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Review

Common bean as a potential crop for future food security: an overview of past, current and future contributions in genomics, transcriptomics, transgenics and proteomics

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ABSTRACT

Common bean is an important legume crop having high quality protein, micronutrients, vitamins and antioxidants, which makes it a "grain of hope" for poor communities. Hence, a good number of breeding activities have been performed on the improvement of various key traits for years. However, recent advancements in molecular markers, sequencing technologies and the completion of the common bean genome sequence have opened numerous opportunities for fine mapping and gene characterization. The availability of these tools together with investigations of quantitative trait loci (QTL) and candidate genes for key traits such as morpho-agronomic, iron and zinc contents, cooking and quality traits, antioxidant activity, biotic and abiotic stresses pave the way to the development of new strategies for common bean genetic improvement. As a food source, it can contribute to the reduction of food scarcity worldwide in the coming years. Therefore, it is very important to take synergic efforts to integrate common bean genetic and genomic resources in breeding activities to ensure food security and contribute significantly to improved livelihoods in developing countries. Moreover, Kompetitive allele specific PCR (KASP) and CRISPR-Cas9 should be used to develop climate resilience common bean varieties. Here, we provide an overview of the evolution of common bean research by highlighting the past and recent advances in genomics, transgenics, transcriptomics and proteomics and also critically discuss the future prospects for further genetic improvement and better expansion of this crop.

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Legume crop; *Phaseolus vulgaris*; genetic resources; genomics; proteomics

Introduction

With the rapid increase in the world's population, it is estimated that 70% more food will be required to meet the food demand for the predicted population of 9.6 billion people by 2050, and this demand will be mainly from developing countries and Africa [1]. To overcome this challenge, there is a need to increase the production of all crops all over the world, especially in Africa [2]. Legumes are the major source of proteins and minerals and an important pillar of agricultural production systems, playing a vital role in the human diet and farming systems of developing countries [3,4].

Common bean (*Phaseolus vulgaris L.*) is an important grain legume crop and mostly used worldwide for its pods and edible seeds [5–9]. It is an important source of protein and provides 15% of protein and fulfills 30% of caloric requirements of the world's population [10]. There are 50 *Phaseolus* species; however, only five species (*P. vulgaris*, *P. lunatus*, *P. coccineus*, *P. acutifolius*,

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and *P. polyanthus*) have been mainly used as human food. Among these five species, common bean (*P. vulgaris*) is most widely used for human consumption [11]. The common bean is an annual herbaceous plant with great diversity in its growth habit, for instance it may be a determinate/indeterminate bush or a climber to semi climber vine [12]. According to FAO, common bean global harvested area was 33.1 million ha and production was 28.9 million tons in 2019 [13]. Asia shares 50% of the global production of common bean (Figure 1), and Myanmar, India, Brazil, China, America were the top five dry bean producing countries in the world in 2000–2019 [13].

Relevance of common bean research

Common bean is a true diploid with a genome size of 587 Mb [14]. It is considered a model crop for comparative genomics studies in different legumes due to its phylogenetic position in the Phaseoloids [15]. It shows very close relatedness to papilionid legumes like soybean (*Glycine max*), pigeon pea (*Vigna radiata*) and cowpea (*Vigna unguiculata*) [16]. Previous studies showed that the divergence of soybean and common bean occurred ~19.2 million years ago; however, they shared a whole-genome duplication event ~56.5 million years ago [14, 17]. Moreover, most segments of any single common bean linkage group showed a higher level of resemblance to two soybean chromosomes on the basis of synteny analysis [18]. Due to its small genome size, it can serve as a model crop to understand the genomics of higher genome size crops, like soybean, with a genome size ~1,100 Mbp [10]. Previously, common bean was considered an "orphan crop". However, this crop entered the modern era crop after the successful genome sequencing in 2014 [14]. Historical advancements in common bean are shown in Figure 2.

Common bean origin and domestication

Mesoamerica is the main region of origin, where maximum numbers of *Phaseolus* species are geographically distributed, and it is assumed that the *Phaseolus* genus originated between 4 to 6 million years ago [19] in this region [12, 19]. Having originated in Mesoamerica, what is now Mexico [20], wild forms of common bean were mainly distributed from northwestern Argentina to northern Mexico and resulted in the formation of unique gene pools (Figure 3), namely the Andean, Mesoamerica and Peru-Ecuador [21,22].

Andean and Mesoamerica gene pools are considered two big gene pools of common bean and their geographical structure is evident from their domestic forms [16]. The Peru-Ecuador gene pool is considered the third gene pool and contains wild populations first

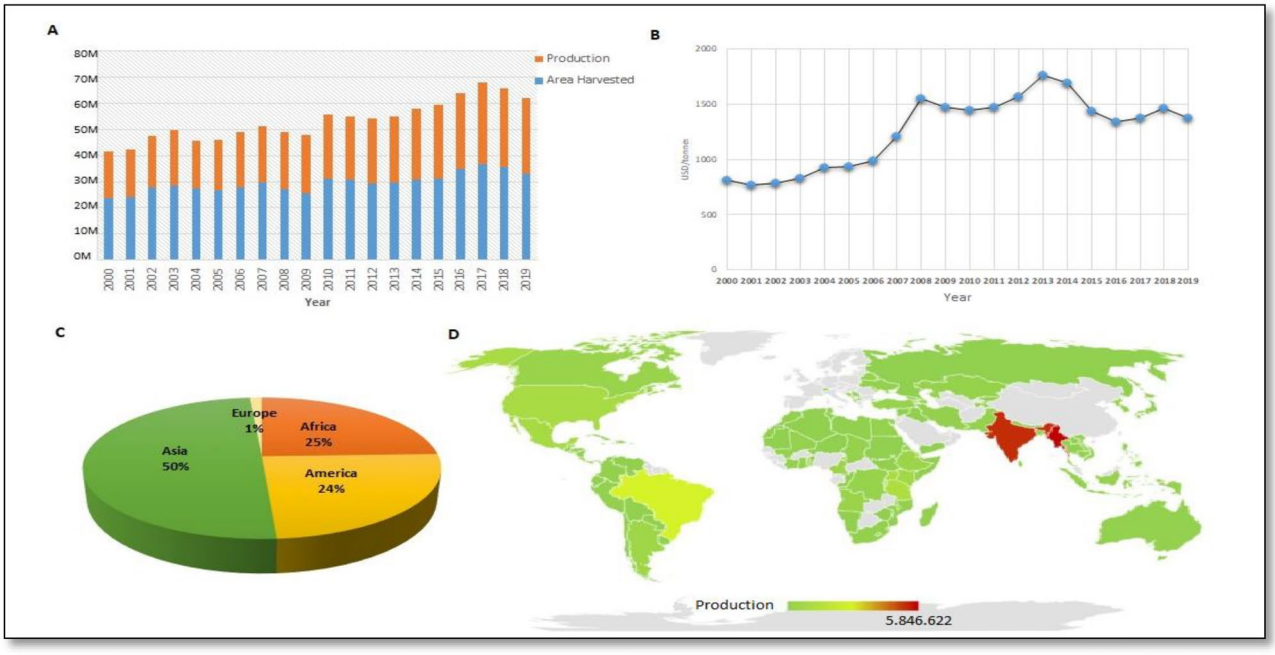

Figure 1. Common bean production in the world. (A) Evolution of common bean seed production and area under cultivation from 2000 to 2019. (B) Evolution of sale prices of common bean seed from 2000 to 2019. (C) Production share of common bean seed by continent in 2019. (D) Map of production quantities of common bean seed by country in 2019 (Source: Food and Agriculture Organization Statistical Databases was used to develop this figure (FAOSTAT) 2020).

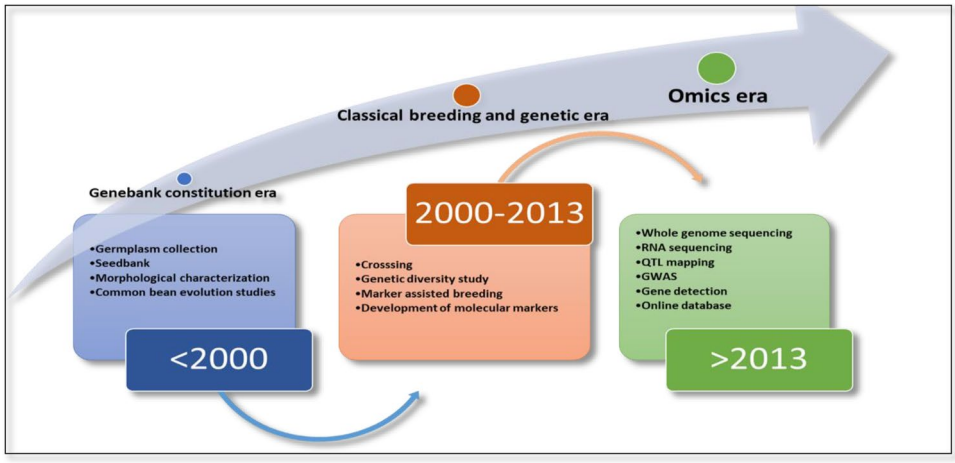

Figure 2. Evolutionary history of the scientific research on common bean.

Figure 3. Representation of common bean gene pool (The figure was adapted from Google Earth (https://earth.google.com/web/) and colored by authors).

discovered in the 1980s and mainly grown in a very small area of Andes western slopes [21]. The Peru-Ecuador gene pool is mainly characterized by its seed protein named Phaseolin type *I,* which is absent in the Andean and Mesoamerican gene pool [22].

Domestication is a very complicated process that plays an important role in the modification of wild relatives into a very useful crop [23]. Domesticated forms of common bean can be differentiated from their wild relatives on the basis of different important characteristics such as growth habit, seed dormancy, photoperiod sensitivity, color, shape and size of the plant. These modifications improve the agronomic performance in different climatic conditions and make the crop plant genetically different from the wild forms [24].

Mesoamerica and the Andes were the main regions where domestication of common bean occurred independently. Domestication events occurring in common bean are still under debate by scientists. Some studies are in the favor of a single domestication event [25–27], while some are in favor of two domestication events that have led to establishment of two gene pools [28–30]. The domesticated Mesoamerican gene pool clearly exhibited reduced genetic diversity in different studies [27, 31,32]. There was three-fold greater genetic diversity reduction in the Mesoamerican gene pool compared to the Andean gene pool [33]. Very recently Trucchi et al. [34], investigated the temporal dynamics of genetic diversity and selection throughout the domestication process of the common bean in the

southern Andes. It was reported that the genomic variation of the pool of cultivars from different Andean regions is higher than the pool of ancient seeds from the central-western and north Argentina.

Diffusion of common bean from its origin to the rest of the world

Several introductions of common bean to different countries were performed with the passage of time. Common bean is now cultivated all over the world and serves as a source of food for millions of people. In Europe, 70% of common bean belongs to the Andean gene pool [35], while the Mesoamerican gene pool is more frequently present in Brazil compared to the Andean gene pool [36]. In China, the Mesoamerican gene pool is more widely spread compared to the Andean gene pool [37], whereas the share of both gene pools is equal in Africa [38]. Additionally, out of the domestication regions, there was less focus on the spatial differentiation between both these gene pools, which resulted in the novel phenotypic and genotypic traits in these gene pools due to hybridization, especially in Europe [35,38].

