraints to bean productivity vary with region, with very different factors likely to concern the subsistence farmer in Latin America and Eastern Africa, and the larger-scale producer more commonly found in the USA and Europe. For the former, the greatest need is to stabilize yield under often marginal conditions and using limited technical inputs: the latter is more likely to be concerned with yield improvement per se. This point is nicely made in the introduction to Schoonhoven and Voysest (1991) which highlights the flexibility of this species.

4.1. Bean diseases

There are a greater array of disease-causing pathogens important in tropical than in temperate bean production. The warm, often humid environment of the tropics and subtropics favors pathogen development, while the planting of 2–3 crop cycles $year^{-1}$ in some regions provides a continuity of inoculum. Further constraints include the small land area available to individual farmers, limiting the possibilities for crop rotation, and the scarcity and the cost of disease-free seed. Beebe and Pastor-Corrales (1991) suggest that more pathogens and more virulent isolates of these pathogens are associated with bean production in Latin America and Africa, than are found in the bean-producing regions of the USA and Europe. Pathogens of major importance include anthracnose (*Colletotrichum lindemuthianum*), rust (*Uromyces appendiculatus* var *appendiculatus*), common bacterial blight (*Xanthomonas campestris* pv *phaseoli*), bean common mosaic virus (BCMV), bean golden mosaic virus (BGMV) and angular leaf spot (*Phaeoisariopsis griseola*). Excellent reviews of this topic are provided by Schwartz and Pastor-Corrales (1989) and Beebe and Pastor-Corrales (1991), and need no further discussion here.

Seed-borne disease is a major issue with beans. Good seed quality, uniform emergence, early seedling vigor and freedom from disease are prerequisites for high yield. Twenty years ago, Ellis et al. (1976) reported farmer's seed from Huila, Colombia to average 40% germination and to have 81% internal contamination with fungus. Such problems persist even though the importance of clean seed is well recognized. Thus Tseng et al. (1995a,Tseng et al., 1995b found seedlots from Taiwan and Ontario to contain 54.8 and 58.5% seed borne fungus with the principal species in the diseased Ontario beans including *Alternaria* (61.1%), *Fusarium* (18.0%), *Rhizoctonia* (6.1%) and *Penicillium* (5.2%). Seed coat characteristics also influence resistance to mechanical damage during harvest (Dickson and Boettger, 1976, 1977).

4.2. Bean insects

Insect pests inflict major damage on beans in both Latin America and Africa. In the former, leafhoppers, chrysomelids and bruchids are the most widely distributed bean pests (Kornegay and Cardona, 1991), while in Africa stem maggots and bruchids are considered most important (Abate and Ampofo, 1996). Storage insects, by forcing farmers to sell their grain shortly after harvest, also have a significant effect on price fluctuations in the developing country bean market.

While less of a concern under field conditions in Europe and the USA, leafhopper damage can be

significant, as shown recently by Lindgren and Coyne (1995).

4.3. Soil mineral nutrition

Sanchez and Cochrane (1980) suggest that 89% of soils in Latin America are deficient in N, and 82%, 54%, 51%, 50%, 49%, and 49% deficient in P, K, S, Zn, Ca and Mg, respectively. Not surprisingly, given these figures, beans grown in this region often suffer nutrient stress. Thus, Malavolta (1972) reported on 232 fertilization experiments undertaken with beans in Brazil, and noted responses to phosphorus and nitrogen in 103 and 67, respectively. Similarly, Franco and Day (1980) noted striking response to Mo in beans from this region, while almost universal deficiency of zinc and a striking response to Zn fertilization have been reported in the bean-producing regions of both Ecuador and Colombia (INIAP, 1994). The constraints to bean production in East Africa appear very similar (Semoka et al., 1990).

Phaseolus vulgaris is widely regarded as weak in nodulation and nitrogen (N_2) fixation. This is partly the result of the marginal soil conditions under which it is commonly grown, partly due to competition from indigenous, but often ineffective soil rhizobia, but also a result of selection for early flowering and short growth season in many areas. Fixation rates reported by Graham (1990) are from only 3 to 125 kg ha^{-1}. Genetic diversity in N_2 fixation has been reported, and a number of centers have breeding programs underway (Bliss and Hardarson, 1993). Giller and Cadisch (1995) suggest that immediate, dramatic enhancement of biological N_2 fixation could be achieved, simply by the implementation of existing technical knowledge. Because gains from nitrogen fixation have proven limited, even monoculture beans are often fertilized, with rates to 60 kg ha^{-1} (Henson and Bliss, 1991), sometimes inhibiting nodulation and N_2 fixation. Bean response to fertilizer N is particularly marked under systems of minimum tillage (Liebman et al., 1995), while the relationship between nitrogen supply and N_2 fixation becomes even more complex for maize-bean associations (see Section 3).

Adequate P nutrition is also essential for vigorous bean growth and N_2 fixation (Graham and Rosas, 1979). More recent studies have sought lines of *P. vulgaris* with tolerance to low levels of soil P, Yan et al. (1995a,b) noting genotypic differences among 16 cultivars of bean. Relative rankings were not affected by soil type, or the degree of rhizobial or mycorrhizal infection, though large-seeded Andean germplasm showed superior P efficiency under conditions of low P availability. Lynch et al. (1992) report bean plants responsive to mycorrhizal infection, a result that could compound differences in P response.

4.4. Drought and heat stress

As much as 60% of bean production in the developing world occurs under conditions of significant drought stress. This includes large areas in Mexico and Africa where the growing season is short and the rainfall, unreliable; regions of Central America where beans are planted after maize, and may be subject to the abrupt cessation of the rains: and areas of Brazil where overall rainfall may be adequate but the growing period interrupted by significant periods without precipitation. Beans are particularly susceptible to drought during flowering, with significant flower and pod abortion occurring when water shortage occurs at this time. Nunez-Barrios (1991) used a rainshelter facility to impose drought on *P. vulgaris* at various stages of plant development. Water deficit hastened flowering and seed fill but delayed leaf appearance. Rapid root expansion was noted at the beginning of the water deficit period, and was followed by root death and compensatory growth in deeper soil layers.

Water management is a critical aspect of bean production in Europe and much of the USA. Irrigation regimes designed to replace 30–150% of evapotranspiration losses have been compared (Di Candilo et al., 1991; Barbieri and de Pascale, 1992) with 90–95% of maximum yield obtained only when 3500–4000 m^3 of water ha^{-1} (100% of evapotranspiration) was applied. Significant interactions between irrigation and N application have also been shown (Dahatonde et al., 1992).

