Chapter 1
Common Bean Genetics, Breeding, and Genomics for Adaptation to Changing to New Agri-environmental Conditions

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Abstract Common bean (*Phaseolus vulgaris* L.) has become, over the last 20 years, a competitive crop in national, regional, and international markets. This situation presents a dynamic environment for producers and researchers of this crop and requires a rethinking of current strategies against research and production needs, the opportunities and challenges of the future, and adaptation to changing agri-

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environmental conditions. Improvement of the common bean means possessing in-depth knowledge of its genetic diversity, the genome and gene functions, to enable the analysis of pathways and networks in response to fluctuating environmental conditions. An important long-term challenge is the discovery of the gene(s) that control important production traits such as pest and disease resistance, abiotic stress tolerance, and biological fixation of nitrogen. This will need to be a cooperative worldwide effort that involves breeders, geneticists, and genomic and bioinformatics experts. Currently, new technologies built around the recently released common bean genome sequence are now being developed, and various genomic resources for common bean are available and include physical maps, bacterial artificial chromosome libraries, anchored physical and genetic maps, and expressed sequence tags. However, these approaches require precise phenotypic data. Complex interactions between the common bean crop genotype, environmental factors in combination with plant population dynamics and crop management greatly affect plant phenotypes in field experiments and are the key for the expansion of the productivity of this crop in traditional and nontraditional growing areas.

Keywords Abiotic stress tolerance · Agronomy · Diseases and pest resistance · Food legumes · Genetic resources · Genetic mapping · Molecular breeding · *Phaseolus vulgaris* L.

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1.1 Challenges, Priorities, and Prospects of Recent Plant Breeding

1.1.1 Background

Understanding the effects of domestication on genetic diversity of common bean (*Phaseolus vulgaris* L.) is of great importance, not only for crop evolution but also for possible applications, such as the implementation of appropriate biodiversity conservation strategies, and the use of genetic variability in breeding programs. One of the most important and generalized features of plant domestication is the reduction in genetic diversity, not only during the initial domestication process but also during dispersion and adaptive radiation from the centers of domestication to other areas. The reduction of genetic diversity is usually more drastic in autogamous species such as common bean, which have restricted genetic recombination and presents a higher population structure as compared with allogamous species (Jarvis and Hodgkin 1999). This reduction is caused by both stochastic events (i.e., a bottleneck and genetic drift due to a reduction in the population size) and selection (i.e., adaptation to a novel agrosystem) (Vigouroux et al. 2002).

A recent hypothesis for the origin of the common bean defended a Mesoamerican origin (Bitocchi et al. 2012, 2013), based on the extensive diversity and population structure within the Mesoamerican gene pool, and the signature of pre-domestication bottlenecks in the south of the Andes detected in five gene fragments across 102 wild bean accessions. This novel structure of population not only evidences a Mesoamerican origin but also excludes an Andean origin of common bean. Additionally, these authors suggested that the wild common bean from northern Peru and Ecuador represents an old relict germplasm including a part of the genetic diversity of the ancestral common bean populations, displaying a type I phaseolin that probably was extinct in Mesoamerica. The resequencing of the genome of the common bean by Schmutz et al. (2014) recently confirmed this hypothesis.

Domestication took place after the formation of the Mesoamerican and Andean gene pools, and thus their structure is evident in both the wild and the domesticated forms (Papa and Gepts 2003; Papa et al. 2005, 2007, Rossi et al. 2009). This clear subdivision of the common bean germplasm is well documented, and it has been defined through several studies (Papa et al. 2007; Angioi et al. 2009; Bitocchi et al. 2012, 2013). However, the number of domestication events within each pool is still debated. Bitocchi et al. (2013) hypothesized a single domestication event within each gene pool and indicated the Oaxaca valley in Mesoamerica and southern Bolivia and northern Argentina as geographical areas of common bean domestication.

The exploration of The Americas by the Europeans, from the 15th century, marked the arrival into the Old World of many plant species such as common bean (*Phaseolus vulgaris* L.), peanuts (*Arachis hypogaea* L.), cocoa (*Theobroma cacao* L.), corn (*Zea mays* L.), potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.), etc. The introduction of these exotic species in a new agricultural area under different environmental conditions raises relevant questions about adaptation, taking into

account the requirements of tolerance to several stresses, as well as competitiveness with other indigenous crops in production and economic value (De Ron et al. 2016).

No records of common bean earlier than 1543 have been found in European herbariums; however, as reported by Zeven (1997), in 1669 it was widely grown in many areas of Europe. The dispersion of the common bean to Europe probably started from the Iberian Peninsula (Spain and Portugal), where the species was introduced mainly from Central America around 1506 and from the southern Andes after 1532, through sailors and traders who brought with them the nicely colored and easily transportable seeds as a curiosity (Brücher and Brücher 1976; Debouck and Smartt 1995). The pathways of dissemination of the crop across Europe were very complex, with several introductions from America combined with direct exchanges between European and other Mediterranean countries (Papa et al. 2007). Over time, the dissemination across Europe surely occurred through seed exchanges among farmers being facilitated by territorial contiguity and similarity of environments. The protein marker phaseolin was used as a marker in describing the worldwide dissemination of common bean (Gepts 1988). A higher frequency of Andean types (T, C, H, and A) was recorded with respect to Mesoamerican ones (S, B, M) (Lioi 1989; Santalla et al. 2002).

As mentioned before, the common bean originated and was domesticated in tropical highlands. This means that abiotic and biotic conditions had an influence on the development of European varieties (Rodiño et al. 2006, 2007). In some cases, bean breeders have had to incorporate tolerances to abiotic stresses from sources outside the primary gene pool of common bean. For example, tepary bean could also provide tolerance to heat or drought, and runner bean, tolerance to low soil fertility (Miklas et al. 2006a, b). In the case of rhizobia symbiotic system, it is possible that migration of the species had not been parallel, so additional efforts are underway to achieve efficient symbiotic genotypes of common bean and rhizobia (Rodiño et al. 2011). As a result of plant-rhizobia coevolution, a spectrum of compatible specific rhizobia is recognized for one or more legume species.

1.1.2 The Common Bean as a Food Resource

Grain legumes (pulses) are considered an essential source of nutrients and are also recognized as poor man's meat, showing their importance for people of developing countries, where the consumption of animal protein is limited by nonavailability or is self-imposed because of religious or cultural habits. Furthermore, legume seeds contain many bioactive and/or antinutritional compounds, such as phytate, oligosaccharides, phenolic compounds, nonprotein amino acids, lectins, enzyme inhibitors that play metabolic roles in humans or animals that frequently assume these seeds. These effects may be regarded as positive, negative, or both (Champ 2002).

From a nutritional point of view, the amino acid profile of legume storage proteins reveals low amounts of the essential sulfur-containing amino acids (i.e., methionine and cysteine) and tryptophan, while lysine, another essential amino acid, is quite

abundant. Legume proteins complement very well those of cereals, which are normally rich in sulfur amino acids and poor in lysine and threonine. Besides the composition in essential amino acids, the nutritional quality of seed proteins is also largely determined by their digestibility. In fact, amino acids composition only represents the potential nutritional quality of a protein, being their bioavailability critical for the supply of amino acids in the diet (Sparvoli et al. 2015).

The common bean is the third most important food legume crop worldwide, surpassed only by soybean (*Glycine max* (L.) Merr.) and peanut (*Arachis hypogea* L.), and it is the first one for direct human consumption. Beans are produced and consumed mainly as a dry food legume, due to the high protein content of the grain, but the use of the fresh pod (snap bean) is common in many countries. Common bean is highly consumed in many areas of Africa and Latin America (as the most important source of plant protein), as well as in traditional diets of the Middle East and Europe (Broughton et al. 2003; Casquero et al. 2006). This legume is part of the healthy diet of the European Mediterranean basin and gaining importance in the USA where consumption has been increasing due to public interest in ethnic and healthy foods (Blair and Izquierdo 2012).

Recently the role of bean in human diet is being focused not only in its protein content but in the functional properties also and some authors have reported that its consumption could contribute to reduce the risk of obesity, diabetes, cardiovascular diseases and colon, prostate, and breast cancer (Hangen and Bennink 2003; Thompson et al. 2009). These health benefits could be due to the fiber content in the grain but also to antioxidant compounds as the phenolic ones. All the molecules present in legumes having anticancer properties are soluble in aqueous-alcohol extracts, while resistant starches, present in high amount in legumes, together with non-starch polysaccharides, are primarily insoluble residues from aqueous-alcohol extracts (Sparvoli et al. 2015). Colon carcinogenesis was induced by azoxymethane treatment in obese ob/ob mice fed with a diet containing cooked navy beans (whole beans), the insoluble or soluble fraction of aqueous-alcohol extracts, or a standard diet (Bobe et al. 2008).

1.2 Prioritizing Climate Smart (CS) Traits

1.2.1 Disease Resistance

1.2.1.1 Introduction

The abnormal functioning of diseased plants generally leads to a reduction in quantity and quality of yield. Disease is the result of an interaction among the plant and its environment and it is often affected by biotic and abiotic factors (e.g., microorganisms, humidity, temperature, etc.) that are detected as signals for the activation of plant response mechanisms (American Phytopathological Society 2005).

When a plant is present in a stress situation (biotic or abiotic), it shows a minimum resistance to this situation, which will slow down their vital functions, reducing their development. This alarm phase is the one that will trigger all the mechanisms to get over it. If this situation persists, the plant will die. However, if it triggers some defense mechanisms, it will enter a resistance phase reaching a maximum level. If the stress continues, the plant will enter a phase of exhaustion. This phase may cause plant death if the stress does not disappear. Nevertheless, if the stress situation ends, plant recovers its physiological functions, being able to regenerate and to reach a new physiological state optimal for the present conditions, which corresponded to the regeneration phase (Tadeo and Gómez-Cadenas 2008).

Crops are affected by a wide diversity of fungal pathogens, for example, *Sclerotinia* spp., *Fusarium* spp., *Botrytis* spp., *Rhizoctonia* spp., etc., causing important economic losses (Mayo et al. 2017). A form of control to diseases is the application of synthetic fungicides. Its application on the seed or directly to the soil can be effective against fungi that affect the crops during or shortly after germination (Beebe and Corrales 1991) because they reduce its incidence and improve the emergence of plants (Valenciano et al. 2004). However, applications with fungicides aimed at avoiding damage caused by fungi that cause root rot or yellowing and wilting are often ineffective and usually impracticable due to the large volume of soil to which they should be directed. Actually, the number of authorized plant protection products has been reduced in order to ensure food safety and its sustainable in the long term. It is therefore proposed to prioritize nonchemical methods in integrated production, organic farming, and others (Mayo et al. 2017).

As a strategy to control plant infectious diseases, mainly those caused by fungi, the use of biocontrol agents can reduce the negative effects of plant pathogens and they also can promote positive responses in the plant (Shoresh et al. 2010). Biocontrol agents are perceived to have specific advantages over synthetic fungicides, including fewer nontarget and environmental effects, efficacy against fungicide-resistant pathogens, reduced probability of resistance development and use in organic farming situations where synthetic fungicides are restricted (Brimner and Boland 2003).

Bacterial species belonging to genera such as *Agrobacterium*, *Pseudomonas*, *Streptomyces*, and *Bacillus*, and fungal genera such as *Gliocladium*, *Trichoderma*, *Ampelomyces*, *Candida*, and *Coniothyrium*, are beneficial organisms that have shown good efficiency as biocontrol agents against pathogenic microorganisms (Vinale et al. 2008a).

1.2.1.2 *Trichoderma* spp.

Trichoderma spp. (Teleomorph: Hypocrea) is a fungal genus that is found in the soil, and it is a secondary fast growing opportunistic invasive (Mayo et al. 2016a, b) producer of chitinases, glucanases and proteases, and metabolites with antimicrobial activity (Lorito et al. 2010). Many *Trichoderma* species are also well known as biocontrol agents of important phytopathogenic fungi. The primary mechanisms of biocontrol used by *Trichoderma* in direct confrontation with pathogenic fungi are

mycoparasitism, antibiosis, and competition for nutrients with the pathogen (Harman et al. 2004). *Trichoderma* species colonize the root surface and cause substantial changes in plant metabolism (Shoresh et al. 2010). The physical interaction between *Trichoderma* and plants is limited to the first cell layer of the epidermis and the root bark. In addition, *Trichoderma* biocontrol strains are able to induce the expression of genes involved in defense response and also to promote plant growth, root development, and nutrient uptake (Hermosa et al. 2012).

Trichoderma spp. is recognized for their important benefits to agriculture such as its ability to protect crops against diseases (Benítez et al. 2004) and increase crop yield under field conditions (Harman et al. 2004). Most species of *Trichoderma* have been linked to biocontrol and biotechnological applications (Monte 2001), and the versatility of *Trichoderma* strains to suppress diseases caused by pathogens (Howell 2003). Since *Trichoderma* strains grow and proliferate best when there are abundant healthy roots, they have evolved numerous mechanisms of action both to attack other fungi and to enhance plant and root growth (Benítez et al. 2004).

In a symbiotic relationship with *Trichoderma*, the transport of sucrose from plants with subsequent intracellular hydrolysis by *T. virens* has been shown (Fig. 1.1). This source–sink communication may be central to the mutualistic interaction, influencing the development of *Trichoderma* in the rhizosphere and root plant (Vargas et al. 2012).

Competition and Mycoparasitism

Competition between *Trichoderma* and pathogens (Fig. 1.1) would be established with the purpose to get more nutrients, oxygen, light, etc. (Paulitz 1990). *Trichoderma* is an excellent competitor for space and nutritional resources. It appears in almost all soils and in habitats that contain high amounts of organic matter. In those niches, it would be an excellent decomposer of plant and fungal material. Moreover, some species of the genus *Trichoderma* show great metabolomic versatility that allows them to grow using a wide range of nitrogen and carbon sources. Furthermore, *Trichoderma* has the ability to colonize the rhizosphere, and this skill might be essential for being used as an excellent biological control agent (Howell 2003).

Mycoparasitism (Fig. 1.1) consists in the recognition of the fungus, attacking it, and penetrating it with the purpose to cause its death. This process involves some different phases. Firstly, *Trichoderma* locates the pathogen without previous contact, beginning to enlarge toward the pathogen by tropism (Chet et al. 1981; Lu et al. 2004). During this process, *Trichoderma* secretes some enzymes that hydrolyze the cell wall of the pathogen (Howell 2003; Woo et al. 2006). It has been studied that *Trichoderma* releases an extracellular exochitinase (Brunner et al. 2003) that might cause the liberation of some oligomers from the fungus, which could induce the expression of toxic endochitinases that would diffuse and would start to attack to the pathogen, even before the physical contact had happened. Some enzymes belonging to these fungi have been purified and used for biocontrol. When they have been

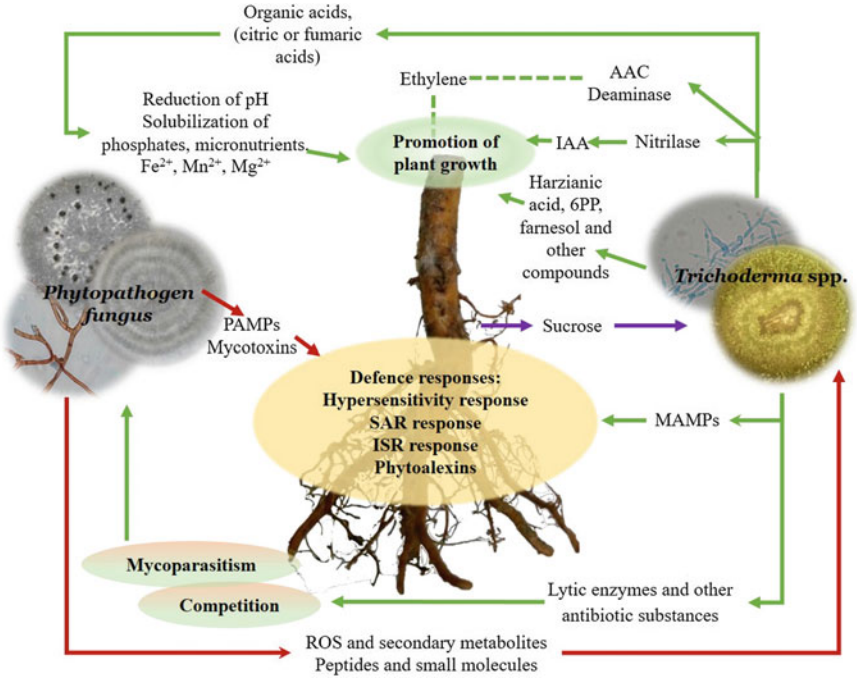


Fig. 1.1 Interactions between phytopathogen fungus, plant, and biocontrol agent *Trichoderma*. The green lines and circles are compounds and actions produced/induced by *Trichoderma*. The red lines are compounds and responses produced/caused by the phytopathogen fungus. The purple lines and circles are the compounds and plant responses produced/induced by the fungi (Altomar et al. 1999; Druzhinina et al. 2011; Howell 2003; Rubio et al. 2009; Vargas et al. 2011; Vinale et al. 2009; Vinale et al. 2008a, b) (*6PP* 6-pentyl-α-pyrone; *AAC* 1-aminocyclopropane-1-carboxylic acid; *IAA* indoleacetic acid; *ISR* induced systemic resistance; *MAMPs* microorganism-associated molecular patterns; *PAMPs* pathogen-associated molecular patterns; *ROS* reactive oxygen species; *SAR* systemic acquired resistance)

assessed, they have shown antifungal activity and have controlled a large number of pathogens, such as *Fusarium*, *Rhizoctonia*, *Alternaria*, *Ustilago*, *Venturia*, and *Colletotrichum* (Lorito et al. 1993; Lorito et al. 1994).