Common bean genetic resources

Domesticated *Phaseolus* species (*P. vulgaris; P. coccineus; P. dumosus: P. acutifolius* and *P. lunatus*) and several wild *Phaseolus* species are preserved in different gene banks. Centro Internacional de Agricultura Tropical (CIAT) Cali, Colombia, preserves the world's largest and most diverse collection of beans with 37,938 *Phaseolus* accessions belonging to 44 taxa, and it holds 71.6% of the preserved bean germplasm (Table 1). Some other stations conserving common bean accessions are Institut für Pflanzengenetik und Kulturpflanzenforschung in Germany (IPK: http://www.ipk-gatersleben.de), the Centro Nacional de Recursos Genéticos e Biotecnologia (CENARGEN/EMBRAPA) in Brazil with more than 1800 common bean accessions (https://www.embrapa.br/en/recursos-geneticos-e-biotecnologia), the National Botanic Garden of Belgium with 2074 accessions from 231 taxa of the *Phaseolus* tribe (http://www.plantentuinmeise.be/RESEARCH/COLLECTIONS/LIVING/PHASEOLUS/index.html), and Western Regional Plant Introduction Station (WRPIS) in the USA with more than 20,000 *Phaseolus* accessions - with *P. vulgaris* as the most abundant species - with 17,000 accessions (https://www.ars.usda.gov/research/publications/publication/?seqNo115=319341). A mini-core collection of nearly 750 Turkish common bean landraces has been recently collected from the different geographical regions of Turkey in different projects funded by The Scientific and Technological Research Council of Turkey. This mini-core collection is maintained at the Abant Izzet Baysal University, Bolu (Turkey) and Sivas University of Science and Technology, Sivas (Turkey), and is available for the bean scientist interested in the Turkish bean germplasm.

A large number of mapping populations have been developed to investigate various traits of interest in common bean [39]. Recombinant inbred (RI) populations from BAT93 x Jalo EEP558 have been taken as core mapping populations because markers resulting from other linkage maps have been mapped in this population [40,41]. Most populations have been produced by making crosses between Mesoamerican and Andean gene pools. For this purpose, diverse parents have been selected exhibiting enough phenotypic variations for agronomic traits, disease resistance, antioxidants, and cooking properties, and also have shown higher polymorphism levels [11, 42].

Breeding activities in common bean

Classical breeding

Several studies have been conducted for the successful breeding of common bean using classical breeding methods such as pedigree, single seed descent (SSD), recurrent selection, gamete selection and backcross method to accomplish the wide arrays of objectives. Main breeding efforts have been done to increase the adaptation of the crop to different environmental conditions, to develop genetically improved cultivars and to increase resistance against various biotic and abiotic

Table 1. Genetic resources of various Phaseolus species conserved in various originations all over the world.

Gene bank	Accessions	Landraces	Wild types
CIAT, Colombia	37.938	30.507	2153
USDA, USA	14.674	9832	880
Embrapa, Brazil	14.460	5784	–
INIFAP, Mexico	12.752	7014 (55)	2168
IPK, Germany	8680	5729 (66)	87
SBTU and BAIBU*	–	750	–

*SBTU, Sivas University of Science and Technology, BAIBU, Bolu Abant Izzet Baysal University.

stresses [43,44]. Common bean is a crop with a low outcrossing proportion [45] and its outcrossing is widely affected by environmental factors [46]. The pedigree method is the most commonly used breeding method for common bean because it facilitates qualitative trait selection in early F_2-F_4 generations, while this selection would be continued for complex traits like yield up to F_5-F_7 generation [47]. The single seed or single pod selection is another method that is much faster than the pedigree method and can also be used in the greenhouse easily. Urrea and Singh [48] developed a single seed descent method in common bean by modifying the pedigree method. This method has been widely used by many breeders to develop the RILs (recombinant inbred lines) for various genetic studies in common bean, while no selection is performed in the RILs development used in QTLs studies [49].

Recurrent selection is another important breeding method, and it is mostly used in the breeding of cross-pollinated crops where pollens are present in the ample quantity in the field. However, it is difficult to make good numbers of crosses between two diverse parents in highly self-pollinated crops like beans to produce enough variations for the next cycle of selection [47]. This method has been successfully applied to introduce plant architecture traits into large-seeded decumbent type-III Durango race pinto beans from type-II Mesoamerican black bean race [50]. Sierra pinto variety was the first variety developed *via* this method with large size seeds of pinto beans and upright type-II short vine habit [51]. Development of Sierra pinto variety served as a genetic bridge for the development of other medium seeded Durango and Jalisco race varieties, and breeders could develop other seed types like Sedona pink bean [52], Merlot small red variety [53] and Matterhorn Great Northern [54].

The selection for multiple traits in a population is possible by crossing the various parents using the gamete selection [55–57]. It was determined to be successful in the development of disease resistant breeding line [58]. The *bc-3* allele for bean common mosaic necrosis virus (BCMNV) resistance and *bgm* gene for bean golden yellow mosaic virus (BGYMV) resistance have been identified through this method [59].

The backcross method is a very useful breeding method mainly used to introduce one or more genes in a variety that lacks such genes [47]. This method has been successfully applied to introduce favorable genetic variations from wild and landraces bean material with introgression between diverse common bean gene pools [60,61]. Intermating between incompatible *Phaseolus* species has been enhanced by applying the congruity backcross method [62]. The congruity backcross method has been used to produce more recombinant events by crossing common bean with tepary bean and their progenies contain genes from both species [63,64].

Advancement in breeding methodologies for common bean

Advancement in DNA molecular markers and sequencing technologies revolutionized and increased the success of breeding activities when compared to the classical breeding methods [65]. Common bean is a diploid plant (2n = 22) with a genome size of 587 Mb [14] and is beneficial in the genome study of crops with higher genome size like soybean [10]. Common bean genetic map has been available since the 1990s by using different types of molecular markers, i.e. restriction fragment length polymorphism (RFLP) markers [66] and random amplified polymorphic DNA (RAPD) markers [67]. The common bean genome was sequenced by Schmutz et al. [14] through the application of the whole-genome shotgun sequencing technique in common bean genotype "G19833". The resulting sequences were assembled on 11 chromosomes and ultimately expressed about 80% of the 587-Mb common bean genome. Assembled genome sequences were annotated through the application of *ab initio* approaches with transcriptome data. A total of 31.632 protein-coding sequences were identified by the 4441 alternately slipped transcripts with 27197 gene models. Moreover, it was reported that transposable elements were present in large amounts and they constituted almost 45% of the genome. The genome of common bean landrace BAT93 was also sequenced by Vlasova et al. [68] under the PhasIbeAm consortium. Based on genetic contents, common bean genome contains some surprises, for instance, it encodes 27,000 genes with a high level of transposons insertion because of the fact that 91% of common bean genes are situated within synteny blocks of soybean. On the other hand, genome duplication is lesser in common bean as compared to the soybean because whole-genome duplication (WGD) occurred in soybean [14]. Recently, the first chromosome-scale version of common bean has been developed by The Joint Genome Institute, Department of Energy) (http://www.phytozome.net/common bean), which is very helpful in common bean genome mapping and marker development. Especially, this database is a very useful

database in gene identification studies because it shows the exon and intron regions within the common bean separately.

Common bean genomic resources

Genome sequencing of common bean has helped in understanding the genomics of not only common bean but also soybean [14]. The first linkage map in common bean was developed in the 1990s by using RFLPs and RAPD markers [41, 69]. Microsatellite markers are very useful for genetic studies, and GenBank sequences and enriched genomic libraries have been used in the development of simple sequence repeats (SSRs). Yu et al. [70,71] firstly developed the GenBank-based microsatellites generating a set of 38 SSR markers that led to the additional development of 57 SSR by Blair et al. [40] and 20 SSRs by Guerra-Sanz [72]. In common bean, more than 2,000 SSRs markers have been developed from various genomic sequences [40, 71, 73,74]. Furthermore, size-fractionated bacterial artificial chromosome (BAC) libraries were used by Caixeta et al. [75] for the development of microsatellite markers linked with angular leaf spot resistance gene. BAC libraries with large DNA insertions have been very beneficial in the development of physical maps and can play a vital role in positional cloning, functional analysis, characterization of the genome for gene structure and transgenic studies [76,77]. These libraries have been used in the cloning of large-sized (100–150 kb) genomic fragments as a vector and applied in various economically important species [78].

Genotyping technologies for common bean

The use of genetic approaches for the investigation and analysis of genetic basis having an association with phenotype has greatly facilitated the improvement of the traits of interest. Advancement in genotyping and sequencing technologies revolutionized the breeding activities for various crops [65]. With the emergence of next generation sequencing (NGS) technologies, whole-genome sequencing data and millions of genome-wide single nucleotide polymorphisms (SNPs) for high-throughput genotyping became available for a variety of genetic studies [79]. Various SNP-genotyping platforms like Taqman, SNPlex, BioMark HD, KASPar, Axiom Biobank, Infinium II, GoldenGate, and iPlex have been developed, and successfully used for the genotyping of the various crop [80]. Specific to common bean Blair et al. [81], reported the first 736 SNP chip. Similarly Song et al. [82], developed the BARCBean6K_1 BeadChip with >5000 SNPs, which have been successfully used in various studies [83–85]. Moreover, genetic studies in common bean have been also performed using other genotyping platforms like Genotyping-by-sequencing (GBS) [86], Fluidigm platform (www.fluidigm.com) or by KASP genotyping at LGC Genomics service provider (http://www.lgcgroup.com, 87].

Development of linkage maps in common bean

Many researchers have conducted studies based on linkage analysis to determine locations of important genes on the related chromosomes of common bean. Freyre et al. [41] first conducted a study to a generate a linkage map for common bean and determined 1258.8 cM genetic distance with 11 linkage groups (LGs). A total of 413 loci are distributed across these 11 LGs having 3.0 cM average distance between neighboring loci. In this study, they developed a RI population (known as BJ population) by crossing BAT93 (Middle American) and Jalo EEP558 (Andean landrace). This BJ population is considered a universal common bean mapping population and has been successfully used to develop linkage maps and other breeding studies in common bean [10, 49, 88–97]. Yu et al. [71] also developed a common bean linkage map with SSRs using similar populations. Blair et al. [40] constructed a genome-wide anchored microsatellite map from DOR364 x G19833 populations and they identified 150 SSRs. It is known that more than 25 linkage maps have been developed for common bean [10]. These genetic maps play a critical role in the development of various types of markers. On the other hand, advancements in sequencing technologies reduced the genotyping cost and resulted in developing millions of SNP markers for common bean [81, 8–101]. The powerful genetic tool has led to the improvement of huge scale molecular markers and the determination of numerous marker–trait associations. Higher numbers of markers resulted in the dense genetic maps that are very helpful for precise localization of major genes and identification of different QTLs controlling various traits of interest [102].

