

Chapter 1

Designing Common Bean (*Phaseolus vulgaris* L.) for Abiotic Stress Tolerance



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Abstract Common bean (*Phaseolus vulgaris* L.) is an important source of carbohydrates, proteins (~22%), minerals, vitamins (e.g., folate) and fiber. Abiotic and biotic stresses are the constraints to high yield and production of common bean. Varieties resistant to biotic and abiotic stresses are among the major breeding objectives for this crop. Most of the agronomically important traits in common bean are controlled by polygenes and therefore it is imperative to understand the mechanism underlying these characters controlled by quantitative trait loci (QTL). Here, we review and compile the information from the studies related to the identification of QTLs for abiotic stresses in common bean. Successful map-based cloning requires handling of major QTLs that behave more or less like single genes which could be isolated in near-isogenic lines, but it also depends on the unambiguous identification of genotypes by progeny testing. Overall, this information will help the common bean breeders to select a suitable method for detection of the inheritance of quantitative traits controlling abiotic stresses and identify donor genes in germplasm resources to ensure that their utilization through introgression.

Keywords Abiotic stress · Common bean · Molecular mapping · QTLs

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1.1 Introduction

Common bean (*Phaseolus vulgaris* L.) is an important legume grown globally. It is a rich source of carbohydrates, proteins (~22% in seeds), minerals, vitamins (e.g., folate) and fiber (Broughton et al. 2003). The valuable products of this legume are snap beans (harvested before complete seed development), shell beans (harvested at physiological maturity), and dry beans (harvested at complete maturity). It is also referred in English to as French bean, string bean, garden bean, etc. According to the morphology and the coloration of the seed, the common bean varieties are called as pinto, pink, kidney, navy, small red, etc. It is cultivated and consumed in countries on all continents from their homelands in America to the Old World and Australia. Among these countries, eight out of the top ten are considered developing countries (Gepts et al. 2008). Common bean is one of the most widely consumed legumes and improving its vitamin and mineral content can address the malnutrition among the poor population in the developing countries (Blair 2013). Due to the domestication of common bean from wild resources that inhabit a narrow ecological niche, it faces many abiotic stresses within its range of agro-ecological zones (Beebe et al. 2006; Briñez et al. 2017). Thus, abiotic stresses are a major drawback for the production and high yield of common bean. Varieties resistant to abiotic stresses are among the primary breeding objectives for common bean (Ochoa et al. 2006; Cichy et al. 2009). Cultivars possessing resistance against stresses can decrease the yield loss from these stresses, thus, enabling stable production of beans across different environments and diverse soil conditions (Lynch 2011).

The genetically simple forms of resistance can be understood by Mendelian ratios, whereas it is difficult to understand the complex forms, often referred to as quantitative trait loci (QTL) (Lopez et al. 2009). Most of the abiotic stresses are under the control of several genes scattered by several genomic regions harbouring more or less numerous candidate genes. A wide set of molecular markers throughout the genome and dense molecular maps (McClellan et al. 2004) are now available in common bean, which provide an opportunity to identify the simple Mendelian factors and complex QTLs governing traits of interest (González et al. 2017). During the past decades, QTLs mapping has been accelerated by new genomic tools such as genomic and transcriptomic sequencing. Sequencing information can be further employed in genome editing and transgenic plants' development that significantly decrease the variety development time in those species in which these technologies are sufficiently fine-tuned. Whereas, given the availability of the common bean's whole genome, this potential expands for this crop (Schmutz et al. 2014; Astudillo-Reyes et al. 2015). The favorable and useful QTLs for abiotic stress tolerance are found scattered in both wild and cultivated populations in different gene pools of the common bean. Several efforts have been made to integrate the different breeding approaches to broaden the genetic base and introduce the QTLs for abiotic stress tolerance (Nietsche et al. 2000; Sartorato et al. 2000; Miklas et al. 2006). This chapter emphasizes on research related to the identification of QTLs for abiotic stress tolerance in common bean.

