

Improving Resource Use Efficiency and Reducing Risk of Common Bean Production in Africa, Latin America, and the Caribbean

Stephen Beebe,^{1*} Idupulapati Rao,¹ Clare Mukankusi,² and Robin Buruchara²

Contents

- 2 Background information and system description
- 3 Major constraints for target production system
- 6 Key eco-efficiency interventions throughout the value chain
- 10 Risk and resilience issues
- 10 Adaptation to and mitigation of the effects of climate change
- 13 Quantifying eco-efficiency and developing indicators
- 14 Opportunities to enhance impact and scale-out from initial studies and interventions
- 14 Perspectives: key lessons and opportunities for research, development, and policy
- 15 Acknowledgements
- 15 References

Abstract

Common bean (*Phaseolus vulgaris* L.) is the most important food legume in tropical Latin America and East and southern Africa. Beans originated in the mid-altitude neotropics with moderate soil fertility conditions. Typically, they are not well adapted to extreme climatic and edaphic environments. Climate change will alter distribution and intensity of biotic constraints to bean production, and more intense droughts will adversely affect important production regions in Mexico, Central America, the Caribbean, and southern Africa. In the tropics the crop is cultivated largely by resource-poor farmers, often on soils that are deficient in nitrogen and phosphorus. Both climatic and edaphic constraints cause severe yield losses. They are widespread, often intense, and occur every year in the case of heat and soil problems. Developing the right root system to cope with root rots, drought, and soil problems in each production environment will be a major research challenge. Genetic improvement for resistance to major biotic and abiotic constraints will have significant and wide impact. Fertilizers that improve plant vigor, root growth, and access to soil moisture, or irrigation to counter drought, are seldom viable options for small-scale farmers. While programs to subsidize such inputs merit consideration, crop improvement through plant breeding will probably be the cornerstone of adapting beans to climate-smart production systems in the tropics. The secondary and tertiary gene pools of common bean cover a range of environments from cool moist highlands to hot semi-arid regions, and will be important resources for the genetic improvement of common bean as it must increasingly confront extremes of heat, drought, and excess moisture.

¹ International Center for Tropical Agriculture (CIAT), Cali, Colombia.

² CIAT, Kawanda Research Station, Kampala, Uganda.

* Corresponding author: s.beebe@cgiar.org

Background Information and System Description

Common bean (*Phaseolus vulgaris* L.) is a traditional crop of the neotropics, where it was domesticated several thousand years ago (Freytag and Debouck, 2002; Chacón et al., 2005). In Central America it formed an essential part of the diet as one of the “three sisters”—maize, beans, and squash. Its central role in the livelihoods of the original inhabitants of the American continent is illustrated by its frequent representation in artwork. It continues to be an essential part of the diet in tropical America, as well as in East and southern Africa, where it was introduced about 400 years ago (Greenway, 1945), and many other parts of the world.

Wild beans

Many of the issues of adaptation of the modern cultivated bean can be traced to its wild ancestor. Knowledge of this wild ancestor and its native environments can elucidate patterns of adaptation of the cultivated bean and identify some of the challenges that breeders and agronomists face in confronting environmental stress.

The wild bean is a vigorous annual liana of 6 to 10 months duration that depends on its vegetative vigor to outcompete surrounding vegetation. It originated in a subhumid premontane forest, typically at mid-altitudes of 1200 to 1800 meters above sea level (masl) and with moderate temperatures (Toro et al., 1990). Soils in this environment typically are organic with reasonable drainage and moderate fertility. Weather patterns are characterized by well-defined wet and dry seasons and abundant total rainfall, but often with a dry period of 2 to 4 weeks or longer in midseason between peaks of bimodal rainfall. Thus, with the possible exception of the dry highlands of Mexico where drought is endemic and occasionally intense, the wild ancestor was not often exposed to extreme environments of soil, temperature, or drought. This fact influences the adaptation range of the species and of cultivated beans, and represents a particular challenge to efforts to adapt the crop to more challenging environments, especially as these evolve under the influence of climate change.

Cultivated beans and genetic diversity

The cultivated bean was domesticated in its mid-altitude environment both in the southern Andes and in Mesoamerica, resulting in two contrasting gene pools that have been subdivided into races (Blair et al., 2009). The Mesoamerican gene pool has been subdivided into four genetic groups or races (Beebe et al., 2000), while three races have been defined in the Andean gene pool based on plant morphology and adaptation range (Singh et al., 1991). From these regions beans were carried into environments with stresses that were different from what they likely confronted in their wild state. The cultivated bean has thus been adapted to wider environments, either by empirical selection by plant domesticators and farmers or through systematic selection by plant breeders (Beebe et al., 2011a).

Beans in cropping systems

Primitive bean varieties in Mexico, Central America, and the Andes were vigorous climbers and were planted with maize for physical support in altitudes from 1200 to 3000 masl. Semidomesticated types might have been collected from the wild with little or no human intervention during the growth cycle (Beebe et al., 1997b). Subsequently, less aggressive plant habits were selected for cultivation as semi-climbing beans in a relay system with mature maize stalks as support, or between rows of maize, cassava or other crops, or as a sole crop.

As beans were moved into still-lower altitudes, they confronted less favorable environments. In Central America and Brazil they are frequently cultivated between 400 and 1000 masl with much higher temperatures than the wild ancestor experienced. In Brazil, currently the largest single bean producer in the world, bean is grown on the drought-prone sandy soils of the northeast and acid infertile soils of the Cerrados (Thung and Rao, 1999).

The crop was probably introduced to Africa by Portuguese traders early in the 17th century, where it met with great success in the Great Lakes region. Highland Africa is now regarded as a secondary center of diversity for the common bean and the crop is an important contributor to

food security in the region (Asfaw et al., 2009). In Africa bean has found its niche in a similar mid-altitude environment as it occupies in the Americas, occasionally interplanted with maize or other crops such as cassava, banana, and pigeon pea (Wortmann et al., 1998). Bush bean varieties are adaptable to various cropping systems due to their short growing cycle, while climbing varieties have been cultivated in the highlands of East Africa for many years at elevations of 2000 masl or higher. In the mid-1980s the International Center for Tropical Agriculture (CIAT, its Spanish acronym) introduced Mesoamerican climbing beans with adaptation to altitudes of 1500–1800 masl. Beans have now been pushed into the dry eastern hills of Kenya and northern Tanzania, into environments that represent frontiers of adaptation for the common bean and a challenge for breeders and agronomists to improve adaptability.

In modern times in Latin America it is more common to find beans planted as a sole crop than as an intercrop. Even in the traditional systems with maize in Central America, most farmers prefer to plant varieties with bush growth habits that require less labor to harvest than the traditional association or relay systems where the bean must be untangled from the maize stalk. In Argentina, Brazil, on the Pacific coast of Mexico, and in the United States, beans have become a commercial crop with high inputs and mechanization. Modern varieties have upright plant habit with an eye to direct mechanical harvest. In these commercial systems, bean cultivation responds to market demand and competes with other commercial crops, especially soybean and maize. In Africa, beans are gaining an important place on the export market and are considered an important source of household income.

Major Constraints for Target Production System

Table 1 lists the major production constraints to common bean production, including biotic (fungal, bacterial, and viral diseases; insect pests) and abiotic (drought, heat, nitrogen [N] and phosphorus [P] deficiency; acid soil) stress

factors. This topic has been reviewed by Singh (1999), Rao (2001), Miklas et al. (2006), and Beaver and Osorno (2009).

