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REVIEW

A review of breeding objectives, genomic resources, and marker-assisted methods in common bean (*Phaseolus vulgaris* L.)

Teshale Assefa · A. Assibi Mahama · Anne V. Brown · Ethalinda K. S. Cannon · Jean Claude Rubyogo · Idupulapati M. Rao · Matthew W. Blair · Steven B. Cannon

Abstract Common bean (*Phaseolus vulgaris* L.), one of the most important grain legume crops for direct human consumption, faces many challenges as a crop. Domesticated from wild relatives that inhabit a relatively narrow ecological niche, common bean faces a wide range of biotic and abiotic constraints within its diverse agroecological settings. Biotic stresses impacting common bean include numerous bacterial, fungal, and viral diseases and various insect and nematode pests, and abiotic stresses include drought, heat, cold, and soil nutrient deficiencies or toxicities. Breeding is often local, focusing on improvements in responses to biotic and abiotic stresses that are particular challenges in certain locations and needing to respond to conditions such as day-length regimes. This review describes the major breeding objectives for common bean, followed by a description of major genetic and genomic resources, and an overview of current and prospective marker-assisted methods in common bean breeding. Improvements over traditional breeding methods in CB can result from the use of different approaches. Several important germplasm collections have been densely genotyped, and relatively inexpensive SNP genotyping platforms enable implementation of genomic selection and related marker-assisted breeding approaches. Also important are sociological insights related to demand-led breeding, which considers local value chains, from farmers to traders to retailers and consumers.

Keywords Marker-assisted breeding · Demand-led breeding · Biotic stress · Abiotic stress

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Introduction

Common bean (*Phaseolus vulgaris* L.) is the arguably the most important edible grain legume worldwide, with global production estimated to be 26.8 million metric tons in 2016 (http://faostat.fao.org/). Common bean (CB) accounts for a high proportion of daily protein intake in many countries, particularly in Latin America, Africa, and parts of Asia. Beans are also an economically significant food legume and vegetable crop in Canada, USA, and Europe. Bean consumption is particularly high in African countries—for example, per capita consumption of bean ranges from 50 to 60 kg per year in Rwanda, Kenya, and Uganda (Broughton et al. 2003; Buruchara et al. 2011). CB is very nutrient rich, with both protein and complex carbohydrates, vitamins (e.g., A, C, folate), dietary fiber, and biologically important minerals such as Ca, Mg, K, Cu, Fe, Mg, and Zn (Broughton et al. 2003; Blair 2013). CB also helps improve soil and environmental health through symbiotic nitrogen fixation (SNF).

The challenges faced by CB as a crop are strongly shaped both by its evolutionary history in particular environments of Central and South America and by the set of new agroecosystems where it is now grown. Several lines of evidence indicate that CB was domesticated at least twice—from northern Andean and from Mesoamerican populations (Bitocchi et al. 2013; Schmutz et al. 2014; Ariani et al. 2016; Cortés and Blair 2017). Ecological niches for both wild populations are relatively specialized and narrow—with the Mesoamerican population, for example, being adapted to a bimodal rainfall regime and a mid-season dry period, typically on relatively fertile volcanic soils, in disturbed areas or transitional forest clearings, in a near-equatorial geographical range, while the Andean wild population, growing on the Andean slopes, is more cold-adapted (Bitocchi et al. 2013; Ariani et al. 2016). Domestication bottlenecks have likely further reduced the capacity for responses to some stresses such as drought conditions and particular pathogens (Bitocchi et al. 2013; Schmutz et al. 2014). These evolutionary and domestication histories arguably leave CB with vulnerabilities to a wide range of biotic and abiotic stresses, particularly as the crop has moved into new agroecological niches worldwide. These constraints, in turn, help set the breeding objectives for CB.

Both traditional and molecular breeding methods are in use in CB (Miklas et al. 2006). New genomic tools promise more rapid progress and the ability to solve some previously intractable breeding challenges. Marker-assisted breeding (MAB) should, in principle, increase the efficiency of selection for both major and minor qualitative and quantitative trait loci (QTL) (Xu and Crouch 2008). There are not only technical challenges; however; in developing countries, breeding programs face additional challenges of correctly identifying the highest value breeding targets and of getting uptake of new varieties where they are needed (Rubyogo et al. 2007). Some approaches, under the name of "demand-led breeding" and "wider impact," have shown successes (Persley and Anthony 2017; Rubyogo et al. 2010).

The review concludes with the following set of recommendations: integration of robust, high-value markers into breeding programs; better characterization of strengths and weaknesses of genomic selection and related methods; better characterization of germplasm resources; solutions for physiological weak points in CB; and combining Marker-Assisted Breeding Methods with Demand-Led Breeding.

Breeding objectives for common bean

Overview of target traits and market classes for breeding

Breeding in CB is guided primarily by improvement with respect to biotic and abiotic stresses, combined with a need to maintain particular quality traits and market class characteristics, which are essential for meeting consumer preference in various markets. For example, most farmers in Africa and Latin America are continuing to plant specific Andean type varieties with lower yield to meet particular quality traits required by consumers, even though the Mesoamerican types commonly yield higher than the Andean types (Beebe 2012). Objectives relative to biotic and abiotic stresses tend to vary by location—varying, for example, by temperature and humidity or by soil fertility and water availability.

Over 80% of bean production in developing countries is from subsistence farming of semi-arid regions and sub-humid to humid growing environments. In these areas, most producers are small-scale farmers who use unimproved bean cultivars. CB tends to face a high incidence of biotic and abiotic stresses, including diseases, insects, drought, and low soil fertility (Singh 1992). Hence, breeding for resistance/tolerance to these stresses has been a major research objective (Singh

1992; Beebe 2012). Table 1 provides an overview of some of the breeding objectives, derived from breeding priorities of the International Center for Tropical Agriculture (CIAT) and Pan-African Bean Research Alliance (PABRA, http://www.pabra-africa.org; described in the "Linkage and association mapping resources" section below), and includes some other traits such as higher content of minerals (iron and zinc), fast cooking time, canning quality, harvest index, and market class/seed color (Beebe et al. 2013; Assefa et al. 2015, 2017).

In the USA, Canada, and European countries, most bean production is by commercial farmers, with much of that production being for export (e.g., small white Navy beans for UK processing and small black beans for Cuba and Mexico) or for specialized markets (e.g. "alubias" white beans for export largely to Argentina and Spain). In these areas, improvement efforts have particularly focused on resistance to major diseases, including white mold, bacterial blight, rust, halo blight, anthracnose, and bean common mosaic virus, and to insect pests such as bean leaf beetle, stinkbugs, and aphids (Table 1).

Major bean classifications are based on market classes and agronomic features (Voysest and Dessert 1991; Santalla et al. 2002). Great variation is found among dry bean market classes—with differences in pod shape, size, and color as well as seed shape (kidney, elongate, and round), seed size (varies from small-medium to large size), seed color (classified into nine groups being white, cream, yellow, brown, pink, red, purple, black, and other = gray/green/etc.), seed pattern or striation (striped, mottled, and bi-color), growth habit, and phenological traits (Singh 2001). Seed size in CB cultivars varies from small (< 25 g/100 seeds) to large (> 40 g/100 seeds). Seed shape varies from round to oblong to kidney-shaped, with different combinations of color patterns (Voysest and Dessert 1991). Seed also varies in terms of surface texture from shiny (brilliant) to opaque to intermediate.