A major part of the *Trichoderma* antifungal system consists of a number of genes encoding an astonishing variety of secreted lytic enzymes (Sanz et al. 2004) including endochitinases, N-acetyl-β-glucosaminidases, chitin 1,4-β-chitobiosidases, proteases, glucan β-1,3-glucosidases, glucan β-1,6-glucosidases, glucan α-1,3-glucosidases, lipases, xylanases, mannanases, pectinases, pectin lyases, amylases, phospholipases, RNAses, DNAses, etc. Some of these proteins have been purified and their corresponding genes have been cloned and characterized by our group: protease PRA1 (Suarez et al. 2004), chitinases CHIT36 and CHIT37 (Viterbo

et al. 2002), α-glucanases AGN13.1 (Ait-Lahsen et al. 2001) and AGN13.2 (Sanz et al. 2005), and β-1,6-glucanases BGN16.2 and BGN16.3 (Montero et al. 2005, 2007).

The direct confrontation assays were used to verify the ability of *Trichoderma* spp. to overgrow the pathogen and its capacity of mycoparasitism. In a study, the percentage of overgrow oscillated between 72.77 and 14.63%, according to the species of *Trichoderma* (Mayo et al. 2015).

Some *Trichoderma* spp. are selected because of their mycoparasitic mechanism but the most efficient biocontrol strains display, simultaneous or sequentially, more than one biocontrol strategy (Howell 2003). *Trichoderma* spp. can also exert marked antimicrobial activity (Vizcaino et al. 2005) due to the production of blends of secondary metabolites (Cardoza et al. 2005; Reino et al. 2007). Currently, better knowledge about *Trichoderma* has facilitated its use in biocontrol as whole microorganisms, able to be monitored in natural environments (Hermosa et al. 2001; Rubio et al. 2005), as enzyme formulations (Benítez et al. 2004) or as sources of genes for transgenic plant development. Since the early description of the capacity of *Trichoderma* to increase plant biomass production (Chang et al. 1986), several new general mechanisms for both biocontrol and plant growth increase have been demonstrated and it is now clear that there must be hundreds of separate genes and gene products involved in these processes.

There are compounds produced by *Trichoderma* that cause inhibitory effects on plants. For example, trichosetin, a secondary metabolite isolated from dual cultures of *T. harzianum-Catharanthus roseus* callus that is an antimicrobial compound with activity against *Staphylococcus aureus* and *Bacillus subtilis* (Marfori et al. 2002), but also inhibited root and shoot growth in some plant species (*Oryza sativa*, *Vigna radiata*, *Medicago sativa*, *Capsicum frutescens*, and *Lycopersicon esculentum*) (Marfori et al. 2003). Additional compounds with negative effects on plant growth (as necrosis in bean, tobacco, and corn) include trichocaranes (A, B, and C) (Macías et al. 2000), koninginins (B, C, E, and G) (Cutler et al. 1989; Parker et al. 1995), cyclonerodiol, and a laevorotatory form of harzianopyridone (Cutler and Jacyno 1991). *T. virens* also synthesizes negative plant growth promoters such as viridiol, a potent herbicidal compound, which is effective for weed control (Héraux et al. 2005).

Recently, they were identified other compounds with antimicrobial, antioxidant, and cytotoxicity activity. However, they inhibited germination of cabbage seeds as alternariol 1′-hydroxy-9-methyl ether, alternariol 9-methyl ether, alternariol, altechromone A, altenuene, 4′-epialtenuene, α-acetylorcinol, and cerebroside C (Zhang et al. 2017).

Promotion of Plant Growth

Trichoderma spp. has developed opportunistic mechanisms for their adaptation to abiotic stresses as well as for nutrient uptake and solute transport. In the plant, these processes are facilitated by the induction of cell wall extension and expansion,

secondary root development, lateral root hair production and a higher photosynthetic rate (Shoresh et al. 2010; Hermosa et al. 2013).

Trichoderma produces some organic acids such as citric or fumaric acids that reduce soil pH and allow the solubilization of phosphates and other micronutrients such as iron, manganese, and magnesium (Fig. 1.1) (Benítez et al. 2004; Harman et al. 2004). On the other hand, there are some *in vitro* studies indicating that *T. harzianum* and other *Trichoderma* isolates could solubilize iron (III) oxide, manganese (IV) oxide, zinc, and phosphates, which are highly insoluble compounds or with low solubility, owing to chelation processes and oxidation-reduction activity (Altomare et al. 1999). The increment of all those nutrients, in particular, phosphorus, could favor the plant growth. It has been shown that *T. atroviride* produces and degrades indoleacetic acid (IAA), which in combination with ethylene by the microorganisms present in the rhizosphere causes a promotion of plant growth (Fig. 1.1) (Gravel et al. 2007).

The volatile pyrone 6-pentyl-α-pyrone (6PP) is a common *Trichoderma* compound that inhibits the growth of the pathogen such as *Fusarium oxysporum*. However, at low concentrations, 6PP significantly promotes the plant growth and it was able to induce the expression of plant defense genes (Viterbo et al. 2007; Vinale et al. 2008a).

Cremenolide is another compound that inhibits the development of plant pathogens. This compound significantly inhibited the growth of *F. oxysporum*, *Botrytis cinerea*, and *Rhizoctonia solani*. Furthermore, in tomato seedlings assays it promoted plant growth in terms of root length and fresh weight (Vinale et al. 2016).

Farnesol is produced by *Trichoderma* and is a signaling molecule that by accumulating in the extracellular space generates a response across the local fungal population. In another study, its effect on the development of bean plant was evaluated. This compound, which farnesol at concentrations of 10 and 100 μM farnesol showed a negative effect on growth of bean plants, which could be related to abscisic acid synthesis. However, 2 mM of farnesol has the opposite effect. Thus, at this concentration bean plants increased the development of aerial parts and root systems (Mayo et al. 2016a, b).

Defense Response

The relationships established between plants and microorganisms are very diverse. Plant's defense against pathogens is regulated through a complex network of signaling pathways involving several molecules such as reactive oxygen species (ROS), salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Kunkel and Brooks 2002; Vitti et al. 2015) and some secondary metabolites with antimicrobial activity that can act also as signaling molecules (i.e., phytoanticipins and phytoalexins) (Mhlongo et al. 2016) (Fig. 1.1). When a plant is exposed to a pathogenic microorganism, the production of molecules associated with SA is increased, which is related to a systemic acquired resistance (SAR) response. The response of plants against non-pathogenic microorganisms is different, resulting in activation of signaling cascades

that are dependent on JA and ET, such as hydroperoxide lyase, peroxidase, and phenylalanine ammonia-lyase, all related to an induced systemic resistance (ISR) response (Druzhinina et al. 2011). Other responses result in rapid cell death in infected tissues. Then, plants activate the hypersensitive response that involves the accumulation of salicylic acid, ROS, and an increased the influx of Ca^{2+} (Guerrero-González et al. 2011).

Hypersensitive Defense and Phytoalexins

Another response exhibited by plants is the necrotic defense or hypersensitive defense (Fig. 1.1) that induces the selective death of some cells to block the progress of phytopathogens through the plant tissues (Tadeo and Gómez-Cadenas 2008). These changes in hypersensitive reactions include loss of cell membranes permeability and increase in respiration and production of phytoalexins. Phytoalexins are not present in healthy plants but are synthesized in response to biotic stress as part of the plant defense response and are restricted to the tissue colonized by the fungus and the cells surrounding the infection site (Morrissey and Osbourn 1999). The result is death and collapse of the infected cells. The necrotic tissues isolate the phytopathogen causing its death because the pathogen depends entirely on the plant to survive. It is likely that the faster the host cells die after they have been infected, the more resistant they become to infection (Agrios 2002). For example, alfalfa (*Medicago sativa*) or barrel medic (*Medicago truncatula*) produce medicarpin, which is an isoflavone, in response to the pathogens *Colletotrichum trifolii* or *Phoma medicaginis*, respectively (Saunders and O'neill 2004; Jasiński et al. 2009). Other example is peanut (*Arachis hypogaea*) that produces resveratrol in response to *Aspergillus* spp., *Botryodiplodia theobromae*, *Ganoderma lucidum*, or *Rhizopus oligosporus* (Sobolev et al. 2009; Condori et al. 2010; Yang et al. 2010; Wu et al. 2011). Soybean (*Glycine max*) produces glyceollin, another phytoalexin, in response to the attack of *Macrophomina phaseolina*, *Sclerotinia sclerotiorum*, *Phytophthora sojae*, *Fusarium solani*, or *Aspergillus* spp. (Lozovaya et al. 2004; Feng et al. 2007; Simons et al. 2011a; Simons et al. 2011b; Eromosele et al. 2013).

In the tripartite interaction of plants with a pathogen and a biocontrol *Trichoderma* species, several changes are produced in the plant, such as the increase in phenolic acid and lignin, accumulation of phytoalexins, and down- or upregulation of defense-related genes expression (Guerrero-González et al. 2011; Mayo et al. 2015).

Different categories of defense-related genes whose expression is modulated by biotic stresses have been described in bean plants interacting with pathogenic and nonpathogenic microorganisms (Mayo et al. 2015).

SAR and ISR Responses

The perception of an external stimulus can active the response genes. There are some components that regulate many processes in response to stimuli (Fig. 1.1).

A component involved in the regulation of plant defense gene expression is WRKY transcription factors (TFs) (Rushton and Somssich 1998; Singh et al. 2002). They

can function up- and downstream of hormones that are involved in the antagonist functions of SA and JA/ET. They also contribute to the development control processes via auxins, cytokinins, and brassinosteroids (Chen et al. 2010; Agarwal et al. 2011; Rushton et al. 2012; Bakshi and Oelmüller 2014). Several ROS-dependent responses are controlled by WRKY TFs, and they also regulate major changes in the plant transcriptome during early phases of root colonization with arbuscular mycorrhizal fungi (Gallou et al. 2012).

Thus, *WRKY33* has a role in biotic stress defense, where it regulates the balance between necrotrophic and biotrophic pathogen responses (Lippok et al. 2007; Pandey and Somssich 2009; Birkenbihl et al. 2012). A rapid pathogen-induced *WRKY33* expression did not require salicylic acid signaling but downregulation of this gene involved a direct activation of jasmonic acid (Bakshi and Oelmüller 2014). Other reports established that *WRKY33* is essential for defense against the necrotrophic fungus *B. cinerea* (Birkenbihl et al. 2012). Loss of *WRKY33* function results in inappropriate activation of the SA-related host response and elevated SA levels post-infection, and in the downregulation of JA-associated responses at later stages. This downregulation appears to involve direct activation of several JA *ZIM*-domain genes, encoding repressors of the JA response pathway, by loss of *WRKY33* function and by additional SA-dependent WRKY factors. Moreover, genes involved in redox homeostasis, SA signaling, ET-JA-mediated cross-communication, and camalexin biosynthesis were identified as direct targets of *WRKY33*. Although SA-mediated repression of the JA pathway may contribute to the susceptibility of *wrky33* plants to *B. cinerea*, it is insufficient for *WRKY33*-mediated resistance. Thus, *WRKY33* apparently directly targets other still unidentified components that are also critical for establishing full resistance toward this necrotroph (Birkenbihl et al. 2012).

In the work of Mayo et al. (2016a), when bean plants (*Phaseolus vulgaris*) were in contact with *T. velutinum* T028 without pathogen, the *WRKY33* gene expression was significantly upregulated while the *PR* genes expression (*PR2*, *PR3*, and *PR4*) was significantly downregulated, compared to expression levels in plants without *Trichoderma* treatment. However, in the same work, when the pathogen *R. solani* was added to the substrate, expression of *WRKY33* was significantly downregulated in plants with *Trichoderma* inoculation, while *PR2*, *PR3*, and *PR4* were downregulated. In the study by Mayo et al. (2015), the expression of *PR1*, *PR2*, *PR3*, and *PR4* was downregulated when beans (*P. vulgaris*) were inoculated with *R. solani*. An overexpression of *PR2* and *PR5* has also been observed in *Arabidopsis thaliana* inoculated by the necrotrophic bacteria *Erwinia carotovora* subsp. *carotovora* (Li et al. 2004). WRKY family members have been shown to be responsible for the regulation of expression of *PR2* and *PR5* in grapevine (Marchive et al. 2013) and *A. thaliana* (Li et al. 2004). *PR1*, together with *PR2*, *PR3*, *PR4*, and *PR5*, is considered marker for SAR.

WRKY33 is also involved in the regulation of expression of genes modulated by components of the ethylene signaling pathway. Expression of *ERF1* and *ERF5* reached similar significant values either with or without *Trichoderma* and/or *R. solani* in the substrate. *WRKY33* would act as a repressor of *ERF1* and *ERF5* expression. Thus, when the expression of *WRKY33* is increased, the expression of *ERF1* and

ERF5 is downregulated (Mayo et al. 2016b). In *Arabidopsis*, *ERF5* may contribute to plant innate immunity against biotrophic pathogens, by regulating SA signaling, while also affected plant resistance to necrotrophic pathogens by regulating JA signaling (Son et al. 2012).

The *CH5b* gene encodes an endochitinase precursor and it is related with the ethylene signaling pathway. In previous works, it has been shown that when this gene was over-expressed the *R. solani* symptoms were reduced in crops like *N. tabacum* and *Brassica napus* (Broglie et al. 1991). However, when *P. vulgaris* plants were in contact with *R. solan*i, the expression of this gene was downregulated but not significantly, while treatment of these infected plants with *T. velutinum* resulted in its significant upregulation. These results are in agreement with previous data, showing that the pathogen represses its expression, and the presence of *Trichoderma* induced it (Mayo et al. 2015). Furthermore, expression of a chitinase encoding gene from *T. harzianum* in transgenic tobacco and potato plants and observed an increase in the resistance to *Alternaria alternata*, *R. solani*, and *B. cinerea*, a much wider protection spectrum than the one obtained when using plant chitinases (Lorito et al. 1998).

Osmotins have also plant protective effects against pathogen infection (Narasimhan et al. 2009). When *T. velutinum* or *R. solani* were present in the soil, the expression of *OSM34* was not significantly upregulated with respect to control plants, but when both fungi were in the soil at the same time, *OSM34* was slightly but significantly downregulated (Mayo et al. 2016b).

PAL (phenylalanine ammonia-lyase) plays an important role in plant defense; it is involved in the biosynthesis of salicylic acid, which is related to plant systemic resistance (Mauch-Mani and Slusarenko 1996; Nugroho et al. 2002; Chaman et al. 2003). *PAL* gene expression is also regulated in response to pathogen infection. The presence of *T. velutinum* and *R. solani* in the soil resulted in a significant downregulation of this gene compared with control plants (Mayo et al. 2016b). Similarly, potatoes inoculated with *T. harzianum* and/or *R. solani*, showed an upregulation *PR1* at 168 h post inoculation (hpi) and a slight upregulation of *PAL* at 96 hpi, in plants inoculated with *T. harzianum* alone (Gallou et al. 2009). This was in apparent contradiction with other studies in which a marked induction after a short time (24 hpi or 48 hpi) of *PAL*, hydroxyperoxide lyase (*HPL*), and *Lox*, *PAL*, ethylene receptor 1 (*ERF1*), ethylene-inducible *CTR1*-like protein kinase-encoding genes was observed (Yedidia et al. 2003; Shoresh et al. 2005). Such differences might be attributed to the absence of root cell penetration and colonization by the *Trichoderma* strain.

HPL (hydroperoxide lyase) is involved in the production of antimicrobial and defense signaling oxylipins (Noordermeer et al. 2001; Huang et al. 2010). The presence of *T. velutinum* and *R. solani* resulted in a downregulation of this gene expression when compared versus control plants. Thus, after 45 days of growth in contact with *T. velutinum* and/or *R. solani*, its expression was downregulated, indicating that the plant identifies *Trichoderma* and *Rhizoctonia* as two invader organisms. Some of the mechanisms activated against the presence of both are similar, independently of the final response that will be specifically activated in the plant by each one (Mayo et al. 2016b).

The expression of dependent genes of JA was studied in common bean plants inoculated by *T. harzianum* ALL-42. They also presented differential expression pattern for defense response such as *BCH1* (chitinase), *Glu1* (β-1-3-glucanase), *Lox* (lipoxygenase encoding gene), and *POD3* (peroxidase) in comparison to control plants, and with plants infected with *F. solani* or *R. solani*. This response is in agreement with previous works which showed that this is a typical host plant response to its colonization by a symbiotic or pathogenic microorganism (Harman et al. 2004; Shoresh et al. 2005; Shoresh et al. 2010). Plants challenged by *T. harzianum* ALL-42 showed upregulation of *Glu1*, *Lox*, and *POD3* compared with plants challenged by phytopathogenic fungi. *T. harzianum* ALL-42 also seems to potentiate common bean (*P. vulgaris*) response to the presence of the phytopathogenic fungus *R. solani*, as shown by the increase in the levels of *Glu1* and *POD3* for the double treatment (*Trichoderma* + pathogen) in comparison to that obtained for plants in the presence of *R. solan*i alone (Pereira et al. 2014).