Bean reproductive development is also very sensitive to temperature. Pollen/stigma interaction, pollen germination, pollen tube growth and fertilization are all negatively affected by high temperature (Gross

and Kigel, 1994) with the lowest pod set observed in plants exposed to high temperature 1–6 days prior to anthesis. Shonnard and Gepts (1994) suggest that selection for improved heat tolerance in beans is possible

4.5. Ozone stress

Air pollution is important in many areas of the world where bean production occurs in proximity to large cities or industrial complexes. Ozone and sulfur dioxide are the principal pollutants. Bender et al. (1990) exposed plants of common bean grown in open-topped chambers to doses of ozone ranging from 24–109 ppb. Exposure to O_3 did not impair vegetative growth, but did reduce foliar chlorophyll concentration. Concentrations below 70 ppb had little effect on yield, but at 80 ppb yield components were reduced 12–20%. Astorini et al. (1995) reported that near-ambient levels of O_3 (48nmol mol^{-1}) reduced dry matter and plant biomass by 52 and 57%, respectively.

4.6. Weeds

The importance and the role played by weeds varies with production system. In many regions of Latin America and Africa, beans are introduced with limited tillage or pesticide application into cereal residues or slashed/burned fallow areas. While the limited inputs used will often constrain yields, Tapia and Comacho (1988) and Thurston (1992) found less damage from insect pests and pathogens in such systems, and better control of soil erosion. Hand-weeding is often used in subsistence agriculture, and is critical during the period until flowering, as weeds can compete for light, nutrients and water. Liebman et al. (1993) compared dry bean seed yield in a no tillage system without fertilizers and herbicide, and attributed lower yields without tillage to limited N availability and competition from weeds. In further experiments with a no tillage-rye mulch system, weed production was greater than for a conventionally-tilled planting, and yield without N fertilization was much reduced (Liebman et al., 1995). N fertilization improved crop yield in both conventional and no-till systems, but the effect was much greater for the no till system under normal rainfall conditions.

5. Design of a complete breeding program

To be successful a new common bean variety must please the grower, the seedsman and the consumer. There can never be a perfect bean because:

- Different end users have different requirements.
- By the time a particular crossing program can generate, test and release a new variety, the perceived needs of agriculture or society are likely to have changed.

The development of common bean varieties is complicated even further by the many different environments and cropping systems under which this species is grown, and by the grain type and color preferences associated with its consumption. The result is that any new variety or breeding line is likely to satisfy only a small fraction of the market, and in consequence that most bean-breeding programs are likely to emphasize beans grown for specific regional or export market requirements.

The typical bean-breeding program includes an array of specific and non-specific objectives. The principal non-specific objective is to identify a useful genetic diversity for plant, pod and seed characteristics, pest and insect resistance, environmental stress tolerance, and physiological properties. Sources include the breeder's own collections, accessible public and/or private breeding materials, current and old cultivars, and those exotic and wild materials which are available through germplasm resource units such as CIAT.

When a specific breeding objective is defined, suitable germplasm is assembled, and a breeding strategy developed which is consistent with available genetic information for the trait or traits in question. Hybridization, or a series of hybridizations is effected, then successive generations both selectively multiplied and screened. When screening is undertaken will depend on the trait in question. Resistance to specific diseases is often simply inherited, and likely to be evaluated in early generation materials, with disease expression encouraged by the use of spreader rows or artificial inoculation. Horticultural or agronomic traits with lower heritability are likely to be evaluated in a defined environment and sequence, and at a later generation. The advent of new molecular techniques for the identification of marker-associated traits is already beginning to have

a profound effect on some aspects of progeny evaluation.

When the target combination of characters is identified in a number of advanced-generation single plant selections, the most promising of these are multiplied, evaluated several years under a range of cultural conditions, and the best lines released as a breeding line or named variety (Ranalli, 1995).

5.1. Using available genetic resources

Cultivars and landraces of a crop species represent the primary gene pool available to plant breeders for hybridization and crop improvement (Harlam and de Wet, 1971). In the case of *Phaseolus vulgaris*, however, the origins of such plant materials needs to be carefully weighed before they are used in breeding programs. The main problem is the potential incompatibility of Andean and Mesoamerican germplasm (Singh and Guttierez, 1984; Gepts and Bliss, 1985). Singh (1995) concluded that the potential for yield improvement in crosses between Andean × Mesoamerican bean races was significantly less than for populations derived only from common bean races of Mesoamerican origin. In parallel studies, Welsh et al. (1995) showed that variation for agronomic traits including yield, and for morphological, protein and isozyme markers was greater in interracial Mesoamerican populations than in those derived from intraracial crossing. Gains from selection for seed yield ranged from 3.9 to 11.4%.

Knowledge of the genetic relationships among cultivars, and between cultivars and landraces is useful to the plant breeder in organizing germplasm resources, and in the efficient sampling and testing of genetic diversity. Some aspects of this were discussed in Section 2.1. Estimates of genetic relationship based on restriction fragment length polymorphisms (RFLPs) have also been applied to *Phaseolus vulgaris*. Thus Khairallah et al. (1991) were able to differentiate the species using mtDNA digested with seven different endonucleases and hybridized with five cosmid clones covering ca. 200 kb of mtDNA sequences. Random amplified polymorphic DNA (RAPD, Welsh and McLelland, 1990; Williams et al., 1990; Skroch et al., 1992) molecular markers are discussed in several of the sections which follow.

5.2. Current goals of breeding programs

The following sections discuss briefly some of the attributes of beans considered important in different regions of the world, and given priority in breeding programs.

5.2.1. Plant architecture and seed yield

The yield potential of common beans is determined by growth habit, pod number and distribution, seed characteristics, maturity features, growing environment, cropping system, agronomic management and inputs applied. Amongst these, only the first five features are intrinsic characteristics of each bean cultivar. Within and across bean production areas these traits, and hence yield, will vary greatly among commercial cultivars and landraces belonging to the different gene pools (Singh and Guttierez, 1984; Nienhuis and Singh, 1986).

Plant growth habit or plant type plays a determining role in the acceptance of a dry bean cultivar by growers. While in a sole cropping system without artificial support, the highest yielding cultivars are likely to be those with indeterminate growth habit and small seeds (Nienhuis and Singh, 1988a,b), other factors can influence the acceptance of particular growth habits by farmers. Thus in the Midwest USA where conditions in the fall can be wet and humid, upright plant types of growth habit I or II may be preferred because the prostrate habit of Type III plants creates a considerable risk of harvest losses and white mold development during the growing season. In contrast, in the semi-arid, often subsistence farming conditions common in parts of Mexico, plants of growth habit III are preferred because their branching and prostrate habit permits compensation for non-germination, low planting density or drought.