CB genotypes can also be grouped into determinate bush types to indeterminate climbing growth habit. This growth habit classification divides beans into four groups: Type I (determinate bush), Type II (indeterminate bush), Type III (indeterminate semi climber), and

Table 1 Summary of breeding objectives in common bean

Disease	• Anthracnose	• *Ascochyta* blight
	• Angular leaf spot	• Curly top virus
	• Bacterial brown spot	• Bean yellow mosaic virus
	• Bean golden mosaic virus	• Bean golden yellow mosaic virus
	• Bean common mosaic virus Common bacterial blight	• Bean calico mosaic virus
	• Halo blight	• *Fusarium solani, oxysporium*
	• Rusts	• *Pythium*
	• Root rot complex	
	• White mold	
	• Web blight	
Pests	• Bean pod weevil	• Aphids
	• Leaf hoppers	• Pod borers
	• Bean fly	• Mexican bean beetles
	• Bruchids	• Mites
	• Thrips	• Nematodes
	• White fly	
Abiotic stress	• Drought	• Cold
	• Low phosphorus	• Manganese toxicity
	• Aluminum toxicity	• Salinity
	• Heat	
Agronomic	• Growth habit	• Pod wall biomass partitioning
	• Plant architecture	• Canopy temperature control
	• Mechanical harvesting	
Quality	• Canning	• Grain composition
	• Cooking time	• Flatulence reduction
	• Iron and zinc	• Adaptation of various market classes
Environment	• Genotype × environment	• Agronomic practices
	• Prediction (site)	

Priorities vary by location and breeding program

Type IV (indeterminate climber) (Singh 1991). Besides growth habit classification, beans are sometimes also classified by origin—specifically, by the major Andean and Mesoamerican gene pools and races within those pools (Singh et al. 1991b; Beebe et al. 2013).

For example, in many developing countries, reduction of cooking time and improvement of mineral composition are of relatively higher importance than in developing countries, and biotic stress challenges such as web blight and nematode are of greater concern in particular locations, while various root rot diseases are a problem worldwide. See references in "Breeding objectives for common bean" section for discussion of relative priorities.

Grain yield and yield-related traits

Grain yield is a product of both plant growth rate and capacity to partition photosynthates to seeds. Significant yield differences are likely due, in part, to differing growth habits and seed sizes for beans from different market classes and gene pools (Beebe 2012). However, yield differences among cultivars within the same gene pool are often small, especially for those in the same maturity group.

Large-seeded cultivars with growth habits I, II, and III belonging to the Nueva Granada and Chile races, respectively, are physiologically less efficient and exhibit narrow adaptation compared with the small-seeded market class genotypes (Beaver et al. 1996; Beebe 2012). Direct selection for seed yield was used to improve CB productivity for Andean bush beans and is thus considered an important selection criterion. However, the progress in increasing CB yield has been modest compared to self-pollinated cereals (Singh 1991). This is due to lower dry matter partitioning efficiency toward grain yield of CB compared to cereals, low response to inputs (nitrogen fertilizer), moderate to low narrow-sense heritability of yield, high intensity of diseases, and large genotype by environment interactions (Singh 1991; Beebe 2012).

Seed yield and yield components are quantitatively inherited and are highly influenced by environments (Singh 1991), so understanding the relation between yield and its components is important to set effective selection criteria and breeding strategies. In several CB studies, high correlations have been found between yield and 100 seed weight, yield and pods/plant, and yield and seeds/plant (Beebe et al. 2013; Assefa et al.

2015; Rao et al. 2017). Hence, yield component traits have been used as selection criteria to improve grain yield and cultivar development.

The majority of efforts toward increasing seed yield under favorable environments has come from improvement in pods/plant, seed/plant, and seed weight (Beebe et al. 2013). However, under unfavorable conditions (e.g., drought), other traits including biomass partitioning indices (pod partitioning index, harvest index, and pod harvest index) have been used as key traits to improve yield (Beebe et al. 2013; Assefa et al. 2013, 2017; Rao et al. 2017).

Improvements in grain yield and related traits in CB have been associated with the improvement of the number of seeds per plant and grain yield per day (Bezaweletaw et al. 2006; Ribeiro et al. 2008). Several studies showed that hybridization of interracial bean varieties had higher yield, particularly in crosses between Mesoamerican with Durango or Jalisco races (Beebe 2012). Increasing yield potential has also been achieved through breeding for abiotic stress tolerance. Beebe et al. (2008) reported that yield could increase under drought conditions through photosynthate remobilization and biomass translocation, implying that yield improvements can be made under drought conditions. Further, CIAT and PABRA have designed new breeding strategies to breed for grain yield and resistance to single biotic and abiotic stresses, based both on grain type and market class. This has led CIAT and PABRA to release numerous new bean varieties in Africa and Latin America (Buruchara et al. 2011).

Biotic stresses

With over 200 different bean diseases reported, the pathogens causing significant yield losses to beans include bacteria, virus, fungi, and plant parasitic nematodes (Table 2). Many of these diseases and insect pests have co-evolved with CB (Beebe 2012; Beebe et al. 2013). Some of the most significant bean diseases in the tropics include bean angular leaf spot (ALS, *Phaeoisariopsis griseola*), anthracnose (ANT, *Colletotrichum lindemuthianum*), common bacterial blight (CBB), and viral diseases *bean golden mosaic virus* (BGMV) and *bean common mosaic virus* (BCMV) (Beebe and Corrales 1991; Duc et al. 2015; Miklas et al. 2017). In temperate regions, the most common diseases are CBB, halo blight, rust, and white mold (Duc et al. 2015).

Table 2 Summary of bean disease and insect pest distribution, transmission, and resistance genes

Disease	Distribution	Seed propagated	Transmission	Resistance	Reference
Fungi					
Anthracnose (Colletotrichum)	Worldwide (cool = 14–18 °C, humid, and > 1000 m in tropics	Yes	Wind and rain; animal & insect	QTL: Pv01, Pv02, Pv04, Pv10, Co-1, Co-2	Zuiderveen et al. (2016)
Angular leaf spot (Phaeoisariopsis)	Worldwide (moderate temp.: 18–25 °C, high moisture)	Yes	Wind	QTL: Pv04, Pv10 (ALS10.1) Phg1, Phg2	Oblessuc et al. (2012), Oblessuc et al. (2015), Keller et al. (2015)
Rust (Uromyces)	Worldwide	No	Wind, crop residue	KASP SS68 marker associated with Pv11	Hurtado-Gonzales et al. (2017), Hanson et al. (1993)
Leafspot (Ascochyta)	Tropics (high altitude: > 1500 m)	Yes	Splash, contact, crop residue	Quantitative (P. polyanthus)	Hanson et al. (1993)
Pythium root rot	Worldwide	Yes	Crop residue, infected soil	QTL:ER3^{XC} (LG3), SV6^{XC}(LG6), Py-1 (LG7)	Campa et al. (2010)
Fusarium	Worldwide	No	Crop residue, infected soil	QTL (FRR3.1^{km} (Pv03), LGs B2 and B3	Román-Avilés and Kelly (2005), Kamfwa et al. (2013)
Web blight	Worldwide (hot-humid)	Yes	Infected soil, Seed	Quantitative	Montoya et al. (1997), Takegami et al. (2004)
Bacteria					
Common blight (Xanthomonas)	Worldwide (cool to moderate temp.)	Yes	Rain, moisture	QTL: BC420 (Pv06), SU91 (Pv08), Xa11.4OV1 (Pv11)	Viteri et al. (2014), Miklas et al. (2017)
Halo blight (Pseudomonas)	Worldwide (cool to moderate temp.)	Yes	Rain, moisture	Quantitative: Pse-1, Pse-2, Pse-3, Pse-4, Pse-6, HB5.1 98BB, 98LFA, 96BBS	Miklas et al. (2011), Jung et al. (2003), Tock et al. (2017)
Bacterial brown spot (Pseudomonas)	Worldwide (warm-humid weather)	Yes	Seed, wind	LG02	Jung et al. (2003), Muedi et al. (2015)
Viruses					
Bean common mosaic virus and Mosaic necrosis virus	Worldwide	Yes	Aphid	Qualitative: bc-1, bc-2, bc-3	Johnson et al. (1997), Strausbaugh et al. (1999)
Bean golden yellow mosaic virus	Central America, Caribbean	No	Whitefly	Qualitative, quantitative, Bgm-1, RNAi	Blair et al. (2007)
Insects					
Leaf hopper (E. kraemeri and E. Fabae)	Central, South, and North America	NA	NA	QTL: Pv01, Pv02, Pv03, Pv06, Pv07, Pv08, Pv09	Murray et al. (2004), Brisco (2012)
Bean pod weevil (A. goodmani)	Central America	NA	NA	Quantitative: Chr2 (b01) Chr3 (b08), Chr4 (b07), Chr6 (b11)	Blair et al. (2006b)
Bean fly or bean stem maggot (Ophiomyia phaseoli Tryon)	Africa and Asia	NA	NA	Qualitative and quantitate	Miklas et al. (2006)
Seed weevils Acanthoscelides obtectus and Z. subfasciatus	Africa and Latin America	NA	NA	APA gene (b04) for Z. subfasciatus	Blair et al. (2010a, 2010b)