The *CNGC* genes can be related to early plant defense responses due to changes in ion flux, including H^+ and Ca^{2+} influx and K^+ and Cl^- efflux (Atkinson et al. 1996). The upregulation of *CNGC2* confirms the importance of ion channels for the plant resistance response (Borges et al. 2012). *CNGC2* was downregulated in plants treated with *T. velutinum* (Mayo et al. 2016b).

GSTa (2,4-D inducible glutathione S-transferase) expression also responds to pathogen attack (Mauch and Dudler 1993) and can be induced by molecules such as salicylic acid, methyl jasmonate, abscisic acid, and H_2O_2 (Dixon et al. 2002; Moons 2005). In *Gossypium arboretum*, *GST* provides resistance to fungal pathogens and oxidative stress (Barthelson et al. 2010). *GST* expression was upregulated during fungal infection in barley, *Arabidopsis*, and cotton (Dowd et al. 2004; Durrant and Dong 2004; Lu et al. 2005). However, in banana *GST* was downregulated following *F. oxysporum* f specialis (f. sp.) *cubense* infection (Wang et al. 2013), which is in agreement with the downregulation of *GSTa* when *T. velutinum* and/or *R. solani* were present in the soil (Mayo et al. 2016b).

hGS encodes a homoglutathione synthetase that is involved in response to oxidative stress. There is not much information about the behavior of this gene in the plant. In the study of Mayo et al. (2016b), when bean plants (*P. vulgaris*) were in contact with *T. velutinum* and/or *R. solan*i, expression of this gene was significantly upregulated compared to control plants. In other studies, treatment of *Medicago truncatula* plants with compounds that release nitric oxide, a key signaling molecule, induced expression of *GST* but not *hGS* in roots (Innocenti et al. 2007). Similarly, common bean plants treated with H_2O_2 showed upregulation of *hGS* in nodules, whereas treatments with cadmium, sodium chloride, or jasmonic acid had no effect (Loscos et al. 2008).

Production of Secondary Metabolites: Changes in Plant Metabolism as Defense Response

When a plant is induced by exposure to a microorganism, it starts to produce diverse metabolites and enzymes. The physiological changes activated in the plant lead to the

activation of various metabolic pathways, which will be different depending on the type and origin of these signaling natural products. Different secondary metabolites are synthesized after perception and recognition of the signals originating from plant or pathogenic microorganism elicitors produced during the first steps of plant defense reactions (Grotewold 2005; Boller and Felix 2009; Veitch 2009). Plant responds after the invasion of a phytopathogen or a biocontrol agent by activating disease-resistance responses (i.e., upregulation of defense-related genes) against the invasion (Mayo et al. 2016b). Also, plant produces some antimicrobial secondary metabolites such as phytoalexins (phenols, isoflavones, terpenes), and some substances that can block pathogen invasion and spread, such as lignin and callose (Chen et al. 2015). Some plants do not produce phytoalexins when are in contact with pathogens but release toxins that are normally stored as less toxic glycosides (Grayer and Kokubun 2001).

Trichoderma spp. are also considered as efficient producers of extracellular enzymes, and some of these enzymes have been involved in the biological control of plant diseases (Monte 2001; Harman et al. 2004). *Trichoderma* species also produce plant hormones and solubilize minerals in the soil, which help to promote plant growth and suppress the disease (Kim et al. 2006).

During the *Trichoderma*–plant interaction, various classes of metabolites could induce resistance such as proteins with enzymatic activity, low molecular weight compounds related to the fungal or the plant cell wall, which can be originated by the enzymatic activity of *Trichoderma* (Woo et al. 2006; Woo and Lorito 2007), and other secondary metabolites. These elements trigger plant defense responses against the pathogen (Hermosa et al. 2012; Malmierca et al. 2014), by inducing the expression of genes encoding for pathogenesis-related (PR) proteins, which further contribute to reduce the disease symptoms.

During the plant–*Trichoderma* interactions, the fungus participates actively in protecting and improving its ecological niche. Leucine-rich repeat (LRR)-containing proteins are signal receptors regulating plant development and defense (Afzal et al. 2008). Marra et al. (2006) observed that LRR proteins increased in bean leaves (*P. vulgaris*) interacting with *T. atroviride*, and that hydrophobins and ABC transporters were accumulated in the proteome of the fungus. Hydrophobins (Rosado et al. 2007) and ABC transporters (Ruocco et al. 2007) support the biocontrol activity of *Trichoderma* and its ability to colonize the roots. In a similar way, a *Trichoderma*-secreted swollenin (an expansin-like 5 protein) remarkably increased fungus plant root colonization efficiency. Due to a cellulose-binding domain was able to trigger defense responses in the plant and afforded pathogen protection, indicating that this domain might, therefore, be recognized by the plant as a microbe-associated molecular pattern (MAMP) in the *Trichoderma*–plant interaction (Brotman et al. 2008). At least four classes of substances that elicit plant defense responses have been identified in *Trichoderma*: polysaccharide oligomers, enzymes, low molecular weight proteins, and peptaibols. Some cell wall oligomers may act as elicitor molecules released by plants following pathogen attack (Woo et al. 2006). The overexpression of *Trichoderma* chitinase genes in tobacco plants generates innate defense responses and enhanced stress tolerance (Dana et al. 2006). Also, it was detected hydrophobin-like cysteine-rich low molecular weight secreted proteins Sm1 from *T. virens* and Epl1

from *T. atroviride* (Djonović et al. 2006; Seidl et al. 2006) that can trigger ISR but, with the exception of peptaibols as elicitors of plant defense responses (Viterbo et al. 2007), the role of secondary metabolites in this task remains unexplored. In fact, the peptaibol alamethicin produced by *T. viride* sprayed on *Phaseolus lunatus* plants activates ISR, resulting in the production of defense compounds against herbivores (Engelberth et al. 2000). A plausible explanation is that the peptaibols produced by *Trichoderma* spp. can affect its own plasma membrane functions, and that the lack of production of these metabolites by the mutant potentiates growth, leading to the production of more aerial mycelium (Velázquez-Robledo et al. 2011).

Trichothecenes are important mycotoxins, which in general have potent phytotoxicity, but they are also toxic for animals and humans. Some *Trichoderma* species can produce trichothecenes (Nielsen et al. 2005). Thus, *T. brevicompactum* produces trichodermin, a phytotoxic compound that enables this species to be used as a biocontrol agent (Tijerino et al. 2011). *T. arundinaceum* produces harzianum A, a trichothecene lacking phytotoxic activity when assayed *in vivo*, but with antifungal activity against *B. cinerea* and *R. solani* (Malmierca et al. 2013). Harzianum A also elicits systemic defense and priming responses in tomato plants (Malmierca et al. 2012). In the antagonistic interaction of *T. arundinaceum* and *B. cinerea*, the former produces harzianum A while the latter inhibits the expression of genes in the trichothecene biosynthetic cluster. *B. cinerea* on tomato activates a typical JA response in the plant; *T. arundinaceum* on tomato activates the expression of SA and JA signaling genes by the plant. In the interaction between *T. arundinaceum*, *B. cinerea*, and tomato, there is a dramatic increase in the expression of tomato plant defense-related genes belonging to the SA and JA pathways, compared to a background of *B. cinerea*–tomato and *T. arundinaceum*–tomato conditions (Malmierca et al. 2012).

In the work of Velázquez-Robledo and et al. (2011) suggest that hydrolytic enzymes and mycoparasitism are more relevant than antibiotics in the control of *R. solani* during seed protection. A similar observation was made in the case of a *T. virens* mutant that did not produce gliotoxin but remained efficient in the protection of plants against infection by *R. solani* (Howell and Stipanovic 1995).

1.2.1.3 Conclusions

Crops are affected by a wide diversity of fungal pathogens and a method of control is the application of synthetic fungicides. However, it is a priority to develop non-chemical methods in integrated production, organic farming, and others such as the use of biocontrol agents. *Trichoderma* is a fungal genus including a huge number of species and strains. A high percentage of these species have the abilities to protect crops against diseases and to increase crop yield under field conditions. Plant can response to attack of pathogen as a hypersensitive defense that induces the selective death of some cells, including loss of permeability of cell membranes, an increase in respiration, and production of phytoalexins. *Trichoderma* and/or a phytopathogen can cause an upregulation or a downregulated response that will depend on the function gene, plant age, tissue, etc.

1.2.2 Cold Tolerance

Low temperature is a collective term, incorporating two distinct but related stresses, chilling, and freezing. Chilling temperatures fall in the range of 0–15 °C, while freezing temperatures are below 0 °C. While there is some commonality between the metabolic impact of chilling and freezing, their physiological impacts differ. However, both chilling and freezing can have extremely harmful effects on plant functions (Thomashow 1999). The sensitivities of plants to low temperatures are broadly correlated with their agro-environmental distribution. Several visual symptoms of chilling injury are exhibited by sensitive plant species. The most noticeable of these is the wilting of aerial organs, resulting from reduced water retention capacity. Moreover, prolonged chilling exposure can cause accelerated aging that is characterized by a loss of leaf coloration (Lukatkin et al. 2012). However, the processes underpinning the initiation and regulation of programmed cell death are not yet fully understood (Van Durme and Nowack 2016).

Despite the proven benefits of legume utilization, yield increases have not kept pace with those of cereal crops. Global increases in legume production are a result of increased land usage, rather than a direct increase in crop productivity (Foyer et al. 2016). Pulse crops are members of a diverse family of plants, the ecological and nutritional characteristics of which are well matched to the varied challenges of climate change, calorific provision, and nutritional demand. However, in order to sufficiently address these challenges a greater level of research must be conducted into legume biology, with a specific focus on the enhancement of legume survival and productivity under stress conditions (Foyer et al. 2016). Low temperatures in particular place a significant constraint on global legume yields and those legumes of significant dietary importance must be studied further.

While the general mechanisms of low-temperature tolerance have been characterized in the plant kingdom, extensive research has not been conducted on the factors underpinning low-temperature tolerance in legumes. Recent evidence has emerged showing that cold tolerance may be enhanced through favorable interactions between plants and the soil microbiome (Subramanian et al. 2016). This finding is particularly interesting when considered in the context of legumes, which are characterized by their intimate links with the soil microbiome.

Low temperature is a phenomenon that impacts agricultural productivity on every continent. In the United States, an estimated 25% of the reduction in crop productivity was attributed to low temperatures (Boyer 1982). Exposure to cold is also a limiting factor in the agricultural distribution of legume crops in Australia (Maqbool et al. 2010) and Africa. Moreover, in Europe severe cold weather events limit overwintering legumes such as faba bean (*Vicia faba*) and chickpea (*Cicer arietinum*) (Link et al. 2010). As such, the development of low-temperature tolerant legume crops is of critical importance for the protection of food security (Link et al. 2010). Yield reduction is the dominant consequence of stress exposure. Plants are vulnerable to cold stress at all stages of development, with susceptibility being particularly high during seedling establishment and seed formation. However, plants

employ numerous strategies for the survival of low-temperature stress. While the genetic and biochemical factors underpinning low-temperature tolerance have been extensively characterized in cereals (Winfield et al. 2010), limited research has been conducted on the mechanisms of low-temperature tolerance in legumes.

Biotechnology has provided some insight into the genetic factors contributing to stress tolerance; however, the focus has been placed on abiotic stresses. Moreover, the resolution of causative genetic factors tends only to extend to the level of genomic loci. As such, progress needs to be made in the elucidation of single gene location and function (Dita et al. 2006). However, some understanding of the mechanisms through which plants protect against abiotic stress exposure has been gained through transgenic studies. In legumes, the most susceptible stages are flowering, early pod formation, and seed-filling stages (Siddique et al. 1999). The cold stress can also lead to other problems, including increased vulnerability to pathogen entry, such as to bacterial blight, which requires a wound to infect the field pea plant. Genetic assessment for frost tolerance in pulses either under natural or controlled frost conditions is a relatively new area of research, with the majority of studies carried out on reproductive frost tolerance in barley (Reinheimer et al. 2004) and cold tolerance in chickpea (Clarke et al. 2004). The timing of the exposure to low temperature or frost is a key factor that determines the disruption of fertilization of flowers in legumes (Stoddard et al. 2006). However, international efforts to breed for frost tolerance, cold tolerance, freezing tolerance, and winter hardiness vary depending on the specific local climatic conditions, whereas the most severe damage may be caused at the seedling stage, the vegetative stage or the reproductive stage.

The genetic improvement strategies could include developing new screening and selection methodologies, including methods for marker-assisted backcrossing and genetic engineering (Stoddard et al. 2006). Only a limited number of studies have been carried out on tolerance in pulse crops (Margesin et al. 2007).

1.2.3 Drought Tolerance

Legumes rank among humanity's most important agricultural food crops. They are grown in almost every climatic region and on a wide range of soil types. Drought is one of the most common abiotic stresses reducing the yield of many crops including legumes. The yield of food legumes grown in arid to semiarid environments or drylands such as the Mediterranean (e.g., faba beans, chickpea, and lentil) is usually variable or low due to terminal droughts that characterize these areas (Mafakheri et al. 2010; Karou and Oweis 2012). Improving the tolerance of crops under water-limited environments is prerequisite if agricultural production is to keep pace with the expected demographic increase. Beyond productivity, the resilience of crops to water-limited environments, i.e., the capacity to yield even under very harsh conditions, will be increasingly important. The economically viable approaches to support crop production under drought are still limited. More importantly, it remains unclear how

the impact of drought on legume production varies with legume species, regions, agroecosystems, soil texture, and drought timing.

Besides soil degradation and heat stress (Abate et al. 2012), drought is the abiotic factor that most adversely affects legume production. It turns out, however, that the largest producers of pulses (70% of global production) (Gowda et al. 2009) are located in regions that experience water shortage (Rockstrom et al. 2009) and their production are highly vulnerable to drought.

1.2.3.1 Differences in Species Response to Drought

There are significant differences among legume species with regard to their adaptability to drought as measured by their ability to maintain high yield following a period of water stress. Lentil and groundnut were the legumes that exhibited the lowest yield reduction (21.7% and 28.6% respectively) while faba bean had the highest yield reduction (40%) under the highest observed water reduction (>65%). Under slightly lower water reduction (60–65%), pigeon pea exhibited the lowest yield reduction (21.8%) followed by soybean (28.0%), chickpeas (40.4%), cowpeas (44.3%), and common beans (60.8%). There are some legume crops (soybeans and common beans) that have migrated successfully from their center of origin while others remain largely confined to their areas of origin. During the evolutionary history of domesticated species, the wild types generally adapt themselves to their environment of origin, ensuring their own survival and that of their progeny. At the same time, genetic variability may exist within a legume species, from extremely drought-sensitive to drought-resistant types. This origin, however, does not always correspond to the adaptability of a legume species to drought. This indicates that most legumes may have the potential to be modified into more drought-resistant species.

1.2.3.2 Differences in Drought Responses Under Different Plant Phenological Stages

Plant phenological stage affected the percentage of yield reduction observed in legume crops, with drought during the vegetative phase resulting in lowest yield reduction (15.5%) compared to drought that occurred during the early and late reproductive stages under the same amount of water reduction. Although drought during the very early vegetative stage may impair germination, most studies that examined the effect of drought usually allowed sufficient water to support good and uniform plant establishment. Therefore, drought that happens during the later vegetative periods was relatively more tolerable to plants even though they might experience retarded cell elongation, division, and differentiation (Farooq et al. 2009). They are still able to maintain their growth functions under stress because early drought may lead to immediate survival or acclimation where the plants modify their metabolic and structural capabilities mediated by altered gene expression (Chaves et al. 2002).

A number of drought-resistant cultivars/lines of different crops have been developed solely using conventional breeding approach. These drought-tolerant lines of different crops provide a sound testament that conventional plant breeding played a considerable role during the last century not only for improving the quality and yield of crops but also for improving abiotic stress tolerance including drought tolerance. While transferring desired genes from one plant to other through the conventional plant breeding, a number of undesired genes are also transferred. Furthermore, to achieve the desired gain through traditional breeding, a number of selection and breeding cycles may be required. The limited success in improving crop drought tolerance could be due to the reason that the drought tolerance trait is controlled by multiple genes having an additive effect (Thi Lang and Chi Buu 2008) and a strong interaction exists between the genes for drought tolerance and those involved in yield potential. Thus, there is a need to seek more efficient approaches for genetically tailoring crops for enhanced drought tolerance.

