Common Bean Improvement in the Tropics

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I. INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) for dry seed harvest is grown annually on over 13 million hectares (ha) in the world, with production of about 9 million tonnes. In addition, there is substantial production and consumption of immature pods of snap, green, or stringless bean (Silbernagel 1986; Davis and Janssen 1987). Green-shelled seeds and tender leaves are also harvested for human consumption in some countries (Nyabyenda et al. 1981; Singh 1989a). Ñuñas or popped beans are consumed as snacks in the highlands of Peru (Debouck 1989).

Dry bean production is concentrated in tropical and subtropical Latin

America (46.7%), sub-Saharan Africa (24.1%), North America (11.6%), Europe (10.4%), and Asia and North Africa (6.5%) (Pachico 1989). In Asia, Iran and Turkey are major producers, whereas Brazil (2.2 million tonnes) and Mexico (1.1 million tonnes) are the largest producers and consumers in the world. The highest yearly per capita consumption (>40 kg) of dry bean is in Rwanda and Burundi (Centro Internacional de Agricultura Tropical, CIAT 1981b).

There are strong preferences for seed types of dry bean in different countries and regions within countries (Voysest 1983, 1989; Vieira, C. 1988; Voysest and Dessert 1991). In Brazil, for example, small-seeded (<25 g/100-seed weight) black, cream, and cream-striped beans are popular. The latter two predominate in the northeastern states, whereas black beans are more popular in the southern region (Vieira, C. 1988). Similarly, small black and/or red beans are consumed in Central America, Mexico, Cuba, and Venezuela, whereas, in the Andean countries of Colombia, Ecuador, and Peru, large-seeded red, pink, beige, and cream types, both solid and with various patterns of mottling, speckling, and spotting, are preferred. These latter types also predominate in most of sub-Saharan Africa. In Europe, North Africa, and western Asia, white, red, and cream-mottled beans of different sizes and shapes (but mostly medium and large) are consumed.

In the past few years, three excellent books edited by Gepts (1988a), Schwartz and Pastor-Corrales (1989), and Schoonhoven and Voysest (1991) have been published on various aspects of Phaseolus beans. Other books, bulletins, and proceedings published on common bean within the past 25 years are those by Vieira (1967, 1978, 1983, 1985), Wall (1973), Drijfhout (1978), Robertson and Frazier (1978), Engleman (1979), CIAT (1981a,b, 1985a, 1989c), Lépiz I. and Navarro (1983), Tapia and Alarcón (1983), Voysest (1983), Davis and Janssen (1987), Lareo and González (1988), White et al. (1988), Zimmermann et al. (1988), Beebe (1989a), Abawi and Pastor-Corrales (1990); Toro et al. (1990), and Pastor-Corrales (1992).

General accounts of common bean are also given by Allavena (1984) and Adams et al. (1985). Debouck (1991) has provided a thorough treatment of systematics and morphology. Tanaka and Fujita (1979), Laing et al. (1984), Wallace (1985), Masaya and White (1991), and White and Izquierdo (1991) have provided comprehensive coverage of physiology of yield and adaptation of common bean. In addition, Smartt (1970), Hucl and Scoles (1985), and Mok et al. (1986) reviewed interspecific hybridization; Zaumeyer and Meiners (1975) reviewed disease resistance; Graham (1981) discussed nitrogen fixation; Schuster and Coyne (1981) have reviewed breeding for resistance to bacterial diseases; Hamblin and Zimmermann (1986) have examined breeding for yield in mixtures; and

Silbernagel (1986) has described snap bean breeding. Yarnell (1965) and Singh (1991a) reviewed results of genetic studies in common bean and Osborn (1988) reviewed genetics of bean seed protein. Silbernagel and Hannan (1988) have described the history and use of germplasm in improvement of common bean in the United States. Therefore, only common dry-bean improvement in the tropics and subtropics will be reviewed here, with special reference to work at CIAT. Readers interested in other details should refer to the above literature.

A. Origin and Domestication

Over 50 species of Phaseolus have been reported from the Americas (Debouck 1991). Of these, only five, namely, common bean (P. vulgaris L.), P. polyanthus Greenman, scarlet runner bean (P. coccineus L.), tepary bean (P. acutifolius A. Gray), and lima bean (P. lunatus L.), are known to be domesticated (Smartt 1969, 1985, 1988, 1990a,b; Evans 1980; Debouck 1988, 1991). Common bean possesses by far the maximum breadth of adaptation of all Phaseolus species and over 90% of cultivated Phaseolus fall under this species worldwide.

Cultivated common bean originated from its wild relatives, with which it crosses easily and produces normal fertile progenies (Burkart and Brücher 1953; Weiseth 1954; Kaplan 1965, 1981; Miranda C. 1967; Gentry 1969; Smartt 1969, 1985, 1988, 1990a; Berglund-Brücher and Brücher 1976; Evans 1980; Brücher 1988; Delgado S. et al. 1988; Kaplan and Kaplan 1988; Debouck and Tohme 1989; Gepts 1990; Gepts and Debouck 1991). Present-day distribution of wild common bean extends from Chihuahua in northern Mexico to San Luis in Argentina (Burkart and Brücher 1953; Miranda C. 1967; Gentry 1969; Harlan 1975; Nabhan et al. 1986; Brücher 1988; Delgado S. et al. 1988; Debouck and Tohme 1989; Toro et al. 1990). Contrasting differences in leaf, flower, pod, seed, allozyme pattern, phaseolin seed protein pattern, and other characteristics are found among accessions from the two most distant geographical regions (Brücher 1988; Debouck and Tohme 1989; Koenig et al. 1990; Toro et al. 1990; Gepts and Debouck 1991). Wild common bean germplasm from intermediate regions (i.e., Costa Rica, Colombia, Venezuela, Ecuador, and northern Peru) exhibits intermediate characteristics. Most of these differences are also found in cultivated forms of common bean from each of the respective regions, leading to two principal domestication centers: Middle America and the Andean highlands (Harlan 1975; Evans 1980; Gepts and Bliss 1985; Gepts et al. 1986; Gepts 1988c, 1990; Vargas et al. 1990; Gepts and Debouck 1991). Morphological, physiological, biochemical, and genetic changes that have occurred in common bean under domestication have been noted by

Kaplan (1965), Miranda C. (1967), Smartt (1969, 1985, 1988, 1990a), Berglund-Brücher and Brücher (1976), Evans (1980), Brücher (1988), and Gepts and Debouck (1991). Major changes include gigantism of leaf, flower, pod, and seed characteristics; appearance of determinate and indeterminate upright growth habits; insensitivity to photoperiod; and reduction or loss of seed dormancy, pod fiber, and impermeability to water. Although there seems to be a much wider range of variation in wild bean for phaseolin seed protein patterns (Gepts et al. 1986; Koenig et al. 1990; Vargas et al. 1990), cultivated common bean exhibits greater variations for such traits as seed size, shape, color, growth habit, leaf and pod characteristics, days to maturity, and ecological adaptation. These variations, however, are not distributed randomly, and some apparent patterns are found.

Cultivated landraces (Gepts 1988b; Debouck et al. 1989) of common bean from its primary centers of domestication in Latin America show specific associations for morphological traits (Evans 1973, 1980; Vanderborght 1987; Singh 1989a; Sprecher and Isleib 1989; Singh et al. 1990a, 1991b; Urrea and Singh 1991), molecular markers (Gepts and Bliss 1985; Gepts et al. 1986; Gepts 1988b, 1990; Sprecher 1988; Khairallah et al. 1990; Koenig et al. 1990; Singh et al. 1991d), breeding behavior (Evans 1970; Shii et al. 1980, 1981; Gutiérrez and Singh 1982; Singh and Gutiérrez 1984; Gepts and Bliss 1985; Koenig and Gepts 1989; Sprecher and Khairallah 1989; Vieira et al. 1989; Singh and Molina 1991), and geographical and ecological adaptations (Laing et al. 1984; Gniffke 1985; Singh 1989a; White and Laing 1989; Masaya and White 1991; Voysest and Dessert 1991). A major separation between Middle American and Andean landraces resulted from the divergence prior to domestication of wild ancestral populations (Singh et al. 1991a; Koinange and Gepts 1992). Within the Middle American and Andean groups, landraces sharing certain distinctive morphological, molecular, agronomic, and adaptive traits and differing from other groups in allelic frequencies of the genes controlling differences in those traits were defined as races by Singh et al. (1991a). Each race may consist of one or more gene pools described by Singh (1988a, 1989a, 1991b) on the basis of growth habit, maturity, yielding ability, and other traits. Six races (Singh et al. 1989b, 1991a) and 12 gene pools (Singh 1988a,b, 1989a, 1991b) have been described in cultivated common dry bean. For the relationship between races and gene pools, please refer to Singh (1988b, 1991b) and Singh et al. (1991a).

B. Principal Dry Bean Types

Common bean is polymorphic for growth habit, seed characteristics, and days to maturity, among other morphoagronomic and molecular

traits. The type of terminal bud on the main stem and branches at flowering, stem strength, angle formed by lateral branches and main stem, number of nodes on the main stem, internode length, presence or absence of guides or leaders (i.e., elongated terminal internodes on the main stem and branches, which are weak and possess ability to intertwine), climbing ability, and fruiting patterns are used to characterize and identify the principal growth habits (Evans 1973; CIAT 1981a; Singh 1982b; Vargas 1982; Adams et al. 1985; Debouck and Hidalgo 1986; Schoonhoven and Pastor-Corrales 1987; Debouck 1991; Voysest and Dessert 1991). The four main growth habits are (1) determinate upright (type I); (2) indeterminate upright (type II); (3) indeterminate, weak-stemmed nonclimbing or semiclimbing (type III); and (4) indeterminate, weak-stemmed climbing (type IV). Seed size (hence weight) varies from <15 to >60 g/100 seeds. Seed shape can be cylindrical, kidney, rhombohedric, oval, or round (Singh et al. 1991a). Similarly, large variations are found in testa color and its spotting, striping, speckling, mottling, etc. (Voysest 1983; Leakey 1988; Singh 1991b, Singh et al. 1991a; Voysest and Dessert 1991). Days to maturity can vary from 50 to > 250 days (Singh 1989a, 1991b). Differences in growth habit, seed characteristics, maturity, and ecological regions of adaptation conform to distinctive characteristics of specific commercial bean classes or seed types, races, and gene pools (Singh 1988a,b, 1989a; Singh et al. 1989b, 1991a; Voysest and Dessert 1991). These traits are also highly associated with yielding ability, bean-growing environments, cropping systems, production problems, and consumer preferences (Singh 1991b). It is therefore essential to consider genetic improvement of common bean in terms of races and their gene pools.

Major production regions and constraints for six races of common cultivated dry bean are listed in Table 7.1. Important bean cultivars of major commercial classes grown in the tropics have been described by CIAT (1981a), Voysest (1983, 1989), Vieira, C. (1988), Singh (1991b), and Voysest and Dessert (1991).

Common bean ($2n = 2x \equiv 22$) is a self-pollinated crop (Elgueta and Baillón 1944; Vieira 1960; Rutger and Beckham 1970; Ortega 1974; Pacova and Rocha 1975; Tucker and Harding 1975; Pereira Filho and Cavariani 1984; Stoetzer 1984) possessing complete, papilionaceous flowers with 10 stamens and an ovary with long, coiled style and hairy introrse stigma. Anthesis occurs in the early morning hours. Hand pollination (with or without emasculation) is required for achieving desired hybrid combinations (Buishand 1956; Bliss 1980). However, genic (van Rheenen et al. 1979; Mutschler and Bliss 1980; Bannerot, personal communication, 1988) and cytoplasmic-genic (Bannerot 1980; Singh et al. 1980; Bassett and Shuh 1982; Mackenzie et al. 1988) male sterility and

Table 7.1. Principal growing regions of common bean (*Phaseolus vulgaris* L.), preferred bean types, cropping systems, and production constraints in the tropics and subtropics.

Growing region	Environmental conditions					Preferred bean types			Growth habit[y]	Cropping systems[x]	Production problems
	Area sown (10⁶ ha)	Mean temperature (°C)	Rainfall (mm)	Crop duration (days)	Race[z]	Size and shape	Color	Commercial classes			
Brazil, coastal Mexico, Central America, Cuba, and Venezuela	6.00	22	500–1000	90–100	Meso-america	Small; kidney, cylindrical, round	Black, cream, cream striped, beige, pink, and red	Negro, Rojo, Carioca, Mulatinho, Jalinho	II, III, IV	Sole crop and subsistence intercropping	Drought, acid soils, BCMV, BGMV, common bacterial blight, anthracnose, angular leaf spot, rust, root rots, leafhoppers, Apion
Semiarid highlands of Mexico	1.50	18	<510	110–120	Durango	Medium; rhombohedric	Beige, pink, and black of solid, spotted, striped, and speckled	Bayo, Pinto, Flor de Mayo, Ojo de Cabra, Negro	III	Sole crop and subsistence intercropping	Drought, root rots, common blight, anthracnose, angular leaf spot, rust, Mexican bean beetle

Table 7.1. Continued.

Growing region	Area sown (10⁶ ha)	Mean temperature (°C)	Rainfall (mm)	Crop duration (days)	Race[z]	Size and shape	Color	Commercial classes	Growth habit[y]	Cropping systems[x]	Production problems
Humid highlands of Mexico and Guatemala	0.25	18	600–800	150	Jalisco	Medium; round, oval, kidney, cylindrical	Beige, pink, and black	Garbancillo, Rosita, Flor de Mayo, Negro Puebla	III, IV	Subsistence intercropping with maize	Rust, anthracnose, angular leaf spot, common blight, Apion, acid soils
Medium altitudes of Andean highlands and sub-Saharan Africa	3.50	20	800–1000	90–100	Nueva Granada	Large; kidney, cylindrical, oval, round	Red, pink, beige, cream, and buff of solid, mottled, spotted, and speckled	Sangretoro, Bagajo, Doré de Kirundo, Kabanima, Canario, Azufrado, Cargabello, Canadian Wonder	I, III	Sole crop and subsistence intercropping	BCMV, BYMV, BGMV, CMV, anthracnose, angular leaf spot, rust, common blight, halo blight, bean fly, acid soils
Highlands of Colombia, Ecuador, Peru, Bolivia, and Argentina	0.15	16	1000–1500	240–260	Peru	Large; round, oval	Red, pink, beige, yellow, and white of solid and spotted	Cargamanto, Bolón Bayo, Bola Roja, Caballero, Ñuñas	III, IV	Subsistence intercropping with maize	Anthracnose, angular leaf spot, rust, powdery mildew, ascochyta blight, halo blight

Continued

Table 7.1. Continued.