1.2 Genetic Resources of Abiotic Stress Tolerance

The backbone of every breeding and QTL mapping study in relation to abiotic stress tolerance is the availability of desirable sources of variation, mainly tracked from its wild relatives or landraces adapted to varying stresses over the evolutionary line. The evolutionary history of common bean is shared by two separate gene pools, i.e. Andean gene pool native to South America and the Mesoamerican gene pool originating from Central America and Mexico. Variation in seed size, plant morphology, seed storage protein content, molecular and biochemical markers have categorized two gene pools, which were domesticated in two independent domestication events (Singh 1991; Blair et al. 2006). Thus, a range of abiotic stress resistance genes can be obtained from such extensively diverse germplasm sources. These two gene pools of common bean are further classified into races based on adaptation, morphology and traits of agronomic importance. The Andean gene pool was subdivided into races including Peru, Nueva Granada and Chile, whereas Mesoamerican gene pool includes races Durango, Jalisco, Mesoamerica and Guatemala (Singh et al. 1991; Beebe et al. 2000). The information on crossing compatibility and valuable genes present across the range of bean germplasm in various pools is expected to add valuable QTLs to existing genetic resources.

Common bean trait enhancement is centered on genetic diversity in the reasonably narrow gene pool of improved landraces and cultivars. At the same time, wild relatives and closely associated species have been underutilized. Even though the wild relatives of common bean have been effective in trait improvement against biotic stresses, their use to improve various other quantitative traits has been restricted. The important traits present in wild germplasm include abiotic stress resistance found in wild relatives such as *P. acutifolius*, *P. coccineus* (Beaver et al. 2005) and *P. costaricensis*, whereas *P. parvifolius* and *P. acutifolius* are known to harbour high iron content (Sperotto and Ricachenevsky 2017). Moreover, there is a need to explore more accessions of wild germplasm sources by analyzing earlier determined ecological niches, along with the usage of geographic information system (GIS) data, and expert knowledge.

Nevertheless, gaps in knowledge must be dealt with to facilitate the usefulness in breeding using wild relatives. This presents a challenge; thus, both high and low throughput evaluation techniques are being employed for the characterization of the common bean wild relatives. Appropriate testing environments have to be identified for both field and greenhouse/growth chamber analysis of abiotic stress-related traits and genomic techniques, determining the genome level changes during the breeding program.

1.3 Molecular Mapping of QTLs Underlying Abiotic Stress Tolerance

Common bean shares its evolutionary history with two independent lineages, i.e. Mesoamerican and Andean. Various inter- and intra-gene pool crosses were generated to produce genetic linkage maps for trait mapping in common bean (González et al. 2017). In this direction, a Mesoamerican genotype ‘XR-235-1-1’ was crossed with Andean genotype ‘Calima’ to generate a backcross population for linkage mapping. This resulted in a total of 11 linkage groups that contained 224 restriction fragment length polymorphism (RFLP) and some isozyme and protein markers covering 960 cm (Vallejos et al. 1992).

The saturated linkage maps are a key foundation in trait mapping studies. An initial linkage map was developed using a recombinant inbred population derived from BAT93 and Jalo EEP558 (McClellan et al. 2004). Linkage maps incorporate genetic information thanks to common markers from other linkage maps, which increases the probability of mapping more loci and fine-tuning the linkage between mapped loci. Furthermore, the same map was enriched with more markers such as expressed sequence tag (EST), simple sequence repeat (SSR), and amplified fragment length polymorphism (AFLP), and aided in the development of new cultivars of common bean by introducing or pyramiding identified genes in the cultivars using marker-assisted selection (MAS) (Hanai et al. 2010). Whereas, saturated linkage maps were developed by Córdoba et al. (2010) carrying out the characterization of SSRs in 89,017 bacterial artificial chromosome end sequences (BES) from the G19833 common bean library. They included a total of 280 SSRs in the linkage map, together with 92 previously mapped BES- and 114 non-BES-derived markers, integrating a total of 8,232 bacterial artificial chromosome clones in 162 contigs from the physical map. In another study, 3,123 ESTs developed from root and leaf cDNA libraries were screened for micro satellites. The study yielded 184 new SSR markers and 120 of these new microsatellite markers were evaluated for their capacity to distinguish bean diversity in a germplasm panel of 18 genotypes (Blair et al. 2011).

Single nucleotide polymorphism (SNP) based markers were first developed in the crop using a method in which Roche 454-FLX system (454) was coupled with Illumina Genome Analyzer (GA) for sequencing and high-throughput SNP identification. A Golden Gate assay was developed for genotyping by integrating approximately 800 working SNP markers among the identified SNPs (Hyten et al. 2010). After this study, 84 genic and 10 non-genic regions comprising SNPs were validated using Kompetitive Allele-Specific PCR (KASP) technology across a panel of 70 diverse genotypes previously used in crossing for developing mapping populations and tested for SSR marker as well (Cortés et al. 2011). Tentative orthologous genes (TOG) from legume species were used to develop an Illumina Golden Gate Assay featuring 768 SNP genic loci for its use in fingerprinting. The amplicons of the commonly used genotypes ‘BAT93’ and ‘Jalo EEP558’ were used in the study for developing markers (Blair et al. 2013). The Illumina Golden Gate Assay designed in this study was used recently by Blair et al. (2018) to locate the SNPs’ genetic and

physical positions, and a new map was compared with the whole genome sequence of common bean.