The role of polygenes in controlling a trait has been widely assessed by traditional means, but the use of DNA markers and quantitative trait locus (QTL) mapping has made it convenient to dissect the complex traits (Humphreys and Humphreys, 2005). Due to the intricacy of abiotic stress tolerance and the problems encountered in phenotypic-based selection, the QTL mapping has been considered as imperative to the use of DNA markers for improving stress tolerance (Ashraf et al. 2008). QTL mapping for the drought tolerance trait has been done in different crops, the most notable being maize, wheat, barley, cotton, sorghum, and rice (Bernier et al. 2008). Molecular mapping and a number of QTL associated with drought tolerance identified in different crops can be effectively used in appropriate breeding programs meant for improving crop drought tolerance. Marker-assisted breeding approach is a prospective alternative to traditional breeding, because of being less time-consuming and labor- and cost-effective. Molecular mapping and analysis of QTL have been carried out for a number of qualitative and quantitative traits including stress tolerance, which has undoubtedly resulted in a great magnitude of knowledge and better understanding of the causal genetic phenomena that regulate these traits.

1.2.4 Insect Resistance

1.2.4.1 Biological Control Agents Against Insect Pests

Nowadays, the priority in pest management is to select compounds with different modes of action, with greater selectivity and less persistence. Thus, to minimize side effects on auxiliary fauna, the environment, and public health, there is an increasing interest on the use of entomopathogenic fungi to control invertebrate pests, weeds, and plant diseases, as shown by the increasing number of commercial products available or under development (Rodríguez-González et al. 2017a). Entomopathogenic fungi have great potential as control agents, constituting a group with more than 750 species, disseminated in the environment and causing fungal infections to arthropods

populations (Pucheta-Díaz et al. 2006). López-Llorca and Hans-Börje (2001) cite the following genera as the most important for arthropod control: *Metarhizium*, *Beauveria*, *Paecilomyces*, *Verticillium*, and *Trichoderma*. The field of biological control is an industry focused on the development of less harmful pest management strategies (Abdul-Wahid and Elbanna 2012). In recent years, this industry has started to use fungi to control populations of insect pests, specifically agricultural pests (Hajek 2004). The ability of entomopathogenic fungi to actively invade live insects through their cuticle and proliferate inside them, make these fungi unique and highly effective tools for the management of insect pests (Rodríguez-González et al. 2016).

Meyling and Eilenberg (2007) pointed out that in order to use entomopathogenic fungi as BCAs it is essential to use agricultural practices which enhance their establishment and development. For this reason, knowledge about the ecology of these fungi is of utmost importance. Different parameters which influence the ecology of these fungi are humidity, temperature, pathogenicity, virulence, and hosts range, among others. These pathogenic fungi have been searched and isolated in plants and crops affected by pests and/or diseases. Different *Trichoderma* species have been isolated and identified in bean seeds (*Phaseolus vulgaris*) (Campelo 2010). Rodriguez-Gonzalez and Carro-Huerga (unpublished data) have also been able to isolate and identify different *Trichoderma* species on vineyard soils and vine wood (*Vitis vinifera*) affected by *Xylotrechus arvicola* Olivier (Coleoptera: Cerambycidae).

Rumbos and Athanassiou (2017) described that most studies using entomopathogenic fungi to control post-harvest insects have been conducted with isolates of *Beauveria bassiana* and, to a lesser extent, *Metarhizium anisopliae* (Metschnikoff) Sorokin (Ascomycota: Hypocreales). These fungal pathogens have a wide host range and have been tested against most of the major storage pests under various conditions and crops.

Some studies have been conducted against *Sitophilus zeamais* (Motschulsky) (Barra et al. 2013), *A. obtectus* (Dal Bello et al. 2006), and *Callosobruchus maculatus* (F.) (Cherry et al. 2005) with *B. bassiana*, while *M. anisopliae* has been tested to control *Rhyzopertha dominica* (F.) (Athanassiou et al. 2008), and *Sitophilus oryzae* (L.) (Batta 2004). *B. bassiana* has shown high effectiveness on the control of other Coleoptera families, as for example *Enaphalodes rufulus* (Coleoptera: Cerambycidae) (Meyers et al. 2013), *Monochamus alternus* (Coleoptera: Cerambycidae) (Maehara and Kanzaki 2013) and *X. arvicola* (Coleoptera: Cerambycidae) under laboratory conditions (Rodríguez-González et al. 2016) or simulating field conditions in laboratory (Rodríguez-González et al. 2017b).

As described for *B. bassiana*, *Trichoderma* has shown good results in the control of different development stages of several insect pests within the orders Lepidoptera and Coleoptera. Examples of these results are shown in Alahmadi et al. (2012) *with Lucanus cervus* (Coleoptera: Lucanidae), Ghosh and Pal (2016) with *Leucinodes orbonalis* (Lepidoptera: Crambidae) and Rodríguez-González et al. (2017a, b) with *X. arvicola* (Coleoptera: Cerambycidae). For all this, the use of *Trichoderma* spp. as BCA against *A. obtectus* (Coleoptera: Chrisomelidae: Bruchinae) may be an economical, simple, and ecologically sustainable alternative.

1.2.4.2 *Trichoderma* spp.

Harman and Kubicek (2002) described *Trichoderma* spp. (Teleomorph: *Hypocrea*) as a genus of filamentous ascomycetes that is among the most commonly found saprophytic fungi in nature. These fungi frequently appear on the ground and grow on wood, bark, other fungi, and many other substrates, having high opportunistic potential and great adaptability to diverse ecological conditions. *Trichoderma* spp. produces chitinases, glucanases, and proteases, as well as other metabolites with antimicrobial activity (Lorito et al. 2010). Many *Trichoderma* species are also well known as biocontrol agents of important phytopathogenic fungi. Its two main mechanisms of biocontrol against these pathogens are mycoparasitism antibiosis (Papavizas 1985) and competition for nutrients with the pathogen (Harman and Kubicek 1998). *Trichoderma* species colonize plant root surface and cause substantial changes in plant metabolism (Harman et al. 2004).

There are several authors (Benítez et al. 2004) who have recognized *Trichoderma*'s important benefits to agriculture, such as its ability to protect crops against diseases and increase crop yield under field conditions (Harman et al. 2004). Benitez et al. (2004) described that once *Trichoderma* strains have grown and proliferated around abundant healthy roots, the fungus develops numerous mechanisms of action both to attack other fungi and to enhance plant and root growth.

1.2.4.3 The Bean Weevil, *Acanthoscelides Obtectus*

The bean weevil is an insect pest of neotropical origin (Fig. 1.2a) that feeds on wild and cultivated common bean (Paul et al. 2009; Thakur 2012; Vilca-Mallqui et al. 2013). Their larvae feed exclusively on the seeds and, cause considerable damage to them (Fig. 1.2b). The galleries they produce in the seed destroy the cotyledons, causing a significant reduction in its weight and germination rate (Gallo et al. 2002; Quintela 2002). Moreover, the commercial depreciation of the damaged beans is also due to the presence of insect excrements and death individuals. These remains favor the development of fungi and other pathogens inside the beans making them unsuitable for human consumption (Ramírez and Suris 2015).

The bean weevil is both a field and a storage pest, although major losses are caused when beans are in storage (Baier and Webster 1992). The bean weevil is a polyphagous species that affects around 35 species of legumes (Romero-Nápoles and Johnson 2004). Adults are straw colored, have an ovoid shape and, measure 2–4 mm in length. They are good flyers and can easily infect new beans, both in the field and in storage (Gallo et al. 2002). Gołębiowski et al. (2008) described that these insect populations grow exponentially when left untreated and can destroy stored crops within a few months. The management of the bean weevil in storage facilities is either nonexistent (by small farmers) or relies on the application of synthetic insecticides (in big storage facilities), such as phosphine, pyrethroids, and organophosphates (Daglish et al. 1993; Oliveira et al. 2013). The application of these compounds causes the development of pest resistance, environmental contamination and also

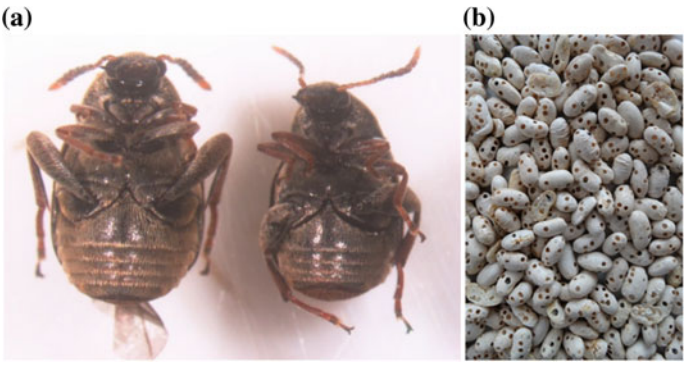


Fig. 1.2 *A. obtectus* adults (left: female; right: male) (**a**). Damage caused in beans by *A. obtectus* larvae (**b**) (images from da Silva 2017)

threats human health (Subramanyam and Hagstrum 1995; Daglish 2008). Therefore, the use of synthetic insecticides has been recently questioned by a society that seeks sustainable alternatives for pest control (Regnault-Roger et al. 2012).

1.2.4.4 *Trichoderma* spp. Against the Bean Weevil

Four *Trichoderma* species were evaluated against bean weevil eggs showing high biocontrol activity. *T. harzianum* had an almost total ovicidal control (96.7% of eggs infected) (Fig. 1.3a). *T. atroviride* and *T. citrinoviride* also inhibited most of the tested eggs (Fig. 1.3b, c), whereas *T. longibrachiatum* was only able to infect half of the eggs (Fig. 1.3d).

T. harzianum has been described in previous reports as a control agent against insect immature stages (Alahmadi et al. 2012) using Trichodex® (Makhteshim Ltd., Makhteshim-Agan of North America, Inc., New York). Trichodex® is a commercial compound made from *T. harzinanum* that controlled *Lucanus cervus* (Coleoptera: Lucanidae) larvae. *T. citrinoviride* also showed a biocontrol effect on *A. obtectus* eggs. There are no previous studies where *T. citrinoviride* was applied to control immature stages of insect pests. Until now, this *Trichoderma* species has been used exclusively against plant diseases, so it may be interesting to test their insecticidal activity on other insect species. Even the lower effect shown by *T. atroviride* could be used to significantly reduce egg density and subsequently diminish the emergence of neonatal larvae in storage conditions. This inhibitory activity shown by *T. atroviride* has also been described by Razinger et al. (2014) treating *Delia radicum* L. (Diptera: Insecta) larvae. To date, no use of *T. citrinoviride* has been described to control insect pests, being its use limited to species of the Plantae kingdom (Mayo et al.

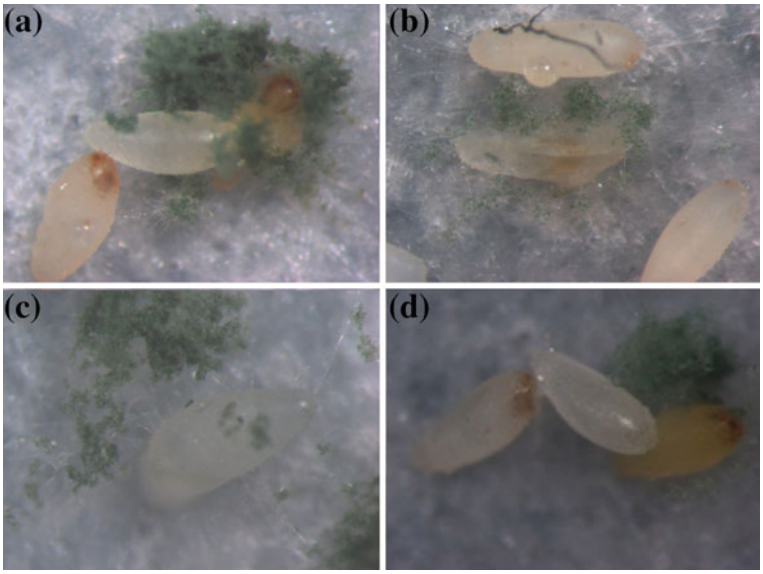


Fig. 1.3 Infection and sporulation of *T. harzianum* (**a**), *T. atroviride* (**b**), *T. citrinoviride* (**c**), *and T. longibrachiatum* (**d**) on bean weevil eggs (images from Rodríguez-González et al. 2017a)

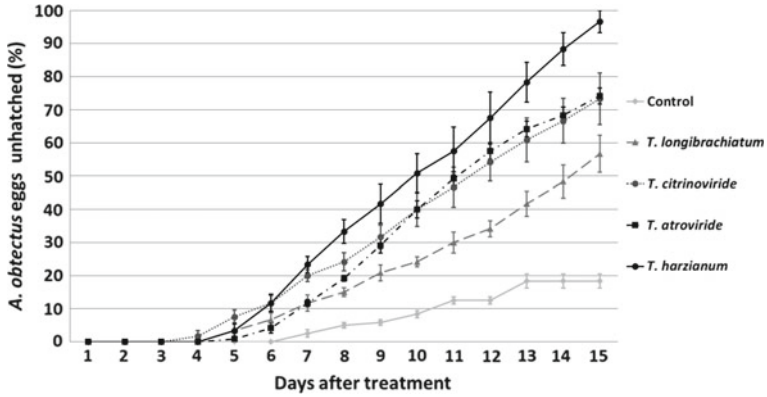


Fig. 1.4 Bean weevil eggs infected by *Trichoderma* species during 15 days after treatment. Upper and lower error bars are represented (image from Rodríguez-González et al. 2017a)

2015). Likewise, *T. longibrachiatum*, *T. citrinoviride*, and *T. longibrachiatum* have been used mainly on plants and have not been described as a biological control agents against insect pests, but for the control of *Leucinodes orbonalis* (Lepidoptera: Crambidae) larvae (Ghosh and Pal 2016).

The Fig. 1.4 shows the percentage of bean weevil eggs hatching during 15 days after they have been treated by the different *Trichoderma* species evaluated.

When these Trichoderma species were applied on bean weevil adults, the results showed that *T. citrinoviride* was able to control all adults evaluated. Furthermore, *T. longibrachiatum*, *T. harzianum*, and *T. atroviride* also showed a high performance, being able to control 98.3, 95.0, and 93.3% of adults evaluated, respectively (Da Silva 2017). *T. longibrachiatum* has also been used to control adult stages of insect pests such as *Bemisia tabaci* (Homoptera: Aleyrodidae) (Anwar et al. 2017) and *Leucinodes orbonalis* (Lepidoptera: Crambidae) (Ghosh and Pal 2016). As for *T. citrinoviride*, it has biological activity against the aphid *Rhopalosiphum padi* (Homoptera: Aphididae), an important pest of cereal crops (Ganassi et al. 2016). *T. atroviride*, on the other hand, proved to be useful against the cabbage root fly, *Delia radicum* (L.) (Diptera: Anthomyiidae) (Razinger et al. 2017). The cited species obtained high control rates in all cases.

Great attention is focused on developing these entomopathogenic fungal species as inundative biopesticides against insect and other arthropod pests (de Faria and Wraight 2007). Many authors highlight the multiple roles played by fungal entomopathogens as a promising potential for their indirect, multifaceted, and cost-effective use in sustainable agriculture (Jaber and Ownley 2018). For instance, they can be used as biofertilizers (Kabaluk and Ericsson 2007; Sasan and Bidochka 2012; Jaber and Enkerli 2016, 2017), as a vertically transmitted fungal endophytes (Quesada-Moraga et al. 2014; Lefort et al. 2016), and dual microbial control agents of plant diseases and arthropod pests (Vega et al. 2009; Ownley et al. 2010; Lacey et al. 2015). Several studies have shown that by inoculating *Trichoderma* on plants, insect behavioral changes occur due to plant emitted volatiles and, plant defensive responses are activated. Previous studies have shown changes on insect development and behavior by treating their plant hosts seeds with fungi. Akello and Sikora (2012) reported that inoculation of fungal isolates in bean seeds reduced the population of *Acyrthosiphon pisum* Harris (Homoptera: Aphididae) 33 fold compared to population growth observed in untreated samples. Menjivar-Barahona (2010) described the reduction of whitefly population in tomatoes inoculated with *T. atroviride*. More recently, Rodríguez-González et al. (2018), demonstrated that the application of different *Trichoderma* species (volatile producers and nonproducers) on beans changed the behavior of *A. obtectus* adults. Accordingly, a new line of research is opened for the control of insects by treating beans with *Trichoderma*. To date, the treatment of bean seeds with different *Trichoderma* spp. has been focused on the control of phytopathogenic fungi. This technique is easy, fast, and saves time and resources (Martínez et al. 2013).

In conclusion, these results show that the *Trichoderma* species evaluated against the bean weevil may be suitable for the control of this insect pest. *T. harzianum* shows good control activity against different *A. obtectus* stages. Meanwhile, *T. atroviride*, *T. citrinoviride*, and *T. longibrachiatum* exhibit high biological control activity only on adults. These fungi can be considered a highly effective tool for the control of this insect species.

1.2.5 Other Crop-Specific Traits: Biological (Symbiotic) N Fixation

Approximately 80% of Earth's atmosphere is nitrogen gas (N_2). Unfortunately, N_2 is unusable by most living organisms. All organisms use the ammonia (NH_3) form of nitrogen to manufacture amino acids, proteins, nucleic acids, and other nitrogen-containing components necessary for life. Biological nitrogen fixation is the process that changes inert N_2 into biologically useful NH_3. This process is mediated in nature only by N-fixing rhizobia bacteria (Sørensen and Sessitsch 2007). Other plants benefit from N-fixing bacteria when the bacteria die and release nitrogen to the environment. In legumes and a few other plants, the bacteria live in small growths on the roots called nodules. Within these nodules, nitrogen fixation is done by the bacteria, and the NH_3 they produce is absorbed by the plant.