	Environmental conditions						Preferred bean types					
Growing region	Area sown (10⁶ ha)	Mean temperature (°C)	Rainfall (mm)	Crop duration (days)	Race[z]		Size and shape	Color	Commercial classes	Growth habit[y]	Cropping systems[x]	Production problems
Chile	0.05	20	<500	120–130	Chile		Medium; oval, round	Gray, white speckled, cream mottled	Tórtolas, Coscorrón, Frutilla, Bolita	III	Sole crop and subsistence intercropping with maize	BCMV, BYMV, CMV, drought, high temperature, salinity

[z] According to Singh et al. (1989b, 1991a).

[y] Growth habit I = determinate, upright bush, II = indeterminate, upright bush, III = indeterminate, prostrate nonclimber or semiclimber, and IV = indeterminate or determinate climber (Singh, 1982b).

[x] Substantial harvest from sole crops is often sold. Intercropping may include strip cropping, relay cropping, and direct association with maize, cassava, banana, sugarcane, potato, and other crops or crop mixtures.

indehiscent anthers (Wyatt 1984), as well as extremely high rates of natural outcrossing in some environments and genotypes (Brunner and Beaver 1988; Wells et al. 1988), have been reported.

C. Major Growing Regions

Growth of common bean is favored by a mean growing temperature of 18–22°C and well-distributed precipitation of 500–800 mm during the growing season. In tropical equatorial regions, the crop matures in less than 100 days in lowlands (<1500 m elevation), but may take up to 270 days in highlands (>2000 m elevation). Performance is the best in near-neutral soil pH. In acid soils deficient in phosphorus and possessing toxic levels of aluminum and manganese, adequate use of lime and/or phosphorus-rich fertilizers may be required for commercial cultivation. In relatively high-pH soils, which are also high in salts, deficiencies of iron and boron and toxicity of some elements might require the use of gypsum, elemental sulfur, and/or sulfur-rich fertilizers. Although some cultivar differences exist, common bean is a poor fixer of nitrogen in the tropics.

Six principal bean-growing regions in the tropics and subtropics, their bean types, and the approximate areas sown in each region are summarized in Table 7.1. The largest area (6 million ha) is sown with small-seeded bean cultivars belonging to Middle American race Mesoamerica, followed by large-seeded Andean race Nueva Granada (3.5′ million ha) and medium-seeded Middle American race Durango (1.5 million ha).

D. Production Systems

A good discussion of different production and cropping systems of common bean is provided by Aguirre and Miranda (1973), Edje et al. (1981), Schoonhoven and Voysest (1989), and Woolley et al. (1991). Common bean production systems in the tropics and subtropics can be grouped into the following four general categories.

1. Subsistence Intercropping. This system is common in bean production regions of Latin America and sub-Saharan Africa. Common bean is grown as a rainfed subsistence crop, in fields usually <3 ha, either in direct association or in strip or relay cropping with maize (*Zea mays* L.), cassava (*Manihot esculenta* Crantz), coffee (*Coffea arabica* L.), banana (*Musa* spp.), cotton (*Gossypium hirsutum* L.), potato (*Solanum tuberosum* L.), sugarcane (*Saccharum officinarum* L.), sorghum (*Sorghum bicolor* (L). Moench), and other crops (Aguirre and Miranda 1973; Francis et al. 1976; Edje et al. 1981; Francis 1981; Nyabyenda et al.

1981; Serpa et al. 1981; Vieira 1985; Woolley et al. 1991). In Central America, the relay cropping system in which beans are sown when maize is approaching physiological maturity is popular. Similarly, in the Andean highlands (>2000 m altitude), growing climbing beans in direct association with maize is the predominant cropping system. Common bean cultivars used for intercropping can be bush (types I and II), semiclimbing (type III), and/or climbing (type IV). In sub-Saharan Africa and in some parts of Latin America, genotypic or varietal mixtures of common bean predominate (Pessanha et al. 1981; Edje and Adams 1985; Dessert 1987; Vieira, C. 1988). Yields are generally low (600 kg ha^{-1}).

2. Semiarid Farming. Over four million hectares of common bean cultivation in monoculture (sole crop) and/or intercropping are found, especially in the central highlands of Mexico (Ibarra 1988; Acosta et al. 1989) and northeastern Brazil (Silveira et al. 1981; Guimarães 1988), where the crop often suffers moisture stress. Predominant cultivars are of semiclimbing growth habit III. Farmers use limited inputs when there are rains. If rain is insufficient, inputs are not used. Yields in these marginal production areas are low (< 500 kg ha^{-1}), and total crop failures are a common phenomenon.

3. Small Monoculture Farming. Often, fields of <5 ha of common bean are cropped either with or without irrigation but with intensive use of agrochemicals and traditional farm implements. These areas are found in small pockets throughout Latin America where bean is grown as a cash crop due to favorable market prices and special demands. Cultivars grown are often bush types or climbers in relay cropping and on trellises or stakes. Yields are relatively high (> 1000 kg ha^{-1}).

4. Large Monoculture Farming. This system represents semicommercial and commercial monoculture operations run by affluent farmers or their associations and cooperatives, which use modern farm machinery and agrochemicals and may or may not use irrigation. These areas can be found in the Pacific and Gulf coastal regions of Mexico, Cuba, Venezuela, central (under winter sowing) and southern Brazil, eastern Bolivia, Chile, and Argentina. While in most of these areas a farmer may grow up to 500 ha of common bean, in Argentina it is not uncommon to find growers with over 3000 ha of bean plantings. Cultivars grown are of growth habits I, II, or III. Yields are often > 1000 kg ha^{-1}.

Most climbing bean and substantial bush and semiclimbing bean hectarage is intercropped with maize and other crops, especially in Latin America (Vieira 1967, 1978, 1985; Lépiz I. 1972, 1974, 1978; Aguirre and Miranda 1973; Francis et al. 1976; Francis 1981; Woolley et al. 1991) and

Africa (Osiru and Willey 1972; Willey and Osiru 1972; CIAT 1981b; Woolley et al. 1991). In these cropping systems, common bean is often a secondary crop. Due to a shortage of labor, long growing season, and buildup of diseases, however, there is a gradual reduction in total area planted to climbing bean and an increase in monoculture cropping systems in Latin America. Moreover, in countries such as Brazil and Mexico, common bean is being pushed away from favorable production regions to marginally fertile and adverse regions by industrial crops such as soybean (*Glycine max* (L). Merr.), sugarcane, sorghum, and maize. Thus, common bean in the tropics is grown mostly as a subsistence crop by resource-limited farmers who often do not use agrochemicals and modern farm technology available in developed countries (Pachico 1989). Consequently, yield is low (600 kg ha^{-1}) and varies from year to year and region to region. Consumer demands for common bean, especially in urban populations, often far exceed the available supply; therefore, bean prices are relatively high in countries where the price is not subsidized.

E. Production Problems

Diseases, drought, and low soil fertility are among the most widespread and endemic production problems of cultivated common bean in the tropics and subtropics (Zaumeyer and Thomas 1957; Vieira 1967, 1983; Zaumeyer 1973; Graham 1978; Schwartz and Gálvez 1980; CIAT 1981a,b, 1985a; Lépiz and Navarro 1983; Tapia and Alarcón 1983; Vieira, C. 1988; Zimmermann et al. 1988; Allen et al. 1989; Schoonhoven and Voysest 1989). Insects such as leafhoppers (*Empoasca kraemeri* Ross & Moore), bean pod weevil (*Apion godmani* Wagner), Mexican bean beetle (*Epilachna varivestis* Mulsant.), and bean fly (*Ophiomyia phaseoli* Tryon) in fields; and Mexican bean weevil (*Zabrotes subfasciatus* Boheman) and bean weevil (*Acanthoscelides obtectus* Say) in storage cause serious crop losses in some areas (CIAT 1981a; Cardona 1989; Karel and Autrique 1989). Among diseases, bean common mosaic virus (BCMV), common bacterial blight caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye, anthracnose caused by *Colletotrichum lindemuthianum* (Sacc. & Magn.) Scrib., angular leaf spot caused by *Phaeoisariopsis griseola* (Sacc.) Ferraris, rust caused by *Uromyces appendiculatus* (Pers.) Unger var. *appendiculatus*, and root rots caused by a group of plant pathogenic fungi (Abawi 1989; Abawi and Pastor-Corrales 1990) are widespread throughout bean production regions of the world (Hernández-Bravo 1973; Zaumeyer 1973; Graham 1978; CIAT 1981a,b, 1985a; Beebe and Pastor-Corrales 1991). Other fungal, bacterial, and viral diseases are often of regional importance, such as halo blight caused by *Pseudomonas syringae* pv. *phaseolicola* (Burkholder) in the cool and humid highlands of

the Andes and Central and eastern Africa (CIAT 1981a, 1981b) and bean golden mosaic virus (BGMV) in the Pacific coastal regions of Mexico, Guatemala, El Salvador, Honduras, Cuba, the Dominican Republic, Haiti, Brazil, and northwestern Argentina (Morales and Niessen 1988; Gálvez and Morales 1989; Morales and Singh 1991). Similarly, deficiencies of soil phosphorus (Thung 1990) and nitrogen are common in bean production areas. Although occurrence, severity, and duration of drought vary from region to region, over 60% of all bean production areas suffer from some sort of drought; it is endemic in northeastern Brazil and the central highlands of Mexico (Silveira et al. 1981; Guimarães 1988; Ibarra 1988; Singh and White 1988; Acosta et al. 1989; White and Singh 1991a). Major production problems of common bean are summarized in Table 7.1.

Different combinations of production problems and their severity vary according to region and year, thus causing great fluctuations in bean production. Hence, in most regions, recovering existing yield potential of commercial cultivars, stabilizing production, and reducing crop losses have been of greater priority than increasing productivity potential per se.

II. HISTORY OF IMPROVEMENT IN THE TROPICS

The earliest reports of organized common bean breeding in Latin America go back to the late 1920s and early 1930s in Brazil, Colombia, and Mexico (Bastidas 1980; Voysest 1983; Vieira, C. 1988). For example, the Instituto Agronômico de Campinas, São Paulo, Brazil, initiated common bean improvement in 1930 (Vieira, C. 1988). The Oficinas de Estudios Especiales in Mexico intensified research on important food crops, including maize, wheat (*Triticum aestivum* L.), and common bean in the 1940s. Similarly, improvement of common bean received impetus in the 1940s, 1950s, and 1960s in Chile, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, and Peru. Some of these programs were initiated in collaboration with, and through, financial support from the Rockefeller Foundation (e.g., in Mexico and Colombia), the U.S. Agency for International Development, and the Organization of American States through IICA (Instituto Interamericano de Ciencias Agrícolas). Those programs helped train the first group of scientists in these countries who made long-lasting contributions to *Phaseolus* germplasm collection and improvement. For example, cultivars such as 'Jamapa,' 'Porrillo,' 'Turrialba,' 'Rojo Zamorano,' and 'San Fernando' in Mexico and Central America and 'Diacol Calima,' 'ICA Pijao,' and 'ICA Bunsi' in Colombia; and 'Canario Divex' and 'Bayo Chimú' in Peru have

been in commercial production for many years and have been the cornerstone for further improvement in several programs. These groups include cultivars that were developed by selection among and within landraces (e.g., 'Jamapa,' 'San Fernando,' and 'Porrillo') as well as those developed by hybridization and selection (e.g., 'ICA Pijao,' 'Diacol Calima,' 'Canario Divex,' and 'Bayo Chimú'). Nevertheless, owing to the fact that large differences in bean types, ecological adaptation, cropping systems, and production problems occur within traditional bean-growing regions of Latin America, the total impact may not be large. This, in part, could also be due to relatively short periods of research, poorly funded programs, and the subsistence nature of this crop grown by farmers with limited resources.

Bean improvement in Africa is a much more recent activity, which was begun by researchers in the 1960s (Leakey 1970; CIAT 1981b; Edje et al. 1981; Karel et al. 1981; Nyabyenda et al. 1981; Rubaihayo et al. 1981; Allen et al. 1989). Organized collaborative research covering important bean production regions in Central, eastern, and southern Africa began only in the 1980s (CIAT 1981b). Information about bean production and research activities of principal bean-producing countries in the tropics and subtropics could be found in the books and bulletins listed earlier and in the proceedings of regional bean conferences for Latin America (Wall 1973), eastern and Central Africa (CIAT 1981b), and West Asia and North Africa (CIAT 1985a). Owing to the crop's importance as a major protein and calorie source in the traditional diets of rural dwellers and urban poor in tropical and subtropical Latin America and sub-Saharan Africa (Bressani 1972; Wall 1973; Scobie et al. 1974; CIAT 1981b, 1985a; Linares et al. 1981), the need for launching a concerted international effort was apparent.

Until 1973, common bean was one of several legumes being investigated at CIAT (Wall 1973). A multidisciplinary team was gradually formed to conduct research on dry, field, or common bean, with emphasis on its genetic improvement (CIAT 1981a). In 1977, the first regional collaborative project with CIAT participation was initiated in Central America to strengthen research, production, and technology transfer capabilities of national programs. This was an adjunct and complement to efforts of PCCMCA (Programa Cooperativo Centroamericano de Mejoramiento de Cultivos Alimenticios), which had been functioning since the 1950s in the region. At present, there are six CIAT-assisted regional projects functioning: three each in Latin America and sub-Saharan Africa.

The bean/cowpea collaborative research support program (CRSP) initiated from 1980 to 1981 is a program in which research projects are developed and executed by researchers in Africa, Central and South

America, and Caribbean countries in collaboration with U.S. institutions (Silbernagel and Hannan 1988). These projects are active in about a dozen countries that are making significant and valuable contributions in research and training of personnel from host countries (MSU 1990).

CIAT is responsible for the collection, preservation, and distribution of all cultivated *Phaseolus* species and their relatives. However, germplasm improvement or enhancement is restricted to common bean. Common bean represents about 90% of the over 40,000 accessions currently maintained at CIAT (CIAT 1990; Hidalgo 1991). Over 23,000 of these accessions have passed quarantine requirements, have had their seed multiplied and registered, and are available for utilization in research and production programs. Other countries possessing major collections of *Phaseolus* germplasm include Belgium, Brazil, Costa Rica, France, Guatemala, Honduras, Italy, Kenya, Malawi, Mexico, Peru, the United Kingdom, United States, and the former United Soviet Socialist Republics.