The recombination rate was estimated using a recombinant inbred line (RIL) population derived from BAT93 x Jalo EEP558, and linkage disequilibrium over the whole genome was calculated based on the SNP marker allele diversity Mesoamerican Andean publically-accessible international diversity panels. An SNP assay named ‘SNP chip-BARC Bean6K_3’ was developed for SNP genotyping by anchoring 6,000 SNPs obtained from sequencing 17 distinct varieties of common bean with the help of Illumina GAIIX platform (Song et al. 2015). Such bead chips for high throughput analysis were valuable and cost-effective, which can also be tested for cross-species genotyping assays. The development of molecular markers accelerates the process of QTL mapping studies (Fig. 1.1). Generally, biparental homozygous mapping populations are employed for associating markers with traits in most of the studies. There is a need of integrating association mapping, multi parent mapping approach and advanced backcross QTL mapping (in the case of the wild donor) for more reliable and transferable linked markers.

Environment plays a crucial role in developing plants, as all the edaphic and climatic factors run parallel during the growth to bring the crop to maturity. During the course of time, deficiency or excess or any environmental factor causes severe yield

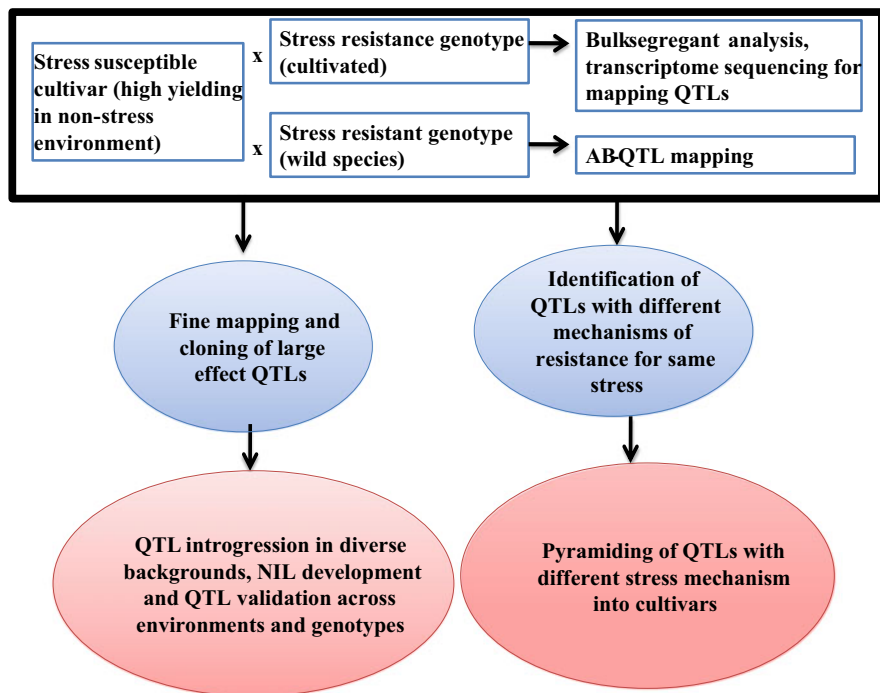


Fig. 1.1 QTL mapping and introgression strategy for stress resistance

constraints. Drought stress is a significant limitation in yield potential of common bean, especially in subtropical and tropical regions (Rao 2014). Southern Africa and Central America face severe and periodic drought stress challenges in 60% of their growing areas (Ambachew et al. 2015; Darkwa et al. 2016). The significant traits controlling resistance to drought include root depth and size, phenology, carbohydrate mobilization and storage, root hydraulic conductivity, and water absorption (Beebe et al. 2013). Food mobilization traits from primary source to sinks gain breeders' focus during drought stress (Rao et al. 2017). The QTLs for resistance to drought have been mapped across *P. vulgaris* L. chromosomes (Table 1.1; Fig. 1.2).