NA not available

Significant progress has been made in developing cultivars with resistance to various diseases using conventional breeding. Some important resistance-mapping studies are summarized in Table 2. Markers associated with established resistance loci can be used for more efficient breeding to develop resistant cultivars. Some early examples of marker-assisted selection for bean diseases include 23 RAPD markers and 5 SCAR markers associated to 15 different resistance genes, described by Kelly and Miklas (1998). Molecular markers and linkage mapping of rust resistance genes have been reviewed by Miklas et al. (2002). Kelly and Vallejo (2004) provided a summary of markers, MAS, map location, and breeding value for anthracnose resistance. Similarly, Miklas et al. (2006) reviewed MAS in breeding for resistance to anthracnose, angular leaf spot, common bacterial blight, halo bacterial blight, bean golden yellow mosaic virus, root rots, rust, and white mold (Table 2).

Abiotic stresses

Drought stress Abiotic (climatic and edaphic) stress factors are major constraints for bean productivity in most tropical and subtropical countries (Rao 2014). In Central America and in eastern and southern Africa, as much as 60% of the bean growing areas in these regions suffer from periodic drought stress (Assefa et al. 2013; Ambachew et al. 2015; Darkwa et al. 2016). Key traits linked to drought resistance include phenology, root size and depth, root hydraulic conductivity, carbohydrate reserve storage and mobilization, and water absorption efficiency (Beebe et al. 2013). Breeders and physiologists are particularly focused on improving the traits related to photosynthate mobilization from vegetative parts of the plant to the pod walls and seeds under drought conditions (Rao et al. 2017). These photosynthate-mobilizing traits include pod harvest index (PHI), pod partitioning index (PPI), and harvest index (HI) (Beebe et al. 2013) which may be used to select drought-adapted beans (Beebe et al. 2008; Assefa et al. 2013; Rao et al. 2013, 2017; Polania et al. 2016a, 2017). Sources of drought resistance have been found in the Durango race and in tepary bean (Beebe 2012; Rao et al. 2013; Asfaw and Blair 2014; Mukeshimana et al. 2014). Several drought-resistant lines have also been identified in Africa (Asfaw et al. 2012; Mukeshimana et al. 2014).

Breeding for improved adaptation to drought is complex because several traits are involved in resistance mechanisms, and the traits are quantitatively inherited and highly affected by environments (Mir et al. 2012). Use of MAS for improving drought resistance was explored by Schneider et al. (1997), who identified QTLs for drought using Random Amplified Polymorphic DNA (RAPD) markers. In this study, yield was improved by 11% under drought and 8% under normal conditions by using five RAPD markers (Schneider et al. 1997).

Genotype by environment interactions affecting drought QTL are reported by Chavarro and Blair (2010), Asfaw et al. (2012), Asfaw and Blair (2012), Blair et al. (2012), and Mukeshimana et al. (2014). Asfaw et al. (2012) identified 9 and 69 QTLs associated with drought using mini-environment mixed model approach and composite mapping approaches, respectively. Asfaw et al. also reported that the phenotypic variation explained by QTLs is up to 37% for SPAD leaf chlorophyll and pod partitioning index traits. This result shows the importance of QTL detection for photosynthate acquisition and remobilization traits. Trapp et al. (2015) also detected two major QTLs on Pv01 and Pv02 for seed yield in several abiotic stresses and drought tolerance conditions. QTL in populations with Durango derived drought tolerance have also been analyzed (Mukeshimana et al. 2014; Briñez et al. 2017). The QTLs identified in all those studies could be important tools for MAS in bean breeding programs to select indirectly for drought tolerance traits that are difficult to screen in large populations.

Heat stress High temperature (HT) stress is a major bean production constraint (Rainey and Griffiths 2005; De Ron et al. 2016). HT (greater than 30 °C day and/or greater than 20 °C at night) causes significant reduction in yield and quality and limits environmental adaptation. The major effect of high temperature is shown as inhibition of pollen fertility that results in blossom drop. This causes reduced seed number and quality of the seed. Researchers have identified heat-tolerant CB genotypes from diverse gene pools (Porch and Jahn 2001; Porch 2006; Porch et al. 2013). Some of these maintain pollen viability up to 5 °C higher during night temperatures compared to temperatures that are normally considered to be limiting (> 18 °C at night). Development of HT varieties under adverse environments would also increase resilience for the future global climate change threats (Porch et al. 2013; Gaur et al. 2015).

Low temperature stress CB is sensitive to low temperatures, which can limit production in the early part of the season. Differences among genotypes for tolerance to suboptimal temperatures were reported by Dickson and Boettger (1984). The unifoliate and the first trifoliolate leaf stages were the most sensitive to freezing temperatures in CB (Meyer and Badaruddin 2001). Their estimated temperature to cause 50% mortality was − 3.25 °C, although regrowth after survival was limited, meaning few plants made it to maturity. Interspecific introgression of portions of the tepary bean genome into CB is a promising method for increasing tolerance to extreme temperatures in CB (Souter et al. 2017). Rodino et al. (2007) reported seven cultivars of *P. coccineus* that showed ability to germinate, emerge, and grow under cold temperature—thus showing potential for as source of cold-tolerant genes in interspecific hybridization with CB.

Low P stress Low soil phosphorus (P) availability causes significant bean yield loss in the tropics (Ramaekers et al. 2010; Beebe 2012). About 50% of bean growing regions worldwide are affected by low soil P (Nielsen et al. 2001; Beebe 2012). More than three million hectares of bean-growing areas of Africa could suffer from P constraints (Wortmann et al. 1998). Progress has been made in developing tolerant cultivars with better P acquisition efficiency, involving higher total root length, root surface, and shallow root angle under low P (Ochoa et al. 2006; Beebe 2012; Rao et al. 2016). One of the key mechanisms identified to increase access to P is greater topsoil foraging resulting from root architectural, morphological, and anatomical traits (Lynch 2011). Shallower root growth angle of axial or seminal roots increases the topsoil foraging and thereby contributes to greater acquisition efficiency of P from low P soils.

Rao (2001) and Beebe et al. (2009) reported that greater photosynthate remobilization to the grain gives better yield under conditions of low P availability. The CIAT Bean Program has reported that bean genotype G21212 and other breeding lines identified for drought tolerance also gave better yield than poor performing lines under low soil P conditions (Beebe et al. 2008). Root QTLs associated with P acquisition in low soil P environments were reported in Beebe et al. (2006), which are linked with root parameters such as total and specific root length. QTLs associated with P use efficiency were also reported by Cichy et al. (2009a).

QTL studies of P deficiency tolerance have also been conducted with other inter-genepool crosses (Ochoa et al. 2006) and within Andean genotype populations (Cichy et al. 2009a, 2009b). Mechanisms of tolerance to low soil fertility have been studied both in terms of root architecture and higher root hair density (Liao et al. 2004).