Germplasm evaluation continues to be one of the main activities of the CIAT bean team and research support units. In addition to routine evaluations of all germplasm accessions by the personnel of the Genetic Resources Unit (Hidalgo 1991), members of the bean team and other research support units actively participate in systematic evaluations of important agronomic traits. For example, most available germplasm has been or is being evaluated for BCMV, leafhoppers, bean weevil, Mexican bean weevil, common bacterial blight, anthracnose, angular leaf spot, response to photoperiod and drought, and other traits. All evaluation information is computerized, forms part of the central data management system, and is available to users. For factors such as BGMV, bean pod weevil, and bean fly that do not occur in Colombia, evaluations are made in the regional programs or by bilateral collaboration with national programs (CIAT 1988). Similarly, for highly variable pathogens, pests, and climatic and edaphic factors, promising germplasm is also tested through regional and international nurseries at contrasting sites (CIAT 1989b, 1990).

Germplasm evaluation information has been important for all common bean improvement activities. Sources of resistance to major production problems and other useful germplasm have been identified and are being utilized (Bannerot 1965; Beebe et al. 1981; Schoonhoven and Cardona 1982; Schwartz et al. 1982; Schoonhoven et al. 1983; Gniffke 1985; Cardona 1988; CIAT 1988, 1990; Menezes and Dianese 1988; White and Laing 1989; Beebe and Pastor-Corrales 1991; Kornegay and Cardona 1991a; White and Singh 1991a,b). Combining ability and recombination studies among and within bean classes, races, and gene pools are being carried out (Foolad and Bassiri 1983; Vaid et al. 1985; Kornegay

and Temple 1986; Nienhuis and Singh 1986, 1988a; Paredes C. 1986; Rodríguez C. 1987; Rodríguez and Kuruvadi 1990; Corrales B. 1991; Morales and Singh 1991; Vizgarra 1991; Singh et al. 1992b) in order to be able to select parents for hybridization, predict performance of populations and lines derived from them, and to thus increase efficiency in creating useful genetic variation.

III. BREEDING OBJECTIVES AND STRATEGIES

Over 80% of common bean in Latin America and sub-Saharan Africa is grown either as a subsistence intercrop, in semiarid regions, or in production environments suffering from diseases, insects, drought, and low soil fertility. In addition, bean farmers are often unable to use necessary amounts of agrochemicals. Therefore, breeding for key production-limiting factors, especially diseases (Orozco et al. 1964; Leakey 1970, 1973; Crispin 1974; Cafati and Alvarez 1975; Mukunya and Keya 1978; Miranda et al. 1979; Bastidas 1980; Pompeu 1980, 1982; Mohan 1981; Alberini et al. 1983; Tay and France 1986; Tay et al. 1986), of widespread importance has been emphasized. Breeding for production-limiting factors helps recover yield potential of commercial cultivars, minimize production losses, reduce production costs, and stabilize yield. It also permits subsistence farmers to take advantage of improved cultivars, minimize the risk of spreading pathogen populations, reduce dependence on chemical pesticides and fertilizers, and increase water use efficiency, thus maintaining a cleaner environment and conserving natural resources.

Initially at CIAT, breeding for resistance to diseases of major economic importance, which included BCMV, anthracnose, angular leaf spot, common bacterial blight, and rust, was emphasized (CIAT 1981a), both in character and cultivar improvement projects (discussed below). This was done because these diseases not only cause severe yield losses but also all except rust are seed-transmitted. Thus, new germplasm resistant to these diseases facilitated production and distribution of a better quality seed and stabilized yield in addition to reducing production costs and occurrence of disease epidemics. Breeding for tolerance to leafhoppers and resistance to bean weevil, Mexican bean weevil, and bean pod weevil was undertaken subsequently. However, increasing attention also needs to be given to breeding for tolerance to drought and low soil fertility, seed yield, early maturity, easily mechanizable upright plant type, and culinary quality.

Breeding for small-seeded black, red, cream, and cream-striped cultivars of growth habits II and III of race Mesoamerica was initiated first

(1974–1975). This was followed by work on large-seeded bush and semiclimbing cultivars of race Nueva Granada (1978–1979), large-seeded climbing beans of race Peru (1980–1981), medium-seeded semiclimbing beans of race Durango (1981–1982), medium-seeded climbing beans of race Jalisco (1983–1984), and medium-seeded semiclimbing beans of race Chile (1989). In each case, improvement of only the most popular seed classes and cultivars has been emphasized. Severe problems of adaptation, however, have slowed the improvement of cultivars belonging to races Peru, Durango, Jalisco, and Chile at CIAT. Active participation and collaboration of national program scientists, at least in the evaluation and selection phases, for improvement of these groups of cultivars is crucial.

Germplasm improvement strategies to accomplish the above-mentioned objectives are organized around two main areas: character and cultivar (CIAT 1987). In some crop improvement programs, there is often no clear separation between character and cultivar improvement projects. At CIAT, the need for this distinction was realized early in the program because of numerous production constraints, a lack of information regarding useful germplasm and screening techniques, and the relative ease or difficulty with which different characters could or could not be improved simultaneously.

A. Character and Cultivar Improvement

Each character improvement project encompasses germplasm evaluation to find desirable genes and mechanisms from diverse sources across races and gene pools of common bean, its wild and weedy forms, and related species that will enhance expression of specific characters, study of their inheritance, and their recombination and accumulation in common backgrounds. Often, little or no attention is given to bean type, plant type, regions of adaptation, and cropping systems. Each major production-limiting factor requires a separate breeding project. Progress achieved in some projects will be discussed later.

For cultivar improvement (or character deployment), growing environments, commercial bean types, cropping systems, production problems, and other factors are taken into account (CIAT 1981a; Singh 1991b; Table 7.1). Program objectives and priorities reflect the urgency with which desirable germplasm is sought. Nevertheless, for each major bean production and cropping system, plant type or growth habit, maturity, and seed characteristics of the most prevalent landraces and commercial cultivars have been emphasized. For example, although climbing type IV and bush determinate type I landraces are found in some regions, in most countries of Central America small-seeded, black- and red-colored cultivars of growth habits II or III predominate. Therefore, in national pro-

grams and regional projects in Central America, and at CIAT, breeding for the latter plant types has been emphasized. Similarly, for semiarid highlands of Mexico where indeterminate semiclimbing type III cultivars have traditionally been grown, no attempts have thus far been made at CIAT to develop bush upright growth habit I or II cultivars. Specific examples of cultivar improvement will be dealt with later.

Lines from character improvement projects usually show superiority only for the specific traits for which they have been improved and may not be suitable for direct utilization in a bean production system where several stresses occur simultaneously. However, these lines are easier to work with than the original donor parents and they increase the frequency of desirable agronomic types in the subsequent hybrid populations made for cultivar improvement. For example, lines XAN 93, XAN 112, and XAN 159 developed for common bacterial blight resistance lack desirable seed characteristics, but they have better tropical adaptation than some of the original sources, such as great northern 'Tara' and 'Jules' from Nebraska, PI 207262 from Mexico, and tepary bean, used in their development. XAN 93, XAN 112, XAN 159, and their sister lines have subsequently been used to develop high-yielding lines that are in commercial cultivation (CIAT 1987; Beebe and Pastor-Corrales 1991).

B. Hybridization

Germplasm from cultivated races and gene pools, wild and weedy forms, and related species has been used in hybridization and improvement of common bean cultivars. The role of each of these for creation of useful genetic variability will be discussed briefly here.

1. Use of Interspecies Variability. Crosses of common bean with *P. polyanthus* Greenman and scarlet runner bean can be achieved without the aid of embryo culture (Smartt 1970; Hucl and Scoles 1985; Mok et al. 1986). Realization of the F_1 hybrid with tepary bean is usually difficult, and embryo rescue for the initial cross with tepary bean and its subsequent backcross with common bean is essential (Smartt 1970; Alvarez et al. 1981; Prendota et al. 1982; Thomas and Waines 1984; Hucl and Scoles 1985; Waines et al. 1988). Genotypic diversity of parents used in hybridization and the cytoplasm of the female parent play a significant role in recovery of interspecies hybrids (Shii et al. 1982; Thomas and Waines 1984; Pratt et al. 1985; Parker and Michaels 1986; Waines et al. 1988). Simple genetic control of incompatibility between tepary and common bean was suggested by Parker and Michaels (1986). Interspecies compatibility in *Phaseolus* beans could be predicted by seed protein patterns using electrophoresis (Sullivan and Freytag 1986). Nonetheless,

transfer of useful traits from these species into stable, true-breeding common bean lines is difficult. Thus far, successful gene transfers between common bean and lima bean have not been possible.

Transfer of useful genes, especially for resistance to common bacterial blight, from tepary and scarlet runner beans to common bean, has been carried out to some extent (Honma 1956; Freytag et al. 1982; McElroy 1985; Park and Dhanvantari 1987). But cultivated and wild germplasm from these and other related species need to be evaluated, and desirable genes transferred, especially for traits not adequately expressed (e.g., resistance to BGMV, drought, low soil fertility) in common bean cultivars. Tepary beans might be especially useful in common bean improvement for fragile moisture deficient and low soil fertility environments because of their higher levels of tolerance (Waines 1978; Thomas et al. 1983; Markhart III 1985). They also possess high levels of resistance to common bacterial blight (Schuster 1955; Drijfhout and Blok 1987) and leafhoppers (CIAT 1985c).

2. Use of Wild and Weedy Forms. Less than 1000 accessions of wild and weedy populations of common bean compared to more than 35,000 entries of cultigens are currently available in the germplasm banks (CIAT 1990; Toro et al. 1990; Hidalgo 1991). Relatively higher levels of polymorphism for phaseolin seed protein patterns in wild populations compared to cultigens (Gepts et al. 1986; Koenig et al. 1990; Vargas et al. 1990) and discovery of immunity for bean weevil and Mexican bean weevil in wild beans from Mexico and its absence in all cultigens evaluated thus far (Schoonhoven and Cardona 1982; Schoonhoven et al. 1983) strongly suggest that not all wild bean populations were domesticated, or some useful genes were left out during domestication.

Wild beans had longer flowering duration, higher number of flowers and mature pods, and more ovules and seeds per pod compared to cultigens (Nakamura 1986). Lynch et al. (1989) reported that Mexican wild and weedy accessions had high photosynthetic rates, low soluble protein content, and the highest instantaneous photosynthetic nitrogen use efficiency. Argentinean accessions had low values for these leaf photosynthesis-related parameters. In a recent study, 39 wild and weedy populations from the two extremes of their distribution range in Middle America and the Andes were crossed to a high-yielding tropically adapted common tester cultivar 'ICA Pijao.' Although final results are not available yet, from the performance of F_1, F_2, F_3, and F_4 population bulks in contrasting environments, it was found that the Middle American populations were superior for seed yield under favorable and water stress environments to their Andean counterparts. However, under low soil fertility, populations involving Andean wild beans performed better

(Singh et al 1991c; our unpublished data). Thus, it is imperative that all wild and weedy bean populations be systematically evaluated for useful genes and used in character and cultivar improvement projects. Also, alternative hybridization and selection strategies need to be tried for effective and efficient gene transfer from wild and weedy forms into cultigens.

3. Use of Interracial Variability. This includes the agronomic evaluation of parental germplasm, predicting parental performance in crosses, and actual planning and making of crosses. Traditionally, bean breeders have restricted hybridization within commercial seed classes, races, or gene pools because of problems of recovering desirable plant, seed, and adaptation characteristics. Also, hybrid incompatibility and segregation distortion (Coyne 1965; van Rheenen 1979; Shii et al. 1980, 1981; Gutiérrez and Singh 1982; Singh and Gutiérrez 1984; Gepts and Bliss 1985; Koenig and Gepts 1989; Sprecher and Khairallah 1989; Vieira et al. 1989; Singh and Molina 1991) prevent effective recombination. Information about combining ability among and within commercial seed classes, races, and gene pools for most agronomic traits has been lacking. Thus, exploitation of genetic variability and gene transfer across commercial seed classes, races, and gene pools, especially among those belonging to different domestication centers, is just commencing. Nonetheless, there is mounting evidence suggesting that crosses within commercial classes, races, and gene pools must be avoided if tangible and sustainable genetic gains are to be achieved, especially for yield (Singh 1989b, 1991b; Singh et al. 1989a, 1991e; Singh and Gutiérrez 1990); resistance to diseases such as anthracnose, angular leaf spot, and rust, which are caused by highly variable pathogens (Bannerot 1965; Junqueira Netto et al. 1969; Oliari et al. 1973; Alvarez-Ayala and Schwartz 1979; Stavely 1984b; Correa V. 1987; Menezes and Dianese 1988); low soil fertility problems (Singh et al. 1989c); and drought.

Between and within commercial seed classes, races, and gene pools, genetic divergence among parents could be determined by their phaseolin seed protein pattern (Brown et al. 1982; Gepts et al. 1986; Koenig et al. 1990; Singh et al. 1991b), allozymes (Bassiri and Adams 1978; Sprecher 1988; Singh et al. 1991d), and morphological marker traits (Singh et al 1989b, 1990a, 1991a; Urrea and Singh 1991). For example, within small-seeded race Mesoamerica, germplasm carrying B phaseolin has a different evolutionary origin from that possessing S type (Gepts and Bliss 1986; Koenig et al. 1990), even within germplasm possessing similar phaseolin, which from cool highlands (i.e., different geographical origins) could be used to improve germplasm from lowlands and vice versa. Similarly, germplasm from the secondary centers of diversity (i.e.,

Europe, Africa, and Asia), especially for large-seeded white and snap beans, might be useful for improvement of germplasm from the Americas because greater range of variation for both these beans is found among accessions from those areas (Singh 1989a). Although precise information is not available, the best guess is that less than 5% of the total genetic variability available in the primary gene pools of common bean (Debouck 1991) has been utilized thus far in improvement programs.