Common bean breeding for biotic and abiotic stresses

More than 200 biotic stress factors causing significant yield and quality losses in common bean have been reported so far [103,104]. Antrachnose (ANT, caused by *Colletotrichum lindemuthianum*), angular leaf spot (ALS, caused by *Phaeoisariopsis griseola*), common bacterial blight (CBB), bean golden mosaic virus (BGMV)

and bean common mosaic virus (BCMV) are known as the most significant bean diseases worldwide [05–107]. Concerning biotic and abiotic stress factors in common bean, numerous quantitative trait loci (QTL) mapping studies have been performed after development of different molecular techniques. For example, several QTLs about white mold (*Sclerotinia sclerotiorum* (Lib.) de Bary) as a major constraint to common bean were reported by Park et al. [91] Kolkman and Kelly [94], Ender and Kelly [108], Mkwaila et al. [109] and Soule et al. [110]. These studies have given valuable information for this disease in common bean. Soule et al. [110] identified QTLs (*WM4.2, WM5.3, WM5.4* and *WM7.3*) first time having an association with white mold. Another important biotic factor is angular leaf spot (ALS) caused by the hemibiotrophic fungus *Pseudocercospora griseola* (Sacc.) Crous and U. Braunis that significantly affects the yield of common bean. Oblessuc et al. [111] identified seven QTLs at ALS effects, four of which were mapped firstly in their research. In another study Keller et al. [112], discovered a region containing 36 candidate genes for ALS resistance. In another realm, two QTLs (*FRR2.2CM* and *FRR2.3CM*) located on Pv02 associated with fusarium root rot, which is a soil-borne disease that constrains common bean yield, were reported by Wang et al. [113]. Regarding thrips resistance (*Thrips palmi* Karny), only a QTL named as *Tpr6.1* located on LG b06 was determined by Frei et al. [114]. Concerning the bean weevil (*Acanthoscelides obtectus* [Say]) which is a crucial postharvest pest of common bean seed Kamfwa et al. [115], discovered three QTLs on chromosomes Pv04 and on Pv06. In addition to these QTLs examples related to biotic stress factors, several QTL studies were also released about abiotic stress factors. For instance Diaz et al. [87], detected 143 QTLs under different stress treatments (drought, P, and Al stresses). Similarly Dramadri et al. [116], identified 18 QTLs, especially those for partitioning and seed yield under drought stress. In another very recent report Sedlar et al. [117], identified QTLs in moderate drought treatment (*Wp10.1, Wp1.1, Wp1.2, Wp1.3, Wp5.1, ΦPSII5.1, and ΦPSII9.1*) and severe drought treatment (*Wp6.2, Wp8.1, Wp9.1, Wp1.2, Wp3.1, Wp7.1, ΦPSII3.1, ΦPSII7.1,* and *ΦPSII11.1*) for leaf water potential (*Wp*) and effective quantum yield of PSII (*ΦPSII*). Additionally, extensive QTLs data obtained from previous studies are presented in Table 2. Also, extensive data for SCAR markers developed to track many significant diseases of common bean are freely accessible on http://bic.css.msu.edu/_pdf/SCAR_Markers_2010.pdf. Such findings will undoubtedly assist breeders in efforts to improve common bean cultivars resistant to biotic and abiotic stresses with super high yield.

Common bean breeding for agronomic traits

Genetic resources are fundamental in improving agricultural productivity. These resources contain a variety of alleles necessary for resistance and tolerance to the different diseases, pests and harsh environments found in their natural habitat, and can be used in various breeding programs. One of the main objectives of the common bean breeding programs is to develop high-yielding cultivars with better quality [43]. Previous studies reported that yield-related traits are controlled by several complex genes [148–150]. During the last twenty years, many QTLs about various agronomic traits in common bean have been identified. In addition, few scientific groups [38, 151] were interested in the nutrition traits QTLs of common bean worldwide. A glimpse of the diverse applications of QTLs/genes for various agronomic traits in common bean research is presented in Table 3. Even though various researchers have determined QTLs with the same chromosomal locations for different agronomic traits, further screening is needed to pinpoint the candidate genes for breeders. Finally, compiling all valuable genomic information related to QTL traits herein will help plant breeders to improve cultivars having higher-yield and resistance to biotic and abiotic factors to meet the diverse demands of humankind.

Genome wide association studies (GWAS) in common bean

Dissecting the genetic control of traits of interest is of pivotal importance to foster common bean breeding and to develop new varieties able to adapt to changing climatic conditions. Genome Wide Association Studies (GWAS) is considered the next step, after QTL mapping, to investigate the genetic basis having significant association with traits of interest. During the last decade, a good number of GWAS studies have been conducted in different genetic resources to uncover the genetic basis controlling various traits like flowering, cooking time, seed traits, mineral and antioxidant activity. Cichy et al. [83] performed a study with a similar approach in a panel of 206 *P. vulgaris* accessions to investigate the genetic diversity and cooking time variations, and focused on chromosomal regions distributed on chromosomes Pv02, Pv03, and Pv06 associated with cooking time. Nemli et al. [164] also reported a study with genotyping by sequencing

Table 2. Biotic and Abiotic stress related QTLs/markers in common bean.

Trait	Gene/QTL	Marker	Linkage group	Reference
Anthracnose	*Co-1*	OF10530	B1	[118, 119]
Anthracnose	*Co-1*	ATA03	B1	[120]
Anthracnose	*Co-u*	NDSU_IND_2_40.3966	B2	[120]
Anthracnose	*Co-2*	PV-ag001	B11	[40, 121]
Anthracnose	*Co-3*	SW12	B4	[120]
Anthracnose	*Co-3*	g1375	B4	[120]
Anthracnose	*Co-3/9*	SCAR (SW12)	B4	[122, 88]
Anthracnose	*Co-4*	SCAR (SC08)	B8	[40, 123]
Anthracnose	*Co-4*^{2}	RAPD (OH 18, OBB14) SCAR (SHI8, SBB14)	B4,B8	[124]
Anthracnose	*Co-5*	SCAR (Phs)	B7	[125, 22]
Anthracnose	*Co-5*	SSR (BM210)	B7	[40, 125]
Anthracnose	*Co-6*	RAPD ((OAH1$_{780}$, OAK20$_{890}$)	B7	[126]
Anthracnose	*Co-7*	BM183	B7	[127]
Anthracnose	*Co-9*	SB12	B4	[128]
Anthracnose	*Co-9*	NDSU_IND_9_29.1822	B9	[120]
Anthracnose	*Co-10*	RAPD (OF10$_{1100}$)	B4	[129, 93]
Anthracnose	*Co-13*	OPV20$_{680}$	B3	[120]
Anthracnose	*Co-17*	*	B3	[120]
Anthracnose	*Ur-5*	SCAR (SI19)	B4	[130, 88]
Rust	*Ur-3*	OK14$_{620}$	B11	[131, 132]
Rust	*Ur-4*	0F10$_{970}$, 0I19$_{460}$	B6:B4	[132]
Rust	*Ur-5*	RAPD (OI19$_{460}$) SCAR (SI19)	B4	[130, 132]
Rust	*Ur-6*	OAY15.200	B11	[133]
Rust	*Ur-7*	OAB18.650	B11	[134]
Rust	*Ur-9*	RAPD (OA4.1050)	B4	[135, 136]
Rust	*Ur-11*	OAE19$_{890}$	B11	[137, 138]
Rust	*Ur-12*	O13.1350	B4	[135]
Rust	*Ur-13*	SCAR (KB126)	B8	[139]
Bean Common Mosaic Virus	*I*	RAPD (OW13$_{690}$)	B2	[131]
Bean Common Mosaic Virus		SCAR (SW13)	B2	[140]
Bean Common Mosaic Virus	*bc-1*	OH14$_{1100}$	B3	[141]
Bean Common Mosaic Virus	*bc-u*	OC16$_{1100}$	B3	[141]
Bean Common Mosaic Virus	*bc-1*^{2}	SCAR (SBD5$_{1300}$)	B3	[88]
Bean Common Mosaic Virus	*bc-3*	ROCII/350/420, ROC20/ 460	B6	[142]
Bean Common Mosaic Virus	*bc-3*	OG6$_{595}$	B6	[143]
Common bacterial blight	-	RAPD (BC420$_{900}$)	B5	[70]
Common bacterial blight	-	SCAR (SAP6)	B10	[88]
Bean golden mosaic virus	*bgm-1*	RAPD (R2$_{570/530}$)	B3	[144]
Bean golden yellow mosaic virus	*bgm-1*	SCAR (SR2: SR21)	B3	[145]
Drought				
Drought	*P5CS2*	Bng126 ; BMd045	B1	[146]
Drought	*Sw6.13*	BM187	B6	[147]
Drought	*Sw9.1*	BM114	B9	[147]
Drought	*Sw9.2*	N201	B9	[147]
Drought	*Sw6.14*	AG1301	B6	[147]
Drought	*Sw6.15*	AB1001	B6	[147]
Drought	*Sw6.16*	BM187	B6	[147]
Leaf water potential	*Wp5.2*	AGTC02 BMd53	Pv05	[117]
Leaf water potential	*Wp6.1*	SSR-IAC47 BMb519	Pv06	[117]
Effective quantum yield of PSII	*ΦPSII7.1*	BMb502 BM150	Pv07	[117]
Effective quantum yield of PSII	*ΦPSII10.1*	BM212 BMd42	Pv10	[117]
Effective quantum yield of PSII	*ΦPSII11.1*	BMd22 BM239	Pv11	[117]
Days to flowering	*Df1.1*	BMb356 ATA3	Pv01	[117]
Days to pod-setting	*Dp1.1*	ATA3 BMb1024	Pv01	[117]
Number of seeds per pod	*Sp2.1*	BM236 BM156	Pv02	[117]
Seed yield per plant	*Syp1.1*	BMb356 ATA3	Pv01	[117]
Seed yield per plant	*Syp2.1*	CAAT04 BM139	Pv02	[117]
Seed yield per plant	*Syp4.1*	CCTA05 AGGT07	Pv04	[117]
100 seed mass	*Hsm2.2*	BM142 PVBR25	Pv02	[117]
Days to flowering (DF)	*DF3.2PR*	ss715639424	Pv03	[116]
Days to flowering (DF)	*DF11.1PR*	ss715646273	Pv11	[116]
Days to maturity (DM)	*DM3.1PR*	ss715639424	Pv03	[116]
Pod weight per plant (PW)	*PW1.1PR*	ss715646076	Pv01	[116]
Pod weight per plant (PW)	*PW2.1PR*	ss715649478	Pv02	[116]
Pod weight per plant (PW)	*PW3.1PR*	ss715646441	Pv03	[116]
Pod weight per plant (PW)	*PW4.2PR*	ss715646215	Pv04	[116]
Seed yield per plant (SY)	*SY1.1PR*	ss715646076	Pv01	[116]
Seed yield per plant (SY)	*SY2.2BR*	ss715649478	Pv02	[116]
Seed yield per plant (SY)	*SY3.3PR*	ss715639424	Pv03	[116]
Seed yield per plant (SY)	*SY3.4PR*	ss715648183	Pv03	[116]
Seed yield per plant (SY)	*SY4.1PR*	ss715640609	Pv04	[116]
Seed yield per plant (SY)	*SY6.1PR*	ss715649019	Pv06	[116]