Diseases and pests

Diseases and pests are universal constraints to bean production, especially fungal pathogens (Schwartz and Pastor-Corrales, 1989; Wortmann et al., 1998). Diseases may cause 80–100% yield loss while pest damage, especially during the early seedling stage and pod formation, also causes severe yield losses. Anthracnose, rust, and angular leaf spot are widely distributed, while rhizoctonia web blight and ascochyta blight can be locally intense in warm-moist and cool-moist environments, respectively. In the past few decades root rots have emerged as a greater problem (Abawi and Pastor-Corrales, 1990), especially those caused by *Pythium* spp. and *Fusarium* spp. Intense cultivation under increasing population pressure, without fallow periods or adequate crop rotations, results in declining soil fertility or soil compaction, or both, and in build-up of pathogen inoculum in the soil (Wortmann et al., 1998). Reduced soil quality inhibits root growth and the potential for plant recovery after infection. *Fusarium* spp. are a major constraint in Mexico (Navarrete-Maya et al., 2002) and Rwanda, and *Pythium* spp. in the moist highlands of Uganda (CIAT, 2007). Several species of *Pythium* have been isolated from infected beans in Uganda, some of which also infect sorghum. While rotation with cereals is a widely accepted practice to reduce inocula in the soil, this practice may not be as effective with pathogens that infect both beans and cereals.

Common bacterial blight is the most important bacterial disease, while halo blight can occur occasionally in cool climates. Although yield losses of up to 40% have been recorded in managed trials, and common blight can be intense in production systems in Argentina and Brazil, in most small-scale farming systems losses seldom reach this level. Rather, common blight is more of a threat in seed production, since the pathogen is seed borne and results in rejection of seed lots. Infection of pods will discolor grain, especially of white seeded types, and reduces commercial quality.

Table 1. Major production constraints of common bean.

Constraint ^a	Regional importance	
	Latin America and Caribbean	East, West, and southern Africa
Abiotic constraints		
Drought	+++	+++
Heat	+++	++
N deficiency	++	+++
P deficiency	+++	+++
Acid soil toxicities (Al, Mn)	++	+
Viral diseases		
BCMV/BCMNV	+	++
BGMV/BGYMV	+++	
Fungal diseases		
Angular leaf spot	++	+++
Anthracoze	++	++
Pythium	+	+++
Fusarium	+	++
Rust	++	++
Bacterial diseases		
Common bacterial blight	+	+
Insect pests		
Bruchids	++	++
Bean stem maggot		+++
Ootheca		+
Whiteflies	+	
<i>Apion</i> sp.	+	

a. Al = aluminum; Mn = manganese; BCMV = bean common mosaic virus; BCMNV = bean common mosaic necrotic virus; BGMV = bean golden mosaic virus; BGYMV = bean golden yellow mosaic virus.

Severity of constraint: += low; ++ = moderate; +++ = high.

SOURCE: Adapted from Beebe et al. (2011a).

Viruses can be especially devastating. In lowland Americas gemini viruses are almost universally present (Anderson and Morales, 2005). Bean common mosaic virus (BCMV) is a seed-borne potyvirus and is distributed throughout the bean-growing world. Its close relative, bean common mosaic necrotic virus, is prevalent in parts of Africa and appears locally in the Americas.

Insects are occasional problems. In Central America the bean pod weevil, *Apion godmani* and *A. aurichalceum*, is the most important pest (Schwartz and Pastor-Corrales, 1989), while in East Africa the bean stem maggot (*Ophiomyia* spp.) is a serious limitation (Wortmann et al., 1998), as are aphids and pod borers. In Mexico the bean beetle causes serious damage.

Leafhoppers (spp.) cause serious damage in drier climates.

Climate change will undoubtedly alter patterns of disease and insect incidence and intensity. Equatorial regions of the northern Andes and the East African highlands are expected to receive more rainfall on average as a result of climate change, although extreme rainfall events induced by the La Niña phenomenon will be the major problem (Yadav et al., 2011). Excess rainfall will exacerbate existing problems with many of the fungal pathogens, particularly soil-borne pathogens and foliar pathogens such as angular leaf spot and anthracnose (Beebe et al., 2011a). Excess rainfall and medium to high temperature will increase the incidence of web blight and angular leaf spot at elevations between 50 and

1400 masl. On the other hand, disease caused by *Fusarium oxysporum* and *Macrophomina phaseoli* can be more severe on drought-stressed crops, and could also become more limiting in Mexico and other countries. Most root-rot pathogens need some soil moisture to support infection. However, once disease has been established in a drought-stressed plant the damage may be much greater than in plants in a non-drought situation. *Macrophomina* is a major problem under conditions of terminal drought (Frahm et al., 2004), whereas *Rhizoctonia solani* and *Fusarium* spp. are major root pathogens in regions where intermittent drought occurs (Navarrete-Maya et al., 2002).

Drought conditions will affect disease by making the environment more or less favorable for infection, disease development, and/or disease spread. Although droughts occur when there is a lack of rainfall, humidity may not be lacking and dew is likely to form if the air is humid and night temperatures fall below the dew point. Dew on leaves creates a favorable environment for some pathogens, and damage from some leaf diseases may be extreme in drought-stressed plants. Dew on leaves often provides enough moisture for the rust pathogen (*Uromyces appendiculatus*) to infect plants. High humidity provides a favorable environment for the infection and development of powdery mildew as well.

Pests such as the bean stem maggot, whiteflies (*Bemisia tabaci*) that transmit bean golden mosaic virus, and aphids that transmit BCMV (*Aphis fabae* and *Aphis craccivora*) are very important in drought conditions. High incidence of BCMV is expected at elevations between 50 and 1400 masl and during drought periods and at high temperatures. Rising temperatures will likely broaden the geographic range of *Bemisia* spp. and will carry the viruses into higher elevations (Beebe et al., 2011a).

Soil constraints

Soil constraints per se are probably the biggest single cause of a persistent yield gap between potential and realized productivity, particularly in developing countries in the tropics (Wortmann et al., 1998; Thung and Rao, 1999). General

symptoms of mineral deficiency or toxicity include poor emergence; slow growth; seedling and adult plant stunting; leaf yellowing, chlorosis, and bronzing; reduced overall growth and dry-matter production; delayed and prolonged flowering and maturity; excessive flower and pod abortion; low harvest index; reduced seed weight; deformed and discolored seeds and severe yield loss (Singh et al., 2003). Root growth may also be adversely affected (Fawole et al., 1982; Cumming et al., 1992).

The wild ancestor of the common bean originated in soils that were typically high in organic matter and that were seldom critically deficient in nutrients. The wild bean is more sensitive to low soil P availability than its cultivated counterparts, suggesting that domestication and selection have actually improved adaptation to P-deficient soils (Beebe et al., 1997a). However, adapting bean to nutrient-poor soils continues to be a challenge.

P and N are the elements most often limiting in tropical soils. Legumes are especially limited by poor P availability; K is limiting only occasionally. Often fertilizer is not applied to the bean crop, but rather to the companion cereal crop, either in association or rotation, and the bean crop benefits from residual fertility. Micronutrients are constraining in some soils, especially those with alkaline pH. In Iran, for example, iron and manganese can be critically limiting.

Low soil fertility is particularly a constraint for bean production in Africa. In central and eastern Africa, the major soil fertility-related problems include low available N and P, low availability of exchangeable bases and soil acidity (Wortmann et al., 1998). In this area, P is deficient in 65–80% of the cultivated area and N in 60% of the area. Although beans are produced primarily in areas where median soil pH is between 5.0 and 6.0, over 23% of the production in eastern Africa occurs in areas where soil pH is below or equal to 5.0.

Beans can fix modest to good amounts of N if conditions permit (Hardarson et al., 1993), and climbing beans can actually contribute substantial

amounts of N to the system. However, low availability of P, high temperatures, or root diseases usually do not permit bean to maximize its N fixing potential. Rising temperatures will represent an even greater limitation on N fixation.

Apart from nutrient availability, various soil physical constraints also limit yields. Soil degradation is severe in Central America and Haiti, and is advancing in Africa (Ayarza et al., 2007; Sanginga and Woolmer, 2009). Erosion and loss of soil organic matter (SOM) is associated with lower availability of plant nutrients, declining soil structure, and reduced water-holding capacity. The vast Mexican plateau boasts a million hectares of beans and is characterized by soils that are frequently thin and with low SOM. The bean root system does not penetrate compacted soil well and can be severely limited by soil physical structure.