The legumes provide a range of nutritional and agroecosystems services to the societies: as important sources of protein-rich food and feed, oil, fiber, minerals, and vitamins, improve soil fertility by contributing nitrogen through atmospheric N_2 fixation in symbiosis with rhizobia; improve soil structure and increase soil organic carbon status; reduce the incidence of pest and diseases in cropping systems; and increase the overall productivity and economic benefits of the production systems (Lupwayi et al. 2011). Legumes also contribute to mitigating the climate change effects by reducing fossil fuel use, ammonia fertilizer production or by providing feedstock for the emerging bio-based economies where fossil fuel sources of energy and industrial raw materials are replaced in part by sustainable and renewable biomass resources.

Thus, the legumes are key components of sustainable agriculture and their use in crop rotation leads to a reduction in agricultural CO_2 emissions and a decrease in nitrogen fertilizer application (Barton et al. 2014) for their capacity for nitrogen fixation. Interestingly, the nitrogen-fixing capacity of legumes is not a ubiquitous trait, with approximately 88% of described legumes showing this ability (Graham and Vance, 2003). The N_2 fixed by the legume crops represents a renewable source of nitrogen for agricultural soils. Globally, legumes in symbiosis with soil rhizobia are reported to fix 20–22 million tons of nitrogen each year in agricultural production systems (Herridge et al. 2008). Nitrogen fixation is achieved through symbiotic interactions with organisms in the soil microbiome, consisting of bacterial species, rhizobia, and arbuscular mycorrhizal fungi. The legumes are able to access atmospheric nitrogen fixed in the forms of ammonia (NH_3), nitrate (NO^{3-}) or ureides (Atkins 1987). This process of symbiotic nitrogen fixation is resulted from the complex interaction between the host plant and rhizobia. This mutualistic relationship is beneficial for both symbiotic partners; the host plant provides the rhizobia with carbon and source of energy for growth and functions while the rhizobia fix atmospheric N_2 and provide the plant with a source of reduced nitrogen in the form of ammonium. Thus, the process offers an economically attractive and ecologically sound mean of reducing external inputs and improving internal resources (Van Hameren et al. 2013).

Legume nodules are very complex organs, containing several interacting processes that operate at distinct levels, including, at least, nodule formation, carbon metabolism, oxygen supply, cellular redox, and transmembrane transport (Udvardi and Poole 2013). Nodule metabolism and regulation have been a topic of intensive research for quite a long time. Despite the enormous progress in this field, more research will still be required to provide a greater understanding of this fantastic process (Oldroyd and Dixon 2014). Pink or red nodules should predominate on a legume in the middle of the growing season. If white, gray, or green nodules predominate, little nitrogen fixation is occurring as a result of an inefficient rhizobia strain, poor plant nutrition, pod filling, or other plant stress. Factors like temperature and water availability may not be under the farmer's control, but nutrition stress (especially phosphorus, potassium, zinc, iron, molybdenum, and cobalt) can be corrected with fertilizers. An increase in soil concentration of nitrate can inhibit N_2 fixation quite severely. When nutritional stress is corrected, the legume responds directly to the nutrient and indirectly to the increased nitrogen nutrition resulting from enhanced nitrogen fixation. Poor nitrogen fixation in the field can be easily corrected by inoculation, fertilization, irrigation, or other management practices.

Plant breeding research in the 1980s and 1990s focused at combining high symbiotic nitrogen efficiency into improved genetic backgrounds in legumes, with some germplasm and breeding lines with high N_2 fixation being released. This becomes more important in the view of advances made in genomics of rhizobium and several model symbiotic nitrogen-fixing (SNF) legumes. Research on SNF suggests that several plant traits are associated with nitrogen fixation in grain legume crops, including nodule number and nodule weight, root and shoot weight, total biomass, and percent and total atmospheric N_2 fixed. An accurate estimation of the total atmospheric N_2 fixed and phenotyping of traits associated with nitrogen fixation is a prerequisite to detect genetic variation associated with nitrogen fixation in crop germplasm. Digital image analysis allows rapid and nondestructive phenotyping of various parameters after segmentation of an image and extraction of quantitative features from the segmented objects of interest (Hatem and Tan 2003). Gray et al. (2013) developed a minirhizotron imaging system as a novel in situ method for assessing the number, size, and distribution of nodules in field-grown soybean exposed to elevated atmospheric CO_2 and reduced precipitation. The performance of the symbiosis depends on the rhizobial attributes of competitiveness, infectiveness, and effectiveness. In the future, the success of SNF will depend on improving host plant, rhizobia, and environment system of the crop. Therefore, plant breeders should consider nitrogen fixation in the breeding programs as mandatory and a prerequisite for the future success of symbiosis.

The discovery of PCR-based DNA markers led to the construction of genetic linkage maps of varying intensity that has revolutionized the use of genomic-led approaches in applied crop breeding. Genetic research in the preceding paragraph clearly indicates that SNF is a complex trait and is possibly governed by various genes with varying effects, and dissecting its genetic basis may provide crop breeders more opportunities to harness marker (QTL)-trait association in crop improvement (Collard and Mackill 2008). A large number of specific genes influencing the

legume–rhizobia interactions have been cloned or analyzed with forward and reverse genetics. Likewise, the sequence variations among rhizobium genomes may provide insights into the genetic basis of SNF. Several data are now available, through classical genetic experiments (screening of mutants, etc.) and whole genome sequences. However, no ultimate markers for the identification of the "best" strains can be defined, since the overall picture of gene interactions during the symbiotic processes is not fully understood, especially for those genes present in the dispensable genome fraction of rhizobial species. Consequently, more effort is needed toward the molecular characterization of gene functions and the modeling of genome–phenotype relationships. A large number of mutants with altered nodulation pattern (nod−, no nodulation; nod+/−, few nodules; fix−, ineffective nodulation; nod++, hypernodulation; nod++nts, hypernodulation even in the presence of otherwise inhibitory nitrate levels) have been reported in several grain legume crops (Bhatia et al. 2001).

Research showed that use of nodulation mutants has indeed contributed to the understanding of the genetic regulation of host–symbiotic interactions, and nodule development and nitrogen fixation (Sidorova et al. 2011). The use of DNA markers may, therefore, facilitate the identification of QTL associated with high SNF and their introgression into improved germplasm (Collard and Mackill 2008). Candidate genes associated with high nitrogen fixation have been identified in the genomes of common bean (Ramaekers et al. 2013), soybean (Schmutz et al. 2010), and model legume *M. truncatula* (Stanton-Geddes et al. 2013). Sequence variation of plant genes that determine the stability and effectiveness of symbiosis may be used for developing DNA markers that will facilitate breeding of legume cultivars with high symbiotic efficiency (Zhukov et al. 2010). The future of rhizobial biology is then directed toward the screening and collection of strains with interesting phenotypes and to link, under a systems biology view, such new or already known phenotypes with genomic information, providing genetic tools to screen and improve plant growth promoting performances of rhizobial strains.

1.3 Genetic Resources of CS Genes

1.3.1 Primary Gene Pool

Daryanto et al. (2015) reported that, among different grain legumes, common beans have among the greatest seed yield reductions in response to drought, with an estimated 70% of bean production areas affected by drought worldwide (Beebe et al. 2012). Middle American races, specifically Durango race bean lines, originating from higher altitude semiarid climatic zones and have the highest levels of drought tolerance (Singh 2001). Hybridization of Mesoamerican and Durango races has resulted in improvements in drought tolerance (Terán and Singh 2002; Frahm et al. 2004).

Limited sources of heat tolerance have been found in common bean, while most current production areas in Africa and Latin America are predicted to be unsuitable

for bean production by 2100 (Ramirez-Cabral et al. 2016). The small-seeded Middle American race Mesoamerica has the highest levels of heat tolerance. Beebe et al. (2013) note that larger seeded Andean beans with determinate growth habits have little heat tolerance. There are a few exceptions such as G122 (collected in India), Sacramento (developed in California), and CELRK (developed in California) that have been selected under high-temperature production environments resulting in higher levels of heat tolerance. "Indeterminate Jamaica Red" (Román-Aviles and Beaver 2003), also originating from the same region as G122 in India, has among the highest levels of heat tolerance yet identified in Andean germplasm and has been used for introgression of this trait into different Andean seed classes, including indeterminate types, e.g., PR9920-171, and determinate types, TARS-HT1 and HT2. The indeterminate growth habit is a common type among Andean bean landraces collected in the Caribbean (Durán et al. 2005), while indeterminacy has been shown to be a source of yield stability under abiotic stress. Beebe et al. (2013) also noted that mid-season bean lines with indeterminate, prostrate habits tend to have better adaptation to intermittent drought. In addition, improved germplasm for drought often combines deep rooting and improved seed fill under stress. Although precise ideotypes for heat or drought have not been suggested, certain characteristics of the shoot and root architecture have been identified and associated with stress tolerance.

Seed size may be associated with abiotic stress tolerance in common bean with smaller seeded types associated with greater heat and drought tolerance. This association could be due to a number of causes including the Middle American geographic origin with inherent abiotic stress selection, reduced diversity in the domestication process (Beebe et al. 2001), shorter seed-filling period less exposed to intermittent stress, or indeterminate plant habit, among others. Beebe et al. (2013) noted that small-seeded beans in the tropics are often produced at lower altitudes where tolerance to both heat and drought are needed. More progress has been made in the development and release of small-seeded (small red, black, and white beans) with enhanced levels of heat and drought tolerance, while less effort has been dedicated to larger seeded Andean beans. Larger seeded beans generally have a lower relative growth rate (RGR), as compared to smaller seeded beans, which has been associated with lower biomass and yield. In Lima bean (*Phaseolus lunatus* L.) a similar relationship has been found in California production environments with Middle American sieva seed types having higher heat tolerance as compared to large-seeded Andean types (Long et al. 2014). As global temperatures rise, producers and consumers of Andean beans at higher altitudes may switch to smaller seeded beans to maintain productivity.

There may be limits for the genetic improvement of common bean for tolerance to drought and high temperature. It may be necessary to introgress genes for tolerance to abiotic stress from related species such as the tepary (*Phaseolus acutifolius* L.) or to consider shorter-season common beans, or altering planting dates to avoid peak periods of heat or drought. As the physiological and genetic basis of drought and heat tolerance is better understood, genome editing techniques may provide opportunities to enhance abiotic stress tolerance. For example, Baltes et al. (2017) inserted a promoter into maize (*Zea mays* L.) to increase the expression ARGOS

genes (negative regulators of the ethylene response to drought and heat stress) that resulted in increased drought tolerance.

There may be greater use of irrigation to meet global demand for grain legumes; however, freshwater reserves are critically low in certain production zones and rainfall patterns are changing in others. Under these conditions, water use efficiency may gain importance as a criterion for selection by bean breeding programs. Beebe et al. (2013) noted that drought tolerance would be beneficial for irrigated production by reducing the amount of water required to produce the crop. In the tropics, bean production may move to higher altitudes where the risks of erosion and soil degradation are greater. Breeding for infertile soils or Al toxicity may need to be added to the list of breeding objectives since these conditions are more prevalent at higher altitudes.

1.3.2 Secondary Gene Pool

The scarlet runner bean (*Phaseolus coccineus* L.) is from the secondary gene pool and originates from high altitudes of Middle America. There are no reports of introgression of drought or heat tolerance from scarlet runner bean although it has been used extensively as a source of disease resistance (reviewed in Porch et al. 2013b) and recently to introgress tolerance to aluminum toxicity into common bean (Butare et al. 2011).

1.3.3 Tertiary Gene Pool

The tepary bean is recognized as having greater heat and drought tolerance than common beans (Federici et al. 1990; Teran and Singh 2002; Acosta-Gallegos et al. 2007). Rao et al. (2013) suggested that the tepary bean could be used as a model to improve drought tolerance of common beans. Beebe et al. (2009) reported that the tepary bean invests in early root growth, limited vegetative growth and efficient partitioning of photosynthates to the seed. Traub et al. (2017) noted that tepary beans have a slower increase in stomatal conductance in response to rainfall after a drought. They suggested that this would be advantageous to conserve water during periods of terminal drought. Souter et al. (2017) identified interspecific (*P. vulgaris* × *P. acutifolius*) lines that had superior performance in trials for drought and tolerance to low temperature.

Beebe et al. (2013) noted that Lima beans are very tolerant to heat and soil constraints. At present, it is not possible to introgress genes for traits such as heat tolerance from lima to common bean. Beebe et al. (2009) reported that crosses between common (*P. vulgaris*) and lima bean (*P. lunatus*) genotypes do not produce fertile hybrids. A better understanding of the physiological and genetic basis of abiotic stress tolerance in lima bean may lead to the identification of traits or breeding strategies that could be used to improve the abiotic stress tolerance of common bean.

In regions where high temperatures or drought stress are expected to become too extreme for common bean production, the commercial production of tepary or lima beans may become a viable alternative. Systematic plant breeding efforts to improve the tepary bean in the lowland tropics (Porch et al. 2013a) and heat tolerance of lima bean in temperate zones (Ernest et al. 2017) have been limited. However, lima bean and tepary bean may have appeal and potential for broader expansion in the Americas, the Caribbean, and Africa (Porch et al. 2013b) as production environments become increasingly marginal.

1.4 Glimpses on Classical Genetics and Traditional Breeding for CS Traits

1.4.1 Breeding Objectives

Rao et al. (2013) and Beebe et al. (2009) reported that globally almost 2/3 of the production areas planted in beans are vulnerable to drought. Singh (1995) noted that the degree and length of intermittent and terminal drought stress are associated with the reduction in common bean yield. Singh (2001) reported that daytime temperatures >30 °C and or nighttime temperatures >20 °C can limit bean production. In temperate bean production regions, a temporary heat wave during a critical period of reproductive development can reduce pod set and yield, especially for Andean beans such as snap beans with a determinate growth habit. Significantly greater yield reduction or complete crop failure would be expected with the occurrence of both heat and drought. Future climatic conditions in most bean production regions are expected to be warmer, drier, and more variable (Williams et al. 2007; McClean et al. 2011). Daryanto et al. (2015) concluded that the common bean could be the grain legume in greatest need of improved drought tolerance given its importance in world production and human nutrition.

As bean production expands in Central America into the tropical lowlands, heat tolerance has gained importance as a trait. Some bean diseases also become more important in higher-temperature environments. For example, bean cultivars lacking the dominant *I* and either the *bc-3* or *bc-1*^{2} recessive genes are susceptible to *Bean common mosaic necrosis virus* (BCMNV) at higher ambient temperatures (>30 °C) (Singh and Schwartz 2010). Resistance to BCMNV must be added to breeding objectives to lowland tropical bean breeding programs where this seed-borne virus is endemic or has the potential to emerge.

Plant breeders need to identify the most appropriate combination of traits needed for adaptation to specific geographic regions and/or cropping systems. It may be necessary to evaluate the performance of bean lines in dryer and or hotter environments, or a combination of both, than current production zones in order to successfully select for future environmental conditions. The USDA/ARS bean research program in Puerto Rico screens beans for drought on the southern coast of the island where

conditions are much dryer than the regions where most beans are currently produced. In Honduras, the bean breeding program at Zamorano University screens beans for heat tolerance at a low altitude site near the Pacific coast that is considered too warm for bean production, but has resulted in the successful selection of improved cultivars for lowland production in Central America (Rosas et al. 2000). The USDA/ARS and University of Nebraska bean breeding programs have screened beans for drought in alternate generations in Puerto Rico and Nebraska. By conducting two field screenings each year, the development of improved bean breeding lines is accelerated. The screening of bean lines in contrasting environments may lead to more robust drought tolerance in breeding lines.

In some regions, beans are exposed to intermittent periods of drought whereas, in other regions, beans are more likely to suffer from terminal drought toward the end of the growing season (Omae et al. 2012). Breeding for these different types of drought will require the selection of distinct sets of traits. The sensitivity of bean to abiotic stress during reproductive development makes intermittent heat or drought during this period, or terminal drought, critically important. Beebe et al. (2009) noted that breeding for abiotic traits such as tolerance to drought and higher temperatures is challenging due to low genetic variability for these traits and the importance of genotype × environment interaction.

Plant breeders recognize that there may be trade-offs when focusing on the selection of specific traits related to greater drought or heat tolerance. Purcell (2009) noted that biomass accumulation in plants is directly linked with water loss due to transpiration. Traits such as deep rooting that increase the amount of water available for transpiration generally benefit crop growth and yield under drought conditions. Although deep and healthy root systems are considered desirable for all types of drought, it has been reported that shallow roots are more efficient in the absorption of nutrients such as P from the soil (Ho et al. 2005). Beebe et al. (2009) reported that deeper and more dense roots do not insure higher yields under drought conditions. In fact, too much investment in root growth may lead to lower seed yield potential. Blum (2009) argued that effective water use, involving improved harvesting of soil water by the plant and efficient use of that water in transpiration and biomass production would ensure continued yield gain, while selection for WUE and TUE (transpiration use efficiency) tends to result in drought resistance, but yield loss. Beebe et al. (2009) suggested that more efficient root systems that require less biomass accumulation may contribute to greater seed yield potential under drought stress.