For many years the possibility of mechanical cultivation and industrial processing of seed in the temperate, intensely-cultivated areas of the USA and Europe led to an emphasis on shorter duration, determinate bush beans with uniform pod maturation, plant height, seed shape and size. The navy-bean ideotype developed in the 1980's (Adams, 1982: Kelly et al., 1984, 1987) was a departure from this model. Plants of this type had a thick hypocotyl,

moderate number of basal branches with most pods borne on the main stem; and a tall stature with a Type II indeterminate semivine growth habit. Kelly and Adams (1987) used a phenotypic recurrent selection program to combine the architectural characteristics of the small-seeded navy bean ideotype with the seed characteristics of pinto beans. Architecture and seed characteristics showed no evidence of recombination until C_3 with the pinto bean ideotype which was then developed having fewer pods plant^{-1} and fewer seeds pod^{-1} (Brothers and Kelly, 1993). It is particularly noteworthy that the system of phenotypic recurrent selection, as practiced in this case, was successful in breaking and reassembling a small number of functionally integrated linkage blocks. Hanson, as early as 1959, had suggested that a breeding program for a self-pollinated species should include at least one and preferably three or four generations of intermating (see Hanson, 1959). Ranalli et al. (1991) and Ranalli (1996) further suggest that the establishment of the C_0 population should include three- and four-way crosses to maximize heterogeneity.

Selection for increased seed yield is difficult in dry beans (Adams, 1967; Coyne, 1968; Sullivan and Bliss, 1983; Nienhuis and Singh, 1986). Coyne (1968) suggested that the failure to improve bean yield was due to low heritability and large environmental effects on the expression of yield and its components. Compensation among yield components (Nienhuis and Singh, 1986) and negative or low general combining ability among the high yielding small seeded cultivars (Nienhuis and Singh, 1988a,b) have also been blamed for lack of progress in this area. Beaver and Kelly (1994) have compared different selection methods for dry bean populations derived from crosses between gene pools.

5.2.2. Disease resistance

All breeding programs must at some point be concerned with plant disease, though the need is perhaps greatest in developing countries in the tropics and subtropics where disease pressure is greatest, and the farmers are less likely to be able to afford pesticides and clean seed. A movement toward sustainability in the USA could also result in reduced pesticide usage in the future, and lead toward a greater emphasis on resistance breeding, and especially the pyramiding of both vertical and horizontal resistance genes. An excellent review of this topic, including methods for the development, inoculation and management of field and glasshouse evaluations, is provided by Beebe and Pastor-Corrales (1991), with only limited additional information provided here.

5.2.2.1. Anthracnose. While a number of pathogenic races of this fungus exist, sexual recombination by this organism is believed to be uncommon, and dispersal over long distances limited to seed transmission (Beebe and Pastor-Corrales (1991). While these factors favor control of the pathogen, it is still a significant disease of beans in Europe, where much of the seed comes from Eastern Africa, and of cooler locations in Central and Latin America. Because of this, breeding for disease resistance has had priority in both regions.

For many years the Cornell line 49-242, source of the ARE resistance gene (Hubbeling, 1957; Mastenbroek, 1960), was used in the development of resistant varieties. When this resistance source proved susceptible to a number of isolates of the pathogen from Latin America and Germany (Oliari et al., 1973; Schnock et al., 1975) additional, different, sources of resistance were identified. These included Mex222 and Mex227, Ecuador 299, PI207262, G2333, G811 and G2641 (Beebe and Pastor-Corrales, 1991); these new sources of resistance are often combined with the ARE gene for more stable resistance. The identification of RAPD markers flanking the ARE gene in both Andean and Mesoamerican backgrounds (Young and Kelly, 1996) will facilitate selection for resistance to this disease. Vilarinhos et al. (1995) have also used RAPD-PCR to characterize anthracnose differential varieties.

5.2.2.2. Rust. Over 200 races of the rust fungus (*Uromyces appendiculatus*) are known (Stavely and Pastor-Corrales, 1991; Stavely et al., 1989; Stavely and Batra, 1991). This pathogenic variability, coupled with mobility of the pathogen makes it a major problem in most bean production regions, but especially in the more humid regions of Eastern Africa and in both North and South America.

Traditionally, breeding for resistance is conducted on a regional basis with the incorporation of single

gene resistance to the predominant races only the first step. Because of the pathogenic variability referred to above, breeding strategy for this disease can also include the use of multilines, non race specific factors such as leaf hairiness (Shaik and Steadman, 1988) or small pustule size and long latent period for the development of infection (CIAT, 1986; Habtu and Zadoks, 1995). The pyramiding of different horizontal and vertical resistance genes has been accomplished for a number of dry bean varieties (Stavely and Grafton, 1991; Beebe and Pastor-Corrales, 1991), but is a difficult task because of the numerous progeny tests required to distinguish different resistance genes. Michelmore et al. (1991) proposed bulk segregant analysis as a means to allow the rapid development of populations useful for the identification of RFLP or RAPD markers linked to important plant genes. Using this methodology two RAPD markers linked to major rust resistance genes have been identified in contrasting DNA bulks obtained from F_2 individuals of known genotype (Haley et al., 1993; Johnson et al., 1995).

5.2.2.3. Root rots. Root rots of common bean are probably the most ubiquitous chronic disease of beans, wherever this crop is grown, but particularly under conditions of poor seed quality and limited crop rotation. Despite their importance, they receive only limited attention from commercial breeders as they are very difficult to control genetically. Reasons for this include:

- The lack of high levels of stable resistance in horticulturally-acceptable plant and pod types.
- The general association of colored seed coat and late maturity with resistance.
- The low heritability of reaction to root rots.
- Variation in the roles played by different organisms in different soils and environmental conditions.

Bean lines with resistance to soil-borne pathogens have been reported by Pastor-Corrales and Abawi (1987, Pastor-Corrales and Abawi, 1988a,b. A discussion of methods used in the evaluation of soil-borne fungal disease is provided by Abawi and Pastor-Corrales (in press).

5.2.2.4. Bacterial blight. Common bacterial blight of beans, caused by *Xanthomonas campestris* pv *phaseoli* is a seed-borne disease prevalent under hot humid conditions. Resistance to this pathogen has been identified in *P. acutifolius*, and has been transferred to *P. vulgaris* (Honma, 1956; Webster et al., 1980; McElroy, 1985). US commercial lines which carry the resistance gene from *P. acutifolius*, and include GN Neb #1 sel 27 in their parentage include GN Tara and GN Chase (Coyne and Schuster, 1975; Coyne et al., 1995). As stated earlier, however, lines derived from PI207262 or GN Neb #1 sel 27 rarely prove adapted to growing conditions in the tropics, and additional searches for resistance to bacterial blight have had to be initiated. Seven lines with moderate resistance to this pathogen were identified at CIAT, then retested with four strains of *X. campestris* pv *phaseoli* (Arnaud-Santana et al., 1993). Of these only G06700 proved resistant to all strains in leaf inoculation studies, while even this cultivar showed a susceptible pod reaction with some isolates. Common bacterial blight resistance loci in *Phaseolus vulgaris* have been mapped using RAPD markers (Jung et al., 1993, 1995).