Drought and excess water

Drought affects up to 60% of bean production regions (Beebe et al., 2011b) and is endemic in Mexico, Central America, parts of the Caribbean, Ethiopia, northern Uganda, eastern Kenya, Tanzania, and southern Africa. Some regions are expected to become progressively drier under climate change, especially Mexico, Central America, and parts of northeast Brazil and southern Africa (Yadav et al., 2011). However, it will be the extreme climatic events that will be

most limiting and the most threatening to food security, especially those associated with El Niño events.

Temperature

As a consequence of their mid- to high-altitude origin, beans are generally sensitive to high temperatures (Porch and Jahn, 2001). Night temperatures in excess of 20 °C can seriously reduce pollen fertility and pollination. However, current analyses suggest that nocturnal temperatures still seldom reach critical levels and that day temperatures may actually be more limiting (Yadav et al., 2011). Regions where bean is currently cultivated at the margins of its temperature adaptation range and that could soon suffer significant losses due to higher temperatures include lowland Central America and central Brazil (Figures 1A and 1B), West Africa in general, northern Uganda, and southern Democratic Republic of the Congo (Figures 2A and 2B).

Key Eco-Efficiency Interventions throughout the Value Chain

Eco-efficiency interventions should be considered throughout the value chain, from farm to consumer. However our analysis suggests that the most successful interventions to favor eco-efficient agriculture will occur in the production arena.

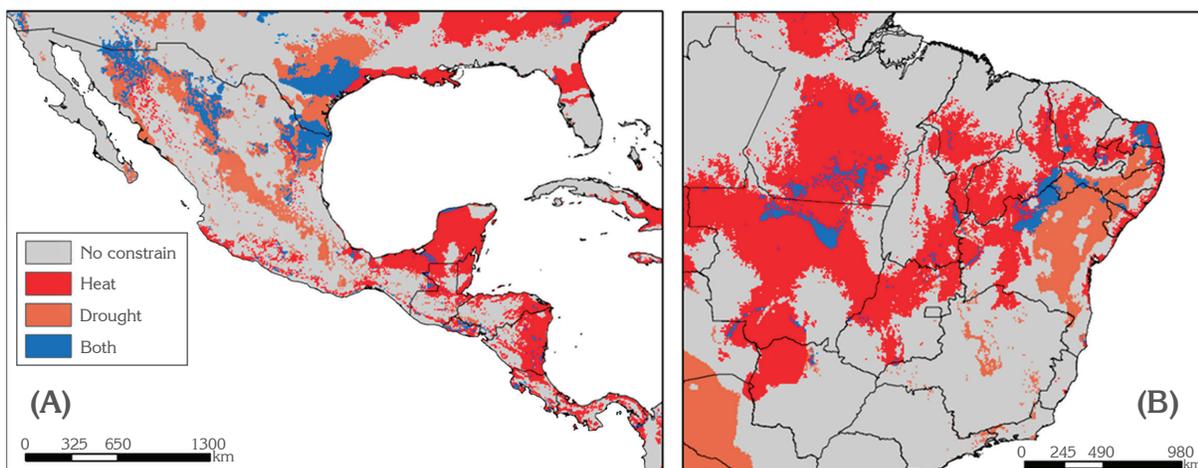


Figure 1. Regions in (A) Central America and (B) Brazil that suffer heat stress, drought stress, or both.

SOURCE: CIAT.

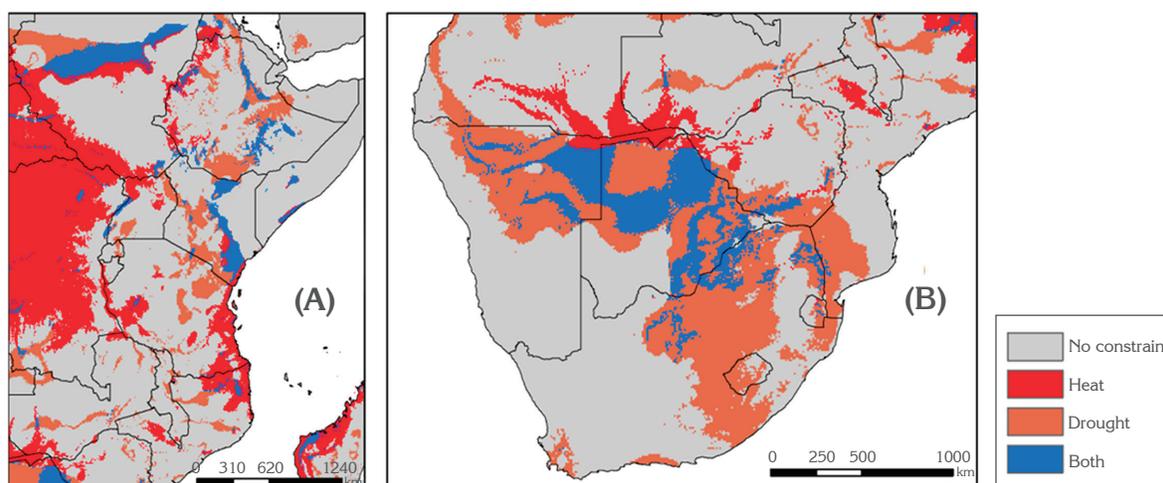


Figure 2. Regions in (A) East Africa and (B) southern Africa that suffer heat stress, drought stress, or both.

SOURCE: CIAT.

Improving host plant resistance to biotic stress factors

Host plant resistance (HPR) as a first line of defense against diseases and insects is a primary goal of plant breeders working at CGIAR centers. In the case of beans, HPR combines several eco-efficiency attributes, especially reduction of pesticide abuse. Breeding for disease resistance is well advanced in the case of dry beans. Nonetheless the use of interspecific crosses with *P. coccineus* and *P. dumosus* should be broadened, especially in breeding for resistance to soil-borne pathogens for which resistance is incomplete and that may become more severe under population pressure and more intense cultivation. In Latin America pesticides are readily available to farmers and pesticide abuse is common, especially on high-value crops such as snap beans (Cardona et al., 2001). High demands for very specific quality traits have slowed progress toward genetic resistance to diseases of snap beans. More intense rainfall will necessitate renewed effort to develop cultivars that are resistant to diseases, especially anthracnose, angular leaf spot, and ascochyta blight.

DNA markers have enormous potential to improve the efficiency and precision of conventional plant breeding via marker-assisted selection (Collard and Mackill, 2008). They are increasingly being used in breeding for resistance to a number of important diseases of the common bean. Several markers have been

identified that are linked to genes conferring resistance to angular leaf spot, anthracnose, common bacterial blight, BCMV and its necrotic strain, bean common mosaic necrosis virus, pythium, and fusarium root rots (Miklas et al., 2006). SCAR (sequence characterized amplified regions) markers have been developed for some of these genes, principally for resistance to anthracnose, BCMV, common bacterial blight, angular leaf spot, and pythium root rot (Miklas et al., 2006).

Extensive work has been done on charcoal rot and one major source of resistance, BAT477, has been studied (Mayek-Pérez et al., 2001; Hernández-Delgado et al., 2009). Quantitative resistance conditioned by four quantitative trait loci (QTLs) with relatively minor effects (13–19%) was reported in the Dorado/XAN 176 mapping population (Miklas et al., 1998). Two of the QTLs with larger effects that expressed across environments were located within resistance-gene clusters on linkage groups B4 and B7 (Miklas et al., 2000).

Improving nutrient acquisition and use efficiency

Fertilizer use efficiency per se has not received much attention in breeding programs, although attention has been directed toward adaptation to infertile soils. Such adaptation could be based on either efficiency of nutrient uptake (acquisition efficiency) or on efficiency of use per unit of

nutrient uptake (use efficiency). Mechanisms include greater root hair density (Yan et al., 2004), exudation of organic acids to solubilize soil nutrients (Ramaekers et al., 2010), or greater root length density in superficial soil strata where nutrients are concentrated (Liao et al., 2004; Beebe et al., 2006; St. Clair and Lynch, 2010). Substantial mechanistic work has been carried out in common bean in this regard, although trait-based selection has seldom been implemented in breeding programs.