Low N stress Low soil N affects bean production in many regions (Wortmann et al. 1998). Beans grown in marginal, generally low-nutrient and moisture-limited soils, also tend to show diminished nodulation activity (Albrecht et al. 1984). Significant genetic variability is known to exist in both the host-plant and rhizobium strains in terms of SNF, which should enable breeders to find cultivars with improved SNF ability (Bliss 1993; Snoeck et al. 2010; De Ron et al. 2015; Drevon et al. 2015; Polania et al. 2016b). Total seed N concentration could be used as selection criterion to screen advanced breeding lines for genetic variability in SNF (Miranda and Bliss 1991). Harvest index and biological yield are also considered indirect measures for genetic improvement of SNF ability in bean (Araújo et al. 2015). Farid et al. (2017) reported that selection of bean lines for their high SNF capacity could be done in both CBB-susceptible and CBB-resistant genotypes. Their work suggests that selection for SNF capacity in CBB-resistant lines of CB may have negative influence on the degree of rhizobial infection.

Aluminum toxicity and acid soil stress Other abiotic stress factors such as aluminum (Al) and manganese toxicities associated with soil acidity are also problems to bean production, particularly in acid soil regions of Latin America and Africa (Rao 2014; Rao et al. 2016). Mechanisms of Al resistance were defined using the Al-resistant genotype 'ICA Quimbaya' and the Al-sensitive 'VAX-1' (Yang et al. 2013). The induced and sustained Al resistance of 'Quimbaya' was shown to be mediated by reducing the stably bound Al in the apoplast, thus allowing cell elongation and division to resume. Resistance to Al is attributed to the release of citrate by the root apex which is mediated by the multidrug and toxin extrusion (MATE) citrate transporter gene. Resistance to Al in CB was mainly dependent on the capacity to sustain citrate synthesis, thereby maintaining the cytosolic citrate pool that enables exudation. The initial Al-induced inhibition of root elongation in both Al-resistant and Al-sensitive genotypes was correlated with the

expression of the 1-aminocyclopropane-1-carboxylic acid oxidase gene (Yang et al. 2013). QTLs for Al stress tolerance were first identified by López-Marín and Rao (2009). Andean genotypes have been screened for Al tolerance, with significant genetic variability identified for this trait (Blair et al. 2009).

Genetic and genomic resources for CB breeding

Germplasm collections and CB diversity

Significant national collections of CB are maintained at the USDA, in Pullman, Washington, USA (about 15,000 accessions), the Institute für Pflanzengenetik und Kulturpflanzenforschung, Germany (about 9000 accessions), in Brasilia, Brazil (CENARGEN/ EMBRAPA, with about 6000 accession), in Beijing, China (CAAS, Institute of Genetic Resources with more than 5000 accessions), and the National Center for Plant Genetic Resources in Alcala de Henares, Spain (with more than 5000 bean accessions). The largest collection of CB genetic resources is maintained under the auspices of the Food and Agriculture Organization (FAO) treaty, under International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), at CIAT in Cali, Colombia (around 36,000 accessions), with a backup at the Svalbard Global Seed Vault in Norway, where more than 50,000 accessions are now held. In addition to CB (*P. vulgaris*) and various wild *Phaseolus* species, these collections include four other domesticated *Phaseolus* species: year-long bean (*Phaseolus dumosus*), runner bean (*Phaseolus coccineus*), tepary bean (*Phaseolus acutifolius*), and lima bean (*Phaseolus lunatus*). Most of these collections were made from the centers of origin, mainly Andean and Mesoamerican regions. Smaller collections of CB accessions exist through non-governmental agencies such as Seed Savers Exchange in Decorah, Iowa or at breeding stations of national, sub-national, or multi-country regional programs (e.g., ECABREN and SABRN bean networks in East and Southern Africa, respectively). Germplasm accessibility is generally not a bottleneck for bean breeding and genetic studies.

Genetic diversity has been extensively studied in bean using different types of markers, including seed protein (e.g., phaseolin) (Gepts et al. 1986; De La Fuente et al. 2012) and isozyme analysis (Koenig and Gepts 1989). Other molecular markers used for genetic

diversity in CB are DNA restriction fragment length polymorphism (RFLP) (Khairallah et al. 1990, 1992), nuclear RFLP (Becerra Velasquez and Gepts 1994), allozymes (Singh et al. 1991a; Santalla et al. 2002), and random amplified polymorphic DNA (RAPD) (Freyre et al. 1998; Beebe et al. 2000). Similar reports have also demonstrated genetic diversity through use of amplified fragment length polymorphism (AFLP) markers (Beebe et al. 2001; Papa and Gepts 2003; Zizumbo-Villarreal et al. 2005), SSR markers (Gaitán-Solís et al. 2002; Blair et al. 2006a), DNA sequencing (Gepts et al. 2008), and single nucleotide polymorphism (SNP) markers (Galeano et al. 2009a, 2009b, 2012; Blair et al. 2013). These tools help answer different questions related to evolution, domestication, and diversity of CB, which is not possible to answer with the use of phenotypic methods alone (Arif et al. 2010). For example, genes related to domestication from the Andean and Mesoamerican domestication events and evolutionary traits such as shattering have been identified (Bellucci et al. 2013; Gaut 2014) as have polymorphism in drought-related genes (Cortés et al. 2012a, 2012b). Due to their cost-effectiveness, efficiency, and simplicity, SNP, SSR, and AFLP markers have been the most commonly used markers studies on CB genetic diversity.

The world's germplasm collections can be characterized in various ways: by genotype (i.e., marker- or sequence-based characterization), by phenotype (e.g., growth habit, seed characteristics, disease responses, photoperiod response, etc.), by pedigree or genepool or race, or by geographic origin. Ideally, these characteristics would be maintained, in combination, for all germplasm accessions, but in practice, the characterizations are incomplete and not fully correlated. Substantial phenotype data is maintained for the U.S. germplasm collection in the GRIN system. Pedigree data is generally lacking, except for selected populations, usually at institutes with long-running breeding programs (e.g., CIAT). For geographic origin, an interesting resource is the geographic information system map of germplasm origin maintained at LegumeInfo (https://legumeinfo. org). This interactive viewer displays geo-coordinates for the bean collection in GRIN, along with the phenotypic data in GRIN. The data in the viewer can then be queried by geographical location or by phenotype (e.g., photoperiod or seed size)—and then phenotypic categories or values can be displayed geographically, to look for correlations such as seed size by location—showing

the Andean material generally having larger seeds than Mesoamerican landraces.

For genotypic data, several projects have generated large SNP datasets. The U.S. Bean Coordinated Agricultural Project (BeanCAP) has generated SNP calls for two diversity panels: the Mesoamerican Diversity Panel (MDP) and the Andean Diversity Panel (ADP) (Moghaddam et al. 2014). These are described and available at LegumeInfo: http://legumeinfo.org/data/public/Phaseolus_vulgaris/G19833.gnm1.div1/.

To access and utilize the highly valuable material in germplasm repositories, arguably the most common approach has been to order a subset of material of interest, on the basis of what phenotype data is available, followed by field trials to screen for particular traits (e.g., resistance to a disease of interest). Availability of genotype data (e.g., for the MDP and ADP panels) makes it possible to select for genotypic diversity as well or even for presence of particular alleles for known genes.

Genomic resources and tools for CB research and breeding

CB has a medium-sized, diploid genome of 588–637 Mbp (Arumuganathan and Earle 1991; Bennett and Leitch 2005; McClean et al. 2008). Genomic resources have advanced dramatically in recent years, with reference genome sequences, dense genetic maps, marker and genotyping sets, and many QTL and genome-wide association studies (GWAS).

Reference genome assemblies provide an important resource for organizing many other genetic and genomic features and resources. At the time of writing, there are three genome assemblies of reference quality: two versions of the Andean G19833 accession (Schmutz et al. 2014) and the Mesoamerican BAT93 assembly (Vlasova et al. 2016) [https://doi.org/10.1186/s13059-016-0883-6]. The G19833 assemblies (v1 and v2) are available for downloading, sequence searching, and browsing at both Phytozome (https://phytozome.jgi.doe.gov) and LegumeInfo (https://legumeinfo.org).

These on-line tools are typically used for basic research toward marker development and selection and for investigation of the genetic basis of traits of interest, rather than directly for day-to-day breeding work.