5.2.2.5. Bean common mosaic virus (BCMV). Most recently-released bean cultivars in Europe, the USA and Latin America now carry dominant I gene resistance to BCMV. This gene prevents chronic systemic infection by all strains of BCMV, but its presence can result in a lethal systemic necrosis following infection by necrotic strains of BCMV (Drijfhout, 1978). Necrotic strains have been identified intermittently in Latin America and the USA, but are particularly common in some bean-producing regions of Africa. Because of this, incorporation of additional recessive genes (bc-u, bc-1, bc-2, bc-3; Drijfhout, 1978) in combination with the I gene is now desirable. Kelly et al. (1995) have suggested that the presence of the epistatic bc-3 gene can interfere with traditional efforts to pyramid desirable recessive resistance genes, and have urged the identification of molecular markers linked to the different resistance genes.

5.2.2.6. Bean golden mosaic virus (BGMV). Bean golden mosaic virus is an important disease of beans in Central America, the Caribbean and Brazil, and has recently been reported in Florida (Blair et al., 1996). This white-fly transmitted disease can be

particularly severe where beans are grown in close proximity to tomato, soybean or other crops that support heavy white fly populations, so control of the vector to reduce transmission is an important aspect of overall control. Thus, in the Dominican Republic, the planting date for beans is regulated to reduce carryover of the vector from one crop to another, while in the Central American region insecticide applications may be coupled with the use of tolerant cultivars to reduce infection. Resistance sources for this disease include Porillo sintetico, DOR364 and Garrapato (Morales and Niessen, 1988; Blair and Beaver, 1993). Beebe et al. (1995) have noted that the relative degree of genetic diversity among lines of common bean selected for BGMV resistance in Central America is significantly less than for unselected lines. A novel alternative to resistance breeding is the injection of genes for BGMV seed coat protein into susceptible lines by particle bombardment (Russell et al., 1993; UW-Madison et al., 1995).

5.2.3. Insect resistance

Empoasca fabae and *E. kraemeri* are both important pests of beans, with *E. kraemeri* the dominant species in Latin America. Tolerance to *E. kraemeri* has been identified, and includes both the ability to withstand high populations of this insect and non-preference to leafhopper oviposition, but progress in breeding for enhanced levels of tolerance to this insect in beans has been slow (Kornegay and Cardona, 1991).

Resistance to the bruchids *Zabrotes subfasciatus* and *Acanthoscelides obtectus* has been identified in wild *P. vulgaris* of Mexican origin (Schoonhoven et al., 1983). Presence of a seed protein, arcelin, has been correlated with resistance to *Z. subfasciatus* (Osborn et al., 1986, 1988). Six arcelin variants have been identified (Kornegay and Cardona, 1991; Suzuki et al., 1995) but not all appear equally effective in providing resistance to *Z. subfasciatus* (Fory et al., 1996). Pereira et al. (1995) found weevil damage in the susceptible variety Goiano, about 7 times higher than in near isogenic lines containing Arc1 and Arc2. A heteropolysaccharide in the wild accession G12953 is suggested as the factor responsible for resistance to *A. obtectus* (Gatehouse et al., 1987).

5.2.4. Nutritional factors

The biochemical and nutritional attributes of grain legumes, including *Phaseolus vulgaris* are reviewed by Norton et al. (1985). Areas identified as concerns included content of S-containing amino acids, digestibility, flatulence factors, and hard to cook characteristics. Liu (1995) and Martincabrejas et al. (1995) have recently reviewed the biochemical basis for the hard to cook characteristic. Nutritional quality and cooking characteristics in beans have generally been traits considered at the beginning (making sure parental lines fall within acceptable norms) and at the end of the breeding process. While some of these traits are costly or difficult to evaluate at the population level, Castellanos et al. (1995) describe a simple test for selection against genotypes having hardshells and needing extended cooking times.

6. Prospects for the crop

Phaseolus vulgaris was for many years an almost forgotten crop beleaguered by so many problems that yields were consistently low, and the crop often grown under subsistence conditions. More recently the focus on this crop by the CIAT Bean program, the Bean/Cowpea CRSP, a number of national bean programs, and various private seed companies and agrochemical organizations is beginning to have a positive impact on bean production in different regions of the world. In part this is due to improved cultivars and their acceptance by growers, it also derives from more effective environmental and pest management strategies.

Nevertheless, improvements in yield and yield stability will not be measured by any large or sudden increase in production per unit area, but by more gradual and subtle increases, and often for relatively small areas of production. What is needed in both the short and long term is greater attention to seed quality, the further development of sustainable agricultural practices, and continued effort toward improved disease and abiotic stress tolerance.

Molecular techniques will play a major role in these changes. For a crop with many disease constraints the ability to quickly and effectively tell which early generation plants carry resistance for

specific diseases will expedite evaluations and often save generations of field testing.

References

Abate, T. and Ampofo, J.K.O., 1996. Insect pests of beans in Africa. Entomol., 41: 45–73.

Abawi, G.S. and Pastor-Corrales, M.A. Root Rots of Beans in Latin America and Africa: Diagnosis, Research Methodologies, and Management Strategies. CIAT, in press.

Adams, M.W., 1967. Basis of yield component compensation in crop plants with special reference to the field bean *Phaseolus vulgaris*. Crop Sci., 7: 505–510.

Adams, M.W., 1982. Plant architecture and yield breeding. Iowa State J. Res., 56: 225–254.

Adams, M.W., Coyne, D.P., Davis, J.H.C., Graham, P.H. and Francis, C.A., 1985. Common bean (*Phaseolus vulgaris* L.). In: ed. R.J. Summerfield and E.H. Roberts, Grain Legume Crops. Collins, London, pp. 433–476.

Anderson, N.O., Ascher, P.D. and Haghighi, K., 1996. Congruity backcrossing as a means of creating genetic variability in self-pollinated crops. Seed morphology of *Phaseolus vulgaris* L. and *Phaseolus acutifolius* Gray, A. hybrids. Euphytica, 87: 211–224.

Arnaud-Santana, E., Mmbaga, M.T., Coyne, D.P. and Steadman, J.R., 1993. Sources of resistance to common bacterial blight and rust in elite *Phaseolus vulgaris* germplasm. Hort Sci., 28: 644–646.

Astorini, G., Margani, I., Tripodo, P. and Manes, P., 1995. The response of *Phaseolus vulgaris* L. cv Lit to different dosages of the anti-ozonant ethylenediurea (Edu) in relation to chronic treatment with ozone. Plant. Sci., 111: 237–248.

Barbieri, G. and de Pascale, S., 1992. Effects of irrigation regimes and methods on the yield of kidney bean (*Phaseolus vulgaris* L.) cultivars. Irrigazione e Drenaggio, 39: 19–23.