Single, three-way, double, and modified double crosses (Singh 1982a), along with backcrosses and multiple crosses, are used for the creation of desired recombinants. From interracial single crosses it is usually extremely difficult to find recombinants with desirable seed, plant, and adaptation characteristics because of their genetic distance. Hence, these are used to make three-way, modified double, double, and/or backcrosses with the most desirable parents to overcome these difficulties and increase frequency of desirable recombinants. For cultivar improvement where several traits have to be combined together (especially from parents belonging to different races), single, three-way, and double crosses often serve only as donor parents of the ultimate modified double, multiple, and backcrosses. Use of more than ten parents in a cross is to be avoided because these usually give inferior recombinants. Similarly, top crosses, intermatings in early segregating generations, recurrent selection, and use of mutagens are not popular at the moment in common bean improvement in the tropics, with some exceptions. However, their relative importance is under investigation. For three-way, modified double, double, multiple, and backcrosses, plant-to-plant hybridizations are made between the male and female parents in order to assure adequate sampling of gametes from all parents involved in those crosses. An average of 200 flower buds from over 75 plants are pollinated for each final hybrid combination.

C. Selection Methods

These may involve (1) determining the value of and selection among hybrid populations; (2) evaluation, identification, and selection of desirable recombinant genotypes within promising populations; and (3) fixation of desirable traits into pure lines or genotypic mixtures. The selection method will depend largely upon the order and combination in which these three activities are carried out in succeeding hybrid filial generations. This in turn depends upon (1) the number of traits to be selected at a time, (2) heritability of traits, (3) facilities available for screening and evaluation, (4) number of populations to be managed, (5) resources available, and (6) collaboration among scientists from different disciplines and institutions.

1. Choice of Selection Methods. Pedigree, mass-pedigree, and conventional backcross methods of selection have been the principal breeding systems used in common bean improvement. Use of recurrent selection (Duarte 1966; Davis and Evans 1977a; Tolla 1978; Sullivan and Bliss 1983a; Kelly and Adams 1987; Fouilloux and Bannerot 1988), congruity backcrosses (Haghighi and Ascher 1988; Hibberd and Ascher 1988), inbred backcrosses (Wehrhahn and Allard 1965; Sullivan and Bliss 1983b; Sullivan 1988), and the single seed descent or recombinant inbred procedures (Brim 1966; our unpublished data) are gradually being tried, especially when desirable genes have to be transferred from distantly related or unadapted parents to otherwise popular cultivars. An important feature of the last two procedures is delaying evaluation and selection within hybrid populations until considerable homozygosity has been reached.

2. Early Generation Yield Test. Early generation yield testing (EGT) is either being used, or its value is being investigated in some projects where high yield is sought (Singh 1989b, 1991b; Singh and Gutiérrez 1990; Singh et al. 1990b), or it must be combined with resistance to production-limiting factors such as drought, low soil fertility, diseases, and insects. For example, the EGT procedure is used in breeding for tolerance to drought (Singh and White 1988; White and Singh 1991a) and leafhoppers (Kornegay and Cardona 1990), for which seed yield is the main selection criterion. Replicated yield trials are conducted under adequate pressure of specific production-limiting factors. Objectives in these cases are to estimate potential of crosses on the basis of their bulk population or family performance and select among, rather than within, populations or families. Hamblin and Evans (1976) and Singh et al. (1990b) were able to determine the potential of common bean populations on the basis of the yield of parents and/or hybrid bulks in early generations. The mean yield of high-yielding populations did not change, but that of poor-yielding populations increased gradually in successive generations of inbreeding (Hamblin 1977).

For bulk method of breeding, single pod bulks (SPB), with or without selection within plots, are formed before harvesting replicated plots for yield measurements. After data analysis, only SPB from selected populations or families are advanced to the subsequent generations. Single plant selection commences in the F_3, F_4, or F_5 in populations that have done well in yield trials and other evaluations in previous generations. For reliable yield estimation, data from two or more locations and/or growing seasons or years are required, depending upon the locations used for evaluation (Singh et al. 1990b).

For single seed descent (SSD) and pedigree methods of breeding, single pods from all plants within each F_2 population are harvested in separate

envelopes before harvesting replicated plots for yield measurements. After data analysis, only single pods from selected populations are saved for planting in the hill plots in the F_3 (each pod in a separate hill). For SSD, from each hill plot only a single plant is harvested for planting in the subsequent generation, and the process is repeated until the desired level of homozygosity is reached. Eventually, a single plant from each hill plot is harvested for progeny testing and obtaining recombinant inbred lines, which are then subjected to agronomic evaluations.

For the pedigree method, all plants from each hill plot in the F_3 are harvested in bulk for yield tests in F_4 and F_5. Thus, single plant harvests are made in high-yielding F_2-derived F_6 lines from high-yielding populations. These are grown in plant-to-progeny rows in the F_7, and if found uniform for principal agronomic traits, all plants within plots are harvested in bulk for subsequent evaluations and identification of high-yielding cultivars.

3. Selection for Multiple Traits. While selecting for two or more traits in the same populations, extremely high selection pressure for any one trait in the early generations is avoided. For simultaneous improvement of two or more traits that could not be screened in the same nursery (e.g., anthracnose and drought), selection is practiced in alternate generations (CIAT 1981a). Alternate selection was also found to be more efficient than simultaneous or independent selection for resistance to anthracnose and angular leaf spot, the two diseases which are often sympatric and can be screened in the same nursery (Singh et al. 1991e). Alternate selection is done at different locations and/or in different growing seasons in the early segregating generations, followed by evaluation of advanced generation lines in separate complementary or parallel nurseries for each of the traits (CIAT 1981a). Use of selection index (Davis and Evans 1977b; Sullivan and Bliss 1983a) or simultaneous improvement of multiple traits is not popular in the tropics.

4. Selection for Durable Resistance. Although precise information regarding different mechanisms and race-specific and race-nonspecific resistances (Beebe and Pastor-Corrales 1991) were not available initially, diverse sources of resistance from both Middle American and Andean domestication centers have been used at CIAT. Presently, for diseases such as rust, angular leaf spot, and anthracnose, extensive evaluation of sources of resistance across production regions over a period of several years and often through international disease nurseries helps identify race-nonspecific and race-specific genes conferring resistance to much broader ranges of pathogen populations (CIAT 1985b, 1987, 1990; Beebe and Pastor-Corrales 1991). Thus, recessive and dominant sources of

resistance (e.g., BCMV and angular leaf spot) and different mechanisms of resistance (e.g., anthracnose and rust) identified through these evaluations and other sources (Drijfhout 1978; Cardona A. 1967; Pastor-Corrales et al. 1985; Stavely 1984b; Zaiter et al. 1989, 1990) are being used in hybridization.

For diseases and pests as well as other production problems, field screening and evaluations (often across contrasting sites) are emphasized. Mixtures of susceptible spreader rows and resistant and susceptible checks are interplanted to facilitate uniform development and spread of diseases and pests. Also, to the extent possible, artificial infestation or inoculations with a mixture of insect biotypes or pathogen populations locally collected from the previous season or an earlier crop are repeatedly made to ensure adequate pressure. Selected materials in advanced generations are then tested under controlled glasshouse conditions (for diseases) and evaluated in regional and international nurseries across contrasting locations and over a period of years to identify and select desirable genotypes with stable resistance and broad adaptation.

5. Plant Density Used for Selection. Because common beans of different growth habits show differential yield response to plant densities (Edje et al. 1974; Crothers and Westerman 1976; Bennett et al. 1977; Kueneman et al. 1978; Costa et al. 1981, 1983; Nienhuis and Singh 1985) and growth habit × environment interactions occur (Nienhuis and Singh 1985), plant densities used for evaluation and selection in segregating populations, and hence the magnitude of intergenotypic competition, are of great importance to bean breeders. Singh and Gutiérrez (1990) reported that for common bean of growth habits II and III, the highest yielding lines originated from the highest density (266,000 plants ha^{-1}) used for selection. Apparently, low density (66,000 plants ha^{-1}) leads to selection of inferior genotypes, and it was neither good for selection nor for evaluation and identification of high-yielding common bean cultivars. In cultivars of growth habits I, II, and III, the highest yields are usually obtained at relatively higher plant densities (Crothers and Westerman 1976; Aguilar M. et al. 1977; Nienhuis and Singh 1985; Singh and Gutiérrez 1990). Because there may be an undesirable physiological mechanism limiting sink size in common bean (Aguilar M. et al. 1977), a high plant density could allow selection to overcome this limitation (Singh and Gutiérrez 1990).

6. Selection for Pure Lines versus Genotypic Mixtures. Intergenotypic competition in common bean is affected by growth habits, seed sizes, methods of planting, and interactions with environments (Miranda C. 1969; Cardoso and Vieira 1971; Hamblin 1975; Lépiz I. 1982; Vieira, R. F.

1988). Common bean cultivars can show undercompensation, overcompensation, or a neutral response when grown in genotypic or varietal mixtures (Vieira, R. F. 1988). In many bean-growing regions of sub-Saharan Africa and other parts of the world, genotypic mixtures still predominate because they minimize diseases, permit harvesting for longer periods, and generally yield higher than the mean of their components when grown in pure stand and in varying environments (Lépiz I. 1982; Mukishi and Trutmann 1988; Panse 1988; Veira, R. F. 1988).

Intergenotypic competition is highest in early generations of hybrid populations. The relationship between competitive ability in heterozygous and heterogeneous conditions of early segregating generations and that of advanced generation bulks, and genotypic mixtures, which are largely heterogeneous, is also worthy of investigation. Because genotype yield in pure culture seems to be generally associated with its yield in genotypic mixtures (Hamblin 1975; Lépiz I. 1982; Dessert 1987; Vieira, R. F. 1988), high-yielding pure lines could be developed and then tested for competitive ability in forming appropriate mixtures if so desired for commercial cultivation. Conversely, bulk method of selection could be used with some negative selection in each generation for disease-susceptible and undesirable seed and plant types, thus leaving the most desirable genotypes in advanced generation bulks, which could then be tested and released for commercial cultivation. Nevertheless, actual problems may not be those of developing and testing desirable genotypic mixtures, but those of their registration, release, and adoption as cultivars. This is because in most tropical and subtropical countries, seed laws, if they exist, come from developed countries which demand varietal purity, and farmers growing mixtures do not accept new mixtures in their entirety, but grow, select, and incorporate only individual components from a new mixture into their own mixtures if found desirable. Although after initial release of 'Jamapa' and 'Porrillo' some genotypic mixtures were also developed through hybridization and released as commercial cultivars (Pompeu 1980, 1982; Alberini et al. 1983), their superiority over pure line cultivars (e.g., 'ICA Pijao,' 'DOR 41,' 'ICTA-Ostúa,' 'EMGOPA-Ouro,' and 'Azufrado Tapatío') has not been established. Nonetheless, genotypic mixtures may become invaluable where a single gene with multiple alleles seems to carry resistance [e.g., *Arc* gene for Mexican bean weevil (Osborn et al. 1986; Cardona et al. 1990)] and biotypes or races of insect or pathogen populations may exist or evolve. However, for disease resistance (e.g., BCMV, anthracnose, angular leaf spot, and rust) controlled by multiple genes distributed within a genome (Yarnell 1965; Singh 1991a), pure lines carrying multiple genes for resistance could also be developed (CIAT 1987, 1990).

7. Selection in Sole Crop versus Intercrop. Common bean is usually grown in a variety of intercropping systems (i.e., mixture of two or more crops in the same field at the same time, or part of the time) in Latin America and sub-Saharan Africa due to its apparent advantages over sole crop (Lépiz I. 1972; Willey and Osiru 1972; Francis et al. 1976; Francis 1978, 1981; Francis and Sanders 1978). Of all field, horticultural, and cash crops and fruit trees that are intercropped with beans, use of maize is probably most popular, especially in tropical and subtropical Latin America. Effects on bean cultivars and interaction and competitive ability of bean cultivars of different growth habits in intercropping systems have been studied (Francis et al. 1978a,b; Santa-Cecilia and Vieira 1979; Chagas and Aquino 1981; Davis and García 1983; Davis et al. 1984; Clark and Francis 1985; Woolley and Rodríguez 1987). Indeterminate climbing bean cultivars are usually more competitive with maize than bush and semiclimbing types, but they too suffer larger yield losses than the latter types when intercropped (Davis et al. 1984; Clark and Francis 1985).

In spite of significant bean cultivar × cropping system interactions, breeding for bush and semiclimbing beans is usually done in sole crop. This is probably due to often positive association between bean yields in sole crop and their yield in intercropping systems (Hamblin and Zimmermann 1986) and difficulties in selecting simultaneously two or more species, each requiring different breeding methodologies (e.g., autogamous bean and allogamous maize). Moreover, sound experimental data are still lacking from long-term selection experiments, which demonstrates the superiority of selection in intercropping over that of selection in sole crop to the extent that it offsets the additional costs involved and still provides the breeder with sufficient genetic gains, which justify evaluation and selection in intercropping.

Characters important to bean yield in intercropping were identified (Paniagua 1977; Francis 1981; Kawano and Thung 1982; Davis and García 1983), gene action and heritability of bean yield in sole crop and intercrop with maize were reported (Zimmermann et al. 1984a,b, 1985), and theoretical considerations and experimental procedures for simultaneous improvement of the two species for intercropping were discussed (Hamblin et al. 1976; Francis 1981; Hamblin and Zimmermann 1986; Zimmermann 1989). Zimmermann et al. (1984a) evaluated F_2-derived F_4 and F_5 bean lines in sole crop and in association with maize. Heritability for yield was higher in intercrop than in sole crop. Direct selection in intercrop and sole crop was superior (although differences were small) to indirect selection in the alternate cropping system. Selection based on the mean performance of both systems gave gains in each system almost as high as those of direct selection. Davis et al. (1980)

evaluated F_2-derived F_3 and F_4 lines of climbing bean in association with maize lines or families and were able to separate them into four groups: (1) low-yielding bean and maize lines; (2) low-yielding bean and high-yielding maize lines; (3) high-yielding bean and low-yielding maize lines; and (4) high-yielding bean and maize lines. However, because bean genotype × cropping system and cropping system × environment interactions are often significant (Francis et al. 1978a,b,c, 1982), more conclusive data from simultaneous selections carried out in both sole crop and in intercrop from early generations followed by evaluations of improved lines in comparative trials over locations and years are long overdue.

That bush upright (types I and II) and semiclimbing (type III) bean cultivars are more extensively grown than true climbers (type IV) in the tropics and subtropics; that the same cultivars of these growth habits are grown both in sole crops and intercrops (Singh 1989a, 1991b; Table 7.1); that they have small effects on maize yields and also suffer fewer yield losses themselves when intercropped (Davis et al. 1984; Clark and Francis 1985); and that correlations between bean yields in sole crop and yield in intercrop are usually positive (Hamblin and Zimmermann 1986) might have led Zimmermann (1989) to conclude that major efforts for a separate breeding of common bean for intercrop were not necessary. Instead, bean lines of growth habits I, II, and III in advanced generations could be yield tested in sole crop as well as in intercrop and their mean yields in both systems taken as a criterion to identify and select superior cultivars.