Together with QTL, marker, and sequence data, comparative genomic analyses are possible through the Legume Information System (LIS or LegumeInfo). The resources at LegumeInfo legume-focused gene families and gene family trees (phylogenies) also include an InterMine instance (https://mines.legumeinfo.org/beanmine) for querying regions and lists of features (e.g., genes within a QTL region, filtered for gene expression).

The legume gene families are an important tool for identifying corresponding genes (orthologs) across legume species and thereby for linking research across various legume species. For example, research on gene function in soybean is often transferrable to orthologous bean genes. A published gene in soybean (e.g., the determinacy gene *Dt1*) could be used to detect the gene family containing the gene (either through a BLAST search against gene families or by entering a gene name), and the family, in turn, identifies both near and more distant orthologs in CB. Expression patterns can then be checked for the bean genes in the genome browser or gene record pages at LegumeInfo.org or in the BeanMine.

To effectively use the genomic resources at LegumeInfo.org or BeanMine, it may be helpful to think of three use-cases, distinguished by starting knowledge. In the first case, one has a gene with known function in another species and wishes to find whether there is evidence for similar functions in the ortholog in common bean. In the second case, one has genetic association information, either in the form of genetic markers from a QTL studies or genomic regions from a GWAS study, and wishes to find candidate genes within that genetic or genomic region. In the third case, one starts with gene enrichment information (e.g., genes upregulated under some condition) and wishes to narrow that list to find causal genes for a trait.

For the first use-case (gene in species 1 to candidate gene in CB), the sequence for the starting gene can be used as a query in a BLAST search at legumeinfo.org—either against the reference genome sequence, which will lead to a genome browser view centered on the BLAST hits, or against gene sequences (protein or coding sequence), which will lead to pages for the respective genes. From either target location (genome browser or gene page), there are link-outs to other resources—for example, from a gene to a gene family

or from a gene to gene expression profiles or from a gene to a genomic synteny in the LegumeInfo Genomic Context Viewer (GCV). Information toward validation of function can be gleaned from expression information, from phylogenetic and genomic context (from the gene tree viewer and GCV), or from overlapping QTL or GWAS regions. For GWAS and QTL regions, additional work typically needs to be done by the researcher to find the locations of flanking markers on the genome browser—which can be done by a search within the genome browser or by a search in LegumeInfo in the marker search page.

For the second use-case (from QTL or GWAS region to candidate genes), the first step is to find the region of interest in the genome browser. This can be done using a search of either flanking- or top-ranked marker, within the browser page or from the LegumeInfo in the marker search page. This needs to be done with caution, particularly for markers identified in QTL studies, because QTL regions are distributions, often with the significance region spanning many very large regions in genomic space. For either QTL or GWAS associations, it is appropriate to extend the region search to include all genes spanned by the flanking *non*-significant markers. For example, if there are significant markers at positions 1,000,000 and 1,100,000 and non-significant markers at 999,000 and 1,200,200, then the region that should be searched for candidate genes is from 999,000 and 1,200,200—because with greater SNP density, it is likely that significant markers would be found outside the two markers that were reported as significant. Once a set of candidate genes has been located in the genome, then functional information for predicted can be used to assess potential function in the plant, and gene lists can be further evaluated for information—either toward confirmation or elimination from candidacy.

For the third use-case (a list of genes of interest from any source to a reduced list of high-value candidates), the initial list could, in principle, come from numerous sources. Take the example of genes with significant differential expression, assayed in an RNA-Seq experiment, for response to some condition, e.g., drought response. Such a gene list can be used in a custom query at the BeanMine (available via LegumeInfo.org: https://mines.legumeinfo.org/beanmine). To be useful, the query should substantially narrow the initial gene list. This could be done by intersecting the genes with one or more genomic regions (likely determined from QTL or GWAS studies) or by another list (for example,

the set of orthologs from a BLAST search from genes known in another species to mediate drought response). Both types of queries and list operations are easily conducted at the BeanMine using similar query templates available from the main page.

Linkage and association mapping resources

Linkage mapping enables identification of associations between traits and markers, for both simple Mendelian traits and quantitatively inherited traits (QTLs) (Ibarra-Perez et al. 1997; Gepts et al. 2008; De Ron et al. 2015). The first widely used genetic map in bean was developed from a backcross (BC) mapping population between Mesoamerican line 'XR-235-1-1' and 'Calima' (Andean cultivar (Vallejos et al. 1992). This linkage map included 9 seed proteins, 9 isozymes, 224 RFLP, and seed and flower color markers. These molecular markers were placed on 11 linkage groups, spanning 960 centimorgans (cM). The second genetic map was developed using RFLP markers, spanning 827 cM. These markers were placed on an F_2 mapping population (cross of BAT93 by Jalo EEP558), with 142 markers being assigned to 15 linkage groups (Nodari et al. 1993).

A third genetic map was developed by Adam-Blondon et al. (1994) from the cross between Ms8EO2 and Core. This map contained 51 RFLPs, 100 RAPDs, and two sequence-characterized amplified region (SCAR) loci and spanned 567.5 cM across 12 linkage groups. These three maps were mainly based on RFLPs, though few seed protein and isozyme markers were also included (McClean et al. 2004). A consensus map was then developed utilizing these linkage maps on BAT93 × Jalo EEP558 (BJ) as a core map (McClean et al. 2004). The creation of this consensus map has provided bean breeders with the means for combining all the genetic information from multiple populations developed from diverse genetic background. It also provided the opportunity to map more loci than from single cross populations and also increased important markers over different genetic backgrounds (Rami et al. 2009).

Numerous subsequent maps have been generated, using a succession of marker types (reviewed by González et al. 2018). Although SNP markers have generally supplanted prior types of markers, important early markers and mapping populations are valuable resources for interpreting new SNP maps and crosses, sometimes through conversion of older marker types to nearby SNP markers. SSR markers (also called

microsatellites), which are also typically though not exclusively PCR-based, have been extensively used in bean genetic studies. SSR markers were first reported in bean by Yu et al. (1999, 2000), with 15 different microsatellite markers included in a molecular linkage map constructed primarily using RAPD and RFLP markers. Blair et al. (2003) integrated 100 SSR markers in two linkage maps along with RFLP, AFLP, and RAPD markers. Much more saturated SSR-based maps were reported by Córdoba et al. (2010) and Blair et al. (2014). Since then, several bean genetic studies have been implemented using SSR markers and have further been employed for map comparison and integration. The sequence-characterized amplified region (SCAR) marker is another PCR-based marker that has been used for comparison of genetic map and integrating genetic maps (McClean et al. 2002). Additional types of PCR-based markers include indel-based markers, including a large set described by Moghaddam et al. (2014).

In the last decade, SNP assay methods have become far more efficient. Researchers can now inexpensively scan the whole genome to identify rare variants that are potentially associated with traits of interest. SNP discovery in maize and soybean is illustrative for many other crop species (Rafalski 2002, 2010; Hyten et al. 2010), though there are species-specific differences—for example, with the SNP frequency being roughly an order of magnitude higher in maize than soybean. In CB, SNP frequency is relatively high, with approximately one SNP per 88 bp across a genome of ~588 Mbp—implying more than six million SNPs are expected in the genome (Gaitán-Solís et al. 2008; Schmutz et al. 2014; Blair et al. 2018). An important recent SNP map is the high-resolution Mesoamerican × Andean cross of Stampede × Red Hawk produced by Song et al. (2015), which utilized 7276 SNP markers in an F2 mapping population of 267 RILs. This was used to anchor sequence scaffolds into pseudomolecules in the first reference genome assembly for CB (Schmutz et al. 2014). Many bean SNPs have been discovered through sequencing and genotyping by sequencing (Bhakta et al. 2015; Ariani et al. 2016; Schröder et al. 2016), and some older markers have been converted to "Kompetitive Allele Specific PCR" (KASP)-based SNP assays (Cortés et al. 2011).