Traub et al. (2017) suggested the use of lower stomatal conductance as a criterion for selection for drought tolerance. Greater stomatal conductance and lower leaf temperatures were associated with deeper rooting in beans under drought although no yield advantage was reported (Beebe et al. 2009). Taub et al. (2017) reported that the common bean line SER 16 and the tepary bean line TB1 had lower stomatal conductance under both drought and well-watered conditions. A trade-off of slightly lower net photosynthesis under nonstress conditions allowed for better performance under drought conditions and led to greater water use efficiency. Beebe (2012) noted that a more rapid stomatal recovery may be advantageous under conditions of intermittent drought, while Ramirez Builes et al. (2011) found stomatal response associated with

yield under drought in the greenhouse and field. Pimentel et al. (1999) proposed the integration of a calculated photosynthetic rate based on the stomatal conductance through the use of intrinsic water use efficiency (WUE) that would allow for selection of efficient genotypes during key developmental stages. Instantaneous measurements of leaf temperatures using high-throughput phenotyping platforms have been used to estimate stomatal response to drought (Andrade-Sanchez et al. 2014), and instantaneous normalized difference vegetation index (NDVI) measurements have been correlated with yield in bean (Sankaran et al. 2018), and could potentially be used for selection of stress-responsive lines. Carbon isotope discrimination (CID), on the other hand, provides a cumulative assessment of WUE over the whole season and can be readily evaluated on the harvested seed. Due to its inverse relationship with WUE, selection for low CID has been recommended (Easlon et al. 2014).

Omae et al. (2012) reported that higher leaf water content was associated with greater drought and heat tolerance. Traub et al. (2017), however, noted that plants must balance the influx of CO_2 and the loss of water. Hoyos-Villegas et al. (2017) indicated that water conservation may limit photosynthesis and the growth and development of plants. In response to severe drought stress, bean plants may produce smaller or fewer leaves that can result in suboptimal leaf area and reduced net photosynthesis. Schneider et al. (1997) suggested selection for increased biomass under drought stress to avoid the reduction in photosynthetic capacity. This practice, however, may result in indirect selection for later maturity.

Daryanto et al. (2015) noted that osmotic regulation through increased solute concentration is less energy demanding than stomatal conductance and allows the roots to extract water at lower soil water potentials. A plant breeding challenge is the selection of an appropriate balance between water conservation and net photosynthesis for a specific cropping system? True tolerance is the ability of plants to withstand drought conditions by having low internal water potential. This trait, however, has limited utility since drought tolerance is more important for survival and is often associated with slow rates of growth and low productivity (Passioura 2012).

Beebe et al. (2013) noted that mechanisms to escape drought include early maturity, phenotypic plasticity, and rapid partitioning of photosynthate to seed. Selection for earlier maturity may help to avoid terminal drought but earliness may reduce seed yield potential during more favorable growing seasons. An early, defined, and un-reversible shift to reproductive development and a shorter period of pod filling could reduce the exposure during the sensitive reproductive period of development and shorten the growing season, thus increasing the chances of escape. In the highlands of Mexico, some bean genotypes use phenotypic plasticity adapt to intermittent periods of drought by delaying flowering until more humid conditions return (Acosta-Gallegos et al. 1989; Acosta-Gallegos and White 1995). Indeterminacy is often key for plasticity, providing for reproductive organ abscission as a result of abiotic stress and reflowering at new flower nodes, thus allowing for a degree of avoidance of short-term dry or hot conditions. However, split-sets in snap beans and late maturity in dry beans can result.

Selection for a greater harvest index has been a successful strategy to increase the yield potential of many crops (Unkovich et al. 2010). Foster et al. (1995) reported that

greater partitioning or higher harvest index contributed to terminal drought tolerance. Cuellar-Ortíz et al. (2008) reported that carbohydrate partitioning toward seed fill is a useful drought tolerance strategy. Beebe et al. (2013) noted that accelerated partitioning of photosynthates toward reproductive development contributed to better adaptation and seed yield under both terminal and intermittent drought. Beebe et al. (2009) reported that pod harvest index (grain as percent of total pod biomass) to be consistently associated with seed yield under drought stress. Blum (2005) noted that selection for greater yield potential can contribute to better performance in environments with moderate levels of drought stress. Recent research has shown variability for pod harvest index, or the extent of dry matter translocation from the pod wall to the seed, and its effectiveness as a trait for breeding (Polania et al. 2016). Some tepary bean germplasm has shown efficiency for pod harvest index, short reproductive period and high harvest index, likely key abiotic stress tolerance mechanisms in the tepary bean ideotype that include a thick taproot, prostrate habit, small phototropic leaves, high pod number, and small seed size.

Screening for heat tolerance in the tropics is more predictable than selection for drought tolerance. Evaluations can be conducted at lower altitudes to ensure higher temperatures. On the other hand, screening may need to be conducted under controlled conditions for response to heat waves during critical stages of development that can occur in temperate regions. Porch (2006) noted that temperatures of >30 °C during the day or >20° at night result in the reduction of seed yields of most common beans. In the evaluation of response of common bean to high temperatures, Porch (2006) found that geometric mean (GM) and the stress tolerance index (STI), as described by (Fernández 1992), to be effective in the identification of lines with superior yields in stress and nonstress trials.

1.4.2 Classical Breeding Achievements

Terán and Singh (2002) noted that considerable progress has been made in breeding beans with greater adaptation to both intermittent and terminal drought. Most progress has been made in the selection of drought tolerance of bean races Durango and Mesoamerica. Crosses between Durango and Mesoamerican races have produced progenies with superior performance under drought, for example, SEA 5 (Terán and Singh 2002) and L88-63 (Frahm et al. 2004). Much less research and genetic progress have been made improving the drought tolerance of other bean races, especially beans of Andean origin. Limited gains in breeding for Andean abiotic stress tolerance may be a result of reduced efforts and to more limited genetic diversity in this gene pool (McClean et al. 2011). Bean germplasm or cultivars reported to have drought or heat tolerance are listed in Table 1.1.

Polania et al. (2016) measured seed yield, canopy biomass, stomatal conductance, and carbon isotope discrimination to evaluate the response of common bean lines to drought. The authors identified lines such as SER 16, ALB 60, ALB 6, BFS 10, BFS 29 that conserve water through lower rates of transpiration, moderate rates of growth,

Table 1.1 Release of bean germplasm and cultivars reported to have heat or drought tolerance

Identity	Seed type	Location (year of release)	Type of tolerance	Citations
Bella	White	Puerto Rico (2017)	Heat	Beaver et al. (2018). J. Plant Reg. 12:190–193
Verdín	Black	Mexico (2016)	Terminal drought	Tosquy Valle (2016). Rev. Mex. Cien. Agríc. 7:1775–1780.
DAB-53	Large-seeded red	CIAT germplasm	Andean bean with terminal drought tolerance	Mayor-Duran et al. (2016). Acta Agron. 65:431–437
CENTA EAC	Small red	El Salvador (2015)	Heat	Parada Cardona et al. (2015). CENTA 7 p.
SER 16	Small red	CIAT germplasm	Terminal drought tolerance	
TARS-LFR1	Small red	Puerto Rico (2014)	Heat	Porch et al. (2013a). J. Plant Reg. 8:177–182
INTA Sequía Precoz	Small red	Nicaragua (2013)	Terminal drought	
TARS-MST1	Black	Puerto Rico (2012)	Heat and drought	Porch et al. (2012). J. Plant Reg. 6:75–80
CENTA Pipil	Small red	El Salvador (2013)	Heat	
PR0401-259	Pink	Puerto Rico (2012)	Heat	Beaver et al. (2012). J. Plant Reg. 6:81–84.
TARS-HT1 and TARS-HT2	Dark and light red kidney	Puerto Rico (2010)	Andean beans with heat tolerance	Porch et al. (2010). HortSci. 45:1278–1280
Verano	White	Puerto Rico (2008)	Heat	Beaver et al. (2008). J. Plant Reg. 2:187–189.

(continued)

Table 1.1 (continued)

Identity	Seed type	Location (year of release)	Type of tolerance	Citations
Cornell 503	Snap bean	New York (2005)	Heat	Rainey and Griffiths (2005). J. Am. Soc. Hort. Sci. 130:700–706.
Amadeus 77	Small red	Honduras (2004)	Heat	Rosas et al. (2004). Crop Sci. 44:1867–1868
Indeterminate Jamaica Red	Striped pink kidney	Germplasm Landrace	Andean bean with heat tolerance	Román-Aviles and J. Beaver (2003). J. Agric. Univ. P. R. 87, 113–121.
UI-239	Small red	Idaho (1997)	Terminal drought	Singh (2007). Agron. J. 99:1219–1225
Pinto Villa	Pinto	Mexico (1995)	Phenotypic plasticity to intermittent drought	Acosta-Gallegos et al. (1995). Crop Sci. 35:1211

and more efficient partitioning of photosynthates. Other groups of bean lines such as NCB 280, NCB 226, SEN 56, SCR 2, SCR 16, SMC 141, RCB 593, and BFS 67 were able to avoid drought by having deep roots and more efficient use of available water by combining early maturity and greater harvest indices. Polania et al. (2016) noted that the former group would be most useful in environments that are prone to severe drought. The latter group would be more suited for intermittent drought and soils that have a greater water-holding capacity.

1.4.3 Limitations of Traditional Breeding and Rationale for Molecular Breeding

Heat and drought tolerance are quantitative traits that require the evaluation of large numbers of later-generation breeding lines. These evaluations should be conducted in several environments using replicated trials to obtain reliable estimates of the performance of the lines. Singh (2001) reported that seed yield remains the most reliable trait to evaluate the performance of common bean under drought stress. Beebe et al. (2013) recommended that sites for screening for drought tolerance should have uniform soil and management practices that are representative of the target production

zone. In general, more replications are needed if the lines are to be screened under high levels of drought stress. Instead of screening bean lines at sites with multiple biotic and abiotic constraints, Beebe et al. (2013) recommended the sequential screening of bean lines for individual traits such as drought. The evaluation of advanced generation lines allows the simultaneous evaluation of several traits at different locations. Regional performance trials can be used to evaluate the performance over a wide range of environments.

Screening for drought tolerance is often conducted by comparing the performance of bean lines in drought and nonstress trials. Selection criteria include geometric mean of the seed yields from drought and nonstress trials, percent reduction in seed yield in relation to the nonstress environment, and drought susceptibility indices (Terán and Singh 2002). Schneider et al. (1997) noted that geometric means allows the identification of lines that perform well under drought and nonstress conditions. This should be followed in a breeding program by evaluating the seed yield under drought to confirm the performance of the selections under stress. These conventional plant breeding practices are costly and time-consuming.

Beebe et al. (2013) noted that yield loss depends on the timing, duration, and severity of the drought. The authors also noted that bean root growth and development is sensitive to soil compaction and low soil fertility. A better understanding of interactions among edaphic conditions, soil management practices, and the physiology of traits associated with drought tolerance should lead to the development of robust molecular markers.

Briñez et al. (2017) noted that the response of beans to drought tolerance is a complex quantitative trait controlled by many minor QTLs. Due to the importance of genotype × environmental interaction, Briñez et al. (2017) noted that the stability of QTL for drought tolerance needs to be confirmed across populations and a wide range of environments in which the type and severity of drought may occur. Due to the variable nature of rainfall patterns across years and locations and the importance of genotype × environment interaction, Beebe et al. (2013) pointed out the need to validate in the field the drought tolerance of bean lines selected using marker-assisted selection.

Purcell (2009) noted that a major limitation for the improvement of quantitative traits such as drought is the difficulty in phenotyping plants. At present, rapid and simple methods of evaluating phenotypes for quantitative traits such as drought and BNF are not available. Meta-analyses using data from different trials have been used to compare the response of beans to drought (Daryanto et al. 2005). The use of drones (Sankaran et al. 2015, 2018) or proximal sensing carts (White and Conley 2012) allow for the collection of field data from a large number of lines in a short period of time for traits such as leaf canopy temperature, NDVI, and normalized difference red edge (NDRE) index. Rapid, high-throughput phenotyping allows for a more representative comparison of bean lines for traits at a particular time and thus stress condition or at different times of the day (Andrade-Sanchez et al. 2014).

Purcell (2009) noted that for most legumes BNF is more sensitive to drought stress than photosynthesis, although both decrease with stress. Castellanos et al. (1996) reported that drought stress significantly decreased biological nitrogen fixation of

common bean. High temperature also inhibits BNF (Hungria and Kaschuk 2014) in common bean. This represents a significant challenge to breeding for environments with multiple climatic and edaphic constraints. However, high-temperature tolerant BNF capacity is another trait that could be introduced from tepary bean, where a range of nitrogen fixation capacity has been identified (Vargas 2016).

In the tropics, charcoal rot caused by *Macrophomina phaseoli* tends to be more severe in drought conditions, but occurs frequently under high-temperature humid conditions. In more temperate climates, root rots caused by *Fusarium* spp. are more common during periods of low rainfall. Beebe et al. (2013) note that resistance to root rots is an important trait for beans produced in areas where drought stress is common. It is also important in high-temperature environments where there are higher rates of transpiration.

Dry and warm climatic conditions favor some pests such as leafhoppers (*Empoasca* spp), aphids (*Aphis* spp.) and whiteflies (*Bemisia* spp.). Resistance to leafhoppers is an especially important trait for beans cultivars growing under these conditions. Likewise, resistance to viral diseases vectored by one these pests, such as BGYMV, BCMNV, BCMV, and CTMV, may need to be included as breeding objectives.

Screening for local adaptation, seed size, and commercial seed type and other highly heritable traits can be conducted in earlier generations. There are numerous molecular markers available for major genes for resistance to specific diseases, and some pests, that could be used for marker-assisted selection in earlier generations (Miklas et al. 2006a, b).

In recognition of the difficulty to improve drought and heat tolerance of Andean beans, CIAT bean breeders have developed Durango race bean breeding lines that have seed types that mirror Andean seed types. This approach would allow breeders to take advantage of superior levels of drought tolerance found in the Durango race, while introducing biotic stress tolerance to regions where mostly Andean races of pathogens currently exist, e.g., sub-Saharan Africa.

Several studies have been conducted to identify QTLs associated with drought tolerance. Briñez et al. (2017) evaluated a RIL population from the cross "SEA 5 × AND 277" and reported that the drought-tolerant line SEA 5 had lower leaf temperature under drought conditions than AND 277. These results suggested that SEA 5 had a greater rate of transpiration than AND 277 in the presence of drought stress. All of the QTLs associated with drought were from SEA 5 including a QTL for seed weight under normal and drought conditions. The authors noted that greater seed weight may suggest better seed fill under drought. Hoyos-Villegas et al. (2017) identified significant QTL associated with drought tolerance that may be useful for MAS for this trait.

Marker-assisted selection of major QTLs associated with heat and drought tolerance in earlier generations would help reduce the number of breeding lines that would need to be screened in later generations. Gamete selection suggested by Singh (1994) may be useful to accumulate alleles for drought tolerance when robust molecular markers for this trait have been identified. Lines harboring key QTL for abiotic stress tolerance could be selected in the F_1 from double crosses, thus accelerating

the pyramiding of key regions of interest. Large F_1 populations would be required necessitating many crosses, but critical QTL often affected by G × E could be combined. Beebe et al. (2013) and Hinkossa et al. (2013) noted that recurrent selection is an appropriate breeding approach for quantitative traits such as tolerance to drought and heat. Recurrent selection also provides for a gradual accumulation or pyramiding of key regions for quantitative traits through successive recombination of superior breeding lines.

A gene-based crop model has been developed that predicts vegetative and reproductive development based on genotype and weather data (Hwang et al. 2017). The development of more sophisticated models may facilitate the study of the interaction of traits related to drought tolerance with varying weather patterns and crop management practices.

1.5 Diversity Analysis

Occasional outcrossing, adaptation to particular environments (in terms of temperature, moisture, photoperiod, soil fertility, diseases, and insects), different cropping systems and strong selection for consumer preferences addressed to particular seed types, might have played a significant role in the evolution of new genetic variation in common bean. As a consequence, each country selected its own set of landraces able to respond to the needs and preferences of local populations. The common bean populations were involved in new evolutionary pathways that were not possible in the American center of origin, due to the spatial isolation between these two gene pools. Thus, new germplasm could have arisen from recombination events between Mesoamerican and Andean gene pools, better adapted to the conditions of the new agrosystems out of The Americas. Evidence of this phenomenon has been detected using phaseolins, allozymes, and morphological data (Santalla et al. 2002; Rodiño et al. 2006), and inter-simple sequence repeats (ISSRs) and simple sequence repeats (SSRs) from both the chloroplast and nuclear genomes (Sicard et al. 2005; Angioi et al. 2009). Gene flow between both gene pools appears to be relatively common in the Andean (Debouck et al. 1989; Beebe et al. 1997; Chacón et al. 2005) and European zones (Santalla et al. 2002; Sicard et al. 2005; Piergiovanni et al. 2006; Rodiño et al. 2006; Sánchez et al. 2008).