Beaver, J.S. and Kelly, J.D., 1994. Comparison of selection methods for dry bean populations derived from crosses between gene pools. Crop Sci., 34: 34–37.

Beebe, S.E., Ochoa, I., Skroch, P., Nienhuis, J. and Tivang, J., 1995. Genetic diversity among common bean breeding lines developed for Central America. Crop Sci., 35: 1178–1183.

Beebe, S.E. and Pastor-Corrales, M.A., 1991. Breeding for disease resistance. In: ed. A. van Schoonhoven and O. Voysest. Common Beans: Research for Crop Improvement. CIAT, Cali, Colombia.

Bender, J., Weigel, H.J. and Jager, H.J., 1990. Regression analysis to describe yield and metabolic responses of beans (*Phaseolus vulgaris*) to chronic ozone stress. Ang. Botanik, 64: 329–343.

Blair, M.W. and Beaver, J.S., 1993. Inheritance of bean golden mosaic virus resistance from bean genotype A429. Ann. Rep. Bean Improve. Coop., 36: 143.

Blair, M.W., Massett, M.J., Abouzid, A.M., Hiebert, E., Polston, J.E., McMillen, R.T., Graves, W. and Lamberts, M., 1996. Occurrence of bean golden mosaic virus in Florida. Plant Disease, 79: 529–533.

Bliss, F.A. and Hardarson, G., Eds., 1993. Enhancement of Biological Nitrogen Fixation of Common Bean in Latin America. Kluwer Academic Publishers, Dordrecht, Netherlands, p. 160.

Brothers, M.E. and Kelly, J.D., 1993. Interrelationship of plant architecture and yield components in the pinto bean ideotype. Crop Sci., 33: 1234–1238.

Castellanos, J.C., Guzman-Maldonado, H., Acosta-Gallegos, J.A. and Kelly, J.D., 1995. Effects of hardshell character on cooking time of common beans grown in the semiarid highlands of Mexico. J. Sci. Food Agric., 69: 437–444.

Centro Internacional de Agricultura Tropical (CIAT), 1975. Annual Report Cali, Colombia, pp. C14–C24.

Centro Internacional de Agricultura Tropical (CIAT), 1976. Annual Report Cali Colombia, pp. A47–A67.

Centro Internacional de Agricultura Tropical (CIAT), 1979. Annual Report Cali, Colombia, pp. F1–F10.

Centro Internacional de Agricultura Tropical (CIAT), 1986. Annual Report Bean Program, Cali, Colombia, p. 331.

Coyne, D.P., 1968. Correlation, heritability and selection of yield components in field beans *Phaseolus vulgaris* L. Proc. Amer. Soc. Hort. Sci., 93: 388–396.

Coyne, D.P., Nuland, D.S., Lindgren, D.T. and Steadman, J.R., 1995. 'Chase' pinto dry bean. Hort. Sci., 29: 44–45.

Coyne, D.P. and Schuster, M.L., 1975. Genetic and breeding strategy for resistance to rust (*Uromyces phaseoli*) in bean (*Phaseolus vulgaris* L.). Euphytica, 24: 795–803.

Dahatonde, B.N., Turkhede, A.B. and Kale, M.R., 1992. Response of french bean (*Phaseolus vulgaris*) to irrigation regimes and nitrogen levels. Ind. J. Agron., 37: 835–837.

Davis, J.H.C., Roman, A. and Garcia, S., 1987. The effects of plant arrangement and density on intercropped beans (*Phaseolus vulgaris*) and maize, II. Comparison of relay intercropping and simultaneous planting. Field Crops Res., 16: 117–128.

Debouck, D., 1991. Systematics and morphology. In: ed. A. van Schoonhoven and O. Voysest, Common Beans: Research for Crop Improvement. CIAT, Cali, Colombia, pp. 55–118.

Di Candilo, M., Giordano, I., Faeti, V., Gaspari, N. and D'Amato, A., 1991. Influence of various irrigation regimes on beans (*Phaseolus vulgaris* L). Riv. Agron., 25: 444–451.

Dickson, M.H. and Boettger, M.A., 1976. Selection for seed quality in white seeded snap bean. Ann. Rep. Bean Improve. Coop., 19: 24–25.

Dickson, M.A. and Boettger, M.A., 1977. Applied selection for mechanical damage resistance in snap bean using the mechanical damage simulator. Ann. Rep. Bean Improve. Coop., 20: 38–39.

Drijfhout, E., 1978. Genetic Interaction Between *Phaseolus vulgaris* and Bean Common Mosaic Virus with Implications for Strain Identification and Breeding for Resistance. Cent. Agric. Publ. Doc., Wageningen, Netherlands.

Duke, J.A., 1981. Handbook of Legumes of World Economic Importance. Plenum Press, New York, 345 pp.

Ellis, M.A., Galvez, G.E., and Sinclair, J.B., 1976. Hongos internalmente portados por la semilla y calidad de la semilla de frijol (*Phaseolus vulgaris* L.) cosechado en fincas de pequenos

agricultores en cuatro departamentos de Colombia. Not. Fitopatol., 5: 79–82.

Fory, L.F., Finardi, F., Quintero, C.M., Osborn, T.C., Cardona, C. Chispeels, M.J. and Mayer, J.E., 1996. Alpha-amylase inhibitors in resistance of common beans to the Mexican bean weevil and bean weevil (Coleoptera, Bruchidae). J. Econ. Entomol., 89: 204–210.

Franco, A.A. and Day, J.M., 1980. Effects of lime and molybdenum on nodulation and nitrogen fixation of *Phaseolus vulgaris* L. in acid soils of Brazil. Turrialba, 30: 99–105.

Gatehouse, A.M.R., Dobie, P., Hodges, R.J., Meik, J., Pustzai, A. and Boulter, D., 1987. Role of carbohydrates in insect resistance in *Phaseolus vulgaris*. J. Insect. Physiol., 33: 943–850.

Gepts, P., Ed., 1988a. Genetic Resources of *Phaseolus* Beans. Kluwer Academic Publishers, Dordrecht, Netherlands.

Gepts, P., 1988b. A middle American and an Andean common bean pool. In: ed. P. Gepts, Genetic Resources of *Phaseolus* Beans. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 375–390.

Gepts, P. and Bliss, F.A., 1985. F_1 hybrid weakness in the common bean: Differential geographic origin suggests two gene pools in cultivated bean germplasm. J. Hered., 76: 447–450.

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

Gepts, P. and Debouck, D., 1991. Origin, domestication, and evolution of the common bean (*Phaseolus vulgaris* L.). In: ed. A. van Schoonhoven and O. Voysest, Common Bean: Research for Crop Improvement. CIAT, Cali, Colombia. pp. 7–53.