Genetic maps for CB are found at LegumeInfo (https://legumeinfo.org/traits_maps#phavu) and at PhaseolusGenes (http://phaseolusgenes.bioinformatics.ucdavis.edu). Both of these websites include various genetic maps, as well as QTL features from numerous studies projected onto a reference genetic map. In the case of LegumeInfo, QTL and markers are projected onto the combined map of three populations (Fig. 1), two of which were inter-genepool, namely DOR364 × G19833 (DG) and BAT93 × Jalo EEP558 (BJ) with one Mesoamerican × Mesoamerican BAT477 × DOR364 (BD) population as described in Galeano et al. (2012). This resource has links to a high-density map for an F2 population for North American researchers based on the Mesoamerican × Andean cross of Stampede × Red Hawk (SR) (Song et al. 2015) and to an integrated map for the BJ reference population. Finally, all the maps are tied into the G19833 sequence information from LegumeInfo (Fig. 2).

A great number of trait-mapping studies in CB have been produced over roughly the last 40 years, involving both mapping of qualitative and quantitative traits in biparental populations, and more recently, through genome-wide association studies in diverse germplasm collections (reviewed by González et al. 2018). A sampling of some of these important trait-mapping follows.

The primary determinacy locus, *FIN*, has been identified on LG01 in CB as *PvTFL1y*, homologous to the *Arabidopsis TFL1* gene (Kwak et al. 2008; González et al. 2016). The allele conferring determinacy is the mutant (recessive) form.

Control of photoperiod has been repeatedly mapped to two loci on LG01 (Koinange et al. 1996; Kwak et al. 2008). A compelling candidate for the PPD (photoperiod) locus is an ortholog of the E3/PHYA3 gene in soybean gene (McClean et al. 2010). A candidate for the other LG01 locus, HR, is orthologous to the Flowering Time (FT) gene in *Arabidopsis* (Gu et al. 1998).

Traits such as seed and pod size and yield are complex, involving multiple genes and numerous epistatic interactions, but loci involved have been identified repeatedly, in various backgrounds, and with increasingly tight genetic bounds (González et al. 2018). For example, pod size and pod length QTLs have been reported in similar locations, including LG01, LG02, and LG04 (Koinange et al. 1996; Hagerty et al. 2016; Yuste-Lisbona et al. 2014).

Current and prospective methods in CB breeding

Genomics-assisted breeding

Conventional bean breeding approaches have produced many improved varieties. However, genetic progress in

Fig. 1 Consensus genetic map, showing QTL from various studies
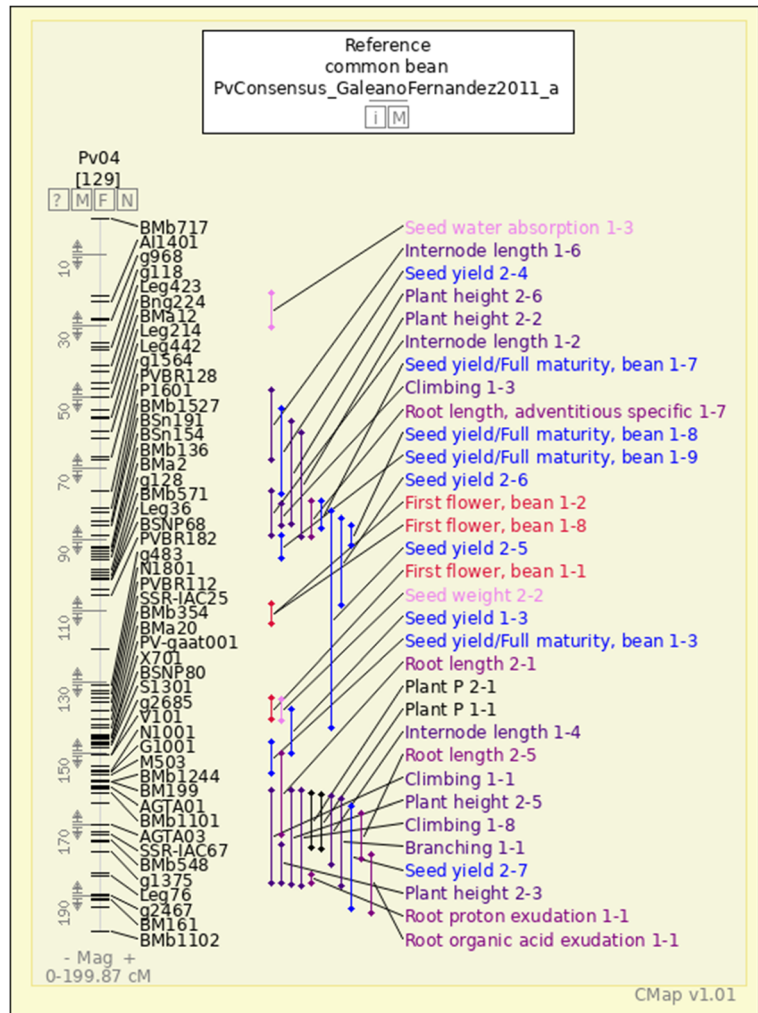
yield has been slow compared to crops such as soybean and maize. Improved molecular marker technologies may enable bean breeders and geneticists to speed up cultivar development. An important intermediate step in this direction is to transfer desirable QTLs (genes) into active breeding populations using MAS—and to transfer multiple traits through gene pyramiding (Das et al. 2017). Progress has been made in applying MAS toward improved resistance and it is described by Miklas et al. (2006) and Tryphone et al. (2013).

A collection of molecular breeding techniques, collectively labeled MAB by Ribaut et al. (2010), includes selection based on marker-assisted back-crossing (MABC), marker-assisted recurrent selection (MARS), and genomic selection (GS) (Fig. 3). The MABC approach is to transfer a major gene from a donor cultivar into an elite line. The MARS approach

is to assemble and involve favorable alleles from various sources for the expression of quantitative traits. The GS approach relies on marker-based selection that might be performed without major testing or even prior marker × trait associations (Bernardo and Yu 2007). MABC and MARS have been effective as indirect selection techniques by selecting for traits without evaluating the trait of interest. MABC is one of the most preferred molecular approaches for transferring desirable genes into well-adapted commercial cultivars. Carneiro et al. (2010) reported that microsatellite markers linked with white mold resistance (genes) were effective in selecting individual plants with a higher resistance relative to the recurrent parent genome. Integrating MABC into bean breeding has been effective for improving traits controlled by major genes and used for stacking of few genes and QTLs
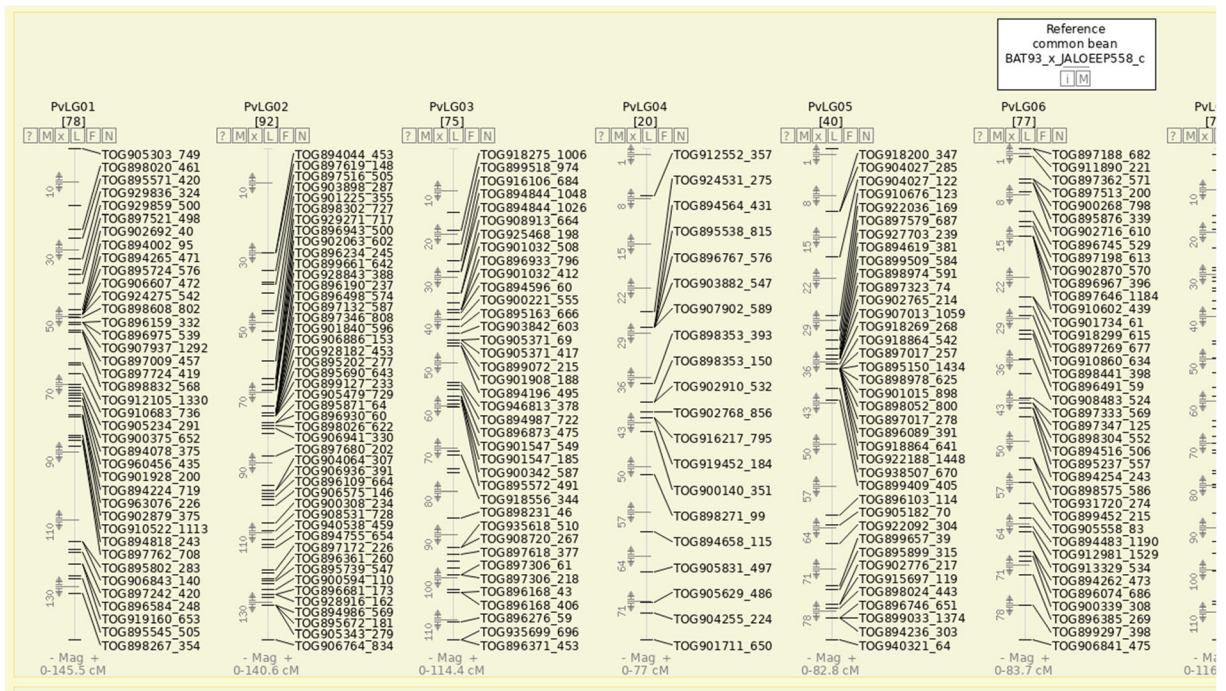
Fig. 2 Reference map of the BAT93 × Jalo EEP558 population using trans-legume orthologous gene-based (TOG) markers