Harvest index (HI)	*HI6.1PR*	ss715649019	Pv06	[116]
Pod partitioning index (PPI)	*PPI1.1PR*	ss715648382	Pv01	[116]
Pod partitioning index (PPI)	*PPI2.1PR*	ss715647234	Pv02	[116]
Pod partitioning index (PPI)	*PPI11.1PR*	ss715648851	Pv11	[116]
Pod partitioning index (PPI)	*PPI11.2PR*	ss715650599	Pv11	[116]
Yield components	*Yd1.1*	Y503 1529725_567896	Pv01	[87]
Yield components	*Yd1.2*	95706_19407 AGTA09	Pv01	[87]
Yield components	*Yd1.3*	R1401 BMa6a	Pv01	[87]
Yield components	*Yd4.1*	V401 PV-CTT001	Pv04	[87]
Yield components	*Yd4.2*	CGAA03 871953_853527	Pv04	[87]
Yield components	*Yd7.1*	745181_210054 701495_548353	Pv07	[87]
Yield components	*Yd8.1*	BMc121 Q1702	Pv08	[87]
Yield components	*Yd8.2*	L201 S1001	Pv08	[87]
Yield components	*100SdW4.1*	T1202 115966_84234	Pv04	[87]
Percent yield loss under stress	*%YdL_D4.1*	806145_731182 CAAA01	Pv04	[87]
Percent yield loss under stress	*%YdL_LP7.1*	AG1003 E101	Pv07	87]
Percent yield loss under stress	*%SdWL_LP7.1*	H1803 235093_128558	Pv07	[87]
Percent yield loss under stress	*%SdWL_LP8.1*	O1502 BM229	Pv08	[87]
Trait for vigor plant	*PBMP4.1*	V401 PV-CTT001	Pv04	[87]
Trait for vigor plant	*SBMP4.1*	V401 PV-CTT001	Pv04	[87]
Dry matter redistribution	*HI8.1*	BM229 T402	Pv08	[87]
Dry matter redistribution	*PHI7.1*	O1501 W1604	Pv07	[87]
Dry matter redistribution	*PHI8.1*	CTTA01 CTTA04	Pv08	[87]
Dry matter redistribution	*PHI7.2*	H1803 235093_128558	Pv07	[87]
Dry matter redistribution	*TNC_Sh8.1*	BMc121 Q1702	Pv08	[87]
Dry matter redistribution	*TNC_Sh8.2*	L201 S1001	Pv08	[87]
Dry matter redistribution	*TNC_Sh8.3*	I703 CGAA07	Pv08	[87]
Phenological trait	*DF1.1*	156216_23400 I701	Pv01	[87]
Phenological trait	*DF1.2*	AGTA09 R1401	Pv01	[87]
Phenological trait	*DF1.3*	BMc324 CGAA05	Pv01	[87]
Phenological trait	*DF8.1*	BMc121 Q1702	Pv08	[87]
Phenological trait	*DF8.2*	C703 CTAT06	Pv08	[87]
Phenological trait	*DF8.3*	L201 S1001	Pv08	[87]
Phenological trait	*DF8.4*	O1502 BM229	Pv08	[87]
Phenological trait	*DH1.1*	156216_23400 1701	Pv01	[87]
Phenological trait	*DH1.2*	R1401 BMa6a	Pv01	[87]
Phenological trait	*DH8.1*	BMc121 Q1702	Pv08	[87]
Phenological trait	*DH8.2*	97394_85972 GGAA03	Pv08	[87]
Phenological trait	*DH8.3*	L201 S1001	Pv08	[87]
Phenological trait	*DH8.4*	I703 CGAA07	Pv08	[87]
Phenological trait	*DH8.5*	CTTA01 CTTA04	Pv08	[87]
Phenological trait	*DH8.6*	O1502 BM229	Pv08	[87]
Resistance to Weevil (*A. obtectus)*				
Percent of perforated seeds	*AO4.1SA*	ss715647359– ss715642594	Pv04	[115]
Percentage of perforated seeds		ss715639347– ss715639525	Pv04	[115]
Percentage of perforated seeds		ss715645757– ss715650286	Pv06	[115]
Seed weight	*SW4.1SA*	ss715642594– ss715640824	Pv04	[115]
Seed weight	*SW7.1SA*	ss715645839– ss715645208	Pv07	[115]
Seed weight	*SW8.1AN,SA*	ss715646527– ss715639591	Pv08	[115]
Seed weight	*SW9.4SA*	ss715647184– ss715647170	Pv09	[115]
Fusarium Root Rot				
Disease severity	*FRR2.2CM*	ss715648472 ss715648481	Pv02	[113]
Disease severity	*FRR2.3CM*	ss715647527 ss715639664	Pv02	[113]
Control root dry wt.	*RTWC2.1*	ss715639514 ss715649049	Pv02	[113]
Control root dry wt.	*RTWC9.1*	ss715645748 ss715645741	Pv09	[113]
Control root dry wt.	*RTWC11.1*	ss715649519 ss715640756	Pv11	[113]
Inoculated root dry wt.	*RTWI1.1*	ss715650911 ss715647371	Pv01	[113]
Inoculated root dry wt.	*RTWI11.1*	ss715649519 ss715640756	Pv11	[113]
Control shoot dry wt.	*STWC2.1*	ss715645964 ss715646140	Pv02	[113]
Control shoot dry wt.	*STWC11.1*	ss715649352 ss715650717	Pv11	[113]
Inoculated shoot dry wt.	*STWI1.1*	ss715650911 ss715647371	Pv01	[113]
Root loss	*RTL3.1*	ss715641329 ss715640990	Pv03	[113]
Root loss	*RTL7.1*	ss715648280 ss715648692	Pv07	[113]
Shoot loss	*STL7.1*	ss715648692 ss715646498	Pv07	[113]
Root dry wt.	*RTW7.1*	ss715648636 ss715648280	Pv07	[113]
Root dry wt	*RTW11.1*	ss715640807 ss715648956	Pv11	[113]
Shoot dry wt.	*STW4.1*	ss715649259 ss715646131	Pv04	[113]
Taproot diameter	*TD11.1*	ss715645475 ss715645476	Pv11	[113]
Lodging MRF	*LDG1.1*	ss715646076 ss715650911	Pv01	[113]
Seed wt.	*SW4.3*	ss715650213 ss715641823	Pv04	[113]
Seed wt.	*SW5.1*	ss715649583 ss715646173	Pv05	[113]
Seed wt.	*SW6.1*	ss715647111 ss715645671	Pv06	[113]
Angular Leaf Spot (ALS) Resistance				
Angular Leaf Spot (ALS)	*ALS4.1GS, UC: ALS10.11DG, UC, GS + ALS9.1GS*	–	4:10 + 9	[112]

Angular Leaf Spot (ALS)	*ALS4.1GS, UC*	Marker50	4	[112]
Angular Leaf Spot (ALS)	*ALS10.1DG, UC*	Marker17	10	[112]
Angular Leaf Spot (ALS)	*ALS4.1GS, UC: ALS10.1DG, UC*	–	4:10	[112]
Angular Leaf Spot (ALS)	*ALS9.1GS*	Marker33	9	[112]
Angular Leaf Spot (ALS)	*ALS5.2UC, GS*	Marker31	5	[112]
Angular Leaf Spot (ALS)	*ALS2.1UC*	IAC134 -IAC18b	B2	[111]
Angular Leaf Spot (ALS)	*ALS3.1UC*	PVBR21 - FJ19	B3	[111]
Angular Leaf Spot (ALS)	*ALS4.1GS,UC*	IAC52 - BMd9	B4	[111]
Angular Leaf Spot (ALS)	*ALS4.2GS,UC*	PVBR92 - Pv-gaat001	B4	[111]
Angular Leaf Spot (ALS)	*ALS5.1UC*	BMd53 - FJ05	B5	[111]
Angular Leaf Spot (ALS)	*ALS5.2UC*	BM175 - IAC261	B5	[111]
Angular Leaf Spot (ALS)	*ALS10.1DG,UC*	GATS11b - IAC137	B10	[111]
Resistance to White Mold				
Straw test	*WM2.3 BR,GC*	Me2Em4.350	B2	[109]
Straw test	*WM3.3 TW*	BM189	B3	[109]
Straw test	*WM9.2 TW*	F6R8.600	B9	[109]
Seed weight	-	BM189	B3	[109]
Seed weight	-	F1R8.300	B9	[109]
Canopy height	-	F5R5.180	B4	[109]
Canopy height	-	BM210	B7	[109]
Lodging	-	BMd-15	B4	[109]
Lodging		F1R1.275	B7	[109]

Table 3. Agronomic traits related QTLs/markers in common bean.

Locus/QTL/gene name	Trait	Chromosome	Approach and population	References
DO	Germination	Pv02, Pv03,Pv04,	Linkage mapping—RILs	[152]
DF (fin), DF df1.1, df2.1, df6.1, df9.1, df9.2, df11.1 ss715646578, ss715646088	Number of days to Flowering (Earliness)	Pv01, Pv08, Pv09 Pv01, Pv02, Pv06, Pv09, Pv11 Pv01, Pv08	Linkage mapping—RILs GWAS—domesticated	[145, 85, 152, 153]
Ref_259_comp19102_c0 Phvul.003G033400, Phvul.002G000500	Vernalisation and flowering time	Pv05 Pv03, Pv02	Candidate gene approach	[16, 33, 14]
DM, DM (fin) DM DM1, Dm5.1, Dm7.1, DM6.1, DM6.2	Number of days to maturity (Earliness)	Pv01 Pv09, Pv10 Pv01, Pv05, Pv07 Pv06	Linkage mapping—RILs Linkage mapping—F2:4 pop Linkage mapping—BC pop Linkage mapping—RILs	[145, 152, 153, 121]
St	Seed dispersal	Pv02	Linkage mapping—RILs	[152]
PvSHP1	Seed dispersal	Pv06	Candidate gene approacha/linkage mapping—RILs	[32]
Fin	Twining	Pv01	Linkage mapping—RILs	[152]
Cab1-1, Cab1-2, Cab2-1	Climbing ability	Pv04	Linkage mapping—RILs	[154]
NM (fin), NM	Number of nodes on the main stem	Pv01	Linkage mapping—RILs	[152]
TB, Brn1		Pv04	Linkage mapping—F2:4 pop, Linkage mapping—RILs	[154, 153]
NP (fin)	Number of pods	Pv01	Linkage mapping—RILs	[152]
NP	Number of pods	Pv08	Linkage mapping—RILs	[152]
NP, PPP	Number of pods	Pv04	Linkage mapping—RILs, Linkage mapping—F2:4 pop	[152, 153]
Pp7.2, Pp9.2 Pp11.3	Number of pods	Pv07 Pv09 Pv11	Linkage mapping—BC pop	[145]
PH PH	Plant height	Pv03 Pv07	Linkage mapping—F2:4 pop	[153]
Ph1.1, Ph6.1, Ph6.2 Ph7.1	Plant height	Pv06 Pv07	Linkage mapping—BC pop	[145]
Plh1-1 Plh1-3,Plh2-1 Plh1-4 Plh2-3	Plant height	Pv03 Pv04 Pv08 Pv11	Linkage mapping—RILs	[154]
PL	Pod length	Pv02,Pv07	Linkage mapping—RILs	[152]
ss715639408, ss715649359,ss715647392	Pod weight	Pv08	GWAS—domesticated	[85]
SW	100-seed weight	Pv01, Pv07, Pv11	Linkage mapping—RILs	[152]
SW	100-seed weight	Pv04, Pv11	Linkage mapping—F2:4 pop	[153]
Sw2.1, Sw2.2, Sw3.1, Sw6.1, Sw7.1, Sw8.1, Sw9.1, Sw10.1, Sw11.1	100-seed weight	Pv01, Pv02, Pv03, Pv04, Pv05, Pv06, Pv07, Pv08, Pv09,Pv10,Pv11	Linkage mapping—BC pop	[145]