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

Giller, K.E. and Cadisch, G., 1995. Future benefits from biological nitrogen fixation – an ecological approach to agriculture, Plant Soil, 174: 255–277.

Graham, P.H., 1978. Some problems and potentials of field beans (*Phaseolus vulgaris* L.) in Latin America. Field Crops Res., 1: 295–317.

Graham, P.H., 1981. Some problems of nodulation and symbiotic nitrogen fixation in *Phaseolus vulgaris* L. Field Crops Res., 4: 93–112.

Graham, P.H., 1990. Problemas de la nodulacion y la fijacion de nitrogeno en *Phaseolus vulgaris* L.: Una reevaluacion. Terra, 8: 71–82.

Graham, P.H. and Rosas, J.C., 1978. Nodule development and nitrogen fixation in cultivars of *Phaseolus vulgaris* L. as influenced by planting density. J. Agric. Sci. (Camb.), 90: 19–29.

Graham, P.H. and Rosas, J.C., 1979. Phosphorus fertilization and symbiotic nitrogen fixation in common bean. Agron. J., 71: 925–926.

Gross, Y. and Kigel, J., 1994. Differential sensitivity to high temperature of stages in the reproductive development of common bean (*Phaseolus vulgaris* L.). Field Crops Res., 36: 201–212.

Habtu, A. and Zadoks, J.C., 1995. Components of partial resistance in *Phaseolus* beans against an Ethiopian isolate of bean rust. Euphytica, 83: 95–102.

Haley, S.D., Miklas, P.N., Stavely, J.R., Byrum, J. and Kelly, J.D., 1993. Identification of RAPD markers linked to a major rust resistance gene block in common bean. Theor. Appl. Genet., 86: 505–512.

Hanson, W.D., 1959. The breakup of initial linkage blocks under selected mating systems. Genetics, 44: 857–868.

Harlam, J.R. and de Wet, J.M.J., 1971. Toward a rational classification of cultivated plants. Taxon, 20: 509–517.

Henson, R.A. and Bliss, F.A., 1991. Effect of fertilizer N application timing on common bean production. Fert. Res., 29: 133–138.

Hidalgo, R., 1991. CIAT's world *Phaseolus* collection. In: ed. A. van Schoonhoven and O. Voysest, Common Beans: Research for Crop Improvement. CIAT, Cali, Colombia, pp. 163–197.

Honma, S., 1956. A bean interspecific hybrid. J. Hered., 47: 217–220.

Hubbeling, N., 1957. New aspects of breeding for disease resistance in beans (*Phaseolus vulgaris* L.). Euphytica, 6: 111–141.

Instituto Nacional de Investigaciones Agropecuarias (INIAP), 1994. Informe Anual Departamento de Manejo de Suelos y Aguas, pp. 60–65.

Johnson, E., Miklas, P.N., Stavely, J.R. and Martinezcruzado, J.C., 1995. Coupling phase and repulsion phase RAPDs for marker assisted selection of PI181996 rust resistance in common bean. Theor. Appl. Genet., 90: 659–664.

Jung, G., Coyne, D.P., Skroch, P.W., Neinhuis, J., Arnaud-Santana, E., Bokosi, J., Ariyarathne, H.M., Steadman, J. and Beaver, J.S., 1995. Construction of a genetic linkage map and locations of common blight, rust and web blight resistance loci in *Phaseolus vulgaris* L. using random amplified polymorphic DNA (RAPD) markers. Hort. Sci., 30: 820.

Jung, G., Skroch, P.W., Coyne, D.P., Neinhuis, J., and Arnaud-Santana, E., 1993. Mapping common blight resistance loci in *Phaseolus vulgaris* L. using random amplified polymorphic DNA (RAPD) markers. Hort. Sci., 28: 456.

Kaplan, L., 1965. Archeology and domestication in American *Phaseolus* beans. Econ. Bot., 19: 358–368.

Kaplan, L. and Kaplan, L.N., 1988. *Phaseolus* in archeology. In: ed. P. Gepts, Genetic Resources of *Phaseolus* Beans: Their Maintenance, Domestication, Evolution and Utilization. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 125–142.

Kelly, J.D. and Adams, M.W., 1987. Phenotypic recurrent selection in ideotype breeding of pinto beans. Euphytica, 36: 69–80.

Kelly, J.D., Adams, M.W., Saettler, A.W., Hosfield, G.L. and Ghaderi, A., 1984. Registration of C-20 navy bean. Crop Sci., 24: 822.

Kelly, J.D., Adams, M.W. and Varner, G.V., 1987. Yield stability of determinate and indeterminate dry bean cultivars. Theor. Appl. Genet., 74: 516–521.

Kelly, J.D., Afanador, L. and Haley, S.D., 1995. Pyramiding genes for resistance to bean common mosaic virus. Euphytica, 82: 207–212.

Khairallah, M.M., Adams, M.W. and Sears, B.B., 1991. Mitochondrial genome size variation and restriction fragment length polymorphism in three *Phaseolus* species. Theor. Appl. Genet., 82: 321–328.

Koenig, R.L., Singh, S.P. and Gepts, P., 1990. Novel phaseolin types in wild and cultivated common bean (*Phaseolus vulgaris* Fabaceae). Econ. Bot., 44: 50–60.

Koinange, E.M.K. and Gepts, P., 1992. Hybrid weakness in wild *Phaseolus vulgaris* L. J. Hered., 83: 135–139.

Kornegay, J. and Cardona, C., 1991. Breeding for insect resistance in beans. In: ed. A. van Schoonhoven and O. Voysest, Common Beans: Research for Crop Improvement. CIAT, Cali, Colombia, pp. 619–648.

Laing, D.R., Jones, P.G. and Davis, J.H.C., 1985. Common bean (*Phaseolus vulgaris* L.). In: ed. P.R. Goldsworthy and N.W. Fisher, The Physiology of Tropical Grain Legumes. Wiley, London, pp. 305–351.

Liebman, M., Corson, S., Rowe, R.J. and Halteman, W.A., 1995. Dry bean response to nitrogen fertilizer in two tillage and residue management systems. Agron. J., 87: 538–546.

Liebman, M., Roew, R.J., Corson, S., Marra, M.C., Honeycutt, C.W. and Murphy, B.A., 1993. Agronomic and economic performance of conventional vs reduced input bean cropping systems. J. Prod. Agric., 6: 369–378.

Lindgren, D.T. and Coyne, D.P., 1995. Injury and yield of leafhopper infested dry beans. J. Amer. Soc. Hort. Sci., 120: 839–842.

Liu, K., 1995. Cellular, biological and physicochemical basis for the hard to cook defect in legume seeds. Crit. Rev. Food Sci. Nutr., 35: 263–298.