(Kelly 2004; Carneiro et al. 2010; Varshney et al. 2010). It is also efficient for gene pyramiding (e.g., combining two or more strains of the same pathogen).

An early example of marker-assisted selection was used to determine and select anthracnose resistance genes Co-5 and Co-42. The markers SAB3 and
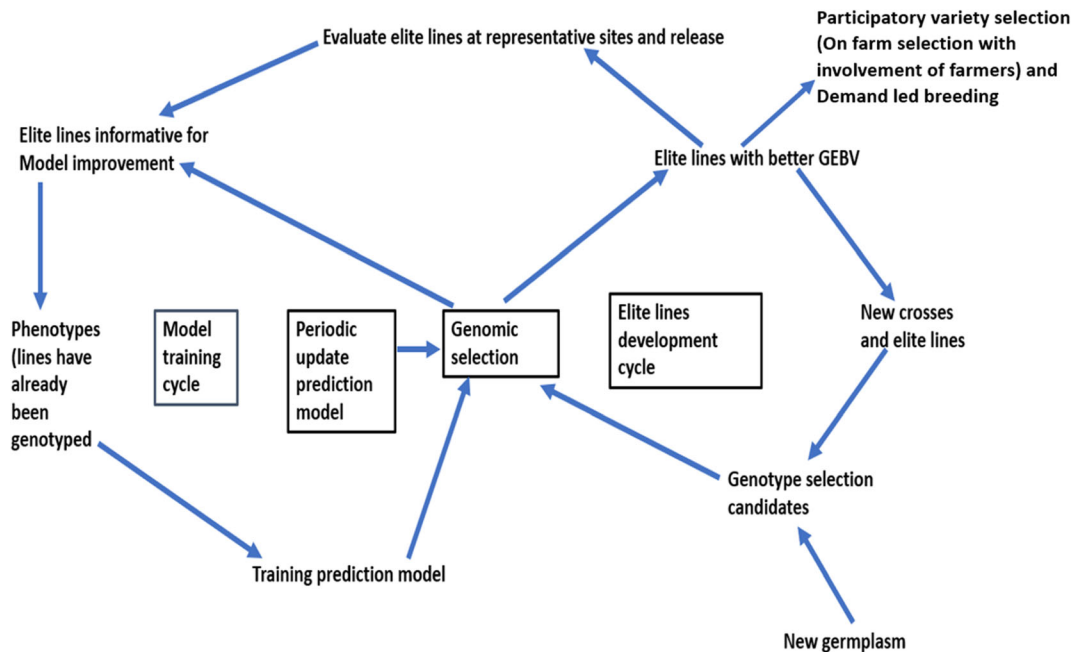

Fig. 3 Genomic selection scheme. GEBV = genomic estimated breeding value. Adapted from Fig. 2 in Heffner et al. (2009), with modifications to show integration of participatory variety selection and demand-led breeding

SAS13 are associated with the anthracnose resistance genes Co-5 and Co-42, respectively, in the donor parent G2333 (the source of resistance genes to anthracnose). This resistant parent was crossed with susceptible commercial cultivars, and resistance was selected for by selecting for these markers (SAB3 and SAS13) in the backcross progeny. The resistance was effectively transferred to the BC_1 population (Garzón et al. 2008). In that study, the Co-5 and Co-42 anthracnose resistance genes associated with the markers (SAB3 and SAS13) can be stacked to increase the level of resistance to anthracnose. Subsequent studies have also selected for bruchid and virus resistance (Blair et al. 2010b).

MAS in bean breeding and the progress that has been made are well explained by Miklas et al. (2006), who describe success toward several diseases of CB. MABC for quantitatively inherited traits including yield and drought tolerance has not yet been well developed in CB (O'Boyle et al. 2007). Markers linked to QTL for disease and insect resistance have been identified and are being utilized to introgress genes into elite varieties (Briñez et al. 2017).

The MARS approach helps breeders identify superior alleles for complex traits such as drought resistance and yield and to develop superior breeding lines from both parents. Bernardo and Charcosset (2006) reported that MARS is effective for identifying multiple genomic regions and to detect both minor and major QTLs. Thus, MARS may be able to achieve greater genetic gain compared to MABC.

GS, another emerging molecular approach, is a form of molecular MAS that enables breeders to increase genetic gain in a short period of time for quantitatively inherited traits (Heffner et al. 2009). GS is different from MABC and MARS in that it directly identifies better genotypes via predicted breeding value (BV), using markers with genome-wide distribution. GS methods use a training population and a validation population. The training population consists of elite lines that are both phenotyped and genotyped with genome-wide markers. These markers are treated as random instead of fixed effects.

In GS, the molecular marker effects on the phenotypes of elite materials are assessed concurrently in a model. It is assumed that one or more markers are in linkage disequilibrium with corresponding QTL associated with the trait. In GS, the model for prediction is fitted to detect the entire additive genetic variances based on totality of the effects of the molecular markers,

to estimate breeding values of individual markers. This model is also applied to the genomic data of a validation population in which the individuals are genotyped but not phenotyped. The model produces genomic estimated breeding values (GEBV), which captures the effects of markers in the training population toward phenotypes of interest. After predicting the breeding value (GEBV) for each genotype in the breeding program, genotypes with higher breeding values are either recycled into the crossing program or dropped. The advantage of using GS over conventional breeding is that it has the potential to reduce the number of breeding cycles and reduce the need for phenotyping in every cycle, while maintaining genetic diversity. GS should be efficient than traditional MAS at selecting for complex traits with low heritability, since models comprised of many markers are able to pick up low-effect genes.

Genomic resources in bean have also enabled the use of GWAS to identify marker-trait associations. A significant advantage of GWAS over QTL studies is that the marker-based associations (typically SNPs) can be integrated with other GWAS, as long as the markers are placed on a common genomic reference assembly. The markers acquire position by virtue of the genomic sequence rather than through genetic mapping and recombination-counting (Schmutz et al. 2014). Significant GWAS research has been conducted in CB to find genetic associations with some traits such as agronomic performance and SNF ability (Kamfwa et al. 2015a, 2015b), anthracnose and angular leaf spot resistance (Perseguini et al. 2016), cooking time (Cichy et al. 2015), anthracnose resistance (Zuiderveen et al. 2016), and drought tolerance (Hoyos-Villegas et al. 2017). More research and a better understanding of different biotic and abiotic stress tolerance traits in the context of GWAS in CB are still needed.