Ref_259_comp6493, Ref_220_comp2070, Ref_25_comp3527, Ref_259_comp4515	Fruit size	Pv03	Candidate gene approach	[16, 33]
SL2 SL3 SL6 SL8 SL10	Seed length	Pv02 Pv03 Pv06 Pv08 Pv10	Linkage mapping—RILs	[121]
WI3 WI6 WI7	Seed width	Pv03 Pv06 Pv07	Linkage mapping—RILs	[121]
SH6 SH8	Seed height	Pv06 Pv08	Linkage mapping—RILs	[121]
Y	Seed yield	Pv05, Pv09, Pv10	Linkage mapping—F2:4 pop	
ss715648538, ss715646178	Seed yield	Pv03, Pv09	GWAS—domesticated	[85]
ct1.1 ct1.2 ct9.1 ct1.3 ct9.2 ct9.3	Cooking time	Pv01 Pv09	Linkage mapping- F2:5	[155]
BC500.400 Q05.850 Y07.1200 G03.1150 D12.700 J09.950 − 1.0 BC406.450 BC457.400	Seed Weight	Pv04 Pv05 Pv06 Pv03 Pv08 Pv07	Linkage mapping- RILs	[156]
BC457.400 AH18.700 + 2. P08.400 D12.700 H18.800 + 1.0 G03.1150 − 5.6 G08.1150	Seed length	Pv03 Pv08 Pv04 Pv11	Linkage mapping- RILs	[156]
G08.1150 BC406.750 G03.850 + 3.0	Seed height	Pv04 Pv06 Pv11	Linkage mapping- RILs	[156]
Int1 Int2 Int3 Int4	Internode length	Pv04	Linkage mapping- RILs	[154]
Swf3.1 Swf4.1 Swf11.1	Seed weight	Pv03 Pv04 Pv11	Linkage mapping—RILs	[157]
Sw6.15 Sw6.16 Sw6.2 Sw2.2 Sw2.3 Sw5.1 Sw6.3 Sw6.4 Sw6.5 Swf3.1	Seed weight	Pv02 Pv05 Pv06	Linkage mapping—RILs	[147]
SY10.1 SY3.3 SY7.3 SY7.4	Seed Yield	Pv10 Pv03 Pv07	Linkage mapping—RILs	[158]
SW8.3 SW9.3	Seed Size	Pv08 Pv09	Linkage mapping—RILs	[158]
DF1.1 DF1.2 DF1.3	Day to flowering	Pv01	Linkage mapping—RILs	[158]
DM81	Days to Maturity	Pv08	Linkage mapping—RILs	[158]
LDG7.1 LDG7.2 LDG1.1	Lodging Score	Pv07 Pv01	Linkage mapping—RILs	[158]
TF1-TF2-TF3-TF4-TF5 TF6-TF7-TF8-TF9-TF10 TF11-TF12	Time to flowering	Pv01 Pv03 Pv04 Pv06 Pv07 Pv11	Linkage mapping—RILs	[159]
SSP-MO14 SSP-MO15 SSP-MO16 SSP-CA14 SSP-CA16 SSP-H2CA16	Stone Seed Percentage (SSP)	Pv01 Pv02 Pv05 Pv07	Linkage mapping—RILs	[160]
HC-MO14 HC-MO15 HC-MO16 HC-CA14 HC-CA16 -HC-H2CA16	Hydration Coefficient (HC)	Pv01 Pv02 Pv07 Pv08	Linkage mapping—RILs	[160]

SW-MO14	100 Seed (SW)	Pv01	Linkage mapping—RILs	[160]
SW-MO15		Pv03		
SW-MO16		Pv07		
SW-CA14 - SW-CA16		Pv08		
SW-H2CA16				
SY-MO14	Seed Yield (SY)	Pv03	Linkage mapping—RILs	[160]
SY-MO16		Pv07		
		Pv08		
CBS381	100 Seed Wight	Pv03	GWAS- 395 common bean accessions	[161]
CBS162		Pv05		
CBS83		Pv07		
P7S191		Pv10		
CBS162	Seed Length	Pv05	GWAS- 395 common bean accessions	[161]
CBS170				
CBS178				
CBS179				
P9S153	Seed Width	Pv01	GWAS- 395 common bean accessions	[161]
CBS345		Pv03		
CBS91		Pv05		
CBS13		Pv06		
CBS23		Pv09		
CBS190				
CBS208				
CBS381	Seed Height	Pv04	GWAS- 395 common bean accessions	[161]
CBS57		Pv02		
CBS149		Pv10		
SW3.1GA	Seed Weight	Pv03	Linkage mapping—RILs	[162]
SW4.1GA		Pv04		
SW5.1GA		Pv05		
SW6.1GA		Pv06		
SW9.1GA		Pv09		
SW9.2GA		Pv11		
SW11.1GA				
SL2.1GA	Seed Lenght	Pv02	Linkage mapping—RILs	[162]
SL8.1GA		Pv08		
SL9.1GA		Pv9		
SWi2.1GA	Seed Width	Pv02	Linkage mapping—RILs	[162]
SP4.1GA	Number of Seed per Pod	Pv01	Linkage mapping—RILs	[162]
SP1.1GA		Pv04		
PP2.1GA	Number of Pod per Plant	Pv02	Linkage mapping—RILs	[162]
PP3.1GA		Pv03		
NS2.1GA	Number of Seed per Plant	Pv02	Linkage mapping—RILs	[162]
NS6.1GA		Pv06		
NB4.1GA	Number of primary Branches	Pv03	Linkage mapping—RILs	[162]
NB4.2GA		Pv04		
NB3.1GA				
NB3.2GA				
PL1.1GA	Pod Length	Pv01	Linkage mapping—RILs	[162]
PL4.1GA		Pv04		
PL4.2GA				
HI1.1GA	Harvest Index	Pv01	Linkage mapping—RILs	[162]
HI2.1GA		Pv02		
SY3.1GA	Seed Yield	Pv03	Linkage mapping—RILs	[162]
SY3.2GA		Pv09		
SY9.1GA				
SY9.2GA				
Yld5.1	Yield	Pv05	Linkage mapping—BC pop	[151]
Sw2.1	Seed weight	Pv02	Linkage mapping—BC pop	[151]
Sw3.1		Pv03		
Sw5.1		Pv05		
Sw9.1		Pv09		
Sw9.2				
Sw2.2				
Sw3.2				
Sw5.2				
Sw5.3				
Fe7.1	Iron conc.	Pv07	Linkage mapping—BC pop	[151]
Fe_cont8.1	Iron content	Pv08	Linkage mapping—BC pop	[151]
Zn_cont2.1	Zinc content	Pv03	Linkage mapping—BC pop	[151]
Zn_cont5.1		Pv05		
Zn_cont5.2		Pv07		
Zn_cont7.1				
Ira2.1	İron reductase activity	Pv02	Linkage mapping—RILs	[163]
Ira11.1		Pv11		

(GBS) approach in 173 common bean accessions for identification of SNPs associated with various pod traits. They identified 43,018 SNPs markers, and 45 of the SNPs showed significant associations with different pod traits. In addition to these reports Moghaddam et al. [165], performed a study using a panel of 280 modern bean genotypes from race Mesoamerica and investigated ~30 candidate genes controlling various agronomic traits. Perseguini et al. [166] performed a GWAS for quantitative resistance loci (QRL) controlling resistance to the anthracnose (ANT) and angular leaf spot (ALS). They reported that statistically significantly 21 and 17 associations were determined for ANT and ALS, and the markers SSR-IAC167 and PvM95 located on chromosome Pv03 and the SNP scaffold00021_89379 were associated with both diseases. Ferreira et al. [167] conducted a GBS study for the investigation of introgressed genomic regions associated with the anthracnose, bean common mosaic virus and bean common mosaic necrosis virus. They investigated 12,697 SNPs distributed on different chromosomes and their results verified the positions of resistance genes (*I*, *Co-3*, *bc-3*, and *Co-2)* on the chromosomes Pv02, Pv04, Pv6, and Pv11, respectively. In addition to these examples, various GWAS conducted to identify genetic loci linked to drought-related traits and drought resistance in common bean [168–171]. Wu et al. [171] identified 196 association loci containing 230 candidate SNPs as being linked to drought resistance in common bean. On the other hand Leitão et al. [172], determined a total of 133 SNPs for transpiration rate, net CO2 assimilation rate, stomatal conductance, chlorophylls a/b, carotenes, and xanthophyll contents. Ninety of these associations were found under water-deficit conditions. To the best of our knowledge, the most notable GWAS studies conducted in common bean are provided in Table 4. To sum up, important breakthroughs in the field of GWAS in recent years have taken common bean research to a new dimension. These resources will provide a new framework for breeders to accelerate the common bean improvement.

Kompetitive allele specific PCR (KASP) technology in common bean

Kompetitive Allele Specific PCR (KASP) is a modern technique of SNP genotyping requiring only a few SNP markers to genotype various samples. This technology was developed by LGC Genomics Ltd., based on fluorescent signals, and emerged as an efficient and very low-cost genotyping method [198,199]. In common bean, very few numbers of KASP genotyping studies have been conducted. For example Hurtado-Gonzales et al. [200], aimed to develop highly specific, tightly linked, effective molecular markers having an association with *Ur-3* rust resistance gene in common bean. They found that SS68 KASP marker has an association with *Ur-3* rust resistance gene. They performed the validation of this marker on a panel of 130 diverse common bean, evaluated SS68 KASP as a highly accurate marker having no false results. Bean yellow mosaic virus (BYMV) is a major limitation to common bean production. Hart and Griffiths [86] aimed to develop markers having resistance to this important disease. They found a total of 44 SNP markers having an association to the phenotype and they converted seven of these markers into KASP assay and found tight linkage of these markers to BYMV resistance in an F2 population of 185 individuals. Anthracnose is considered one of the most destructive diseases of common bean. Recently Gilio et al. [201], aimed to perform fine mapping for anthracnose-resistance *locus* and to develop markers tightly linked to this locus. They found KASP markers ss56 and ss92 the as most tightly linked markers to Co-AC locus.