Alternatively, adaptation to infertile soils can be manifested as efficiency in production of grain per unit of nutrient taken up from the soil (nutrient use efficiency). Genotypic variability in this trait has been observed in common bean when grown in low-P soils or aluminum-toxic acid soils (Rao, 2001; Beebe et al., 2009; Table 2).

Although studied to date in the context of low native fertility of soils, increases in either nutrient acquisition efficiency or nutrient use efficiency would contribute to the increasing efficiency with which added fertilizer inputs are used as well. This would be one of the most important contributions to increasing yield in common bean in an eco-efficient way. In cropping systems where beans benefit from residual fertility following application of fertilizer to a cereal crop, either strategy would make better use of existing inputs and prevent mining the soil in the long run. In tropical soils with high P-fixing capacity, it is important to recover applied P before it is irretrievably fixed by iron and aluminum oxides (Rao et al., 1999). This implies an efficient root system that aggressively accesses soil nutrients. Combined with conservation agriculture, this could have great practical impacts.

Symbiotic nitrogen fixation (SNF) received ample attention in CIAT's research program in its early years, in genotype selection and especially in the search for efficient rhizobial strains (Graham, 1981; Kipe-Nolt et al., 1993). While *Rhizobium etli* typically gives better fixation in optimal conditions, *R. tropici* is more tolerant of heat and acid soil, and *R. tropici* strain CIAT 866 has been widely employed in inoculation studies (Hardarson et al., 1993; Graham and Vance, 2000). The

quantity of N fixed is normally in direct proportion to the length of the crop cycle. Climbing beans have a longer growth cycle than bush beans, and are a good option for improving soil quality and contributing to the associated or subsequent maize crop yields (Pineda et al., 1994; Sanginga and Woolmer, 2009). In contrast, bush beans often present a negative N balance, removing more N from the system than they contribute. However, in optimal conditions of moderate temperature, adequate P supply in the soil, and modest starter N, even bush beans can fix up to 50 kg N/ha (Hardarson et al., 1993). However, such optimal conditions seldom exist, and bush beans therefore seldom contribute significant N to the system. Nitrogen fixation is one of the most sensitive plant processes to environmental stress and is reduced dramatically by P deficiency (Vadez et al., 1999) or drought (Serraj and Sinclair, 1998).

That said, significant progress has been made in recent years in improving tolerance to several of the physiological stresses that limit fixation, including drought (Beebe et al., 2008); aluminum (Beebe et al., 2009; Table 2); low P (Singh et al., 2003; CIAT, unpublished data), and combined stress factors of drought and low P (Table 2). It is therefore timely to revisit the issue of N-fixation capacity of common bean, to determine if alleviating other stresses through genetic improvement has had a beneficial effect on N fixation in suboptimal conditions.

This could also be an opportunity for studies on gene expression. The very high sensitivity of SNF to environmental factors suggests that the plant is actively shutting down its N fixation in the face of other limiting factors. Understanding this plant reaction could lead to selection criteria to recognize genes that are less prone to react negatively to external factors and to maintain fixation activity.

Improving agronomic management

Agronomic management is clearly necessary to improve bean yields, and conservation agriculture offers important opportunities for increasing production of common beans. Beans respond well to improvement in soil structure with

Table 2. Differences in grain yield, shoot phosphorus uptake, and phosphorus use efficiency of common bean genotypes grown under combined stress from drought and low P at Darién, Colombia, and under aluminum toxicity on an acid soil at Quilichao, Colombia.

Genotype	Combined drought and low-P stress			Aluminum toxicity		
	Grain yield (kg/ha)	Shoot P uptake (kg/ha)	P use efficiency (g/g) ^a	Grain yield (kg/ha)	Shoot P uptake (kg/ha)	P use efficiency (g/g)
A 774	913	2.34	390	427	3.11	137
BAT 477	805	2.17	371	637	1.81	352
Carioca ^b	614	1.05	585	693	3.23	215
DOR 390	958	1.81	529	358	2.03	176
EAP 9653-16B-1	549	1.64	335	762	3.71	205
G 40001 ^c	212	0.67	316	431	1.89	228
NCB 226	1047	1.40	748	522	2.03	257
Perola ^b	992	1.69	587	493	1.63	302
San Cristóbal 83 ^b	721	1.61	448	427	2.14	200
SEN 56	471	1.56	302	721	4.78	151
SER 16	584	1.64	356	381	1.35	282
SER 78	542	1.89	287	568	2.35	242
SER 128	590	1.80	328	501	3.08	163
SXB 412	1127	3.27	345	594	2.49	239
SXB 415	922	2.57	359	698	2.48	281
Tio Canela 75 ^b	641	1.50	427	514	2.64	195
Mean	702	1.86	420	594	2.70	227
LSD _{0.05}	243	0.64	ND	250	1.80	ND

a. Grams of grain produced per gram of shoot P uptake.

b. Check cultivars.

c. *P. acutifolius* (tepary bean) germplasm accession.

ND = Not determined because P use efficiency was calculated based on mean values of grain yield and shoot P uptake.

SOURCE: J. Ricaurte, C. Cajiao, M. Grajales, S. Beebe, and I. Rao (unpublished results).

enhanced SOM. The root system of beans is less aggressive than that of cowpea, for instance, and heavy soils or soil compaction can be serious impediments of its root system. Conservation agriculture improves soil structure, water penetration, root development, and plant nutrition and therefore deserves more attention in a systems context, such as in the maize–bean system in Central America (Castro et al., 2009) or the mixed maize system in East Africa where bean is a common component (Hyman et al., 2008). For example, crop water productivity (kilograms of grain produced per cubic meter of water used) of common bean was higher in a slash–and–mulch agroforestry system than in the traditional slash–and–burn agricultural system (Castro et al., 2009).

Reducing carbon footprints through reduced transport and cooking time

The most energy-demanding process in the whole market chain is probably cooking. Even in the United States, where agriculture is almost entirely mechanized and production consumes large amounts of energy, 48% of energy in the food chain is spent in industrial processing and home cooking, compared with 21% used in production and 13% in transportation (CSS/UoM, 2011). Cooking common bean has a particularly high energy requirement because of its relatively long cooking time. Short cooking time regularly emerges as a consumer-preferred trait in studies in the developing world. There is ample variability in cooking time among bean lines, and exploiting this variability systematically would be both a

contribution to energy efficiency and a welcome improvement among bean consumers.

In recent years there has been a move toward consumption of locally produced foods. While this movement is based on multiple motivations, an important one is to reduce the carbon footprint along the food chain. For common bean, this could imply increasing production close to important urban centers that absorb large quantities of beans moved over long distances, including Mexico City, Sao Paulo, Kinshasa, Nairobi, and Johannesburg. The southern region of Mexico, although a traditional bean-producing area, is not self-sufficient in beans and imports beans from other parts of Mexico and from abroad. Local production would seem to be an attractive option, but further studies are needed to determine the competitiveness of different production regions and the yield levels needed on a local level to compete with beans carried over long distances.

Risk and Resilience Issues

We have referred to the likely effects of climate change, including changes to the distribution and intensity of biotic constraints; exacerbating effects of drought; and reducing yields due to higher temperatures in low-lying areas of Central America, Brazil, and Africa.

While soil conditions are similar year after year and temperatures vary within certain limits for a given site and time of year, drought, pests, and diseases are sporadic problems that make predictions of expected yields difficult. Investments that could raise yields, e.g., fertilizer, labor, or capital improvements, are unattractive in the face of such sporadic risks. Thus, while reducing risk may not affect average yields dramatically, it is a primary step toward other improvements in a system.