High-throughput phenotyping approaches for CB breeding

Progress in high-throughput phenotyping (HTP) in CB has generally lagged genomic progress. It remains difficult and costly to do precise phenotyping of simple and complex traits such as plant height, biomass, flowering, and yield for a large breeding population with replicated tests across different environments, requiring large number of plant measurements—many of which are time-sensitive and growth-stage dependent. This bottleneck has led to some new HTP approaches, unlocking

prospects for non-destructive field and lab-based phenotyping (Cobb et al. 2013; D'Agostino and Tripodi 2017; Varshney et al. 2018).

Currently, most plant trait phenotyping is heavily dependent on visual observation and manual measurements, which are time consuming, labor intensive, costly, error-prone, and liable to miss subtle phenotypic variations (Kumar et al. 2015). Some HTP imaging techniques are non-invasive and accurate, reducing dependence on invasive or destructive methods (Bhat et al. 2015)—employing, for example, multi-spectral imaging for different traits such as phenology, leaf disease (chlorosis, necrosis), plant structure, and biomass accumulation. For example, near infra-red cameras are used for measuring tissue water content and chlorophyll fluorescence analysis to assess photosynthetic efficiency (Kumar et al. 2015). A combination of new imaging techniques and robotic and conveyer belt systems in greenhouse could be used for bean HTP (McDonald et al. 2016). At a smaller plot level, ground-based HTP including tractor-based system or modified vehicles such as phenomobiles and phenocarts equipped with global positioning system (GPS) and sensors could be easily applied to bean phenotyping.

Demand-led breeding

Although many aspects of bean improvement depend on technical factors, we would also like to highlight an important sociological approach that has demonstrated success in CB breeding. CB has steadily evolved from primarily a smallholder subsistence crop (Katungi et al. 2009) to market-oriented production (Buruchara et al. 2011). This shift in focus has necessitated a revision in the varietal development process and seed system. The hands-on nature of participatory variety selection (PVS) has evolved from more contractual and consultative to demand-led breeding (Persley and Anthony 2017) where multidisciplinary researchers work closely with bean value chain actors to develop bean varieties that meet the needs of farmers and others in the value chain. This paradigm shift in bean breeding has been toward a value chain-focused approach, with relatively less emphasis placed on the farmer-focused approach of a few farmers engaged in selecting varieties for ecological suitability. Currently, nearly all the bean breeders in

PABRA are employing demand-led breeding approaches. A variety of factors that include different users groups (women/men, more market-oriented/home consumption), a range of agroecological zones, and preference information (from participants including households, farmers, traders, and processors) are resulting in fine-tuning of formal breeding programs. Conventional plant breeding has been successful in developing bean cultivars that can be used in environments that are fairly homogenous and stable, but it has been less effective in developing cultivars in complex and marginalized drought affected environments (Ceccarelli et al. 2000; Fufa et al. 2010; Assefa et al. 2014) Conventional plant breeding is also framed to accommodate limited requirements and the particular needs of farmers and particular growing environments (Assefa et al. 2014). Through demand-led breeding (DLB), bean breeders can also enhance varietal diversity through involvement of actors throughout the value chain, as well as minimizing effort that might be invested in developing varieties that are unacceptable to farmers and local communities, and traders/processors. DLB is also able to exploit genotype by environment interaction by taking advantage of specific adaptations to particular locations and growing conditions, such as periodic drought or soil mineral toxicity.

Tremendous gains have been made in getting conventionally selected varieties released through the formal cultivar release system. Through collaborative efforts, PABRA has succeeded in fast-tracking the release of bean varieties selected for a range of preferred traits. The number of varieties released rose from 73 in 1990–2000 to 130 in 2001–2008 to 340 in 2009–2016, including seven PABRA members with less resourced breeding programs: Burundi, Cameroon, Democratic Republic of Congo, Swaziland, Congo Brazzaville, Lesotho, and Guinea (http://www.pabra-africa.org/pabra-annual-report-20162017-20th-anniversary-special-edition). As result of use wider impact seed systems approach (Rubyogo et al. 2010), within the PABRA region, improved bean varieties occupy 56% of the bean-growing area. More importantly, yields have nearly doubled in Ethiopia (Berhanu et al. 2018), while they have increased by 55% in Uganda, 20% in Burundi, and 12% in Rwanda over the last decade (PABRA 2017). This significant increase of yield for improved bean cultivars is found to be related to the positive impacts (CIAT 2013; Larochelle et al. 2013).

Gaps in common bean improvement and potential future developments

Although a great deal of work is underway globally toward bean improvement, we see several areas of current weakness—and, concomitantly, areas for opportunity.

Integration of robust, high-value markers into breeding programs There remains a lack of some key information for CB improvement, including easily assayed markers tightly linked to important traits and more complete understanding of the mechanisms underlying quantitative traits. In the absence of that mechanistic understanding, single markers will generally be of limited use, particularly given the complexity and heterogeneity of genetic backgrounds in CB. Further, even the best markers for high-value traits are of limited utility in a breeding program unless the breeder has access to efficient, low-cost assays, integrated as a regular part of the annual breeding cycle.

Better characterization of strengths and weaknesses of genomic selection and related methods Although GS methods have been in use for more than a decade (Bernardo and Yu 2007) and have been shown to be useful in multiple species (being particularly helpful in avoiding the need to do expensive phenotyping during each selection round), the method remains challenging to do well—generally requiring careful phenotyping in the first generations in for distinct populations and breeding projects. It works better in some germplasm collections than others and can be highly affected by population structure, which may not be straightforward to identify or correct for.

Better characterization of germplasm resources Complete genome sequence assemblies are available for several bean accessions, and there are available methods for high-throughput genotyping, e.g., genotyping-by-sequencing (Schröder et al. 2016; Ariani et al. 2016) or SNP chips (Song et al. 2015). Nevertheless, no complete catalog of variants across the global germplasm collections exists for CB. This would be helpful in identifying both unique germplasm as well as redundancies across collections.

Solutions for physiological weak points in CB CB remains a vulnerable crop in several ways. It has limited tolerance to high temperatures, particularly during flowering. It also generally has poor tolerance to cold temperatures and to drought and is vulnerable to many diseases and pests. Improvements in any of these areas remain a daunting challenge, but there are opportunities for improvements through introgressions, both from wild *P. vulgaris* accessions with valuable traits and by interspecific crosses to gain traits for tolerance to broader environmental ranges from species such as *P. acutifolius* and *P. coccineus*.

Combining marker-assisted breeding methods with demand-led breeding While DLB and MAB have each been highly selective where applied, DLB has typically been an approach used in developing countries and MAB (summarized in Fig. 3) more often used in resource-wealthy breeding situations. Merging the two should have promise—although the technical requirements of MAB are significant enough to require substantial coordination by experienced organizations (e.g., CIAT or ICRISAT or focused international grant-led projects). The types of methods to incorporate into DLB include MAB and GS (Fig. 3). MAB or GS can further improve the efficiency of selection for biotic and abiotic stress resistance/tolerance traits that typically have a low heritability and also help to increase the initial frequency of favorable alleles in bulk populations. Then, the farmers select the elite lines in their own field (Steele et al. 2004; Kanbar and Shashidhar 2010), helping reduce program costs in the breeding project while also helping build buy-in by farmers.

Summary

Conventional plant breeding and a collection of worldwide germplasm have been the primary source of improvements in CB. However, enormous opportunities still exist to improve the efficiency and accuracy of bean breeding and to increase genetic gain with the use of genomic tools, improved phenotyping methods, and well-coordinated DLB projects. Genomic data facilitate the identification of traits and regions for introgression by direct selection of specific alleles. Genomic approaches are also used for diversity analysis, germplasm characterization, and identification of tightly linked markers for important traits. Linkage maps and identification of QTLs for important traits have enabled MAS, which is now commonly used, and is important for

simply inherited traits, sometimes several at a time, through pyramiding. GWAS and genomic selection are also poised for broader use. Reference genome sequences are now available in CB, which will help breeders identify genes involved in major traits. Sociological insights related to DLB outcomes include participation of local value chains, from farmers to traders to retailers and consumers.

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