Functional genomics studies in common bean

Functional genomics (FG) is crucial for crop improvement and provides a deep insight into molecular plant breeding by classifying the expressed genes, metabolites and proteins related to specific characteristics [202]. FG helps to identify the genes regulating crop improvement, resistance to abiotic/biotic stress factors, yield and multiple different components influencing the economic importance in legumes. A cell contains a complete set of transcriptomes, so understanding the transcriptome is very beneficial for interpreting the functional elements of the genome. Transcriptomics is mainly applied to investigate the transcriptional structure of genes, changes in each transcript due to various conditions. Different types of techniques have been developed and applied in various crops to deduce and quantify the transcriptome [203]. As common bean is an important legume crop, a lesser amount of short expressed sequence tags (ESTs) was only identified with conventional processes. Hatey et al. [204] described ESTs as partial sequences of transcribed genes that represent gene expression in various tissues in which mRNA was obtained in different genotypes. Various studies have been conducted to create cDNA libraries for various legume crops [205–208] and stated that the number of ESTs currently available for all plant species are more than 21 million

Table 4. Genome-wide association studies for common bean to investigate the genetic basis associated with trait of interests.

Trait	Material Type	Marker Type	Idenfied Markers	Chromosome Number	Reference
Pod fibre	Genotype	SSR	5	Pv03, Pv06, Pv09, Pv10	[173]
Pod fibre	Genotype	SNP	3	Pv01, Pv05, Pv06	[173]
Plant type	Genotype	SSR	4	Pv06, Pv07	[173]
Plant type	Genotype	SNP	1	Pv01	[173]
Growth habit	Genotype	SSR	5	Pv06, Pv07, Pv10	[173]
Growth habit	Genotype	SNP	3	Pv01, Pv02	[173]
Seed per pod	Genotype	SSR	1	Pv01	[173]
Days to flowering	Genotype	SSR	4	Pv07, Pv08, Pv10	[173]
Days to flowering	Genotype	SNP	12	Pv01, Pv02, Pv11	[173]
Water uptake	Line	SNP	7	Pv01, Pv03, Pv06, Pv07	[83]
Cook time	Line	SNP	11	Pv02, Pv03, Pv06,	[83]
Days to flowering	Genotype	SNP	2	Pv01, Pv08	[85]
Days to maturity	Genotype	SNP	1	Pv01	[85]
Biomass	Genotype	SNP	2	Pv02, Pv08	[85]
Harvest index	Genotype	SNP	2	Pv03	[85]
Pod harvest index	Genotype	SNP	1	Pv04	[85]
Number of pods	Genotype	SNP	2	Pv05, Pv07	[85]
Pod weight	Genotype	SNP	3	Pv08	[85]
Seed number	Genotype	SNP	2	Pv03, Pv05	[85]
Yield per plant	Genotype	SNP	3	Pv08, Pv09	[85]
Seed yield	Genotype	SNP	2	Pv03, Pv09	[85]
Days to flowering	Genotype	SNP	6	Pv01, Pv07	[165]
Days to maturity	Genotype	SNP	5	Pv04, Pv11	[165]
Growth habit: with determinate genotypes	Genotype	SNP	9	Pv01, Pv07, Pv08	[165]
Growth habit: determinate genotypes excluded	Genotype	SNP	7	Pv04, Pv06, Pv07, Pv11	[165]
Lodging	Genotype	SNP	5	Pv07, Pv08	[165]
Canopy height	Genotype	SNP	4	Pv07	[165]
Seed weight	Genotype	SNP	4	Pv03, Pv08, Pv10	[165]
Anthracnose	Genotype	SNP	21	Pv03, Pv08	[166]
Anthracnose Resistance	Lines	SNP	6	Pv01, Pv02, Pv04	[174]
Angular leaf spot	Genotype	SNP	17	Pv04	[166]
Halo blight	Genotype	SNP	1	Pv5	[175]
Shoot biomass at harvest under irrigation	Genotype	SNP	7	Pv11	[170]
Shoot biomass at harvest under rainfed conditions	Genotype	SNP	5	Pv11	[170]
Shoot biomass at flowering under irrigation	Genotype	SNP	2	Pv02, Pv08	[170]
Seed size under irrigated and rainfed conditions	Genotype	SNP	2	Pv09	[170]
Leaf elongation	Genotype	SNP	1	Pv03	[170]
Wilting	Genotype	SNP	1	Pv11	[170]
Anthracnose	Cultivars	NBS-SSR markers	9	Pv02, Pv11	[176]
common bacterial blight	Cultivars	NBS-SSR markers	7	Pv03, Pv04, Pv07	[177]
Days to flowering	Genotype	DArTseq	6	Pv02, Pv03, Pv07, Pv08, Pv10	[178]
Protein	Genotype	SNP	5	Pv03, Pv06, Pv07	[179]
Zn	Genotype	SNP	6	Pv07, Pv10	[179]
Ca	Genotype	SNP	5	Pv01, Pv02, Pv04, Pv11	[179]
FeBIO	Genotype	SNP	5	Pv06, Pv07, Pv11	[179]
Days to first flowering	Genotype	SNP	1	Pv02	[180]
Days for flowering	Genotype	SNP	7	Pv01, Pv02, Pv03, Pv07, Pv10, Pv11	[180]
Days to flowering	Genotype	SNP	14	Pv03, Pv4, Pv08	[181]
Days to maturity	Genotype	SNP	14	Pv03, Pv4, Pv08	[181]
Days to flower in heat condition	Genotype	SNP	19	Pv01, Pv02, Pv03, Pv11	[181]
Bruchid Resistance	Genotype	SNP	24	Pv5, Pv7	[182]
Flowering	Genotype	SNP	8	Pv01, Pv04, Pv06, Pv08	[183]
Soybean cyst nematode	Genotype	SNP	37	Pv01, Pv02, Pv04, Pv05, Pv06, Pv07, Pv08, Pv09, Pv10, Pv11	[184]
Rhizoctonia solani	Genotype	SNP	Many	Many	[181]
Seed coat traits	Genotype	SNP	4	Pv08, Pv10	[185]
HG 2.5.7 soybean cyst nematode resistance	Genotype	SNP	6	Pv01, Pv09	[186]
HG 1.2.3.5.6.7 soybean cyst nematode resistance	Genotype	SNP	1	Pv07	[186]
Bean Fly	Genotype	SNP	5	Pv01	[187]
Heat tolerance	Genotype	SNP	120	All chromosomes	[188]
Seed coat color	Genotype	SNP	10	Pv02, Pv03, Pv06, Pv09	[186]
Seed weight	Genotype	SNP	14	Pv02, Pv03, Pv07, Pv11	[186]

Total Phenolic Content	Cultivars	SNP	11	Pv01, Pv03, Pv04,Pv07, Pv09, Pv10,Pv11	[189]
Pod color	Cultivars	SNP	6	Pv02, Pv03, Pv05	[189]
Flower color	Cultivars	SNP	13	Pv01, Pv03, Pv09	[189]
Zinc	Genotype	SNP	3	Pv01	[190]
Ca contents	Genotype	SNP	16	Pv02, Pv03, Pv04, Pv08, Pv10, Pv11	[191]
Mn contents	Genotype	SNP	31	Pv01,Pv02, Pv03, Pv05, Pv08, Pv10, Pv11	[191]
Anthracnose resistance (race 3, 87, and 503)	Genotype	SNP	Many	Pv04 (Strongly)	[192]
Anthracnose resistance (race 73)	Genotype	SNP	Many	Pv08 (Strongly)	[192]
Anthracnose resistance (race 2047)	Genotype	SNP	Many	Pv03,Pv09, Pv11 (Strongly)	[192]
Anthracnose	Accessions	SNP	9	Pv01, Pv04, Pv05, Pv08, Pv10	[193]
angular leaf spot	Accessions	SNP	8	Pv02, Pv03, Pv04, Pv06, Pv08	[193]
Sclerotinia sclerotiorum	Lines	SNP	Many	Many	[194]
Pythium root rot	Genotype	SNP	8	Pv01,Pv02, Pv04, Pv05, Pv09	[195]
Anthracnose resistance (race 73)	Genotype	SNP	3	Pv07	[196]
Antioxidant Activity	Genotype	DArT	4	Pv03,Pv07	[7]
Colletotrichum lindemuthianum	F2 population	SNP	8	Pv04	[197]

sequences. More than 3 million of all sequences have been produced from legumes. Development of ESTs to common bean started with moderate amounts of GenBank entries by groups from CIAT-Colombia, UNESP-Brazil and UNAM-Mexico organizations [209–211]. Ramirez et al. [211] served as the starting point for the common bean functional genomics. The project conducted by Ramirez et al. [211] was basically started to generate EST profiles of P-deficient roots and N_2-fixing root nodules. However, EST resources for pods and leaves of common bean was also determined during the project. A total of 21,026 ESTs obtained from five different cDNA libraries containing phosphorus-deficient roots, nitrogen-fixing root nodules, developing leaves and pods of the Negro Jamapa 81 (Mesoamerican genotype). The details of statistics of common bean ESTs are presented in Table 5. These sequences were separated into four main sections, such as plant development and cell cycle, metabolism, interaction with the environment, and unknown function. The investigated resources have contributed to genetic and genomic studies in common bean worldwide because these sequences have played a greater role in the understanding of common bean improvement, metabolism, and adaptations to various stresses [33].

Melotto et al. [210] used the anthracnose resistant breeding line SEL 1308 as the source of mRNA. cDNA libraries (PVEPLE1, PVEPSE2, and PVEPSE3) were generated from leaves, shoots and inoculated shoots of bean seedlings. A total of 5255 single-pass sequences were involved in the database after selection based on the quality of the sequences. Then, these EST sequences were trimmed and constructed a UniGene collection including 3126 sequences. Among these, 314 unigenes revealed important resemblances to genomic sequences of common bean and ESTs, which shows that 2818 unigenes of the database represent recently identified common bean genes. Additionally, 387 out of all unigenes were determined as common bean specific. Tian et al. [212] constructed the cDNA library to classify genes related to phosphorous starvation where a comparatively well-adapted cultivar to low Pi conditions and Pi-efficient genotype (G19833) was used as material. They identified Pi starvation-responsive genes (+240 putative) and identified clones were sequenced, and BLASTx/BLASTn analysis showed an array of 82 genes revealing a high ratio of sequence homology to known and unknown proteins in the database. Following this, differentially expressed genes were divided into five categories: signaling-transcription, transporter-channel, stress-defense, carbon metabolism and another metabolism.

McClean et al. [213] utilized all available EST sequences to improve contig sequences representing gene space in the genome. Their results revealed that most genes had only one copy in common bean, while there were duplicated genes in the soybean genome. This situation is an indication of the diploid history of common bean compared to the soybean polyploidy

Table 5. Sequencing and contigging statistics of common bean ESTs (adapted from Blair et al. [214]).