Resilience of a system is reflected in its ability to adapt to and recover from adverse conditions. Soil quality is an important determinant of the resilience of a farming system. Soil quality, and especially enhanced SOM, permits better root

development, increasing accessibility of moisture, soil water-holding capacity, and availability of nutrients. Greater access to moisture will in turn permit the crop to transpire more, which cools the canopy and allows the key processes of leaf expansion and grain development to continue in the face of high air temperatures. While these effects would benefit all crops, beans would benefit in particular given their sensitivity to shortages of water and nutrients. Such system-based interventions are typically adopted more slowly than simpler interventions such as improved seeds or fertilizer, given their complexity and the fact that they often require capital investment. System interventions that benefit multiple crops will likely have a better chance of adoption by farmers than those that benefit only a single crop.

Adaptation to and Mitigation of the Effects of Climate Change

While common beans are relatively more sensitive to abiotic stress than other legumes such as cowpea, considerable progress has been made in breeding for tolerance to various abiotic stresses. For example, drought tolerance has been improved through intraspecific crosses, employing the naturally occurring variability within *P. vulgaris* (Beebe et al., 2008). However, interspecific crosses with sister species of the genus *Phaseolus* offer prospects of further progress. The genus *Phaseolus* originates in a remarkably wide range of ecologies, from tropical rainforest to arid desert (Freytag and Debouck, 2002), and species that are cross compatible with common bean cover most of this range. The secondary gene pool, including cultigens *P. coccineus* (runner bean) and *P. dumosus* (year-long bean) and wild species *P. costaricensis* and *P. albescens*, is readily crossed with common bean. The secondary gene pool is adapted to cool, moist environments and is a source of traits for environments that will likely receive excess moisture. At the other extreme, *P. acutifolius* (teparty bean) and its wild relative *P. parvifolius* evolved in semi-arid or arid environments and are a source of traits for hot, dry climates.

Improving drought tolerance

Drought tolerance has been the object of bean genetic improvement for at least 3 decades in CIAT and other institutions. Early work suggested that deep rooting was a critical tolerance mechanism (Sponchiado et al., 1989). Singh (1995) found superior drought tolerance in crosses that combined the genetic diversity found in the Mesoamerica and Durango bean races. This formula has continued to produce materials that perform well under drought stress.

Enhanced remobilization of photosynthate to grain under drought stress is another important mechanism of drought tolerance (Beebe et al., 2011b). The wild bean appears to suppress reproductive development in the face of stress (Beebe et al., 2011b). In the wild this strategy is effective under a bimodal rainfall pattern, where late rains permit resumption of reproductive development. However, in a short-season cultivar this strategy results in poor yields. Improved yield under stress is associated with maintaining reproductive development and photosynthate transport to seed. This trait also appears to be beneficial under favorable conditions and to a certain extent in conditions of low soil-P availability (Beebe et al., 2008).

Continued progress in breeding for drought tolerance will likely require accessing genetic variability in sister species of common bean. For example, tepary bean is reported to possess multiple drought-resistance traits, including dehydration avoidance (Mohammed et al., 2002). It has fine roots with high specific root length (Butare et al., 2011) and it expresses rapid root penetration to access moisture at deeper soil levels. Although crosses with common bean normally require embryo culture to obtain viable plants, intensive intercrossing has led to enhanced genetic exchange (Mejía Jiménez et al., 1994), and a stock of introgression lines exists in CIAT (Muñoz et al., 2004) that can be mined for useful traits.

Although runner bean would seemingly not be a promising source of traits for drought tolerance, given its origins in moist environments, in fact it

displays a unique root system with traits that could be valuable in some circumstances. For example, it is highly tolerant of toxic levels of soil aluminum and has a coarse root system that might be able to penetrate compacted soil more readily than that of common bean (Butare et al., 2011).

Our experience suggests that poor soil fertility is a serious constraint on the expression of drought tolerance. A crop that is poorly nourished will have a limited root system and will not have the vigor to resist additional stress from drought. Addressing soil fertility is a critical component of any strategy to combat drought.

Improving tolerance to excess rainfall

Climate change will result in some bean-growing regions receiving more precipitation than at present. Waterlogging and associated root rots may increase in east-central Africa and the northern Andes. Restricting the amount of oxygen roots receive inhibits both symbiotic N₂ fixation and N uptake, reducing root growth and nodulation. Tolerant genotypes may have various adaptive responses (Colmer and Voesenek, 2009). More adventitious roots and/or larger aerenchyma in roots, nodules, and the base of the stem may enhance tolerance of waterlogging. Rapid, reliable screening methods are needed to evaluate waterlogging tolerance.

Improving heat tolerance

Beans are grown over a wide range of latitudes with mean ambient temperatures ranging from 14 to 35 °C. Temperatures of more than 30 °C during the day or more than 20 °C at night result in yield reduction. High night temperatures at flowering (and to a lesser degree, high day temperatures), cause flower and pod abortion, reduced pollen viability, impaired pollen-tube formation in the styles, and reduced seed size. Acclimation to occasional high night temperatures may be a genotypic resistance mechanism. A pollen-based method developed to evaluate heat tolerance in soybeans might be used to screen common-bean genotypes for tolerance to nocturnal heat stress (Salem et al., 2007).

To date there has been limited activity to identify tolerance to heat stress in common bean. Work has been carried out in controlled conditions at Cornell University (Rainey and Griffiths, 2003) but this has not been extended systematically to dry beans in the tropics. There is active interest in improving heat tolerance in Central America (Porch et al., 2007). Evaluation under high temperatures of advanced breeding lines developed for bean golden yellow mosaic virus resistance has been carried out in Central America, and the variety CENTA Pipil developed by the Pan-American Agricultural School of Zamorano, Honduras, has proven to be relatively tolerant in El Salvador. While incremental quantitative progress may be made with further efforts, tepary bean may be a promising source of heat tolerance in the long run. Some interspecific lines of tepary and common bean have been evaluated in Central America and in Puerto Rico, and while some appear to be promising it remains to be seen if they represent an advantage over available genetic diversity within common bean germplasm. Nonetheless, mining the diversity of tepary bean would seem to be high priority for the future.

Improving disease resistance and grain yield

Bean diseases will be exacerbated in some regions as a result of climate change. Efforts to breed for resistance may need to resort to sister species for broader genetic variability. Runner bean has long been employed as a source of resistance for such difficult diseases as white mold caused by *Sclerotinia* spp. (Abawi et al., 1978) and fusarium root rot caused by *Fusarium solani* (Wallace and Wilkinson, 1965). More recently progeny of crosses between runner bean and common bean have proven to be resistant to both *Fusarium* spp. and *Pythium* spp. (CIAT, unpublished data). While using runner bean or year-long bean as a source of resistance is not novel, the utility of interspecific progenies has always been limited by their poor agronomic quality and low harvest index. A recent study suggests that the quality of crosses with the secondary gene pool can be improved by using common bean with enhanced remobilization of photosynthate to grain (Klaedtke et al., 2012).

Such parents can “tame” the excessive vegetative growth of these sister species and result in superior progenies.

Integrating beans into cropping systems to cope with high temperature

While specific agronomic interventions can be made to address the impacts of climate change, broader-based solutions may involve transformation of the whole cropping system. For example, high daytime temperatures might be addressed by adopting a cropping system that provides partial shade to the bean crop. Some such cropping systems already exist; for example, the bean–banana system of Uganda and northwest Tanzania (Wortmann et al., 1998). Beans could be intercropped with coffee to provide shade after pruning of the coffee and while the coffee plantation returns to production. Alley cropping, especially with profitable tree crops such as mangos or other fruits, offers some promise. Such a system could be better exploited if shading tolerance were enhanced in the bean crop.

One option that has emerged in past years and that is likely to expand in response to higher temperatures is the use of alternative planting dates. In Central America bean production has expanded dramatically on the Atlantic coast of the isthmus, in the cool, dry, winter season when the crop survives on residual moisture. In Brazil the cool dry season has seen the expansion of high-input production under center-pivot irrigation. Given that such changes have been largely the result of pressure on land resources or to produce when beans are normally scarce and prices are high, the attraction of producing in a season with more favorable temperatures will only enhance this tendency.