Lynch, J., Lauchli, A. and Epstein, E., 1992. Vegetative growth of the common bean in response to phosphorus nutrition. Crop Sci., 31: 380–387.

Malavolta, E.1972. Nutricao e adubacao. In: Anais do I Simposio Brasileiro de Feijao. Univ. Fed. de Vicosa, Brasil, pp. 211–242.

Martincabrejas, M.A., Esteban, R.M., Waldron, K.W., Maina, G., Grant, G., Bardocz, S. and Pusztai, A., 1995. Hard-to-cook phenomenon in beans-changes in antinutritional factors and nitrogenous compounds during storage. J. Sci. Food Agric., 69: 429–435.

Mastenbroek, C., 1960. A breeding programme for resistance to anthracnose in dry shell haricot beans, based on a new gene. Euphytica, 9: 177–184.

McElroy, J.B., 1985. Breeding dry beans *Phaseolus vulgaris* L. for common bacterial blight resistance derived from *Phaseolus autifolius* A. Gray. Ph.D. thesis, Cornell University.

Michelmore, R.W., Paran, I. and Kisseli, R.V., 1991. Identification of markers linked to disease resistance genes by bulked segregant analysis. A rapid method to detect markers in specific genomic regions using segregating populations. Proc. Nat. Acad. Sci. USA, 88: 9828–9832.

Miranda, S., 1967. Origen de *Phaseolus vulgaris* L. (Frijol comun). Agrociencia, 1: 99–109.

Mok, D.W.S., Mok, M.C. and Rabakoarihanta, A., 1978. Interspecific hybridization of *Phaseolus vulgaris* with *P. lunatus* and *P. acutifolius*. Theor. Appl. Genet., 52: 209–216.

Morales, F.J. and Niessen, A.I., 1988. Comparative responses of selected *Phaseolus vulgaris* germplasm, inoculated artificially and naturally with bean golden mosaic virus. Plant Dis., 72: 1020–1023.

Nienhuis, J. and Singh, S.P., 1986. Combining ability analysis and relationships among yield, yield components, and architectural traits in dry bean. Crop Sci., 26: 21–27.

Nienhuis, J. and Singh, S.P., 1988a. Genetics of seed yield and its components in common bean (*Phaseolus vulgaris* L.) of Middle American origin. I. General combining ability. Plant Breed., 101: 143–154.

Nienhuis, J. and Singh, S.P., 1988b. Genetics of seed yield and its components in common bean (*Phaseous vularis* L.) of Middle American origin. II. Genetic variance, heritability and expected response from selection. Plant Breed., 101: 155–163.

Norton, G., Bliss, F.A. and Bressani, R., 1985. Biochemical and nutritional attributes of grain legumes. In: ed. R.J. Summerfield and E.H. Roberts, Grain Legume Crops. Collins, London, pp. 73–114.

Nunez-Barrios, A., 1991. Effects of soil water deficits on dry beans (*Phaseolus vulgaris* L.) at different growing stages. Ph.D. Thesis, Michigan State University.

Oliari, L., Vieira, C. and Wilkinson, R.E., 1973. Physiologic races of *Colletotrichum lindemuthianum* in the state of Minas Gerais, Brazil. Plant Dis. Rept., 57: 870–872.

Osborn, T.C., Blake, T., Gepts, P. and Bliss, F.A., 1986. Bean arcelin2: genetic variation, inheritance and linkage relationships of a novel seed protein of *Phaseolus vulgaris* L. Theor. Appl. Genet., 71: 847–855.

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

Paredes, O.M. and Gepts, P., 1995. Extensive introgression of middle American germplasm into Chilean common bean cultivars. Gen. Resources Crop Evol., 42: 29–41.

Pastor-Corrales, M.A. and Abawi, G.S., 1987. Reactions of selected bean germplasms to infection by *Fusarium oxysporum* f.sp. *phaseoli*. Plant Dis., 71: 990–993.

Pastor-Corrales, M.A. and Abawi, G.S., 1988a. Reactions of selected bean accessions to infection by *Macrophomina phaseolina*. Plant Dis., 72: 39–41.

Pastor-Corrales, M.A. and Abawi, G.S., 1988b. Bean accessions with resistance to *Rhizoctonia solani* under field conditions in Colombia. Turrialba, 38: 83–86.

Pereira, P.A.A., Yokoyama, M., Quintela, E.D. and Bliss, F.A., 1995. Bean weevil control (*Zabrotes subfasciatus*) (Coleoptera Bruchidae) through the use of specific seed proteins on near isogenic bean lines. Pesq. Agropec. Bras., 30: 1031–1034.

Pineda, P., 1992. Mejoramiento de la Fijacion Biologica de Nitrogeno en Frijol (*Phaseolus vulgaris* L.) en el Peru. CIAT Documento de Trabajo 118, 63 pp.

Ranalli, P., 1995. Improvement of pulse crops in Europe. Eur. J. Agron., 4: 151–166.

Ranalli, P., 1996. Phenotypic recurrent selection program in common bean (*Phaseolus vulgaris* L.) based on performance of S_2 progenies. Euphytica, 87: 127–132.

Ranalli, P. Ruaro, G. and del Re, P., 1991. Response to selection for seed yield in bean (*Phaseolus vulgaris*). Euphytica, 57: 117–123.

Raposo, J.A.D., Schuch, L.O.B., Deassis, F.N. and Machado, A.A., 1995. Intercropping of corn and bean in different plant arrangements and populations. Pesq. Agropec. Bras., 30: 639–647.

Russell, D.R., Wallace, K.M., Bathe, J.H., Martinell, B.J. and McCabe, D.E., 1993. Stable transformation of *Phaseolus vulgaris* via electric discharge mediated particle acceleration. Plant Cell Rep., 12: 165–169.

Sanchez, P.A. and Cochrane, T.T., 1980. Soil constraints in relation to major farming systems of tropical America. In: Priorities for Alleviating Soil-Related Constraints to Food Production in the Tropics. IRRI, Los Banos, Philippines, pp. 107–139.

Schnock, M.G., Hoffman, G.M. and Kruger, J., 1975. A new physiological strain of *Colletotrichum lindemuthianum* infecting *Phaseolus vulgaris* L. Hort. Sci., 10: 140.

Schoonhoven, A. van, Cardona, C. and Valor, J., 1983. Resistance to the bean weevil and the mexican bean weevil (Coleoptera: Bruchidae) in noncultivated common bean accessions. J. Econ. Entomol., 76: 1255–1259.

Schoonhoven, A. van and Pastor-Corrales, M.A., 1987. Standard System for the Evaluation of Bean Germplasm. CIAT, Cali, Colombia, 53 pp.

Schoonhoven A. van and Voysest, O., 1991. Common Beans: Research for Crop Improvement. CIAT, Cali, Colombia.