For climbing beans, which always require support, evaluation and selection are carried out from early generations either in intercropping with maize or any other companion crops, or by using stakes or trellises. Climbing bean lines developed by using stakes or trellises in early segregating generations are tested in intercropping systems in advanced-generation yield trials before their release for commercial production. This is more common when bean lines are developed in a region away from their commercial production or when a maize cultivar different from the one eventually used by farmers for intercropping is used in early generations for evaluation and selection.

IV. BREEDING PROGRESS

Before discussing progress made in the tropics and subtropics, a clarification needs to be made regarding steps involved in finding genetic solutions to bean production problems. Usually, this process takes in three phases: (1) development of experimental lines, (2) evaluation of experimental lines and identification of new cultivars, and (3) com-

mercialization of new cultivars. In most countries in the tropics, commercialization of new cultivars (i.e., seed production, distribution, and marketing) is done by a separate institution or by a separate department within an institution. Also, experimental lines may sometimes be developed by a team of researchers independent from the one responsible for their evaluations. In regional and international collaborative programs involving CIAT and other institutions, most of the responsibility for evaluation of experimental lines and all commercialization of new cultivars is held by national and state programs. Thus, the degree of coordination and collaboration among researchers belonging to different institutions and their active participation in different phases of the process have been decisive for progress made in most character and cultivar improvement projects.

Comparatively more progress has been achieved in specific character improvement projects because selection for only one or a few traits at a time has been emphasized. For example, this is the case for traits, such as BCMV and anthracnose, for which large genetic variation often controlled by major genes and reliable and fast screening techniques are available. Breeding progress for cultivars has been slow because several desirable traits need to be combined in specific seed and plant types for a particular growing region and cropping system. Moreover, it has been rather difficult to recover certain desirable seed traits such as red and pink mottled and speckled seed color (e.g., 'Flor de Mayo,' 'Diacol Calima,' and 'Cargamanto' types) with resistance to BCMV conditioned by the *II* gene (Cáceres and Morales 1985; Temple and Morales 1986; Kyle and Dickson 1988).

A. Cultivar Improvement

Large variations found in consumer preferences for seed type (Ghaderi et al. 1982; Voysest 1983, 1989; Myers and Wallace 1990; Voysest and Dessert 1991) and growth habit in common bean within and across production regions (CIAT 1981a; Singh 1991b; Table 7.1) do not permit a discussion of breeding progress for each commercial bean type. Instead, breeding progress will be discussed in relation to races and their predominant commercial seed types and cultivars. Since landraces belonging to most races were never improved before or very few genetic gains were realized in the tropics, because they lacked several desirable traits, and since breeding projects were not initiated at the same time, progress in improvement has been slow and uneven.

1. Races of Andean-American Origin.

a. Race Peru: Large-Seeded Climbers. Race Peru comprises determinate and indeterminate climbing bean cultivars of Andean South

America. These possess large round or oval seeds. Important groups of cultivars include 'Cargamanto' and 'Mortiño' in Colombia; 'Bola Canario,' 'Bola Roja,' and 'Bolón Bayo' in Ecuador; 'Caballeros,' 'Amarillo Gigante,' 'Tiachos,' and 'Ñuñas' in Peru; and 'Overitos' in Bolivia and Argentina. These are highly sensitive to photoperiod and are cultivated in cool and humid highlands with favorable moisture in association with maize (Table 7.1). They require 6–9 months to reach maturity. Diseases such as anthracnose, angular leaf spot, rust, powdery mildew caused by *Erysiphe polygoni* DC., ascochyta blight caused by *Phoma exigua* var. *diversispora* (Bub.) Boerema, halo blight, root rots, root-knot nematodes (*Meloidogyne* spp.), and root-lesion nematodes (*Pratylenchus* spp.) are endemic in this region and cause serious losses. Although some breeding for disease resistance, early maturity, and reduced climbing ability has been carried out in Colombia by ICA (Instituto Colombiano Agropecuario) at Tibaitatá, La Selva, and Pasto (Bastidas 1989), it has been difficult to recover desirable seed characteristics and yield potential in improved cultivars carrying resistance to diseases.

A project involving food legume researchers from different countries of the region was initiated in 1988. The use of germplasm from other races and gene pools as donor parents, some form of backcrossing using multiple donor parents simultaneously, advancing early generations at relatively warmer sites in order to have at least two crops per year, and multilocational evaluation and selection would accelerate improvement of important landraces of this group. A separate breeding program might be required for 'Ñuñas' (popped beans) from Peruvian highlands.

b. Race Chile: Medium-Seeded Semiclimbers. Among important bean types of this race are 'Tórtolas,' 'Coscorrón,' 'Frutilla,' and 'Bolita' or marrow types of indeterminate semiclimbing growth habit III, of which the first two are cultivated only in Chile. 'Frutilla,' also known as or similar to cranberry, 'Speckled Sugar,' 'Borlottos,' 'Cacahuate,' 'Barbuyans,' 'Carnaval,' 'Chita Fina,' 'Chitti,' and 'Bagajo,' is grown in other parts of Latin America, the United States, Asia, Europe, and Africa. In Italy and the United States, some breeding work has been done for cranberry types. In Chile, the Instituto de Investigaciones Agropecuarias (INIA) has emphasized breeding for resistance to viruses (e.g., BCMV and BYMV), and cultivars such as 'Tórtolas Diana,' 'Tórtolas INIA,' 'Araucano-85-INIA,' 'Suaves-85-INIA,' and 'Coscorrón INIA' have been developed (Cafati and Alvarez 1975; Tay and France 1986; Tay et al. 1986). High yield, tolerance to low soil fertility, drought tolerance, earliness, development of upright plant type, and other desirable traits also need to be emphasized in future breeding activities.

c. Race Nueva Granada: Large-Seeded Bush and Semiclimbers. Within common bean germplasm of Andean-American origin, determinate cul-

tivars of this race exhibit maximum breadth of adaptation. Large kidney, cylindrical, oval, and round-seeded cultivars of red, pink, beige, white, and cream color (of solid and mottled colors) are popular. In sub-Saharan Africa and the Andes, cultivars of race Nueva Granada are grown at medium altitudes (e.g., coffee regions of Colombia and Ecuador). Considerable breeding efforts have gone into these types, especially in the United States and Europe. Resistance to BCMV, anthracnose, angular leaf spot, common bacterial blight, halo blight, and bean yellow mosaic virus (BYMV) has been emphasized, while little attention has been given to breeding for yield potential per se. Because cultivars of this group yield significantly less and are physiologically inefficient (Myers and Wallace 1990; White and González 1990; White and Izquierdo 1991; White et al. 1992), and are relatively unstable compared to their small-seeded counterparts belonging to race Mesoamerica (Ghaderi et al. 1982; Santos et al. 1982; Beaver et al. 1985; Kelly et al. 1987), they need to have desirable genes for yield improvement transferred from races of Middle American origin.

Difficulties have been encountered in combining *II* gene resistance to BCMV with desirable large red-mottled (e.g., 'Diacol Calima,' 'Cargabello,' and 'Pompadour') and cream-mottled (e.g., 'Bagajo,' 'Chita Fina,' 'Jatu Rong,' and 'Cacahuate') seed characteristics (Cáceres and Morales 1985; Temple and Morales 1986; Kyle and Dickson 1988). Use of *II* gene cultivars with desirable seed colors such as 'Cran 28,' 'Cran 75,' and 'San Cristóbal 83' and those possessing recessive resistance such as 'Great Northern 31,' 'Pinto UI 114,' and IVT 7214 is helping overcome this problem lately.

2. Races of Middle American Origin.

a. Jalisco: Medium-Seeded Climbers. Cultivation of these medium-seeded, indeterminate climbing beans is restricted to the humid highlands of Mexico and Guatemala. Cultivars of black, beige, and pink seed color are more popular. These are always grown in association with maize. Anthracnose, angular leaf spot, rust, common bacterial blight, ascochyta blight, and bean pod weevil are among the most frequent production problems. Very little varietal improvement has been carried out in this group of germplasm. Local landraces such as 'Garbancillo Zarco,' 'Frijola,' 'Cejita,' 'Conejo,' 'Apetito,' and 'Flor de Mayo' are still among the most popular cultivars.

In the highlands of Mexico, there is a gradual reduction in hectarage largely because farmers are switching to sole crop of maize, labor costs are excessively high, and there is heavy disease buildup. Thus, development of semiclimbing and bush plant types with desirable characteristics would also be required for farmers interested in sole cropping of beans in

that region. Some progress has been made recently in developing BCMV-
and rust-resistant cultivars of Flor de Mayo grain type by INIFAP (Insti-
tuto Nacional de Investigaciones Forestales y Agropecuarias)
researchers at Celaya, Guanajuato.

b. Race Durango: Medium-Seeded Semiclimbers. This race includes
indeterminate, semiclimbing medium-seeded cultivars of beige (bayo),
black, pink, red, pinto, ojo de cabra, and great northern or dermason
types. Of these, pinto, great northern, pink, and red Mexican types are
also grown outside the Mexican highlands (e.g., in Chile, the United
States, Europe, and western Asia). Some of these types possess rela-
tively short internodes and leaves, thin stems and branches, a high
harvest index, and positive general combining ability for seed yield.
Hence, they are unique and useful germplasm for yield improvement of
other races and gene pools (Nienhuis and Singh 1986, 1988a; Singh
1989b, 1991b; Singh et al. 1989a; Singh and Gutiérrez 1990).

Cultivar improvement has been carried out mostly in the United States,
for pinto, great northern, pink, and red Mexican commercial classes.
Resistance to BCMV, root rots, common bacterial blight, rust, and white
mold caused by *Sclerotinia sclerotiorum* (Lib.) de Bary has been
emphasized there. In the Mexican highlands, some breeding work has
been done for beige (bayo), ojo de cabra, and pinto types. Improved cul-
tivars include 'Alteño,' 'Bayo Mecentral,' 'Bayo Madero,' 'Bayo
Zacatecas,' 'Pinto Villa,' and 'Azufrado Tapatío.' Tolerance to drought,
low soil fertility, and root rots; resistance to anthracnose, angular leaf
spot, common bacterial blight, and rust; and early maturity would be
required in these cultivars for successful adoption in the Mexican
highlands.

*c. Race Mesoamerica: Small-Seeded Bush, Semiclimbers, and
Climbers.* Black, red, cream, and cream-striped cultivars of indetermi-
nate growth habits II and III of this race are the most popular in Latin
America. Climbing bean cultivars of black and red seed colors are grown
in humid highlands of some Central American countries. Cultivation of
small reds, pinks, and purples is restricted to Central America and Brazil.
Similarly, cream and cream-striped cultivars are largely grown in Brazil.
Small black-seeded cultivars of this group are grown either for local
consumption or for export in the United States and most Latin American
countries from Mexico to Chile, except in Panama, Colombia, Ecuador,
and Peru. Although the cultivation of small whites is not popular in Latin
America (exceptions are coastal Peru and Chile), they are grown in the
United States, Canada, Europe, Asia, and Africa, especially for the can-
ning industry. In the Latin American tropics and subtropics, BCMV,
common bacterial blight, rust, angular leaf spot, anthracnose, BGMV,
nematodes, web blight caused by *Rhizoctonia solani* Kühn, root rots,

leafhopper, low soil fertility, and drought are among the most important
production problems. Because cultivars of this race occupy the largest
area in Latin America (6 million ha), considerable breeding efforts have
gone into improvement of these types. Improved cultivars such as 'ICA
Pijao,' 'ICTA Quetzal,' 'ICTA Ostúa,' 'Negro Huasteco,' 'Brunca,' 'Rico
1735,' 'BR1-Xodo,' 'Milionário 1732,' 'Rio Negro,' 'Capixaba Precoce,'
'Dorado,' 'EMGOPA-Ouro,' 'IPA 6,' and 'Carioca 80,' among others of this
race, have found considerable acceptance by farmers in Mexico,
Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Cuba,
Argentina, Bolivia, Brazil, Ethiopia, Zambia, and South Africa. Breeding
for high seed yield, easily mechanizable upright plant type, early
maturity, and tolerance to root rots, drought, low soil fertility, and BGMV
needs to be emphasized.

B. Character Improvement

1. Seed Yield. Large differences in seed yield and adaptation are found
among common bean cultivars of different growth habits and seed sizes
belonging to different commercial classes, races, and gene pools (Singh
1989a, 1991b). However, differences among cultivars within a gene pool
or race are often small, especially when comparisons are made within the
same maturity classes. Moreover, in common beans of growth habits I,
II, and III, large-seeded cultivars belonging to races Nueva Granada and
Chile are often lower yielding, have reduced overall growth and harvest
index, and are physiologically less efficient in yield and adaptation than
their small- and medium-seeded counterparts from Middle America
(Ghaderi et al. 1982; Santos et al. 1982; Beaver et al. 1985; Kelly et al.
1987; Myers and Wallace 1990; White and González 1990; White and
Izquierdo 1991; White et al. 1992).

Bean breeders have thus far emphasized breeding for stress resistance
(e.g., diseases) under the premise that by reducing losses from stresses,
yield and yield stability will increase automatically. Breeding for yield
potential per se was not pursued seriously until recently.

Selection for morphological traits (e.g., plant height, node and leaf
number, and branching patterns), which are positively associated with
yield in common beans of growth habits I, II, and III, did not increase
seed yield in tropical environments (Nienhuis and Singh 1985). However,
a similar strategy was effective under Michigan conditions (Adams 1982;
Izquierdo and Hosfield 1983).