Expected impacts of improved adaptation to climate change

A modeling exercise was carried out to estimate the distribution and relative importance of climatic constraints to bean yields, and the potential value of genetic improvement (Beebe et al., 2011a; Figures 1 and 2). Breeding drought tolerance into bean could improve suitability of some 3.9 million hectares of land where bean is currently grown (the equivalent of 31% more land classified as

highly suitable) and would allow the crop to be grown on another 6.7 million hectares currently not suitable. Heat tolerance could increase the suitability of 7.2 million hectares of land where bean is currently grown. Drought tolerance would also improve productivity on some of this land and could increase the area designated as highly suitable by some 54%. Thus, both drought tolerance and heat tolerance are important objectives for genetic improvement. Although heat tolerance may offer wider impact, drought causes great year-to-year yield variability and must also be given priority.

Quantifying Eco-Efficiency and Developing Indicators

In rainfed agriculture, water use efficiency will be a useful parameter to identify eco-efficient bean genotypes (Table 3). In trials at the CIAT-Palmira

(Colombia) testing site, several breeding lines were identified to be superior to the checks.

Phosphorus use efficiency will be a useful parameter to identify bean genotypes for use on P-deficient soils or those suffering from aluminum toxicity (Table 2). Some breeding lines performed better than the check lines under combined stress conditions of drought and low P and under aluminum toxicity (Table 2).

On small-scale farms with minimal use of fossil fuel, energy input is in the form of work done by humans and animals—calculation of which would be irrelevant for the world's energy balance but highly meaningful to the farmer. Similarly, reduced cooking time would make a miniscule contribution to reducing CO₂ emissions but would be highly significant for the people who must search for firewood, usually women and children.

Table 3. Differences in grain yield and agronomic water efficiency^a of common bean genotypes grown at CIAT-Palmira, Colombia.

Genotype	Grain yield (kg/ha)		Agronomic water efficiency (kg/mm) ^a	
	Irrigated	Rainfed	Irrigated	Rainfed
A 774	2731	839	9.59	6.52
BAT 477	2213	722	7.77	5.61
Carioca	2563	797	9.00	6.19
DOR 390	2345	674	8.23	5.24
EAP 9653-16B-1	2685	1054	9.42	8.19
G 40001 ^b	2190	1144	7.69	8.89
NCB 226	2571	1269	9.02	9.86
Perola	1926	654	6.76	5.08
San Cristóbal 83 ^c	2136	495	7.50	3.85
SEN 56	2888	1102	10.14	8.56
SER 128	2453	1263	8.61	9.81
SER 16	2696	1025	9.46	7.96
SER 78	2352	1361	8.25	10.57
SXB 412	2838	850	9.96	6.61
SXB 415	2806	999	9.85	7.76
Tio Canela 75 ^c	2398	771	8.42	5.99
Mean	2307	898	8.10	6.98
LSD _{0.05}	426	319	1.49	2.47

a. Kilograms of grain produced per millimeter of water applied through either irrigation or rainfall.

b. *P. acutifolius* (teparry bean) germplasm accession.

c. Check cultivars.

SOURCE: J. Polanía, M. Rivera, M. Grajales, S. Beebe, and I. Rao (unpublished results).

Reducing the amount of energy expended in transport by promoting local production could be measured by cost differentials between local and imported products. Such a differential would in fact reflect multiple factors but transport cost per ton can readily be obtained. Translating this cost into carbon emissions would require an added level of assumptions.

Opportunities to Enhance Impact and Scale-Out from Initial Studies and Interventions

Impact from seed-based solutions would follow from the models of seed dissemination that have been used for standard agronomically improved materials. Recent years have seen a diversity of models emerging, from formal revolving seed models, to decentralized seed production, to small packets of seed and fertilizer and seed loans. Nonetheless, no novel system will alter the fact that long-term adoption will depend on the farmer appreciating added value in the new materials. In the case of germplasm that is resistant to the effects of climate change, farmers will likely be able to see the value of drought tolerance or disease resistance within 2 or 3 years where these stresses are endemic. Tolerance to high temperatures may be more difficult to appreciate, as its effects will be felt more gradually.

Agronomic solutions are typically more difficult to deploy. Participatory research should be practiced from the outset, given the complexity of incorporating what are often system-level interventions.

Soil-management practices cut across the entire farming system and go far beyond individual crops (Sanginga and Woolmer, 2009). The contribution of a particular crop could be in generating synergistic benefits that make the system more attractive for adoption. For example, climbing beans are far more productive than bush beans, and anecdotal reports suggest that agroforestry was more readily adopted where it served as a source of staking material for climbing beans. Similarly, planting beans among trees during the establishment phase of plantations was reported to

have made planting of trees more attractive to farmers by creating a source of income in the short term, and to have aided tree establishment by encouraging weed control. These cases have not been documented, but such potential interactions should be sought.

Perspectives: Key Lessons and Opportunities for Research, Development, and Policy

Experience in breeding for drought tolerance suggests that stress tolerance does not necessarily imply a yield penalty (Beebe et al., 2008, 2009). However, the greater the degree of stress that we encounter, the greater will be the demands on obtaining adequate levels of tolerance. Once again, dealing with average conditions will not be nearly so challenging as dealing with extreme events of drought, excess rainfall, and high temperature. Breeders would benefit from more precise estimations of the frequency and intensity of these extreme events.

The *Phaseolus* genus spans a wide range of stressful environments, offering the prospect of finding the necessary genes for stress tolerance. Tolerance to heat and drought can be found in the tertiary gene pool, for example, and tolerance to excess rainfall can be found in the secondary gene pool. Interspecific crosses, by their very nature, require long-term effort, with the need to overcome negative genetic linkages and/or poor chromosome pairing and slow introgression. These are obstacles that are best overcome with time and patience rather than a frenetic investment of research funds on a 3-year project time scale. Thus, such crossing should receive more systematic attention as of now, albeit at a modest level.

If at some time gene expression can be manipulated, then studies of other *Phaseolus* species might reveal which genes will confer tolerance, and these can become targets for enhanced expression or for gene cloning and eventual transgenesis. Efficient transformation remains a challenge in common bean, and the development of an efficient and effective system is yet another area of research.

Little is yet understood about what might be the effects of higher CO₂ concentrations in the atmosphere. Crop experiments conducted in different parts of the world suggested that a doubling of CO₂ from current levels will lead to approximately a one-third increase in grain yield of C₃ crops such as common bean. However, more recent field studies on CO₂ enrichment indicated that this may be an overestimate (Long et al., 2006; Ainsworth and Ort, 2010) and a more realistic estimate is about half of that, i.e., a one-sixth increase. One study on common bean suggests that different genotypes will react differently to higher CO₂, with seed yield at high CO₂ levels ranging from 0.89 to 1.39 times that at ambient CO₂ (Bunce, 2008). There may be opportunities to exploit this dimension of climate change to the benefit of the crop and possibly the system. However, research is lacking in the tropics to determine the impact of higher CO₂ in cropping systems that are limited by other factors. For example, does CO₂ have a positive effect when the crop is simultaneously limited by low available soil P and/or drought and high temperature? In this respect and others, agricultural research in the tropics must be more integrative (Thung and Rao, 1999; Keating et al., 2010; Chen et al., 2011) and less reductionist so that farmers as end users can benefit from research to improve their livelihoods.

Acknowledgements

The authors acknowledge the support of the German Federal Government (Bundesministerium für wirtschaftliche Zusammenarbeit und Entwicklung, BMZ), the Bill & Melinda Gates Foundation, and the Generation Challenge Programme of the CGIAR for financial support of research on improving genetic adaptation of common beans to stressful environments.

References

Abawi GS; Pastor-Corrales, MA. 1990. Root rots of beans in Latin America and Africa: diagnosis, research methodologies, and management strategies. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. 114 p.