Heavy metal toxicity such as aluminum (Al) and manganese (Mn) result in elevated levels of acidity in the soil, which is problematic in bean productivity (as in many other crops), especially in Africa and Latin America (Rao et al. 2016). Al toxicity resistance was identified using root traits such as primary root elongation rate, length of roots, and higher diameter of roots in the Andean gene pool (Blair et al. 2009a, b) and QTLs for Al toxicity tolerance were identified by López-Marín and Rao (2009). Soils with low phosphorus (P) are unfit for breaking the yield ceiling of common bean in tropical regions (Beebe 2012). Traits fighting against low soil P include more considerable root length, P uptake efficiency and root area (Ochoa et al. 2006; Rao et al. 2016) (Table 1.1).

Common bean grows well under an optimum range of temperature (14–30 °C) and day temperature more than 30° or night temperature above 20 degrees is detrimental to bean productivity (De Ron et al. 2016). Blossom drop is a significant problem due to pollen sterility triggered by high temperature and resulting in fewer seeds. Transpiration cooling is achieved by diffusion of carbon dioxide through the stomatal opening at elevated air temperatures (Porch and Hall 2013). Bean genotypes capable of opening stomata at high temperature are valuable sources of resistance to heat stress (Prasad et al. 2017). Therefore, more significant thermal cooling under stress conditions could be an objective for mapping QTLs for heat stress response (McClean et al. 2011; Deva et al. 2020). A total of 50% mortality rate and limited growth after survival were reported at a temperature below freezing temperature (−3.25 °C) (Meyer and Badaruddin 2001). The sources of resistance to low temperature can serve as a valuable material for QTL mapping in common bean (Rodino et al. 2007; Souter et al. 2017).

1.4 Genomic and Transcriptomic Resources

The advancement in molecular marker technology is directly related to the genomic and transcriptomics resources of a crop. The availability of the genome sequence of common bean has broadened molecular research horizons and ultimately speeded up the cultivar development process (Schmutz et al. 2014). A total 473 Mb-genome was assembled out of total 587 Mb, and 160 genotypes belonging to two different gene pools were resequenced, which included wild species and landraces. The insights of domestication related genes and the abundance of sequence information were

Table 1.1 QTL mapping studies for abiotic stresses in common bean

Molecular marker/QTL	Source	Trait/objective	References
5 RAPD markers	RILs [Sierra × AC1028(S/A), Sierra × Lef-2RB (S/L)]	Drought tolerance	Schneider et al. (1997)
36 QTL for various traits, QTLs on b01 near <i>fin</i> locus	RILs (A55 × G122)	Phenological, architectural and yield traits under abiotic stress	Córdoba et al. (2010)
9 QTLs on 6 linkage groups	RILs (DOR364 × BAT477)	Photosynthate acquisition, accumulation, and remobilization under drought	Asfaw et al. (2012)
15 QTLs on 5 linkage groups	RILs (DOR364 × BAT477)	Drought tolerance	Blair et al. (2012)
QTLs, i.e. <i>SY1.1</i> , <i>SY2.1</i> , <i>PW1.2 BR</i> , <i>NDVI 1.1 BR</i>	RILs (Buster × Rosa)	Drought tolerance	Trapp et al. (2015)
QTLs <i>SW</i> , QTL <i>SY3.3SC</i> on <i>Pv03</i> , 14 other QTLs	RILs (SEA5 and CAL96)	Drought tolerance	Mukeshimana et al. (2014)
22 QTLs linked to drought-tolerant traits	F ₈ (SEA 5 × AND 277)	Drought tolerance	Briñez et al. (2017)
QTLs <i>Df1.1</i> , <i>Df1.2</i> , <i>Dp1.1</i> , <i>Sp2.1</i> , <i>Wp1.1</i> , <i>Wp5.1</i> , <i>Syp1.1</i> , <i>Syp1.2</i> , <i>Sp2</i>	RILs (Tiber × Starozagorskičern)	Drought tolerance	Sedlar et al. (2020)
2 major QTLs on B2 and B9, 17 minor QTLs	RILs (G2333 × G19839)	Adventitious root traits under low P	Ochoa et al. (2006)
26 QTLs	RILs (G19833 × DOR 364)	Root architecture traits under low P	Beebe et al. (2006)
QTLs linked to <i>fin</i> gene	RILs (G19833 and AND696)	Root architecture traits and low P tolerance	Cichy et al. (2009)
24 QTLs	RILs (DOR364 × G19833)	Root morphology traits in Al toxicity	López-Marín and Rao (2009)

obtained from the study for future breeding work. The genome and the transcription atlas of coding and non-coding genes of the Mesoamerican BAT93 genotype of common bean was further published (Vlasova et al. 2016). The genome and transcriptome data generated for a Mesoamerican genotype represented a counterpart to the genomic resources already available for the Andean gene pool. Transcriptional sequences add additional details of the expressed genome for developing genic