Seed yield has moderately low heritability (Coyne 1968; Chung and
Stevenson 1973; Sarrafi 1978; Zimmermann et al. 1984a, 1984b, 1985;
Nienhuis and Singh 1988b; Singh et al. 1991f). Nevertheless, among yield

and its components, yield was found to be the best selection criterion (Nienhuis and Singh 1988b), and selection for seed yield among early generation populations or lines was effective (Davis et al. 1980; Zimmermann et al. 1984a; Singh and Gutiérrez 1990; Singh et al. 1990b). Large differences in general combining ability were found among common bean cultivars belonging to different races and gene pools (Chung and Stevensen 1973; Sarrafi 1978; Vaid et al. 1985; Nienhuis and Singh 1986, 1988a; Paredes C. 1986; Rodríguez C. 1987; Singh et al. 1992b). From crosses within races and gene pools, small or no yield gains were realized in common bean because of insufficient genetic variance (Singh et al. 1989c; Singh and Gutiérrez 1990). Similarly, visual selection in F_2 and F_3 for seed yield was ineffective (Patiño and Singh 1989). Knowledge of parental performance and their combining ability, crosses among races, and selection for yield per se were essential for breeding for higher seed yield (Singh 1989b, 1991b; Singh et al. 1989a; Singh and Gutiérrez 1990). Also, where permissible, yield gains could be made by delaying maturity (Laing et al. 1984) and changing growth habits from determinate to increasing indeterminacy, while assuring that these traits are not associated with reduced sink size and assimilate partitioning.

2. Nutritional Quality. Nutritional quality in common bean encompasses several traits, such as cooking quality, which may cover seed hardness, cooking time, color and consistency of broth, cooked bean texture, and differences in taste and aroma; protein quantity and quality; antinutritional factors (trypsin inhibitors, phytohaemagglutinin, arcelin, and lectins); flatulence-producing carbohydrates; and others (Bressani 1972; Bliss and Brown 1983; Lareo 1988; Shellie-Dessert and Bliss 1991). Some antinutritional factors such as phytohaemagglutinin or lectins and arcelin in uncooked seed are to a large extent heat labile and are thus reduced upon cooking (Fernández et al. 1981; Grant et al. 1982; Coffey et al. 1985; CIAT 1989a).

Differences in most seed quality characteristics are found (Ghaderi et al. 1984). Genetics of some physicochemical seed characters related to culinary quality was reported recently (Hosfield et al. 1988; Wassimi et al. 1990). Absence of phytohaemagglutinin in some accessions of wild and cultivated common bean was reported by Brücher (1968). A major gene responsible for the absence of phytohaemagglutinin was found in 'Pinto UI 111' and other cultivars (Brücher et al. 1969; Brown et al. 1981; Osborn and Bliss 1985). Similarly, a gene responsible for the absence of phaseolin was found in runner bean (Gepts and Bliss 1984). The total amount of protein and amino acids is quantitatively inherited (Leleji et al.

1972; Kelly and Bliss 1975). Common bean, although fairly rich in total protein, is low in sulfur amino acids (e.g., methionine and cystine) and is only moderately digestible (Bressani 1972; Márquez and Lajolo 1981; Navarrete and Bressani 1981; Bressani et al. 1984; Lareo 1988). Discrete differences in phaseolin protein patterns, which are under monogenic control, are found (Brown et al. 1981; Bliss and Brown 1982; Romero Andreas and Bliss 1985; Osborn 1988), and cultivars possessing T or H phaseolin pattern are relatively more digestible (CIAT 1990). Breeding strategies for processing and consumer acceptance (Adams and Bedford 1973) have been suggested, and some breeding for protein quantity and quality has been proposed and carried out (Evans and Gridley 1979; Bliss and Brown 1983; Sullivan and Bliss 1983a, 1983b; Osborn 1988). Shellie-Dessert and Bliss (1991) have discussed genetic improvement of culinary quality factors in common bean. However, improvement of bean culinary quality in the tropics is just beginning (Lareo and González V. 1988). Genetic solution by breeding to reduce cooking time, hard-to-cook phenomenon and discoloration of seed coat upon storage, and flatulence-producing carbohydrates might considerably increase global production and consumption of common bean.

3. Plant Type. It is generally believed that evolution in common bean has been from weak-stemmed indeterminate climbing to determinate upright plant types (Miranda C. 1967; Gentry 1969; Smartt 1969, 1985, 1988, 1990a; Evans 1973, 1980). Presently, indeterminate semiclimbing (type III) and climbing (type IV) landraces predominate in bean production areas lying within the range of domestication centers in the Americas. However, cultivation of large-seeded erect determinates (type I) and small-seeded erect indeterminates (type II) has been increasing steadily for the past several decades in the tropics and subtropics. This is largely because of the ease of cultivation of these types in sole cropping systems, the low cost of mechanization, and their ability to avoid some diseases, which will reduce crop losses and produce better quality seed.

Breeders have transferred genes for stem erectness from donor parents into desired cultivars (Adams 1982; Kelly and Adams 1987), but very little has been done for improvement of the erect plant type per se. Stem erectness, as well as determinacy, are recessive traits. Plant height, internode length, number and thickness of internodes, branching pattern, and root morphology need to be modified to improve the upright characteristics of bean cultivars. Acquaah et al. (1991) suggested that hypocotyl diameter, plant height, branch angle, and pods on the main stem should be emphasized for selection of erect bean plant architecture. Some of these

morphological traits seem to be highly heritable (Paniagua and Pinchinat 1976; Ghaderi and Adams 1981; Nienhuis and Singh 1986; Santos and Vencovsky 1986). Our limited experience would indicate that these traits can be easily manipulated in a breeding program (Singh and Gutiérrez 1982; Nienhuis and Singh 1985). However, the value of each of these component traits and their complementarity are poorly understood. Variation in leaf size, pod size, raceme orientation, and other traits related to plant architecture also needs to be explored. One should bear in mind, however, that determinate and indeterminate erect plant type (e.g., lines A 54, A 55, A 57, A 132, A 156, A 170, A 240, A 525, BAT 881, etc.) is associated with low yield potential in traditional cropping systems, planting densities, and crop management practices of the tropics. How to improve their yield without compromising their stem erectness or how to improve both traits simultaneously are indeed real challenges to bean breeders in the tropics.

Some reduction in plant height, climbing ability, and sensitivity to photoperiod would be required in climbing bean cultivars of growth habit IV, which are grown in the highlands of the Andes (race Peru), Central America (race Mesoamerica), and Mexico (race Jalisco), so that these could be grown in association with newer, improved, short-duration and lower-height maize cultivars or could be grown in sole crop. Similarly, modifications in plant architecture (e.g., branch number, branching pattern, and length of main stem and branches) of type III landraces currently grown in semiarid areas of northeastern Brazil, Central America, and the highlands of Mexico might be necessary.

4. Early Maturity. Large differences (50–250 days) in days to maturity are found in cultivated common bean. These differences, however, are associated with differences in growth habit, degree of sensitivity to photoperiod and temperature, and growing environments (Singh 1989a, 1991b). Growth habit and response to temperature and photoperiod are under major-gene control (Coyne 1966, 1967; Davis and Frazier 1966; Miranda C. 1966; Ortega 1968, 1971; Padda and Munger 1969; Bliss 1971; Masaya and Wallace 1978; Kretchmer et al. 1979; Al-Mukhtar and Coyne 1981; Leyna et al. 1982; Masaya et al. 1986; Cerna and Beaver 1990; White and Singh 1991b); hence they can be manipulated with relative ease. However, use of these photoperiod-temperature insensitive or sensitive genes to manipulate maturity has been casual (Davis and Evans 1977a; Masaya 1989). Lately, due to increasing demands, especially in drought endemic areas and regions with short growing seasons, breeding for early maturing cultivars is being emphasized. Dozens of sources of early maturing lines in a variety of bean types and from different

geographical origins (e.g., 'Lime Light,' G 1344, 'Pata de Zope,' 'Pinto UI 114,' 'Blanco INIA,' G 3017, G 2993, 'Ojo de Cabra Santa Rita,' 'Jatu Rong') have been identified, and their genetics have been studied (Cerna and Beaver 1990; White and Singh 1991b). Some improved early maturing lines carrying resistance to BCMV (e.g., ZAA 2, AFR 180, PEF 9, PEF 15, A 774, A 775) have been developed. These are being tested for their usefulness in contrasting environments. Some of these (e.g., A 774 and A 775) have significantly outyielded high-yielding cultivars such as 'ICA Pijao' and 'Carioca' in repeated trials in Colombia and elsewhere (our unpublished data). Development of upright and indeterminate early maturing types seems to be difficult. Why this is so is not clearly understood.

5. Drought Tolerance. Over 4 million ha of common bean are grown annually in the drought endemic areas of northeastern Brazil and the central highlands of Mexico alone. Drought in these regions is unpredictable in duration, intensity, frequency, and stages of crop growth affected. It can be predicted somewhat in areas (e.g., Central America and coastal Peru) where rains cease toward the end of the growing season, or where it seldom rains.

Drought tolerance in a broad sense as defined by White and Singh (1991a) encompasses all mechanisms that allow greater yields under soil moisture deficits. This includes deep root system, earliness, and other traits. Genotypic differences, measured by seed yield per hectare, for response to moderate drought stress have been found in Brazil (Silveira et al. 1981; Guimarães 1988), Mexico (Ibarra 1988), and at CIAT (CIAT 1985c; Singh and White 1988; White and Singh 1991a) in Colombia. These differences for seed yield have been observed in repeated evaluations. However, genetic studies and long-term selection experiments for drought tolerance have yet to be realized in the tropics and subtropics. A single gene responsible for heat-drought tolerance was reported in snap bean (Bouwkamp and Summers 1982), but its value in dry bean improvement is not known, especially in the tropics and subtropics. The little attention dedicated to breeding for drought tolerance has been due to lack of information on its inheritance, difficulties in using seed yield as a selection criterion in early segregating generations, an overriding effect of local adaptation, and unavailability of any other dependable and easily usable selection criterion. Thus far, work has been restricted to systematic evaluations of germplasm accessions and advanced breeding lines under field conditions. Through this procedure, over 25 accessions and breeding lines (e.g., BAT 477, V 8025, A 170, 'San Cristóbal 83,' 'Apetito,' 'Durango 222,' 'Rio Tibagi,' and 'Bayo Criollo del Llano') have been found to possess a moderate level of drought tolerance. In order for

any of these lines to be further improved for commercial production, genes for tolerance to root rots, anthracnose, leafhoppers, angular leaf spot, common bacterial blight, rust and BCMV, and/or adaptability to low soil fertility, must be combined to minimize yield losses and increase stability of performance.

The value of traits such as early maturity, deep root system (Sponchiado et al. 1989; White and Castillo 1989; White et al. 1990), small and thick leaves, and leaf pubescence as drought avoidance or tolerance mechanisms needs to be explored and exploited. In addition to seeking genetic differences, fast, nondestructive, and reliable screening methods need to be developed; and complementary and useful traits combined in otherwise drought-tolerant cultivars (Singh and White 1988; White and Singh 1991a). Although tepary beans possess higher levels of drought tolerance than common beans (Waines 1978; Thomas et al. 1983; Markhart III 1985) and are hybridized with them, transfer of useful genes for drought tolerance from tepary to common beans has yet to be accomplished.

6. Acid-Soil Tolerance. In Brazil, and in the humid and subhumid highlands of the Andes, Mexico, and sub-Saharan Africa, common bean is grown in soils that are characterized by low pH (<6) and deficiency of P and that sometimes contain toxic levels of aluminum and manganese. Without added lime and/or phosphorus-rich fertilizers, it is not possible to harvest a satisfactory crop of common bean. Cultivar differences in utilization of and tolerance to low soil phosphorus have been reported (Whiteaker et al. 1976; Salinas 1978; Fawole et al. 1982; CIAT 1985c; Schettini et al. 1987; Thung 1990). In field conditions in the tropics, the highest levels of tolerance have been found in small-seeded indeterminate cultivars of growth habits II and III (Singh et al. 1989c) of the race Mesoamerica, such as 'Carioca,' G 5059, 'Cuilapa 72,' 'Rio Tibagi,' 'Compuesto Chimaltenango 2,' and 'ICA Pijao.' At present, the genetic potentials for tolerance to acid soils of other races and gene pools are being studied. In preliminary evaluations, some accessions from the highlands of Peru and Bolivia in the Andes and from Rwanda, Burundi, Brazil, and Mexico seem to show moderate tolerance (CIAT 1990; S. E. Beebe, personal communication, 1991). Because, evolutionarily, these medium- and large-seeded accessions are of different origin than small-seeded germplasm from race Mesoamerica, they may possess different mechanisms and genes for tolerance to acid soils.

Inheritance of P absorption, P utilization, and tolerance to low soil P are controlled by quantitative genes with low to intermediate heritabilities (Lindgren et al. 1977; Fawole et al. 1982; Urrea and Singh 1989). However, by crossing among tolerant germplasm from small-seeded race

Mesoamerica, it was not possible to increase the levels of field tolerance measured by seed yield (Singh et al. 1989c). Thus, it is imperative that the best sources of tolerance from race Mesoamerica be crossed with those recently identified in germplasm of races Peru, Nueva Granada, and Jalisco to broaden the genetic base and breed for tolerance to low soil fertility.

7. Nitrogen Fixation. Nitrogen fixation (NF) by *Rhizobium leguminosarum* bv. *phaseoli* in common bean cultivars is estimated by the amount of nodulation, time and duration of nodulation, foliage color, acetylene reduction, and determination of ^{15}N and total nitrogen in inoculated versus uninoculated plots. Selection strategies and cultivar differences for various NF parameters have been reported (Graham 1981; Rennie and Kemp 1981; McFerson et al. 1982; Kipe-Nolt and Vargas 1989). The differences for NF parameters are inherited quantitatively with low to moderately high heritability (McFerson 1983; Pereira et al. 1986; Miranda and Bliss 1987). Asokan (1981) reported a single recessive gene controlling low nitrogenase activity.

Graham (1981) reviewed problems and prospects of nitrogen fixation in the tropics and subtropics. Bean cultivar and *Rhizobium* strain interaction, competition among efficient and inefficient strains, suppression of nodulation by residual soil nitrogen, high demand for phosphorus and photosynthate by *Rhizobium,* sensitivity to moisture stress, and interactions of these factors with environments have slowed the development of high NF cultivars in the tropics and subtropics. A recessive gene mutation responsible for super-nodulation was reported recently (Park and Buttery 1988). Although its usefulness in tropical and subtropical soils remains to be determined, in Canada the mutant yielded significantly less than the parental cultivar (Buttery et al. 1990).

NF in common bean is more a rule than an exception; beans are usually a poor fixer, especially in the tropics; increased nitrogen fixation is not necessarily associated with increased seed yield (Alvarez-Solís et al. 1990; Buttery et al. 1990; St. Clair and Bliss 1991); and over 15 years of research have been conducted at CIAT and elsewhere. However, a critical review is overdue to assess how much genetic gains in NF have been and could be realized over and above what naturally occurs without any additional efforts and whether or not that contributes to actual gains in bean yield. Also, breeding for NF alone versus a more pragmatic approach of simultaneous improvement of tolerance to low soil fertility, including deficiency of nitrogen and phosphorus and toxicity of other nutrients, should be critically examined.