- Abawi GS; Prowidenti R; Crosier DC; Hunter JE. 1978. Inheritance of resistance to white mold disease in *Phaseolus coccineus*. *Journal of Heredity* 69(3):200–202.
- Ainsworth EA; Ort DR. 2010. How do we improve crop production in a warming world? *Plant Physiology* 154:526–530.
- Anderson P; Morales F, eds. 2005. Whiteflies and whitefly-borne viruses in the tropics: building a knowledge base for global action. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. p 341–345.
- Asfaw A; Blair MW; Almekinders C. 2009. Genetic diversity and population structure of common bean (*Phaseolus vulgaris* L.) landraces from the East African highlands. *Theoretical and Applied Genetics* 120(1):1–12.
- Ayarza M; Barrios E; Rao IM; Amézquita E; Rondón M. 2007. Advances in improving agricultural profitability and overcoming land degradation in savanna and hillside agroecosystems of tropical America. In: Bationo A; Waswa B; Kihara J; Kimetu J, eds. *Advances in integrated soil fertility research in sub-Saharan Africa: challenges and opportunities*. Springer, Dordrecht, The Netherlands. p 209–229.
- Beaver JS; Osorno JM. 2009. Achievements and limitations of contemporary common bean breeding using conventional and molecular approaches. *Euphytica* 168:145–175.
- Beebe S; Lynch J; Galwey N; Tohme J; Ochoa I. 1997a. A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. *Euphytica* 95:325–336.
- Beebe SE; Toro O; González AV; Chacón MI; Debouck DG. 1997b. Wild-weed-crop complexes of common bean (*Phaseolus vulgaris* L., Fabaceae) in the Andes of Peru and Colombia, and their implications for conservation and breeding. *Genetic Resources and Crop Evolution* 44:73–91.
- Beebe S; Skroch PW; Tohme J; Duque MC; Pedraza F; Nienhuis J. 2000. Structure of genetic diversity among common bean landraces of Mesoamerican origin based on correspondence analysis of RAPD. *Crop Science* 40:264–273.
- Beebe S; Rojas-Pierce M; Yan X; Blair MW; Pedraza F; Muñoz F; Tohme J; Lynch JP. 2006. Quantitative trait loci for root architecture traits correlated with phosphorus acquisition in common bean. *Crop Science* 46:413–423.

- Beebe S; Rao IM; Cajiao I; Grajales M. 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favorable environments. *Crop Science* 48:582–592.
- Beebe S; Rao IM; Blair MW; Butare L. 2009. Breeding for abiotic stress tolerance in common bean: present and future challenges. Paper presented at the 14th Australian Plant Breeding & 11th Society for the Advancement of Breeding Research in Asia and Oceania (SABRAO) Conference, 10–14 August, 2009, Brisbane, Australia.
- Beebe S; Ramírez J; Jarvis A; Rao IM; Mosquera G; Bueno JM; Blair MW. 2011a. Genetic improvement of common beans and the challenges of climate change. In: Yadav SS; Redden R; Hatfield JL; Lotze-Campen H; Hall A, eds. *Crop adaptation to climate change*. Wiley-Blackwell, Oxford, UK.
- Beebe SE; Rao IM; Blair MW; Acosta-Gallegos JA. 2011b. Phenotyping common beans for adaptation to drought. In: Ribaut JM; Monneveux P, eds. *Drought phenotyping in crops: from theory to practice*. CGIAR Generation Challenge Programme, Texcoco, Mexico. p 311–334.
- Blair MW; Díaz LM; Buendia HF; Duque MC. 2009. Genetic diversity, seed size associations and population structure of a core collection of common beans (*Phaseolus vulgaris* L.). *Theoretical and Applied Genetics* 119:955–972.
- Bunce JA. 2008. Contrasting responses of seed yield to elevated carbon dioxide under field conditions within *Phaseolus vulgaris*. *Agriculture, Ecosystems & Environment* 128:219–224.
- Butare L; Rao IM; Lepoivre P; Polania J; Cajiao C; Cuasquer J; Beebe S. 2011. New genetic sources of resistance in the genus *Phaseolus* to individual and combined aluminium toxicity and progressive soil drying stresses. *Euphytica* 181(3):385–404.
- Cardona C; Rendón F; García J; López-Avila A; Bueno J; Ramírez J. 2001. Resistencia a insecticidas en *Bemisia tabaci* y *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) en Colombia y Ecuador. *Revista Colombiana de Entomología* 27(1–2):33–38.
- Castro A; Rivera M; Ferreira O; Pavón J; García E; Amézquita E; Ayarza M; Barrios E; Rondón M; Pauli N; Baltodano ME; Mendoza B; Wélchez LA; Cook S; Rubiano J; Johnson N; Rao IM. 2009. Quesungual slash and mulch agroforestry system improves crop water productivity in hillside agroecosystems of the sub-humid tropics. In: Humphreys E; Bayot RS, eds. *Increasing the productivity and sustainability of rainfed cropping systems of poor smallholder farmers*. Proceedings of the international workshop on rainfed cropping systems, Tamale, Ghana, 22–25 September 2008. CGIAR Challenge Program on Water and Food, Colombo, Sri Lanka. p 89–97.
- Chacón MI; Pickersgill S; Debouck D. 2005. Domestication patterns in common bean (*Phaseolus vulgaris* L.) and the origin of Mesoamerican and Andean cultivated races. *Theoretical and Applied Genetics* 110:432–444.
- Chen XP; Cui ZL; Vitousek PM; Cassman KG; Matson PA; Bai JS; Menga QF; Hou P; Yue SC; Römhelde V; Zhang FS. 2011. Integrated soil–crop system management for food security. *PNAS* 108(16):6399–6404.
- CIAT (Centro Internacional de Agricultura Tropical). 2007. Annual report 2007: Outcome line SBA-1: Improved beans for the developing world. Cali, Colombia. p 210–216.
- Collard BCY; Mackill DJ. 2008. Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Philosophical Transactions of the Royal Society B* 363(1491):577–572.
- Colmer TD; Voesenek LACJ. 2009. Flooding tolerance: suites of plant traits in variable environments. *Functional Plant Biology* 36:665–681.
- CSS/UoM (Center for Sustainable Systems, University of Michigan). 2011. U.S. food system factsheet. Pub. No. CSS01-06. (Available at http://css.snre.umich.edu/css_doc/CSS01-06.pdf.)
- Cumming JR; Cumming AB; Taylor GJ. 1992. Patterns of root respiration associated with the induction of aluminum tolerance in *Phaseolus vulgaris* L. *Journal of Experimental Botany* 43:1075–1081.
- Fawole I; Gabelman WH; Gerloff GC. 1982. Genetic control of root development in beans (*Phaseolus vulgaris* L.) grown under phosphorus stress. *Journal of the American Society for Horticultural Science* 107:98–100.