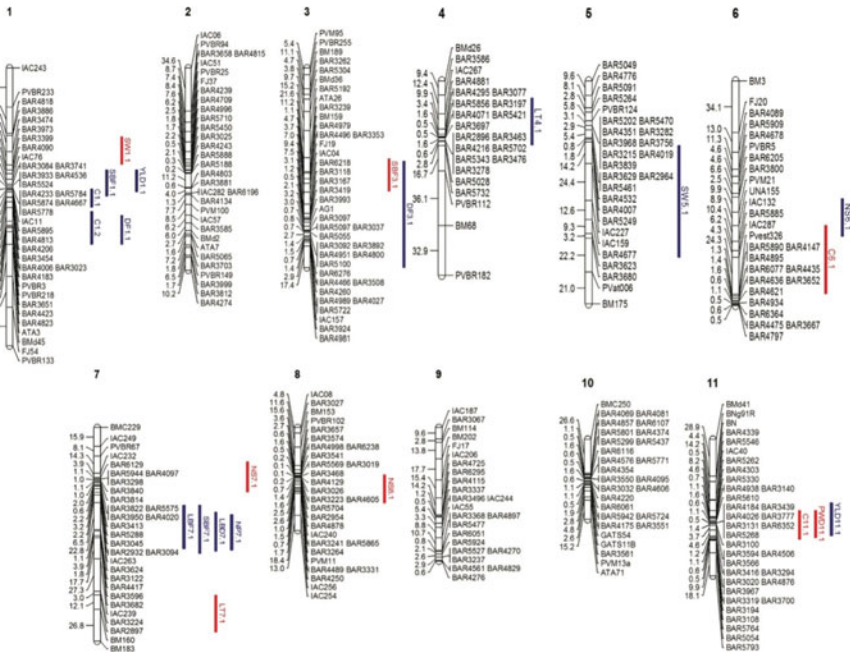


Fig. 1.2 Common bean linkage map from Briñez et al. (2017). This map was produced using 107 recombinant inbred line (RIL) populations obtained from a cross of SEA 5 × AND 277. The QTLs for drought (blue) and irrigated treatments (red) are marked across the chromosomes. Chromosomes were allocated based on the genomic sequence of *P. Vulgaris* L. Available at <http://www.phytozome.net/>

markers and depict various development pathways in the different stages of plant growth and tissues. Transcriptomes have been sequenced for many abiotic stresses in common bean (Table 1.2).

Zinc (Zn) is an essential micronutrient for higher plants; yet, at higher concentrations it is toxic. Transcriptome sequencing of differential lines (Voyager and Albion) for Zn content was performed using Illumina Genome AnalyzerII. The two cultivars had the same levels of Zinc in their pods and leaves but 52% more Zn was present in seeds of ‘Voyager’ cultivar in comparison to ‘Albion’. RNA sequencing of developing pods revealed that three gene families were involved in Zn transport, i.e., zinc-regulated transporter, iron-regulated transporter-like (*ZIP*), the zinc-induced facilitator (*ZIF*) and heavy metal associated (*HMA*) among a total of 381 differentially expressed genes (DEGs) along with potent SNPs from 11 genes for marker-assisted selection (MAS) (Astudillo-Reyes et al. 2015). Transcriptome sequencing was also performed for revealing genes for resistance to abiotic stresses in common bean, such as salt tolerance, drought resistance and phosphorus responsive genes (Hiz et al. 2014; Pereira et al. 2020). Candidate genes for regulation of energy metabolism, trans-membrane activity and secondary metabolites were identified as

Table 1.2 Transcriptome sequencing and resulting candidate genes for important traits in common bean