8. Leafhopper Tolerance. Kornegay and Cardona (1991a) have described

in considerable detail breeding for insect resistance in common bean. Nonetheless, it should be noted that breeding for insect resistance has not received the same attention as disease resistance, until recently, for several reasons. This is because (1) there is a lack of adequate sources of resistant germplasm, (2) there is an excessive and preventive use of agrochemicals in some regions, and (3) because cultural control practices, including intercropping, help reduce some insect populations, economic losses may not always be apparent.

Leafhoppers (*Empoasca kraemeri* Ross & Moore) are pests of common bean in warm and dry production regions/seasons. Feeding damage is caused by nymphs and adults and is most severe during flowering and pod set (Schoonhoven et al. 1978). Under heavy insect pressure, yield losses of susceptible cultivars can be 90%. Among 19,000 common bean accessions, only low levels of tolerance in small-seeded black and cream-colored germplasm of race Mesoamerica have been found (Kornegay and Cardona 1990). Tolerance to feeding damage and antixenosis to oviposition (Kornegay et al. 1986) were controlled by quantitative genes with dominance effects and low heritability (Galwey and Evans 1982; Kornegay and Temple 1986). Both additive and dominance gene effects were significant for damage scores and nonprotected seed yield, although for the latter, dominance effects were larger. General combining ability mean squares were greater than specific combining ability (SCA) for nymphal counts and damage scores. However, for nonprotected seed yield, only SCA was significant. Lines EMP 124 and EMP 125 were found to possess high levels of antixenosis resistance (Kornegay et al. 1989).

Selection based on damage scores and/or nymphal populations alone was not effective. However, mass-pedigree selection based on these criteria combined with yield tests of the bulk F_3 populations, F_5 plant-progeny rows, and lines was effective in increasing both the levels of resistance and seed yield (Kornegay and Cardona 1990). Tolerant and high-yielding small-seeded lines such as EMP 86, EMP 135, EMP 175, EMP 201, EMP 202, and others have been developed (Kornegay et al. 1989; Kornegay and Cardona 1990).

9. Bean Pod Weevil Resistance. Bean pod weevil (*Apion* species) causes serious damage to common bean in Mexico and Central America (Díaz 1988a). *A. godmani* Wagner is a serious pest of bush and semiclimbing cultivars of common bean in El Salvador, Guatemala, Honduras, and Nicaragua. Both *A. godmani* Wagner and *A. aurichalceum* Wagner attack climbing cultivars in the highlands of Guatemala and Mexico. Adults lay eggs in developing, young tender pods. The larvae feed on developing seed, thus causing serious yield losses. Damage caused by *A. godmani* is distributed over the entire pod, but *A. aurichalceum* attacks only at the

pod tips. Also, damage due to the latter is often higher in intercropping with maize and could come late in the season; therefore, short-duration cultivars may escape its attack. High levels of resistant germplasm such as 'Negro 150' (G 5767), 'Amarillo 154' (G 3982), 'Amarillo 169,' 'Mexico 1290' (G 11506), 'Pinto 168,' 'De Celaya' (G 13614), G 3578, G 8142, and others have been identified among Guatemalan and Mexican germplasm (Cardona 1988). Although some accessions are resistant to both insects, it is not uncommon to find germplasm that is resistant to one but not to the other pest. For *A. godmani*, antibiosis principally due to the death of eggs and larvae by encapsulation by healing pod tissues (e.g., APN 83 and APN 84) and ovipositional antixenosis in other (e.g., 'Amarillo 154') germplasm seem to be responsible for resistance (R. Garza, personal communication, 1990).

Evaluation and selection of single plants based on insect damage in the F_2 followed by progeny tests in the F_3 or F_4 in replicated plots have been effective. Small-seeded black and red cultivars with high levels of resistance have been developed for Honduras, El Salvador, and Guatemala (Ajquejay et al. 1988; Beebe 1988; Díaz 1988b; Monzón and Masaya 1988).

10. Bean Weevil and Mexican Bean Weevil Resistance. The Mexican bean weevil, *Zabrotes subfasciatus* (Boheman), and bean weevil, *Acanthoscelides obtectus* (Say), are very important pests of common bean when no precautionary measures are taken during seed storage. Damaged seed loses quality and weight and has an ugly appearance, thus reducing consumer acceptance, germinability, and market value. Among several thousand germplasm accessions of cultivated common bean, no resistance was found (Schoonhoven and Cardona 1982). Instead, very high levels of resistance to both pests were found in a few accessions of wild common bean from Mexico (e.g., G 11051, G 12858, G 12952) (Schoonhoven et al. 1983). Later studies have confirmed that antibiosis is the mechanism of resistance to both pests (Cardona et al. 1989).

A seed storage protein arcelin, found in the cotyledons, was responsible for antibiosis resistance to *Z. subfasciatus* (Osborn et al. 1988; Cardona et al. 1989). The presence of arcelin is monogenic dominant to its absence (Osborn et al. 1986; Romero Andreas et al. 1986). There are five alleles known at the *Arc* locus, of which Arc^5 found in G 2771 has the highest level of resistance (Cardona et al. 1990). The presence of arcelin can be detected easily by SDS-PAGE electrophoresis or by serological methods using Ouchterlony plates (Cardona et al. 1990). Availability of these two fast, simple, reliable, and nondestructive screening techniques applicable on single seed has greatly facilitated and expedited breeding for resistance to *Zabrotes*. However, commercial deployment

and use of this resistance was on hold until 1989, when it was confirmed that arcelin is heat labile, and its adverse effects are reduced upon cooking. Thus, the *Arc* gene does not have any harmful effects on humans (CIAT 1989a). Its utilization in breeding was initiated recently.

The biochemical basis of resistance to *A. obtectus* is not well understood as yet. The resistance in wild bean accession G 12952 is controlled by two complementary recessive genes (Kornegay and Cardona 1991b). Evaluations dependent on insect feeding trials are slow and expensive, require more seed, and are affected by environment, seed age, and other factors. Consequently, progress has been slower in breeding for resistance to this pest.

11. Bean Common Mosaic Virus Resistance. Beebe and Pastor-Corrales (1991) have examined breeding for disease resistance in common bean in the tropics. Among viral diseases, BCMV is an endemic problem in most countries of the world, where susceptible common bean cultivars are still grown. The virus is transmitted by aphids and through seed (Gálvez 1980; Morales and Castaño 1987). Yield losses of over 90% can occur in systemically infected cultivars (Burke and Silbernagel 1974b; Gálvez 1980; Sarrafi and Ecochard 1986). Symptom expression depends upon bean cultivar, virus strain, and growing environment. For example, in small-seeded germplasm, symptoms are usually more severe in warm tropical environments. In large-seeded cultivars grown in relatively cooler climates, symptom expression is generally mild and, consequently, yield losses are not apparent. Also, aphid vector populations are lower. Nevertheless, in the Andean highlands, BCMV may be a problem during the main growing season.

Different strains of the virus have been identified (Drijfhout 1978; Drijfhout et al. 1978). Monogenic dominant (*II*) and recessive gene (*bc-u, bc-1, bc-2, bc-3*) resistances have been reported (Drijfhout 1978; Walkey and Innes 1979). Some cultivars with recessive gene resistance include 'Pinto UI 114,' IVT 7214, and 'Great Northern 31.' Reliable mass-screening facilities available at CIAT have permitted the incorporation of *II* gene resistance in all improved lines of small black, red, cream, cream-striped, and other seed types since 1979. However, it has been extremely difficult to incorporate *II* gene resistance into bean cultivars such as 'Azufrado,' 'Diacol Calima,' 'Flor de Mayo,' 'Cargamanto,' and 'Frutilla' (Cáceres and Morales 1985; Temple and Morales 1986). Apparently, the *II* gene is linked (< 2 cM) with darkened testa color conditioned by the *BB* gene (Kyle and Dickson 1988). Use of cream-mottled (e.g., 'Cran 75') and red-mottled (e.g., 'San Cristóbal 83') cultivars possessing the *II* gene and those possessing recessive gene resistance (noted previously) is facilitating breeding for BCMV resistance in these difficult grain types.

Bean cultivars carrying the *II* gene may develop systemic necrosis (black root) when exposed to necrosis-inducing strains of the virus (e.g., NL_2, NL_3, NL_5, NL_6) (Burke and Silbernagel 1974a). This is a potential problem in South Africa, Rwanda, Burundi, Zaire, and Uganda; but, in most countries of Latin America, deployment of *II* gene resistance has sufficed because these necrotic strains are not common in bean production fields. Incorporation of recessive gene resistance (e.g., the $bc-2^2$ or *bc-3* gene) and its combination with the *II* gene is a strategy that is effective against the known BCMV strains (CIAT 1990).

12. Bean Golden Mosaic Virus Resistance. BGMV is a geminivirus transmitted by the whitefly (*Bemisia tabaci* Gennadius). BGMV is a severe problem of common bean on the Pacific coast of Mexico, and in El Salvador, Guatemala, Honduras, the Dominican Republic, Haiti, Cuba, Brazil, and northwestern Argentina. Pathogenic variation has not been clearly shown to occur among virus isolates collected from different ecological regions (Gilbertson et al. 1990, 1991), because all bean genotypes tested to date are susceptible. Variation to date is greatest with respect to aggressiveness, genome organization, and mechanical transmission properties. Recently, new mechanisms of resistance have been identified among common bean germplasm of diverse origins (CIAT 1988; Morales and Niessen 1988; M. J. O. Zimmermann, personal communication, 1991). However, these mechanisms of resistance must be combined in an adequate genetic background to increase the level of resistance to BGMV in common bean cultivars adapted to the tropics. Protection from the virus for the first few weeks of crop growth is still critical.

For virus symptoms and other associated traits, general combining ability mean squares were more important than specific combining ability (Morales and Singh 1991; Vizgarra 1991). This suggested that parental performance per se could be a good predictor of the performance of their hybrid populations and progenies derived from them. Selection should be effective in hybrid populations involving parental sources of resistance from diverse origins.

Some breeding work has been carried out in Guatemala, Mexico, and Brazil, where tolerant black-seeded cultivars have been developed by using 'Porrillo' and 'Turrialba' sources belonging to the race Mesoamerica. Non-black-seeded lines, such as A 427, A 429, DOR 303, DOR 364, and DOR 476, which combine resistances from two or more sources, seem to perform better under field conditions in Guatemala and Brazil and in inoculated controlled conditions in the glasshouse (F. J. Morales, personal communication, 1991). Therefore, combining the various resistance traits recently identified among germplasm belonging

to different races might facilitate the development of cultivars with higher levels of resistance. Moreover, germplasm resistant to the whitefly vector could be identified and combined with those cultivars carrying resistance to the virus. However, for successful adoption of improved cultivars, the high level of resistance to BGMV must be combined and simultaneously improved with resistance to other diseases (e.g., common bacterial blight, anthracnose, and angular leaf spot), high yield, and tolerance to low soil fertility and drought. Under heavy disease pressure (e.g., Argentina and Brazil), deployment of BGMV-tolerant cultivars with proper agronomic management and some use of insecticides (i.e., an integrated pest-management strategy) may be essential, economical, and long-lasting.

13. Common Bacterial Blight Resistance. Common bacterial blight caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye occurs throughout most bean production regions, but the disease is favored by mild-to-warm temperatures and high relative humidity (Yoshii et al. 1978; Yoshii 1980). The pathogen is seed transmitted (Weller and Saettler 1980). Variation in virulence (Schuster and Coyne 1975; Ekpo and Saettler 1976; Freytag 1989), differential reactions in leaves and pods (Coyne and Schuster 1974b,c; Valladares-Sánchez et al. 1979, 1983), and association between delayed maturity and resistance have been reported (Coyne and Schuster 1974a; Mohan 1981).

Resistant germplasm has been found in tepary bean (Schuster 1955; Schuster et al. 1983; Drijfhout and Blok 1987), runner bean (Mohan 1982; Park and Dhanvantari 1987), and common bean (Pompeu and Crowder 1972; Zapata et al. 1985; CIAT 1987; Rava et al. 1987; Beebe 1989b). Resistance from tepary bean (Honma 1956; McElroy 1985; Scott and Michaels 1988) and runner bean (Freytag et al. 1982; Park and Dhanvantari 1987) has been transferred into common bean. However, most of these original and derived sources of resistance (e.g., great northern 'Tara' and 'Jules,' XAN 159, XR-235-1-1, A 8-40, and PI 207262) are poorly adapted in the tropics (Webster et al. 1980; our unpublished data). Resistance is controlled by a single gene or by a few major genes, the effect is additive and/or dominant, and heritability varies from low to high (Coyne et al. 1965, 1966; Coyne and Schuster 1974a,b; Webster et al. 1980; Valladares-Sánchez 1983; McElroy 1985; Finke et al. 1986; Drijfhout and Blok 1987; Rava et al. 1987; Adams et al. 1988; Scott and Michaels 1988; Beebe 1989b; Freytag 1989; Silva et al. 1989).

Most commercial cultivars grown in Latin America are susceptible to common bacterial blight. Resistance from common, tepary, and runner beans is being transferred into important commercial cultivars (CIAT 1987). Although production of bacterial inoculum is easily accom-

plished, the development of disease under field conditions can be problematic if proper weather conditions do not occur. Resistance in some cases seems to be associated with undesirable seed color and low yield (Beebe 1989b). In order to overcome some of these problems, selection based on the performance of the F_4 or F_5 progeny rows is preferred over single plant selections in the F_2 (Silva et al. 1989). Also, there is a need to combine all known sources, especially those not associated with negative traits (Beebe 1989b), of resistance within common bean (e.g., PI 207262, 'Tara,' XAN 263, G 6700, G 6772, G 4399) and to combine these with other resistances available from tepary and runner beans. Some progress in this direction has been made recently by Dr. R. E. Wilkinson, of Cornell University (M.A. Pastor-Corrales, personal communication, 1989).