Schwartz, H.F. and Pastor-Corrales, M.A., 1989. Bean Production Problems in the Tropics, 2nd Ed. CIAT, Cali, Colombia.

Semoka, J.M.R., Edje, O.T. and MnKeni, P.N.S., 1990. Prospects for phosphate rock utilization in the development of sustainable cropping systems with bean. In: ed. J.B. Smithson, Progress in Improvement of Common Bean in Eastern and Southern Africa. CIAT Africa Workshop Ser. 12, pp. 551–559.

Shaik, M. and Steadman, J.R., 1988. Nonspecific resistance to bean rust and its association with leaf pubescence. Ann. Rept. Bean Improve. Coop., 31: 62–63.

Shonnard, G.C. and Gepts, P., 1994. Genetics of heat tolerance during reproductive development in common bean. Crop Sci., 34: 1168–1175.

Silbernagel, H.J., Janssen, W., Davis, J.H.C. and Montes de Oca, G., 1991. Snap bean production in the tropics: Implications for genetic improvement. In: A. van Schoonhoven and O. Voysest (Editors), Common bean: research for crop improvement. CIAT, Cali Colombia, pp. 835–862.

Singh, S.P., 1995. Selection for seed yield in middle American versus Andean × middle American interracial common bean populations. Plant Breed., 114: 269–271.

Singh, S.P. and Guttierez, J.A., 1984. Geographical distribution of the DL_1 and DL_2 genes causing hybrid dwarfism in *Phaseolus vulgaris* L., their association with seed and their significance to breeding. Euphytica, 33: 337–345.

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

Singh, S.P., Nodari, R. and Gepts, P., 1991b. Genetic diversity in cultivated common bean: I. Allozymes. Crop Sci., 31: 19–23.

Skroch, P., Tivang, J. and Nienhuis, J., 1992. Analysis of genetic relationships using RAPD marker data. In: Applications of RAPD Technology to Plant Breeding. Crop Sci. Soc. Amer., Madison, pp. 26–30.

Smartt, J., 1976. Tropical Pulses. Trop. Agric. Ser. Longman, London.

Stavely, J.R., Steadman, J.R. and McMillan, R.T., 1989. New pathogenic variability in *Uromyces appendiculatus* in North America. Plant Dis., 73: 428–432.

Stavely, J.R. and Batra, L.R., 1991. Recently identified new pathogenic variability in *Uromyces appendiculatus*. Phytopath., 81: 704.

Stavely, J.R. and Grafton, K.F., 1991. Release of seven erect short vine navy bean germplasm lines, Belmidak rust resistant -1, -2, -3, -4, -5, -6 and -7. ARS_USDA release notice.

Stavely, J.R. and Pastor-Corrales, M.A., 1991. Rust. In: ed. H.F. Schwartz and M.A. Pastor Corrales, Bean Production Problems in the Tropics, 2nd Ed. CIAT, Cali, Colombia, pp. 159–194.

Sullivan, J.G. and Bliss, F.A., 1983. Recurrent mass selection for increased seed yield and seed protein percentage in the common bean (*Phaseolus vulgaris* L.) using a selection index. J. Amer. Soc. Hort. Sci., 108: 42–46.

Suzuki, K., Ishimoto, M., Iwanaga, M., Kikuchi, F. and Kitamra, K., 1995. Inheritance of seed alpha amylase inhibitor in the common bean and genetic relation to arcelin. Theor. Appl. Genet., 90: 762–766.

Tapia, H. and Comacho, A., 1988. Manejo Integrado de la Produccion de Frijol Basado en Labranza Zero. GTZ, Eschborn, Germany.

Tohme, J., Gonzales, D.O., Beebe, S. and Duque, M.C., 1996. AFLP analysis of gene pools of a wild bean core collection. Crop Sci., 36: 1375–1384.

Thurston, H.D., 1992. Sustainable Practices for Plant Disease Management in Traditional Farming Systems. Westview Press, Boulder, CO.

Tseng, T.C., Tu, J.C. and Soo, L.C., 1995a. Comparison of the profiles of seed-borne fungi and the occurrence of aflotoxins in mold-damaged beans and soybeans. Microbios, 84: 105–116.

Tseng, T.C., Tu, J.C. and Tsean, S.S., 1995b. Mycoflora and mycotoxins in dry bean (*Phaseolus vulgaris*) produced in Taiwan and in Ontario, Canada. Bot. Bull. Acad. Sin., 36: 229–234.

University of Wisconsin-Madison, University of California-Davis and Asgrow Seed Co., 1995. Transgenic Plants Expressing Gemini AC1/C1. Patent.

Vilarinhos, A.D., Vidigal, M.C.G., Debarros, E.G., Depaula, T.J., Cruz, C.D. and Moreira, M.A., 1995. RAPD-PCR characterization of varieties of the common bean (*Phaseolus vulgaris* L.) used to identify races of anthracnose (*Colletotrichum lindemuthianum*). Rev. Bras. Genet., 18: 275–280.

Webster, D.M., Temple, S.R. and Schwartz, H.F., 1980. Selection for resistance to *Xanthomonas phaseoli* in dry beans. Crop Sci., 20: 519–522.

Welsh, J. and McLelland, M., 1990. Fingerprinting genomes using PCR with arbitrary primers. Nucleic Acid Res., 18: 7213–7218.

Welsh, W., Bushuk, W., Roca, W., and Singh, S.P., 1995. Characterization of agronomic traits and markers of recombinant inbred lines from intraracial and interracial populations of *Phaseolus vulgaris*. Theor. Appl. Genet., 91, 169–177.

Williams, G.J.K., Kubelik, A.R., Livak, K.J. Rafalski, J.A. and Tingev, S.V., 1990. DNA polymorphism amplified by arbitrary primers are useful as genetic markers. Nucleic Acid Res., 18: 6531–6535.

Wooley, J., Lepiz, R., Aquinas-Portes y Castro, T. and Voss, J., 1991. Bean cropping systems in the tropics and subtropics and their determinants. In: ed. A. van Schoonhoven and O. Voysest, Common Beans: Research for Crop Improvement. CIAT, Cali, Colombia, pp. 679–706.

Yan, X.L., Lynch, J.P. and Beebe, S.E., 1995a. Genetic variation for phosphorus efficiency of common bean in contrasting soil types. I. Vegetative response. Crop Sci., 35: 1086–1093.

Yan, X.L., Beebe, S.E. and Lynch, J.P., 1995b. Genetic variation for phosphorus efficiency of common bean in contrasting soil types. II. Yield response. Crop Sci., 35: 1094–1099.

Young, R.A. and Kelly, J.D., 1996. RAPD markers flanking the ARE gene for anthracnose resistance in common bean. J. Amer. Soc. Hort. Sci., 121: 37–41.