Traits	Candidate genes/markers	Breeding strategy	Sequencing platform	References
Zinc content	Three genes involved in Zn transport- <i>ZIP</i> , <i>ZIF</i> and <i>HMA</i> , 12,118 SNPs	Bio-fortification of common bean for curbing malnutrition	Illumina Genome AnalyzerII	Astudillo-Reyes et al. (2015)
Salt tolerance genes	Candidate genes for regulation of energy metabolism, trans-membrane activity and secondary metabolites identified	Validation and pyramiding of candidate genes in common bean	Illumina HiSeq 200	Hiz et al. (2014)
Drought resistance genes	SSRs and SNPs identified along with differentially expressed genes for drought stress	Useful for breeding Common bean for drought affected areas	Illumina platforms (GAII and HiSeq 2000)	Pereira et al. (2020)
Phosphorus responsive genes	<i>WRKY</i> , <i>ERF</i> , and <i>MYB</i> families, phosphatase related genes	Breeding for phosphorus responsive genes improves the quality of crop and also resistance against biotic and abiotic stresses in Common bean	Illumina Hiseq 2500	Silva et al. (2019)
Spider mite resistance	Flavonoid biosynthesis, pathogenesis-related (PR) proteins and heat shock proteins	Breeding spider mite resistant cultivars	Illumina HiSeq 2500	Hoseinzadeh et al. (2020)

salt-tolerant related genes in the crop using Illumina HiSeq 200 of “Ispir”, a salt-tolerant cultivar under two variant environments. Among 2,678 transcription factors (TF) identified in the study, 441 were involved in the salt tolerance mechanism (Hiz et al. 2014). The drought resistance mechanism was elucidated by transcriptome sequencing of roots and leaves of two Mesoamerican cultivars (i.e., Pérola and BAT 477) with contrasting phenotypes for drought tolerance (Pereira et al. 2020). Prominent families of genes involved in drought resistance mechanism were oxidative stress, kinase activity and response to the stimulus. Oxidation–reduction genes were triggered early in the roots of drought-tolerant genotype, indicating a tolerance mechanism by decreasing the damage from reactive oxygen species (ROS). RNA sequencing of IAC Imperador (phosphorus responsive) and DOR 364 (phosphorus unresponsive) in various environments differing for phosphorus concentration was carried out, and *ERF*, *WRKY* and *MYB* gene families were found to be involved in phosphorus restriction along with phosphatase related genes such as acid phosphatase, pyrophosphatase, phosphate transporters and purple acid phosphatase (Silva et al. 2019).

1.5 Prospects and Conclusions

Wild species and crop landraces are goldmines for significant trait improvement in crops. As plant breeding is a number game, one needs to attempt more and more crosses every year with diverse germplasm including wild species and generate mapping populations for obtaining genetic gains and releasing new cultivars. Thus, the populations must be evaluated precisely with advanced phenomic tools, and genomic tools can be employed for dissecting the traits and their functional behaviour. Genomic and transcriptomic studies are growing in common bean, but there is still a need to focus on material used for sequencing and the right stage of plant for transcriptome analysis. The precision in experimental material and methods employed in transcriptomic analysis is the sole criterion for getting accurate and reliable information. Genomic databases for individual crops are being developed, and the purpose of a database is fully released only if there is a balance between outflow and inflow information. The databases are growing as virtual diversity in crop plants and must be used frequently in molecular breeding traits. The amalgam of conventional and genomic techniques generates numerous valuable QTLs. A number of QTL mapping studies for abiotic stresses has been conducted, mostly retaining QTLs specific to a population or environment. To accelerate the desirable genotype development in ever-changing climatic conditions, one needs more stable QTLs. The QTLs express less epistatic background genotype for their efficient marker-assisted backcross breeding programs under varying environmental conditions. The concept of mega-QTLs is a crucial strategy for overcoming the problem and utilizing QTLs among distinct backgrounds. The mapping studies are not entirely accomplished until the product

is not used in developing sustainable genotype. There is an urgent need for comprehensive, collaborative testing of genotypes and QTLs among institutions and countries for validation and deployment in cultivars which is the ultimate goal of plant breeding. The information regarding the genetic basis of inheritance determined by previous studies is useful for the improvement of the common bean is essential. The powerful progression opens brand new research perspectives about the dynamics of combining different traits in one breeding program. This info will help the common bean breeders choose a suitable technique for the inheritance analysis of quantitative characteristics and determine the novel genes in germplasm assets. Overall, the review is an update of common bean genomics and genetics. The vast availability of crop diversity and its utilization to map traits of interest using conventional and genomic breeding has been compiled in the present review. The information is expected to attract advancements in the current scenario of common bean breeding and broaden horizons for future research.

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