14. Halo Blight Resistance. Halo blight caused by *Pseudomonas syringae* pv. *phaseolicola* (Burkholder) occurs in some cool, humid, and subhumid bean production regions, such as highlands of the Andes, Mexico, and sub-Saharan Africa. In certain areas of Turkey, Bulgaria, and other European countries, and the United States, severe crop losses may also occur if growing conditions are favorable, infected seed of susceptible cultivars is sown, and no control measures are taken. Pathogenic variation (Schroth et al. 1971; Schuster and Coyne 1975; Buruchara and Pastor-Corrales 1981; CIAT 1987) and different reactions in foliage and pods (Hill et al. 1972) have been reported. Both race-specific (e.g., 'Red Mexican U.I.3' and 'U.I.35,' V 4604) and race-nonspecific (P.I. 150414, 'Edmonds,' 'G.N. Nebraska #1 Sel. 27,' G 2829, G 11766, G 12592) resistances have been reported (Patel and Walker 1966; Taylor et al. 1978; Innes et al. 1984; CIAT 1987). Inheritance of resistance is controlled by one or two complementary dominant or recessive genes (Patel and Walker 1966; Coyne et al. 1966, 1971; Hill et al. 1972; Taylor et al. 1978; Kelly et al. 1985; CIAT 1987), depending upon the source of resistance, isolates (or race) used for inoculations, and environments (Dickson and Natti 1967). Hagedorn et al. (1974) used P.I. 150414 to develop two halo blight-resistant lines, WBR 40 and WBR 72.

A breeding project for the tropics and subtropics, especially for sub-Saharan Africa, was initiated recently. Pathogen survey, screening of some germplasm, and genetics of resistance have been determined (Taylor et al. 1978; CIAT 1987). Also, some resistant lines (e.g., 'Edmonds') combining two or more different sources are available.

15. Anthracnose Resistance. Anthracnose, caused by *Colletotrichum lindemuthianum* (Sacc. & Magn.) Scrib., is a very destructive disease of common bean in cool and wet production regions of Latin America and

Africa, because susceptible cultivars still predominate in most of these areas. Crop losses are often considerable (Guzmán et al. 1979). The pathogen is highly variable (Bannerot 1965; Oliari et al. 1973; Garrido R. 1986; CIAT 1987, 1990; Menezes and Dianese 1988; Pastor-Corrales 1992) and is transmitted through seed; it can survive in plant debris or in their remains in the soil for a long time. In cool, dry areas, such as the semiarid highlands of Mexico and northeastern Brazil, the disease could be endemic, but severe losses do not occur unless weather conditions remain favorable during most of the cropping season.

Extensive germplasm evaluations have been carried out, and effective sources of resistance have been identified (Mastenbroek 1960; Bannerot 1965; Schwartz et al. 1982; Menezes and Dianese 1988; our unpublished data). Pastor-Corrales et al. (1985) identified four different mechanisms (or types) of common bean reactions to the anthracnose pathogen: susceptibility in all stages of plant growth, moderate resistance in all stages of growth, seedling susceptibility but adult-plant resistance, and resistance in all stages of plant growth. Resistance is controlled by major genes working independently or interacting in a different fashion (Mastenbroek 1960; Cárdenas et al. 1964; Bannerot and Richter 1968; Bannerot et al. 1971; Fouilloux 1976; Muhalet et al. 1981; Peloso et al. 1989). Recently, the utilization of these resistant genes in the tropics and subtropics has been intensified. In Brazil, Cornell 49-242 (Are gene) was initially used to develop resistant cultivars in the states of São Paulo and Paraná (Pompeu 1980, 1982; Alberini et al. 1983), although its resistance is overcome by races of pathogen in some areas (Menezes and Dianese 1988). Breeders and pathologists at CNPAF (Centro Nacional de Pesquisa de Arroz e Feijão), Goiânia, and elsewhere in the country are now using different sources of resistance against a broader range of pathogen populations (e.g., A 322, A 252, A 483, A 475, AB 136, G 811, G 2641, G 2333, G 2338, G 4032, Mexico 222, TO, and TU) (Menezes and Dianese 1988; Beebe and Pastor-Corrales 1991). Accession Ecuador 1056 (G 12488) and cultivar 'Rio Negro' (from Brazil) have anthracnose resistance under field conditions (but are susceptible in the greenhouse in seedling tests) in Brazil, Colombia, Africa, and Peru to varying pathogen populations (Beebe and Pastor-Corrales 1991). The value of such resistance and its combination with apparently race-specific resistance, which is also effective against a wide range of pathogen populations, needs to be determined.

At CIAT, the search for and utilization of diverse sources of resistance against a broad spectrum of pathogen isolates have been emphasized (Schwartz et al. 1982; Singh et al. 1992a). A three-pronged breeding strategy is being used: (1) improvement of important sources of resistance per se for other factors such as resistance to BCMV and tropical

adaptation; (2) combination of two or more different sources and mechanisms of resistance in order to broaden the genetic basis of resistance and to maximize its expression; and (3) transfer of resistance into commercial cultivars. Field screenings at different cool and humid sites across bean-growing regions combined with evaluations in greenhouses of germplasm bank accessions and advanced generation lines, which show resistance in repeated field evaluations, have permitted substantial progress in breeding for resistance to this important disease (CIAT 1987; Beebe and Pastor-Corrales 1991). For example, all small- and medium-seeded cream and cream-striped or spotted lines developed recently at CIAT carry resistance to anthracnose in addition to other desirable traits.

16. Angular Leaf Spot Resistance. Angular leaf spot caused by *Phaeoisariopsis griseola* (Sacc.) Ferraris is also a widely distributed disease of common bean in semihumid and relatively cool areas, and it causes serious yield losses (Rava et al. 1985). The pathogen is seed transmitted and disease development is favored by intermittent hot and cool weather combined with high and low humidity. Pathogenic variation is great (Alvarez-Ayala and Schwartz 1979; CIAT 1987; Correa V. 1987). Levels of resistance are high, but no immunity was found in over 20,000 accessions evaluated thus far. Nonetheless, a relatively large number of resistant sources have been identified (Schwartz et al. 1982; our unpublished data). Both recessive (Santos-Filho et al. 1976) and dominant (Cardona A. 1967) major genes confer resistance.

Breeding strategies employed for angular leaf spot are similar to those for anthracnose. Important sources of resistance found in landraces are improved by backcrossing for BCMV resistance and tropical adaptation. Lines combining multiple sources of resistance have recently been developed (e.g., MAR 1, MAR 2, and MAR 3). Attempts must be made, however, to combine sources of resistance of Andean origin (e.g., G 5686 and Jalo EEP 558) with those from Middle America (e.g., G 3991, G 4032, and G 5653) to develop broader and more stable resistance in commercial cultivars.

17. Bean Rust Resistance. Bean rust, caused by *Uromyces appendiculatus* (Pers.) Unger var. *appendiculatus*, although widely distributed, rarely has caused severe yield losses except in Cuba, Brazil, and the cool and humid highlands of Colombia, Ecuador, and Mexico, where particularly favorable conditions exist for disease and/or long-season cultivars are grown. Pathogenic variability is extremely great (Junqueira Netto et al. 1969; Carvalho et al. 1978; Vargas 1980; Stavely 1984b). A large

number of germplasm accessions carrying high levels of resistance have
been identified, some of which have shown stable resistance across loca-
tions and years (CIAT 1985b). Differences in resistance mechanisms (e.g.,
pustule size, slow rusting, necrotic lesions, field tolerance) have been
reported (Stavely 1984b). Resistance was found to be controlled by one or
more dominant independent or epistatic genes (Lépiz I. 1971; Augustin et
al. 1972; Coyne and Schuster 1975; Carvalho et al. 1978; Christ and Groth
1982; Kolmer and Groth 1984; Stavely 1984a; Grafton et al. 1985; Finke et
al. 1986). The presence of trichomes in germplasm of Andean origin is
controlled by major genes and was found to be associated with race-
nonspecific resistance (Shaik and Steadman 1988; Zaiter et al. 1989,
1990).

Information from the International Bean Rust Nurseries (IBRN) (CIAT
1985b) and other sources should be utilized in parental selection for
hybridization. For screening and selection among segregating genera-
tions, multilocational testing with or without inoculation would be
required for development of stable resistance in cultivars. However, this
is not often practiced, partly because of problems of moving seed of
segregating populations around due to plant quarantine restrictions.
Instead, advanced breeding lines possessing other desirable traits are
subjected to such screening through IBRN and other nurseries.

V. TESTING

Common bean germplasm is tested at department (province or state),
national, regional, and/or international levels. This often comprises a
three-stage testing program: (1) adaptation nursery; (2) yield trials; and (3)
evaluations in farmers' fields. At each stage, 1–3 years of testing at con-
trasting sites (covering bean production regions within the mandate of a
research institution) and in complementary nurseries is required to
identify superior cultivars.

At CIAT, improved lines from all cultivar and character improvement
projects, and those received from other state, national, regional, and
international programs, are systematically tested in uniform nurseries:
the Bean Team Nursery (VEF), which is equivalent to an adaptation
nursery; Preliminary Yield Trials (EP); and the International Bean Yield
and Adaptation Nursery (IBYAN). Since the 1970s, these nurseries have
been operated on a yearly basis (CIAT 1981a, 1989b). All materials
entering this testing scheme are expected to be uniform or nonsegregat-
ing for principal agronomic traits, such as growth habit, seed charac-
teristics, flower color, and maturity, in addition to the characters for

which they have been bred. All materials are grouped according to com-
mercial bean classes, growth habit, maturity, and ecological regions of
adaptation (CIAT 1989b). Evaluations are unbiased and systematic. They
are carried out in separate complementary nurseries at different sites and
in different growing seasons by a pathologist, agronomist, virologist,
entomologist, nutritionist, and physiologist, among others. All evalua-
tion information is computerized, published, and made available to bean
researchers.

Collaborative germplasm testing systems on a regional basis have been
operating among Central American and Caribbean countries (Ensayo
Centroamericano de Adaptación y Rendimiento, ECAR), Andean zone
countries (Vivero de Adaptación y Rendimiento para la Zona Andina,
VIARZA), and Central and East African countries (African Bean Yield
and Adaptation Nursery, AFBYAN) for the past several years. In a
regional nursery, such as ECAR, each participating country contributes
its best entries. The coordination of trials is rotated among member coun-
tries. A regional meeting is usually held once a year to present and dis-
cuss results and make future work plans. In Central America, the
PCCMCA annual meetings have been the venues for presenting and dis-
cussing results from regional and national bean trials since the 1950s and
1960s. Similarly, in the Andes, the RELEZA (Reunión de Leguminosas de
Grano de la Zona Andina) annual meetings have served this purpose since
1990. Some commercial cultivars that have been released recently
through this system include 'Catrachita,' 'Revolución 81,' 'ICTA-Ostúa,'
'Brunca,' and 'CENTA Jiboa.' More recently (1990–1991), line DOR 364,
from the BGMV project, was jointly released under the name of
'Cuscatleco' in El Salvador, 'Doricta' in Guatemala, and 'Dorado' in
Honduras (S. E. Beebe, personal communication, 1991). Similarly, for
example, from state and national trials within Brazil, several cultivars
have been released within the past few years. More recent releases
include 'IPA 6,' 'Capixaba Precoce,' 'Rio Negro,' 'Rico 1735,' 'BR1-Xodo,'
and 'EMGOPA-Ouro.'

All international nurseries, including IBYAN and IBRN (CIAT 1989b,
1990), are operated on a global basis from CIAT headquarters. An inter-
national conference is usually held once every three years at CIAT to dis-
cuss results of common bean germplasm distribution, testing, and utiliza-
tion and thus assess progress as well as future needs (CIAT 1989c).

Systematic testing through these uniform nurseries facilitates avail-
ability of promising germplasm, monitors genetic progress, determines
deficiencies of bred lines, and provides feedback of information to bean
researchers. Several dozen cultivars have been released in Africa, Asia,
and Latin America through state, national, regional, and international
testing schemes within the past few years.

VI. CONCLUSIONS AND PROSPECTS

Common bean is an important food legume, especially in tropical and subtropical Latin America and sub-Saharan Africa. Large differences are found in bean types, plant types, growing environments, cropping systems, and production constraints among countries and regions within countries. Nevertheless, common bean is grown mostly by subsistence farmers, with varying use of agrochemicals. Diseases, drought, low soil fertility, and insects are the principal production problems. Thus, bean improvement in the tropics and subtropics, especially in Latin America where pest and pathogen populations have coevolved, offers both opportunities and challenges.

Genetic improvement of common bean in the tropics is a relatively recent activity. More breeding progress has been made in individual character improvement projects such as resistance to BCMV, anthracnose, common bacterial blight, bean pod weevil, and leafhoppers. For cultivar improvement, landraces and germplasm belonging to races Jalisco and Peru have received little or no improvement, whereas those of races Mesoamerica and Nueva Granada have been emphasized. Improved disease-resistant small-seeded black, red, cream, and/or cream-striped cultivars belonging to the race Mesoamerica have been adopted by farmers in Argentina, Australia, Bolivia, Brazil, Costa Rica, Cuba, El Salvador, Ethiopia, Guatemala, Honduras, Mexico, Nicaragua, South Africa, and Zambia, among other countries. Improved cultivars belonging to the race Nueva Granada are commercially grown in Argentina, Colombia, Peru, Rwanda, and Turkey.

High-yielding cultivars tolerant to drought and low soil fertility, also possessing durable resistance to important diseases and insects, are needed for each of the major bean types to achieve rapid adoption of improved cultivars, reduce production costs, and help to conserve valuable natural resources and cleaner environments. The vast amount of genetic variability available in primary and secondary gene pools represented by over 35,000 accessions of *Phaseolus* beans is mostly unexploited. Hybridization among (rather than within) races of common bean (especially from different domestication centers), based on their performance per se and knowledge of combining ability, would be a key for creation of useful genetic variation for most agronomic traits, especially resistance to variable pest and pathogen populations, tolerance to drought and low soil fertility, and high yield. In addition, alternative hybridization and selection methods need to be tried for efficient and effective selections in interracial populations. Seed yield measured from replicated trials in representative environments must be an integral part of all character and cultivar improvement projects for achieving tangible gains.

The cultivation of climbing beans and intercropping systems may gradually decrease in countries facing labor shortages, and in ones that are exposed to modernization of agriculture and industrial development. High-yielding bean cultivars suitable for mechanization would be required under such circumstances in order to stay competitive with other crops and keep pace with current levels of bean consumption. However, horticultural crop growers near urban markets (especially for their green pods) and farmers in the Andean highlands and elsewhere may still find climbing beans attractive because of their high yield and long fruiting period. It is expected that private, state, national, regional, and international programs dedicated to bean research, production, and development will become more interdependent in their work.

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