Tissues	Mesoamerican nodules	Mesoamerican pods	Mesoamerican roots	Mesoamerican leaves	Andean leaves (5′-3′)	Total ESTs
Total No. of ESTs Sequenced	4.636	3.667	4.329	3.456	4.938	21.026
Sequencing Success Percentage	81.6	82.7	74.2	78.2	67.0	76.3
Good-Quality ESTs Used for Contigging	3.745	2.951	3.165	2.677	3.243	15.781
ESTs in Contigs	2.441	1.929	1.774	1.983	1.951	10.078
EST Singletons	1.304	1.022	1.391	694	1.292	5.703

background. Similarly, McConnell et al. [10] used new sequence-based sources to characterize SNPs and InDel density in the genome. Sequence data were obtained from 550 gene fragments of two commonly used common bean genotypes (BAT93 and Jalo EEP558) for research activities. They identified over 1,800 SNPs and InDels, 300 of which were screened in the RI population, and 395 polymorphic gene fragments were obtained from nearly 593 kb sequence data. The sequences of BAT93 and Jalo EEP558 were compared with each other, and with the contig sequences to determine SNPs and InDel polymorphisms. Blair et al. [214] conducted a study using full-length cDNA technology to develop ESTs. They constructed the library to relate genes expressed in various conditions, such as low soil phosphorus, drought and high soil aluminum toxicity, using BAT477 and G19833 genotypes. It was determined that 4,219 unigenes were recognized consisting of 1,238 singletons and 2,981 contigs. Nearly half of the sequences were found as unique or represented the 5′ ends of known genes compared to other EST sequencing in common bean Table 6. These results can be beneficial to functional gene explanation, investigation of splice site variants, discovery and validation of drought or abiotic stress-associated genes in common bean.

The ESTs in databases are suitable resources for the identification of EST-derived SSRs. As a good example, 302 new EST-SSR markers from 9.583 ESTs revealing good amplification quality were developed based on transferability and polymorphism information by Garcia et al. [73]. Their results showed that 82% of them were transferable across at least one species. The average PIC value was determined as 0.53-genomic SSRs, 0.47-EST-SSRs, and the average amount of alleles per locus was 4 and 3, respectively. Another set of genomic data was constructed by Kalavacharla et al. [216] as they sequenced many cDNA libraries from different plant tissues (leaves, flowers, pods, and roots) using the Roche 454-FLX pyrosequencing platform. The 59,295 unigenes containing 39,572-contigs and 19,723-singletons were identified, and they provided a substantial transcriptome dataset to common bean. It was determined that 31,664 unigenes had no matches to GenBank and could be thought of as new common bean transcripts. Literally, the study resulted in a 150% increase in the amount of common bean ESTs.

In summary, the EST sequences of common bean present the foundation for genome-wide transcript studies. They are sources of established molecular markers to map linkage groups and anchored to physical maps. Additionally, full-length cDNA technology can be very functional for sequencing of the transcriptome, gene annotation, comparative genomics and identification of the genetic basis of agronomically important traits.

Transcription factors in common bean

Transcription factors (TFs) are important genes synchronizing signal transduction and expression of genes during biotic and abiotic stress responses [176]. Due to the importance of TFs, in the regulation of stress-related genes, investigations on plant TFs have been rising rapidly in recent years. In line with this purpose, various studies have been conducted to identify different TFs and to determine the expression levels of these genes under biotic and abiotic stress conditions in common bean. For instance, Apetala2-ethylene-responsive element binding factor (*AP2-ERF*) gene family was identified by Kavas et al. [217]. It was noted that the expression levels of 9 *PvAP2-ERFs* genes were determined in salt-stressed leaf/root tissues. Similarly Kavas et al. [218], classified 155 *bHLH* (basic helix-loop-helix) genes by using bioinformatics tools and investigated the expression levels of 16 *PvbHLH* genes to salt stress in the root/leaf tissues. In another study Büyük et al. [219], investigated a total of 24 candidate *HSP7*0 (heat shock protein 70) genes in leaf/root tissues. In a more comprehensive study, a total of 86 *NAC* (*NAM, ATAF1/2* and *CUC2*) genes were identified by Wu et al. [220]. It was noted that the expression patterns of the 22 *NAC* genes were varied under drought stress conditions.

Another important TF gene named *C2C2-YABBY* was identified İnal et al. [221]. They aimed to investigate some potential genes associated with salt tolerance

Table 6. Comparison of major EST sequencing efforts in common bean (adapted from Blair et al. [214]).

Sequence read	Clones	Sequence reads*	Singletons	Contigs	Unigenes	PUPS (%)	MEL (nt)	MCL (nt)	MSL (nt)
Blair et al. [214]	9.984	7.079	1.238	2.981	4.219	59.6%	563.8	677.9	568.3
Ramírez et al. [211]	21.096	15.781	5.703	2.266	7.969	50.5%	606.2	606.2	594.7
Tibivilliers et al. [215][1]	21.096	37.919	3.544	7.510	10.581	27.9%	656.4	1024.2	691.7

*After LQ & vector trimming, PUPS, Proportion of unigenes per sequence; MEL, Mean EST length; MCL, Mean contig length, MSL, Mean singleton length. Two EST sequencing was compared to the ESTs produced for the full-length cDNA libraries by Blair et al. [214]. Tibivilliers et al. [215] sequenced from both ends of the insert, Ramírez et al. [211] and Blair et al. [214] were 5′end sequenced.

and used two common bean genotypes (sensitive and tolerant) under salt stress conditions and studied the gene expression levels of *C2C2-YABBY* genes. Concerning the *WRKY* gene family, 88 *WRKY* genes were reported, and the response of 19 *WRKY* genes was discovered under drought stress [177].

SBP (SQUAMOSA promoter binding protein family) genes as other important TF genes were identified by Ilhan [222]. Some of the *Phvul-SBP* genes in the roots, leaf, and floral organs were up- or down-regulated. Buyuk et al. [223] reported 42 candidate *PvDOF* genes, and the expression levels of 9 out of the *PvDOFs* genes were up- or down-regulated under salt stress in different tissues. They also identified *CAMTA* (The calmodulin-binding transcriptional activator) gene family and investigated the expression levels of genes to figure out some potential genes that confer resistance to salt stress. On the other hand, *Whirly* and *ArrB* gene families were studied by Gökdemir [224]. The expression levels of the selected genes (*Phv-Why-1, –2, –3* and *Phv-ArrB-5, –8, –13, –16, –19*) were determined under artificial epidemic of *Sclerotinia sclerotiorum* in two registered varieties (Önceler and Akman). It was seen that the expression levels of *Phv-Why-1, –2, –3* and *Phv-ArrB-13, –19* genes were up-regulated in Önceler compared to Akman. On the other hand, *Phv-Arr-5, –8, –16* genes were up-regulated in Akman compared to Önceler. However, the change in the expression levels in the *Phv-Why-2* gene in both varieties was determined as statistically significant compared to the rest of the genes under biotic stress Zhang et al. [225]. studied the expression levels of six *PvB3* genes under salt stress in cotyledon, hypocotyl, radicle, and some *B3* family members revealed a relatively high expression in the radicle and hypocotyl.

Another study by Silva et al. [226] investigated the expression levels of genes in genotypes of common bean IAC Imperador (P-responsive) and DOR 364 (P-unresponsive) under different P concentrations. P-responsive genotype reported 1538 up-regulated genes under P restriction and 1679 up-regulated genes in the control level, while the P-unresponsive genotype reported 13 up-regulated genes in the control level and only 2 up-regulated genes under P restriction. Similarly, Hernández et al. [227] reported identifying 372 bean transcription factor (TF) genes. A total of 126 genes showed significant differential expression (response to P: 62%) in P-deficient roots. The studies described above related to transcription will provide significant information for plant breeders and geneticists to conduct genomic studies of the common bean in the near future.

Common bean proteomics

During 1970s and 1980s, most breeding activities were concerned to improve the protein quality in crops by improving the seed protein contents and balancing the composition of different essential amino acids [228]. However, protein quality was less focused on common bean and it contains lesser concentrations of methionine, cysteine, and sulfur amino acid [229]. Phasolin or 7S globulin phaseolin is the most plentiful seed protein and constitutes up to 50% of total protein in common bean [230]. Lectins are the second most abundant protein (5-10% of total protein) and 11S globulin legume present in very low levels in common bean [231]. Several efforts have been done to improve the protein quality in common bean; however, these efforts are dependent on the availability of alleles conferring phaseolin and erythroagglutinating phytohemagglutinin deficiency [232–234]. Bollini et al. [235] identified a unique genetic source for the deficiency of phytohemagglutinin. A very low concentration of sulfur amino acids is present in 7S globulin, and phaseolin levels are positively correlated with the methionine [233]. To improve and balance the seed protein contents, it is necessary to remove the phytohemagglutinin that enhances the phaseoline concentration in the seeds [234].

During the last decade, most common bean studies have been conducted for the improvement of biotic stress, abiotic stress, diversity and seed storage protein. For the separation of protein and its quantification in various plants, 2-dimensional (2-D) gel electrophoresis has been used, followed by either liquid chromatography coupled to tandem mass spectrometry (LC-MS/MS) or matrix-assisted laser desorption/ionization-mass spectrometry coupled to time of flight (MALDI-TOF) [236]. Robison et al. [237] identified 640 protein species using two common bean lines, A195 and Sacramento. During abiotic stress, the effects of gaseous pollutant ozone were observed and showed distinct changes in protein in the affected common bean leaves by two-dimensional electrophoresis (2- DGE; [238]. Zadražnik et al. [239] performed various proteomic analyses to investigate the drought stress in the common bean leaves using two cultivars Tiber (less drought sensitive) and Starozagorski čern (more drought sensitive). They identified 58 proteins in Tiber and 64 in Starozagorski čern by using LC-MS/MS analysis. Parreira et al. [240] applied high-throughput gel-free proteomics approach (LC–MS/MS) for the investigation of hallmarks of seed development. They identified 418 proteins and 255 of them were characterized. According to Badowiec and Weidner [241], the response of common bean toward the chilling stress was totally dependent on the exposure of

common bean to low temperature and duration of low temperature. They identified various proteomic variations in the root during different periods of low temperature. Salavati et al. [42] used two-dimensional polyacrylamide gel electrophoresis (2-DE) coupled with mass spectrometry (MS) for the proteome analysis of common bean to investigate the symbiosis between common bean roots and bacteria. They identified 483 different proteins, among these only 29 plant and 3 bacterial proteins were associated with early-stage symbiosis. Among the 29 plant proteins, while 19 proteins showed up-regulated expression patterns, 10 showed down regulated expression patterns. These up-regulated proteins were associated with the storage, energy production and protein synthesis; unlike these, down regulated proteins were associated with metabolism. Rust is an important disease in common bean and when rust infected leaves were studied, they showed that R-gene based defense modulates a protein that was identical to the basal defense system [243]. Phenol is an old protein extraction method and now protein extraction is performed with TCA–acetone as a new method and followed by a clean-up step that provides a higher amount of storage and defense protein [236]. Natarajan et al. [244] used the TCA-acetone method with 2-DGE analysis for the analysis of improved common bean by maintaining various changes in protein components. Phaseolin is the major seed storage protein of common bean and phosphorylation is post-translational protein modification (PTM) playing a vital role in proteome complexity López-Pedrouso et al. [245]. performed proteome analysis in two common bean cultivars Sanilac and Tendergreen to investigate the phosphorylation presence and its degradation in the dormant and germinating seeds. They identified remarkable variations in the levels of phosphorylation of the phaseolin from dormancy to seed germination. Mensack et al. [246] performed 2-DGE analysis for the investigation of differences between wild and domesticated common beans and they identified various protein changes between wild and domesticated cultivars. The Database LegProt (http://bioinfo.noble.org/manuscript-support/legumedb) contains the sequences of all legumes, including common bean, and would play a beneficial role in the identification of legumes proteins in a better way [247].