To date, considerable efforts have been made toward DNA polymorphisms discovery in common bean. Several thousand single-nucleotide polymorphisms (SNPs) and insertions–deletions (InDels) have been discovered through expressed sequence tags data mining and partial resequencing of several genotypes (Hyten et al. 2010; Souza et al. 2012; Felicetti et al. 2012; Blair et al. 2013; Goretti et al. 2014; Zou et al. 2014). At the transcriptional level, expressed sequence tags (ESTs), sequencing has been used to discover and identify genes differentially expressed under different conditions. Whole genome transcriptome analysis is also an effective way to exploit key factors for common bean responses to biotic and abiotic stress that are involved in transcriptional and metabolic activities. The data obtained from these technologies

will serve as an invaluable genomic reference to further our knowledge about the common bean at the molecular level and can be applied to molecular breeding for plants with enhanced biotic and abiotic tolerance.

The genome of an Andean common bean genotype (G19833) was sequenced and recently released (Schmutz et al. 2014). A combination of Sanger, 454, and Illumina HiSeq 2000 reads and a genetic map based on 7015 SNP markers were used to assemble the common bean reference genome sequence (Schmutz et al. 2014), with a total genome size of 521 Mb that represents 89% of the 587 Mb bean genome. Also, a first draft of the entire common bean genome sequence of a Mesoamerican genotype (BAT93) was also developed by Vlasoba et al. (2016).

1.6 Molecular Mapping of CS Genes and QTLs

1.6.1 A Brief History of Mapping Efforts

Linkage maps are important genetic tools for common bean improvement and other biological approaches. These maps have been used in several types of studies, including cloning of agronomically important genes, marker-assisted selection (MAS), comparative mapping, and analysis of germplasm diversity (Gepts 1999). Accordingly, several linkage maps have been developed in common bean (Table 1.2), and they differ in several characteristics, such as the types of parents and segregating population used, the type of markers and traits segregating in each population, the total map length and the degree of genome saturation. However, a common feature among the first maps is that they were generated based on low-throughput markers, resulting in low-density maps. Therefore, to increase the precision of bean maps, researchers have exerted much effort in generating new genomic-based tools that are supported by bioinformatics. Different projects, such as the Phaseomics international consortium and the BeanCAP project (USDA Common Bean Coordinated Agricultural Project), were developed to establish the necessary framework of knowledge and materials for the advancement of bean genomics, transcriptomics, and proteomics (reviewed by Gepts et al. 2008; Hyten et al. 2010). As a result, genome sequencing and high-throughput genotyping approaches are enabling the development of high-density functional maps that assist in accelerating bean genetic improvement through MAS.

1.6.2 Evolution on Marker Types

Common bean genetic maps have evolved in parallel with the development of molecular marker technologies. Linkage maps were once based on phenotypic markers (Lamprecht 1961), though molecular markers greatly increase the number of poly-

Table 1.2 Molecular linkage maps in common bean

Parents	Map size (cM)	Markers/traits mapped[a]	References
XR235-1-1/Calima (BC_1)	960	224 RFLPs, 9 seed proteins, 9 isozymes, *P*	Vallejos et al. (1992)
BAT 93/Jalo EEP558 (F_2)	1226	194 RFLP, 24 RAPDs, 15 SSR/ ALS, ANT, CBB, *V*, *C*, rhizobium	Nodari et al. (1993), Gepts (1999), Yu et al. (2000a, b)
Corel/Ms8EO2 (BC_1)	567.5	51 RFLP, 100 RAPD, 2 SCAR/ANT	Adam-Blondon et al. (1994)
Midas/G 12873 (RIL)	1,111	77 RFLPs, 5 isozymes/domestication traits	Koinange et al. (1996)
DOR364/XAN176 (RIL)	930	147 RAPDs, 2 SCARs, 1 ISSR/ ASB, BGYMV, CBB, *R*, *V*, *Asp*, rust	Miklas et al. (1996, 1998, 2000)
BAC6/HT7719 (RIL)	545	75 RAPDs/CBB, WB, rust	Jung et al. (1996)
PC50/XAN159 (RIL)	426	168 RAPDs/ CBB, *C*, *V*, rust, WM	Jung et al. (1997), Park et al. (2001)
BAT 93/Jalo EEP558 (RIL)	1226	120 RFLP, 430 RAPD, 5 isozymes/ BCMV	Freyre et al. (1998)
BelNeb-RR-1/A55 (RIL)	755	172 RAPDs, 2 SCARs/BBS, HB, BCMV	Ariyarathne et al. (1999), Fourie et al. (2004)
Eagle/Puebla152 (RIL)	825	361 RAPDs/ RR	Vallejos et al. (2001)
Jamapa/Calima (RIL)	950	155 RAPDs, 88 RFLPs/RGA	Vallejos et al. (2001)
OACSeaforth/OAC 95-4 (RIL)	1,717	49 AFLPs, 43 RFLPs, 11 SSRs, 9 RAPDs, 1 SCAR/ CBB, agronomic traits	Tar'an et al. (2001, 2002)
CDRK/Yolano (RIL)	862	196 AFLPs, 8 RFLP/SY, *C*	Johnson and Gepts (2002)
DOR364/G19833 (RIL)	1,720	78 SSR, 48 RFLPs, 102 RAPDs, 18 AFLPs	Blair et al. (2003)
ICA Cerinza/G24404 (RIL)	869,5	80 SSRs, 1 SCAR/ *C*, *fin*, *st*, agronomic traits	Blair et al. (2006a, b)
G14519/G4825 (RIL)	915.4	46 RAPDs, 68 SSRs/seed Fe and Zn concentrations and contents	Blair et al. (2010)
BAT 93/Jalo EEP558 (RIL)	1,545	199 gene-based, 59 core and 17 other markers	Hanai et al. (2010), McConnell et al. (2010)

(continued)

Table 1.2 (continued)

Parents	Map size (cM)	Markers/traits mapped[a]	References
DOR364/BAT477 (RIL)	2,041	1,060 (SSR, EST-SSR, BES-SSR, gene-based markers)/SW, Y, DF, DM	Blair et al. (2012), Galeano et al. (2011, 2012)
IAC-UNA/CAL143 (RIL)	1,865.9	198 SSRs, 8 STS-DArT, 3 SCAR/ALS	Oblessuc et al. (2012, 2013)
SEA5/CAL96 (RIL)	1,351	2,122 SNPs/SW, Y	Mukeshimana et al. (2014)
Stampede/Red Hawk (RIL)		7,276 SSRs and SNPs	Schmutz et al. (2014)

[a]*ALS* angular leaf spot, *BCMV* bean common mosaic virus, *CBB* common bacterial blight, *HB* halo blight, *RR* root rot, *WM* white mold, *SW* seed weight, *SY* seed yield, *DF* days to flowering, *DM* days to maturity, *Y* yield, *fin* determinacy, *Ppd* gene for photoperiod sensitivity, *V* flower color, *C* seed color

morphic loci in mapping populations. Thus, the first maps were developed based on restriction fragment length polymorphism (RFLP) markers, a technique that involves DNA hybridization. Later, new markers based on polymerase chain reaction (PCR) were used for genetic mapping, including random amplified polymorphic DNA (RAPD) (Williams et al. 1990), simple sequence repeats (SSRs) (Tautz 1989), amplified fragment length polymorphisms (AFLPs) (Vos et al. 1995) and inter-simple sequence repeats (ISSRs) (Zietkiewicz et al. 1994).

Due to their great robustness and repeatability, RFLP markers have allowed the development of the first DNA-based genetic maps in common bean (Vallejos et al. 1992; Nodari et al. 1993); these markers have also been used to compare and integrate different genetic maps (Adam-Blondon et al. 1994; Koinange et al. 1996; Freyre et al. 1998; Gepts 1999; Yu et al. 2000a, b). In addition, PCR-based molecular markers have been employed for saturating RFLP maps and for generating new ones using additional mapping populations (Freyre et al. 1998; Ariyarathne et al. 1999; Yu et al. 2000a, b; Blair et al. 2003, 2010; Fourie et al. 2004). For example, the first RFLP-based genetic map was constructed with 224 RFLP marker loci; the seed and flower color marker *P*, nine seed proteins, and nine isozyme markers were also included (Vallejos et al. 1992). These markers were distributed into 11 linkage groups (LGs) spanning 960 cM of the common bean genome. A second RFLP-based genetic map was developed by Nodari et al. (1993). This map included 108 RFLPs, seven RAPDs, seven isozymes and 18 loci corresponding to 15 known genes, the *I* gene for bean common mosaic virus (BCMV) resistance, a flower color gene, and a seed color pattern gene; these loci are spread among 15 LGs covering 827 cM of the bean genome, with an average interval of 6.5 cM between markers. A third map constructed by Adam-Blondon et al. (1994) included 157 markers: 51 RFLPs, 100 RAPDs, 2 SCARs (sequence characterized amplified regions), and four morphological markers

that covered 567.5 cM of the bean genome. Moreover, Adam-Blondon et al. (1994) established a preliminary correspondence with the map developed by Vallejos et al. (1992) because 19 RFLP markers were shared between these maps.

The first core linkage map of common bean was constructed by Freyre et al. (1998) on the basis of the shared RFLP markers among these previous maps (Vallejos et al. 1992; Nodari et al. 1993; Adam-Blondon et al. 1994). The Freyre et al. map involved 563 markers, including 120 RFLPs and 430 RAPDs, in addition to a few isozymes and phenotypic marker loci; the markers were grouped into 11 LGs spanning 1226 cM. In successive years, RFLP markers were replaced by SSR markers, which are highly polymorphic PCR-based markers, for anchoring of different genetic maps. Yu et al. (2000a, b) published the first successful assignment of 15 SSRs to a framework map based on RAPD and RFLP markers. Moreover, with the availability of common bean EST (expressed sequence tag) sequencing programs, several functional markers, which are specifically developed from coding genomic regions, were identified and incorporated into bean linkage maps. The linkage map produced by Blair et al. (2003) was the first to incorporate SSR markers developed from EST databases, integrating these markers into a base map comprising 246 loci (78 SSR, 48 RFLP, 102 RAPD, and 18 AFLP markers) spanning 1720 cM. Indeed, EST libraries have become an important source of gene-based markers, such as EST-SSRs, single-nucleotide polymorphisms (SNPs) and insertions/deletions (InDels), which are valuable markers because they represent transcribed sequences that can be associated with phenotypic characteristics (Hanai et al. 2010; Galeano et al. 2012; Oblessuc et al. 2012). Furthermore, because EST-based markers are highly conserved between species, they allow for synteny comparisons between the common bean genome and those of other species (McConnell et al. 2010).

Additionally, with the advent of next-generation sequencing (NGS) technology, the sequencing of complete plant genomes has become increasingly more accessible and routine. The whole genome of common bean has recently been sequenced, and the complete genomes of the Mesoamerican and Andean beans BAT93 and G19833 are also available (Schmutz et al. 2014; Vlasova et al. 2016). In general, whole genome sequence availability accelerates the development of markers for high-throughput genotyping in plant breeding and genetic studies promoting the identification of markers tightly linked to agronomically important traits (Moghaddam et al. 2014; Mukeshimana et al. 2014; Meziadi et al. 2016; Valentini et al. 2017).

1.6.3 Mapping Populations Used

As shown in Table 1.2, several segregating populations are employed for mapping in common bean. Considering that many different economic traits of interest have been considered in bean breeding programs, divergent parents were chosen in each case to maximize phenotypic variation and genetic polymorphism. Moreover, in most cases, the parents chosen belonged to different gene pools, as experiments have shown that polymorphism among genotypes markedly increases in that situation (Nodari et al.

1993; Haley et al. 1994). For example, the mapping population used by Vallejos et al. (1992) to develop the first linkage map consisted of backcross progeny (BC_1) between the Mesoamerican line XR-235-1-1 and the Andean cultivar Calima (XC). Adam-Blondon et al. (1994) also utilized a BC_1 population derived from an inter-gene pool cross between two European bean genotypes: Ms8EO2 and Corel (MsCo). In contrast, Nodari et al. (1993) applied an F_2 population derived from a cross between the Mesoamerican line BAT 93 and the Andean cultivar Jalo EEP558 (BJ).

In addition, recombinant inbred line (RIL) populations, which are derived from single-seed descent from F_2 individuals, have been widely used in bean mapping because of their advantages (Table 1.2). For example, the BJ F2 mapping population was advanced to an RIL for the generation of the first core linkage map of common bean (Freyre et al. 1998), which was later improved (McConnell et al. 2010; Hanai et al. 2010). Furthermore, the base map developed by Blair et al. (2003) using SSR markers was produced using an RIL from the cross between the Mesoamerican variety DOR364 and the Andean landrace G19833 (DG). Similarly, numerous RIL populations were developed during the following years and used for bean genetic mapping studies and QTL identification (Blair et al. 2006b, 2010; Hanai et al. 2010; Oblessuc et al. 2012; Mukeshimana et al. 2014). Overall, the RIL populations derived from BJ and DG inter-gene pool crosses have been widely employed for genetic mapping studies because they are considered core mapping populations (Freyre et al. 1998; Blair et al. 2003, 2006a; Galeano et al. 2009, 2011, 2012; McConnell et al. 2010; Hanai et al. 2010).

1.6.4 Enumeration of Simply Inherited CS Trait and CS QTL Mapping

1.6.4.1 Disease Resistance

Fungal Diseases

Resistance to anthracnose (ANT), caused by *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara, is conferred by single, independent genes named and mapped to date (Table 1.3). Most of these genes are identified with the *Co* symbol: *Co-1* with four alleles; *Co-2* and *Co-3* with four alleles; *Co-4* with two alleles; *Co-5* with one allele; *Co-6*, *Co-11*, *Co-12*, *Co-13*, *Co-14*, *Co-15*, *Co-16*, and *Co-17*; and a new genes provisionally named *Co-Pa* and *Co-AC* (Kelly and Vallejo 2004; Gonçalves-Vidigal et al. 2006, 2007, 2009, 2011, 2012, 2013, 2016; Alzate-Marin 2007; Rodrigues-Suarez et al. 2008; Campa et al. 2011; Sousa et al. 2014; Lacanallo and Gonçalves-Vidigal 2015; Trabanco et al. 2015; Lima Castro et al. 2017; Gilio et al. 2017). An additional allele of *Co-1*, provisionally named $Co\text{-}1^{HY}$, was published in 2017 (Chen et al. 2017). Other genes with the *Co* symbol include *Co-x*, *Co-w*, *Co-y*, *Co-z*, *Co-u*, *CoPv02*, *Co-v* (*Co-6*), and *CoPv09c* as well as a QTL named

PMBO225 (Geffroy 1997; Geffroy et al. 2008; Richards et al. 2014; Campa et al. 2014). However, some previously known single, independent genes were renamed based on new allelism tests: *Co-7* as *Co-3*^{5}, *Co-9* as *Co-3*^{3}, *Co-10* as *Co-3*^{4}, and *Co-6* as *Co-v* (Geffroy 1997; Geffroy et al. 2008; Sousa et al. 2014; Gonçalves-Vidigal et al. 2006; 2013; Richards et al. 2014). Eleven genes (*Co-1*, *Co-12*, *Co-13*, *Co-14*, *Co-15*, *Co-Pa*, *Co-AC*, *Co-x*, *Co-w*, *Co-y*, and *Co-z*) belong to the Andean gene pool; the other 15 genes belong to the Mesoamerican gene pool. Chromosomes containing clusters of ANT resistance genes (shown in parenthesis) include Pv-01, (*Co-14*, *Co-Pa*, *Co-x*, *Co-AC*, and *Co-w*), Pv-02 (*Co*-u and *CoPv02*), Pv-03 (*Co-13* and *Co-17*), Pv-04 (*Co-3*, *Co-15*, *Co-16*, *Co-y*, and *Co-z*), and Pv-07 (*Co-5*, *Co-6*, and *Co-v*). All ANT resistance genes on chromosome Pv-01 (*Co-1* and five alleles including *Co-1*^{hy}, *Co-14*, *Co-x*, and *Co-w*) and other genes for resistance to rust and angular leaf spot are present in cultivars belonging to the Andean gene pool (Gonçalves-Vidigal et al. 2011; 2013; Richards et al. 2014; Chen et al. 2017). Additionally, recent studies conducted by Azevedo et al. (2018) have revealed that COK-4, a putative kinase encoded in the ANT resistance locus *Co-4* that is transcriptionally regulated during the immune response, is highly similar to the kinase domain of FERONIA (FER) in *Arabidopsis thaliana*, a factor that has a role in balancing distinct signals to regulate growth and defense.