- Frahm MA; Rosas JC; Mayek-Pérez N; López-Salinas E; Acosta-Gallegos JA; Kelly JD. 2004. Breeding beans for resistance to terminal drought in the lowland tropics. *Euphytica* 136:223–232.
- Freytag GF; Debouck DG. 2002. Taxonomy, distribution and ecology of the genus *Phaseolus* (Leguminosae–Papilionoideae) in North America, Mexico and Central America. Sida, Botanical Miscellany 23. Botanical Research Institute of Texas, Fort Worth, TX, USA. 300 p.
- Graham PH. 1981. Some problems of nodulation and symbiotic nitrogen fixation in *Phaseolus vulgaris* L. *Field Crops Research* 4:93–112.
- Graham PH; Vance CP. 2000. Nitrogen fixation in perspective: an overview of research and extension needs. *Field Crops Research* 65:93–106.
- Greenway PJ. 1945. Origins of some East African food plants. *East African Agricultural Journal* 10:34–39.
- Hardarson G; Bliss FA; Cigales Rivero MR; Henson RA, Kipe-Nolt JA; Longeri L; Manrique A; Penacabriales JJ; Pereira PAA; Sanabria CA; Tsai SM. 1993. Genotypic variation in biological nitrogen fixation by common bean. *Plant and Soil* 152:59–70.
- Hernández-Delgado S; Reyes-Valdés MH; Rosales-Serna R; Mayek-Pérez N. 2009. Molecular markers associated with resistance to *Macrophomina phaseolina* (Tassi) Goid. in common bean. *Journal of Plant Pathology* 91(1):163–170.
- Hyman G; Fujisaka S; Jones P; Wood S; de Vicente MC; Dixon J. 2008. Strategic approaches to targeting technology generation: assessing the coincidence of poverty and drought-prone crop production. *Agricultural Systems* 98:50–61.
- Keating BA; Carberry PS; Bindraban PS; Asseng S; Meinke H; Dixon J. 2010. Eco-efficient agriculture: concepts, challenges and opportunities. *Crop Science* 50:S-109–S-119.
- Kipe-Nolt JA; Vargas H; Giller KE. 1993. Nitrogen fixation in breeding lines of *Phaseolus vulgaris* L. *Plant and Soil* 152:103–106.
- Klaedtke SM; Cajiao C; Grajales M; Polanía J; Borrero G; Guerrero A; Rivera M; Rao I; Beebe SE; León J. 2012. Photosynthate remobilization capacity from drought-adapted common bean (*Phaseolus vulgaris*) lines can improve yield potential of interspecific populations within the secondary gene pool. *Journal of Plant Breeding and Crop Science* 4(4):49–61.
- Liao H; Yan X; Rubio G; Beebe SE; Blair MW; Lynch JP. 2004. Basal root gravitropism and phosphorus acquisition efficiency in common bean. *Functional Plant Biology* 31:959–970.
- Long SP; Ainsworth EA; Leakey ADB; Nösberger J; Ort DR. 2006. Food for thought: lower-than-expected crop yield simulation with rising CO₂ concentrations. *Science* 312(5782):1918–1921.
- Mayek-Pérez N; López-Castañeda C; López-Salinas E; Cumpián-Gutiérrez J; Acosta-Gallegos JA. 2001. Resistencia a *Macrophomina phaseolina* en frijol común bajo condiciones de campo en México. *Agrociencia* 35:649–661.
- Mejía Jiménez A; Muñoz C; Jacobsen HJ; Roca WM; Singh SP. 1994. Interspecific hybridization between common and tepary beans: increased hybrid embryo growth, fertility, and efficiency of hybridization through recurrent and congruity backcrossing. *Theoretical and Applied Genetics* 88:324–331.
- Miklas PN; Stone V; Urrea CA; Johnson E; Beaver JS. 1998. Inheritance and QTL analysis of field resistance to ashy stem blight. *Crop Science* 38:916–921.
- Miklas PN; Stone V; Daly MJ; Stavely JR; Steadman JR; Bassett MJ; Delorme R; Beaver JS. 2000. Bacterial, fungal, and viral disease resistance loci mapped in a recombinant inbred common bean population ('Dorado'/XAN 176). *Journal of the American Society for Horticultural Science* 125:476–481.
- Miklas PN; Kelly JD; Beebe SE; Blair MW. 2006. Common bean breeding for resistance against biotic and abiotic stresses: from classical to MAS breeding. *Euphytica* 147:105–131.
- Mohamed MF; Keutgen N; Tawfik AA; Noga G. 2002. Dehydration-avoidance responses of tepary bean lines differing in drought resistance. *Journal of Plant Physiology* 159:31–38.
- Muñoz LC; Blair MW; Duque MC; Tohme J; Roca W. 2004. Introgression in common bean × tepary bean interspecific congruity-backcross lines as measured by AFLP markers. *Crop Science* 44:637–645.
- Navarette-Maya R; Trejo-Albarrán E; Navarette-Maya J; Prudencio-Sains JM; Acosta-Gallegos JA. 2002. Reaction of bean genotypes to *Fusarium* spp. and *Rhizoctonia solani* in central Mexico. Annual Report of the Bean Improvement Cooperative 45:154–155.

- Pineda P; Kipe-Nolt JA; Rojas E. 1994. *Rhizobium* inoculation increases of bean and maize yields in intercrops on farms in the Peruvian sierra. *Experimental Agriculture* 30:311–318.
- Porch TG; Jahn M. 2001. Effects of high-temperature stress on microsporogenesis in heat-sensitive and heat-tolerant genotypes of *Phaseolus vulgaris*. *Plant, Cell and Environment* 24:723–731.
- Porch TG; Bernsten R; Rosas JC; Jahn M. 2007. Climate change and the potential economic benefits of heat-tolerant bean varieties for farmers in Atlántida, Honduras. *Journal of Agriculture of the University of Puerto Rico* 91:133–148.
- Rainey K; Griffiths P. 2003. Evaluation of common bean yield components under heat stress (abstract). *HortScience* 38(5):682.
- Ramaekers L; Remans R; Rao IM; Blair MW; Vanderleyden J. 2010. Strategies for improving phosphorus acquisition efficiency of crop plants. *Field Crops Research* 117:169–175.
- Rao IM. 2001. Role of physiology in improving crop adaptation to abiotic stresses in the tropics: the case of common bean and tropical forages. In: Pessaraki M, ed. *Handbook of plant and crop physiology*. Marcel Dekker, NY, USA. p 583–613.
- Rao IM; Friesen DK; Osaki M. 1999. Plant adaptation to phosphorus-limited tropical soils. In: Pessaraki M, ed. *Handbook of plant and crop physiology*. Marcel Dekker, NY, USA. p 61–96.
- Salem MA; Kakani VG; Koti S; Reddy KR. 2007. Pollen-based screening of soybean genotypes for high temperatures. *Crop Science* 47:219–231.
- Sanginga N; Woolmer PL, eds. 2009. *Integrated soil fertility management in Africa: principles, practices and developmental process*. Tropical Soil Biology and Fertility Institute of the International Center for Tropical Agriculture, Nairobi, Kenya. 263 p.
- Schwartz HF; Pastor-Corrales MA, eds. 1989. *Bean production problems in the tropics*, 2nd edn. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. 726 p.
- Serraj R; Sinclair TR. 1998. N₂ fixation response to drought in common bean (*Phaseolus vulgaris* L.). *Annals of Botany* 82:229–234.
- Singh SP. 1995. Selection for water-stress tolerance in interracial populations of common bean. *Crop Science* 35:118–124.
- Singh SP, ed. 1999. *Common bean improvement in the twenty-first century*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Singh SP; Gepts P; Debouck DG. 1991. Races of common bean (*Phaseolus vulgaris*, Fabaceae). *Economic Botany* 45:379–396.
- Singh SP; Terán H; Muñoz CG; Osorno JM; Takegami JC; Thung MDT. 2003. Low soil fertility tolerance in landraces and improved common bean genotypes. *Crop Science* 43:110–119.
- Sponchiado BN; White JW; Castillo JA; Jones PG. 1989. Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. *Experimental Agriculture* 25:249–257.
- St. Clair SB; Lynch JP. 2010. The opening of Pandora's Box: climate change impacts on soil fertility and crop nutrition in developing countries. *Plant and Soil* 335:101–115.
- Thung M; Rao IM. 1999. Integrated management of abiotic stresses. In: Singh SP, ed. *Common bean improvement in the twenty-first century*. Kluwer Academic Publishers, Dordrecht, The Netherlands. p 331–370.
- Toro O; Tohme J; Debouck DG. 1990. Wild bean (*Phaseolus vulgaris* L.): description and distribution. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. 106 p.
- Vadez V; Lasso JH; Beck DP; Drevon JJ. 1999. Variability of N₂-fixation in common bean (*Phaseolus vulgaris* L.) under P deficiency is related to P use efficiency. *Euphytica* 106:231–242.
- Wallace DH; Wilkinson RE. 1965. Breeding for Fusarium root rot resistance in beans. *Phytopathology* 55:1227–1231.
- Wortmann CS; Kirkby RA; Eledu CA; Allen DJ. 1998. *Atlas of common bean (Phaseolus vulgaris L.) production in Africa*. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. 133 p.
- Yan X; Liao H; Beebe S; Blair M; Lynch J. 2004. QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant and Soil* 265:17–29.
- Yadav SS; Redden RJ; Hatfield L; Lotze-Campen H; Hall A. 2011. *Crop adaptation to climate change*. Wiley-Blackwell, Oxford, UK.