Bioinformatics tools and online functional database resources

Various integrative bioinformatics tools and online databases have been constructed to assemble common bean information and the genomic data related to common bean, such as Phytozome database v12.1 (https://phytozome.jgi.doe.gov/pz/portal.html), Legume Information System (LIS: http://phavu.comparative-legumes.org/gb2/gbrowse/Pv1.0/), KnowPulse (https://knowpulse.usask.ca/), National Center for Biotechnology Information (NCBI-https://www.ncbi.nlm.nih.gov/), Hidden Markov model (HMM, http://www.ebi.ac.uk), Pfam databases (http://pfam.xfam.org/) [248], The decrease redundancy tool (http://web.expasy.org/decrease_redundancy), ProtParam Tool (http://web.expasy.org/protparam), Gene Structure Display Server v2.0 (GSDS) (http://gsds.cbi.pku.edu.cn/) [249], the Multiple EM for Motif Elicition tool (MEME v4.11.1; http://meme-suite.org/) [250], The PlantCARE database (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/), the WoLF PSORT (http://www.genscript.com/psort/wolf_psort.html) [251], TargetP 1.1 (http://www.cbs.dtu.dk/services/TargetP/) [252], psRNA Target Server (http://plantgrn.noble.org/psRNATarget/) [253], Blast2GO (http://www.blast2go.com) Software [254], Plant Genome Duplication Database (PGDD; https://chibba.agtec.uga.edu/duplication/) [255], iTAK - Plant Transcription factor & Protein Kinase Identifier and Classifier (http://itak.feilab.net/cgi-bin/itak/index.cgi) [256], Phyre2 database (Protein Homology/Analogy Recognition Engine; http://www.sbg.bio.ic.ac.uk/phyre2) [257] and PAL2NAL (http://www.bork.embl.de/pal2nal) [258]. The above listed online databases have been commonly used in genome-wide studies in common bean. Moreover, a web-accessible TFs database for common bean known as *PvTFDB* has been developed Gautam et al. [259] with 2370 putative TF gene models distributed in 49 TF families. The tools and databases can provide valuable information to breeders related to gene expression, genome functional components, functional genes, comparative genomics, gene family, genetic maps studies etc. in common bean.

Transgenics/genetic transformation in common bean

Common bean is not a much responsive species to genetic transformation with the objective to investigate the genes and their functions. This is the reason why very few efforts have been done in the transformation of common bean as compared to its genomic mapping, transcriptomic and candidate genes identification [260]. Transformation in common bean has been achieved by direct and indirect methods. Electroporation or particle bombardment is a direct gene transfer method and *Agrobacterium tumefaciens* is an indirect method [261–265]. According to Aragão et al. [266], exotic genes can be effectively transferred to superficial cell layers when bombardment is performed on the meristematic cells of

embryonic axes. An electrical particle acceleration device was used by Russell et al. [267] for the production of transgenic navy bean plants. The protocol of [267] showed limitation as it was very time-consuming with less transformation frequency (0.03%). However, studies by Kim and Minamikawa [264] resulted in the recovery of transgenic bean plants when the bombardment was performed on apical meristematic regions [268,269]. According to the literature, the first gene transformation in common bean was achieved in 1993, and till now very few genes have been introduced for agronomic traits [39]. The *be2s1* gene was introduced in common bean to improve the seeds methionine contents. Aragão et al. [270] used five transgenic lines and found that two lines resulted in 14% and 23% increase in methionine content as compare to controlled lines. The *bar* gene is responsible for the coding of phosphinothricin acetyl transferase (PAT) and it confers resistance against the herbicide glufosinate ammonium and phosphinothricin. The introduction of the *bar* gene was performed by Russell et al. [267] and for the production of virus-resistant plants; they also introduced the coat protein gene from bean golden mosaic geminivirus (BGMV). While Faria et al. [271] used mutated AC1 viral gene for the production of plants having higher resistance against the BGMV and Bonfim et al. [272] used RNA interference (RNAi) to produce higher resistance against the BGMV. Molecular characterization of the first commercial transgenic common bean was performed by Aragão et al. [273]. According to Aragão et al. [273], this transgenic common bean showed immunity to BGMV and when crossed with a non-transgenic commercial variety, it exhibited stability of transgenes up to eight self-pollinated generations. *Rep-TrAP-REn* and *BC1* genes were transferred in the common bean to produce resistance against golden mosaic geminivirus (BGMV-BR) by Aragão et al. [274] and transgenic lines showed resistance against this disease.

Agrobacterium-mediated transformation remained unsuccessful as compared to particle bombardment in common bean [275,276] because it was recalcitrant to *Agrobacterium* due to poor regeneration in tissue culture [277–278]. Genga et al. [279] used different strains of *Agrobacterium* in the transformation of cotyledonary node and primary leaf explants, and they produced callus on kanamycin selection media, but they failed to obtain full explants. *A. rhizogenes* strain A4RS and *A. tumefaciens* strain C58Z707/pGA482 were applied by McClean et al. [280] for the transformation of cotyledons and hypocotyls; however they failed to regenerate the full plant successfully. Franklin et al. [275] used the *A. tumefaciens* strain EHA 101 for transformation in kidney bean and they produced GUS positive callus from it. Lewis and Bliss [281] used C58 strain with stab inoculation for the transformation of various shoot types of meristematic regions; however they were unsuccessful in regenerating any shoots during their study. Common bean intact leaves were transferred by Kapila et al. [282] using the vacuum infiltration of *Agrobacterium* for transient gene expression studies and they found higher GUS expression (20-90%). Embryo axis explants were applied by Mukeshimana et al. [283] for the common bean transformation and obtained chimeric plants, which were unsuccessful to acclimatize in the soil. According to Estrada-Navarrete et al. [284] *A. rhizogenes* resulted in a higher transformation level (75-90%) as compared to *Agrobacterium tumefaciens*. Estrada-Navarrete et al. [284] developed an easy and efficient protocol of gene transformation for common bean. Several common bean accessions, landraces and cultivars were used in their study, which resulted in 75-90% transformation efficiency. Four strains of *A. rhizogenes* were used in their study and root hairs were effectively induced due to strain K599. Later in 2007, a detailed and more effective protocol for gene transformation in common bean with strain K599 was presented by Estrada-Navarrete et al. [285]. Colpaert et al. [278] developed a composite method for the production of common bean having transgenic roots. In a very recent study reported by Xue et al. [286], they identified a *PvPOX1* gene from CAAS260205 (*Fusarium* wilt resistant genotype) and transferred the resistant allele in to BRB130 (*Fusarium* wilt susceptible genotype) through the root hairs with the help of *Agrobacterium rhizogenes*. Liu et al. [287] developed a transformation protocol by combining sonication and vacuum infiltration methods using *A. tumefaciens*. This approach is also known as Sonication assisted *Agrobacterium*-mediated Transformation (SAAT) and it resulted in 12% transformation in common bean. The study by [288] resulted in the higher transformation efficiencies between 10-28% with the *A. tumefaciens*.

Several protocols have been developed for the regeneration of common bean from the meristem cells based on the direct organogenesis. Intact seedling and cotyledonary nodes were used from two common bean cultivars Fonix and Maxidor to regenerate full plants [289,290]. In other studies, embryonic axis explants were used to regenerate full plants [291–292]. Veltcheva and Svetleva [293] selected three Bulgarian common bean varieties and used their leaf petioles for the plant regeneration and found genotype dependent reactions. The regeneration process in 10 common bean cultivars using apical meristems was studied by Sabzikar et al. [294] and they found that the race of the cultivar has a direct effect on the multiplication of apical shoot meristem. Apical meristem and

cotyledonary node explants were used by Arellano et al. [277] for the regeneration of 10 different common bean cultivars using indirect organogenesis, but they found a low regeneration frequency in their study.

Current hot topics in common bean and future directions

A good number of studies QTL/linked markers regarding agronomic, cooking quality, biotic and abiotic stresses are available. There is need to validate these identified genetic bases for their usage in marker assisted breeding of common bean.

1. In wheat 660K SNP array, in potato 12K, 20K and 22K SNP chips are available. These arrays techniques fasten the breeding activities in these crops. As a nutritionally potential crop, there is a need to develop such type of arrays having a higher number of SNPs for speed breeding in common bean.
2. Kompetitive Allele Specific Polymerase Chain Reaction (KASP) assays have been used by some scientists in common bean. There is a need to develop and validate the KASP assay for genes that underpin economically important traits in common bean including adaptability, grain yield, quality and biotic and abiotic stress resistance.
3. Characterization of genetic resources is considered as a prerequisite of breeding activities. There is a need to collect, conserve and characterize the genetic resources to explore novel variations for future breeding.
4. Common bean can be crossed with its relative species like tepary bean and also confirmed the occurrence of useful genes that can be used for the common bean improvement [295]. Therefore, there is a need to cross the common bean with its wild relatives to increase the chance of incorporating useful novel chromosomal regions for accelerated breeding.
5. There is a scarcity of information regarding the interaction among various stresses. There is a need to conduct studies in common bean to investigate the combined effects of various stresses like salt versus drought, heat versus drought, drought×salt×nutrition, among others.
6. CRISPR/Cas has opened a new window for plant breeders in recent years. However, to our knowledge, till now CRISPR/Cas has not been used in common bean by the scientific community. This technique can be used to generate a broad range of genetic diversity for common bean breeding in an unprecedented way and can be utilized to develop modern cultivars resistant to biotic and abiotic stress factors by plant breeders.

Conclusions

Common bean, known as "poor man's meat", is a globally important legume crop and appeals both to farmers and consumers. As the world is confronting with simultanious problems of climate change and rapidly increasing population, there is a need to utilize various breeding and biotechnological tools for the development of climate resilient cultivars. Regarding these factors, present efforts comprehensively reported limiting factors, previous and ongoing efforts for the study of common bean in the field of structural and functional genomics, transcriptomics, gene transformation, genome editing and proteomics. We envisage that the information presented herein will be helpful for the breeding community to take more efforts to serve the world population with high quality food in sufficient quantity [153, 296,297].

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