Several sources of resistance to angular leaf spot (ALS), which is caused by the fungus *Pseudocercospora griseola*, (Sacc.) Crous and Braun, have been identified in common bean. Furthermore, single, dominant resistance loci as well as QTLs conferring resistance to ALS have been reported (Miklas et al. 2006a, b; Mahuku et al. 2009, 2011; Gonçalves-Vidigal et al. 2011, 2013; Oblessuc et al. 2013; Keller et al. 2015). The genes conferring resistance to ALS formally accepted by the Bean Improvement Cooperative (BIC) Genetic Committee are presented in Table 1.3. *Phg-1* on chromosome Pv01 is tightly linked (0.0 cM) to the ANT locus *Co-1*^{4} in cultivar AND 277, which led to the designation of the locus as *Phg-1/Co1* ^{4}(Gonçalves-Vidigal et al. 2011). The *Phg-1* locus was discovered using F_2 plants from crosses of AND 277 × Rudá and AND 277 × Ouro Negro inoculated with *P. griseola* race 63-23. A previous study conducted by Carvalho et al. (1998) used the name *Phg-1* before describing a resistance locus in AND 277 crossed with Rudá. The molecular markers CV542014^{450} and TGA1.1^{570} have been found to be linked with the *Co-1*^{4}*/Phg-1* loci at 0.7 and 1.3 cM, respectively (Gonçalves-Vidigal et al. 2011).

The ALS resistance gene *Phg-2* in Mesoamerican cultivar Mexico 54 was discovered by Sartorato et al. (1999) using a cross between Mexico 54 × Rudá and *P. griseola* race 63-19. The authors identified RAPD markers OPN02^{890}, OPAC14^{2400}, and OPE04^{650} as being linked to *Phg-2* at 5.9, 6.6 and 11.8 cM, respectively, on chromosome Pv08. Similarly, the RAPD marker OPE04 was found in all resistant individuals but was absent in those scored as susceptible based on virulence data (Namayanja et al. 2006). Additionally, an allelism test between Mexico 54 and BAT 332 inoculated with *P. griseola* race 63-39 showed that a single, dominant gene controls ALS resistance, suggesting that the resistance to ALS in Mexico 54 and

Table 1.3 Enumeration of mapping of simply inherited CS traits and CS QTLs associated with biotic stress resistance in common bean

Disease	Gene symbol	LG	Resistant parent	Reference
Angular Leaf spot (ALS)	*Phg-1*	1	AND277	Gonçalves-Vidigal et al. (2011)
	Phg-2	8	Mexico 54	Namayanja et al. (2006)
	Phg-2^2		BAT332	Mahuku et al. (2011)
	Phg-3	4	Ouro Negro	Gonçalves-Vidigal et al. (2013)
	Phg-4	4	CAL143	Mahuku et al. (2009), Oblessuc et al. (2012)
	Phg-5	10	G5686	Keller et al. (2015)
Anthracnose (ANT)	*Co-1*	1	Michigan Dark Red Kidney	McRostie (1919)
	Co-1^2		Kaboon	Melotto and Kelly (2000)
	Co-1^3		Perry Marrow	Melotto and Kelly (2000)
	Co-1^4		AND277	Vallejo and Kelly (2002)
	Co-1^5		Widusa	Gonçalves-Vidigal and Kelly (2006)
	Co-AC		Amendoim Cavalo	Gonçalves-Vidigal et al. (2011)
	Co-14		Pitanga	Gonçalves-Vidigal et al. (2012); (2016), de Lima Castro et al. (2017) Gilio et al. (2017)
	Co-Pa		Paloma	

(continued)

Table 1.3 (continued)

Disease	Gene symbol	LG	Resistant parent	Reference
	Co-2	11	Cornell 49-242	Adam-Blondon et al. (1994)
	Co-3	4	Mexico 222	Geffroy et al. (1999); Mendéz-Vigo et al. 2005; Rodríguez-Suárez et al. (2008) Sousa et al. (2014) Coimbra-Gonçalves et al. (2016)
	Co-15		Corinthiano	
	Co-16		Crioulo 159	
	Co-4^3/*Co-3*^{3}	8, 4	PI207262	Alzate-Marin et al. (2007)
	Co-4	8	TO	Fouilloux (1979) Young et al. (1998) Awale and Kelly (2001)
	Co-4^2		SEL1308	
	Co-5	7	TU	Gonçalves-Vidigal (1994), Young and Kelly (1996), Kelly and Young (1996), Young et al. (1998), Vallejo and Kelly (2009), Sousa et al. (2014)
	Co-5^2		MSU 7-1	
	Co-6		AB136	
	Co-4^2/*Co-5*^{2}/*Co-3*^{5}	8, 7, 4	G2333	Young et al. (1998)
	Co-12	–	Jalo Vermelho	Gonçalves-Vidigal et al. (2008)
	Co-11		Michelite	Gonçalves-Vidigal et al. (2007)
	Co-13	3	Jalo Listras Pretas SEL1308	Trabanco et al. (2014)
	Co-17			Lacanallo and Gonçalves-Vidigal (2015)

(continued)

Table 1.3 (continued)

Disease	Gene symbol	LG	Resistant parent	Reference
Rust	*Ur-3*, *Ur-6*, *Ur-7*, *Ur-11*, *Ur-Dorado53*, *Ur-BAC6*	11	P94207 P94232 Beltsville DOR 364 BAC6 BelNeb-RR-1	Stavely (1998), Miklas et al. (2002)
	Ur-5, *Ur-14*, *Ur-Dorado108*	4	DOR 364 Ouro Negro Mexico309	Miklas et al. (2000), Souza et al. (2011)
	Ur-4	6	BAT93	Miklas et al. (2002)
	Ur-9	1	PC50	Miklas et al. (2002)
	Ur-12	7	PC50	Jung et al. (1998)
	Ur-13	8	Kranskop	Mienie et al. (2005)
White mold (WM)	*WM1.1*, *WM7.1*	1, 7	G122	Miklas et al. (2001)
	WM2.1, *WM4.1*, *WM5.1*, *WM8.1*	2, 4, 5, 8	PC-50	Park et al. (2001)
	WM2.2, *WM7.2*	2, 7	Bunsi	Kolkman and Kelly (2003)
	WM2.3, *WM5.2*, *WM7.2*, *WM8.4*	2, 5, 7, 8	Bunsi	Ender and Kelly (2005)
	WM1.2, *WM2.4*, *WM8.2*, *WM8.3*, *WM9.1*	1, 2, 8, 9	G122	Maxwell et al. (2007)
	WM2.2, *WM5.4*, *WM6.1* *WM7.5*	2, 5, 6, 7	I9365-31 VA19	Soule et al. (2011) Vasconcellos et al. (2017)
	WM3.3, *WM7.5*, *WM9.2*, *WM11.1*	3, 7, 9, 11	Tacana PI 318695 PI 313850	Mkwaila et al. (2011)
	WM1.3, *WM3.1*, *WM6.2*, *WM7.1*, *WM7.4*	1, 3, 6, 7	Xana	Pérez-Vega et al. (2012), Vasconcellos et al. (2017)

(continued)

Table 1.3 (continued)

Disease	Gene symbol	LG	Resistant parent	Reference
Common bacterial blight (CBB)	*D2*, *D5*, *D7*, *D9*	2, 5, 7, 9	BAT93	Nodari et al. (1993)
	CBB-2LL, *CBB-2S*, *CBB-2P*, *CBB-2FL*, *CBB-1LL*,	1, 2, 3, 4, 5, 6	BAC 6	Jung et al. (1996)
	CBLEAF, *CBPOD*	1, 2, 9, 10	BelNeb-RR-1	Ariyarathne et al. (1999)
	Bng40, *Bng139*	7, 8	XR-235-1-1	Yu et al. (1998)
	CBB-GH-leaf, *CBB-GH-pod*, *CBB-GH-field*	7, 10	DOR 364	Miklas et al. (2000)
	SU91, *SAP6*, *Xa11.4*^{OV1,OV3}	8, 10, 11	Vax1, Vax3	Viteri et al. (2015)
	Xa3.3^{SO}	3	BOAC 09-3.	Xie et al. (2017)
Halo blight (HB)	*Rpsar-1*, *Rpsar-2*	8, 11	BAT93	Fourie et al. (2004)
	Pse-1, *Pse-2*, *Pse-3*, *Pse-4*, *pse-5*, *Pse-6*	2, 4, 10	UI-3 ZAA12 BelNeb-RR-1	Fourie et al. (2004), Miklas et al. (2009, 2011, 2014)
	HB4.1, *HB6.1*	4, 6	Cornell 49-242	Trabanco et al. (2014)
	HB83, *HB16*	2, 3, 4, 5, 9, 10	BelNeb-RR-1	Ariyarathne et al. (1999)
	SDC^{7}*-6*, *SAUDPC*^{3}*-2*, *PLAUDPC*^{3}*-2*, *PDC*^{3}*-2*, *PDC*^{4}*-2*, *PDC*^{5}*-2*, *PAUDPC*^{3}*-2*, *PAUDPC*^{4}*-2*	2, 6	P1037 PHA1037	González et al. (2016)
	HB4.2, *HB5.1*	4, 5	PI 150414 Rojo CAL 143	Tock et al. (2017)

(continued)

Table 1.3 (continued)

Disease	Gene symbol	LG	Resistant parent	Reference
BCMV/BCMNV	*I*	2	BelNeb-RR-1	Ariyarathne et al. (1999)
	bc-1^2, *bc-u*	3	Olathe Sierra	Strausbaugh et al. (1999)
	bc-3	6	BAT93	Johnson et al. (1997)
ClYVV	*cyv*, *desc*	3	Black Knight	Hart and Griffiths (2013)

BAT 332 is conditioned by the same resistance locus (Namayanja et al. 2006). The *Phg*-22 allele of BAT 332 is the only allele officially accepted by the BIC Genetics Committee.

Phg-3 was originally published as *Phg-ON*, as first described by Corrêa et al. (2001) in cultivar Ouro Negro. This cultivar is an important source of resistance for ALS and other diseases in common bean, such as ANT and rust. Inheritance studies in an F_2 population derived from the Ouro Negro × US Pinto 111 cross revealed one dominant resistance gene conferring resistance to race 63-39 (Corrêa et al. 2001). To investigate associations between *Co-3*^{4} (previously named *Co-10*) and the *Phg-3* genes, Gonçalves-Vidigal et al. (2013) conducted co-segregation analysis of resistance to *C. lindemuthianum* races 7 and 73 and *P. griseola* race 63-39 in Ouro Negro using an F_2 population from the Rudá × Ouro Negro cross and $F_{2:3}$ families from the AND 277 × Ouro Negro cross. This co-segregation analysis showed that *Co-3*^{4} and *Phg-3* are inherited together. Additionally, the genes *Phg-3* and *Co-3*^{4} were found to be tightly linked to marker g2303 at a distance of 0.0 cM (Gonçalves-Vidigal et al. 2013) on chromosome Pv04 (Fig. 1.5).

Furthermore, seven QTLs on five LGs have been reported by Oblessuc et al. (2012). Among these, the major QTL *ALS4.1*^{GS,UD} on Pv04 and *ALS10.1*^{DG,UC} and *ALS10.1*$^{DG,UC,\ GS}$ on Pv10, identified in G5686 and CAL143 (Mahuku et al. 2009; Oblessuc et al. 2012; Keller et al. 2015), have been recently named as *Phg-4* and *Phg-5* (Souza et al. 2016). The *Phg-4* locus was first discovered by evaluating the G5686 × Sprite F_2 population with race 31-0 and was published as Phg_{G5686A} (Mahuku et al. 2009). This QTL was later fine mapped to a 418-kb region on chromosome Pv04 and named *ALS4.1*^{GS,UC} (Keller et al. 2015). As this major locus had consistent and significant effects across different environments and populations (Mahuku et al. 2009; Oblessuc et al. 2012, 2013; Keller et al. 2015), the BIC genetics committee accepted the name QTL *ALS4.1*^{GS,UC} for *Phg-4* in G5686 (Souza et al. 2016). The resistance *Phg-5* locus on chromosome Pv10 was discovered using the CAL 143 × IAC-UNA RIL population. The RILs were evaluated under natural infection in the field and in the greenhouse inoculated with race 0-39, whereby QTL *ALS10.1* exhibited a strong effect in all environments (Oblessuc et al. 2012). Keller et al. (2015) confirmed the QTL *ALS10.1* in G5686. Because of its strong effect on resistance to

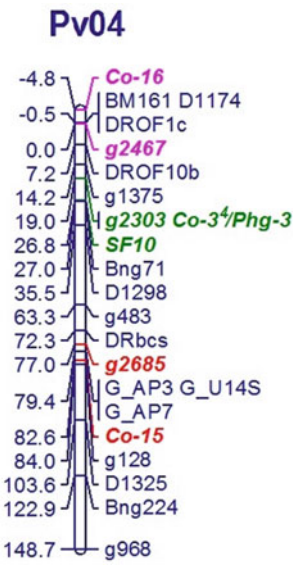


Fig. 1.5 Genetic distances and locations of the *Co-3*^{4} gene for resistance to common bean ANT, the *Phg-3* gene for resistance to ALS, and the molecular markers g2303 on linkage group Pv04 of *Phaseolus vulgaris* L. The map was drawn with MapChart (Voorrips 2002)

ALS in different environments, the BIC Genetics Committee proposed officially named *Phg-5 ALS10.1* in both G5686 and CAL143 (Souza et al. 2016).

Correspondingly, several genes conferring race-specific resistance to the rust pathogen *Uromyces appendiculatus* (Pers.) Unger have been identified, named, and mapped in different LGs in the common bean genome (Table 1.3). Indeed, three large clusters harboring a number of resistance genes located at the ends of chromosomes have been identified on Pv04, Pv10 and Pv11 of the *Phaseolus vulgaris* genome (Schmutz et al. 2014). Among these, one of the most complex disease-resistance clusters containing a large number of genes that confer resistance to various common bean pathogens has been identified at the end of the short arm of chromosome Pv04 (Geffroy et al. 2009; Richards et al. 2014). Moreover, 10 major rust resistance genes have been named and mapped in six different LGs of the common bean genome (Pv01, Pv04, Pv06, Pv07, Pv08, and Pv11) (Kelly et al. 1994, Miklas et al. 2002, Kelly and Vallejo 2004; Miklas et al. 2006a, b; Rodríguez-Suárez et al. 2008; Hurtado-Gonzales et al. 2017a, b). Mesoamerican rust resistance genes include *Ur-3*, *Ur-5*, *Ur-7*, *Ur-11* and *Ur-14* (Augustin et al. 1972; Ballantyne 1978; Stavely 1984; Stavely 1990; Souza et al. 2011). Andean rust resistance genes include *Ur-4*, *Ur-6*, *Ur-9*, *Ur-12* and *Ur-13* (Ballantyne 1978, Finke et al. 1986; Jung et al. 1998; Liebenberg and Pretorius 1997).

In addition, several genes conferring resistance to various common bean pathogens are arranged in clusters of tightly linked genes, often located at the end of the chromosomes. For example, *Ur-9* (Pv01), *Ur-5* (Pv04) and *Ur-3* (Pv11) co-localize with ANT resistance genes *Co-1* (Pv01), *Co3* (Pv04) and *Co-2* (Pv11), respectively (Geffroy et al. 1999, 2000; Kelly et al. 2003). Similarly, *Ur-13* maps close to the *Phg-2* gene for ALS resistance on Pv08 (Garzon and Blair 2014). Recently, co-segregation

analysis inoculating $F_{2:3}$ families from the Rudá × Ouro Negro cross with of *C. lindemuthianum* (ANT) and *U. appendiculatus* (Rust) races reported the genetic linkage between *Ur-14* and *Co-3*^{4} genes (Valentini et al. 2017). In this study, the authors did not evaluate the *P. griseola* in the $F_{2:3}$ families from the Rudá × Ouro Negro cross. Hurtado-Gonzales et al. (2017a, b) evaluated an F_2 population of Pinto 114 (susceptible) × Aurora (resistant *Ur-3*) for its reaction to four different races of *U. appendiculatus*, and bulked segregant analysis using the SNP chip BARCBEAN6K_3 placed *Ur-3* on the lower arm of chromosome Pv11. Specific SSR and SNP markers and haplotype analysis of 18 sequenced bean varieties positioned *Ur-3* in a 46.5-kb genomic region from 46.96 to 47.01 Mb on Pv11. The authors identified in this region the SS68 KASP marker that is tightly linked to *Ur-3*, and validation of SS68 using a panel of 130 diverse common bean cultivars containing all known rust resistance genes showed SS68 to be highly accurate.

Genetic resistance to white mold (WM), caused by the fungus *Sclerotinia sclerotiorum*, is quantitatively inherited, and several QTLs have been identified thus far (Schwartz and Singh 2013). A comparative map composed of 27 QTLs for WM resistance and 36 QTLs for disease-avoidance traits was developed by Miklas et al. (2013). Recently, Vasconcellos (2017) identified 37 QTLs condensed into 17 named loci (12 previously named and five new), nine of which were defined as meta-QTLs WM1.1, WM2.2, WM3.1, WM5.4, WM6.2, WM7.1, WM7.4, WM7.5, and WM8.3; these are robust consensus QTLs representing effects across different environments, genetic backgrounds, and related traits.

Bacterial Diseases

Xanthomonas axonopodis pv. phaseoli (*Xap*) and *X. fuscans subsp. fuscans* cause common bacterial blight (CBB), a damaging disease of common bean worldwide. CBB resistance has been reported to be quantitatively inherited, often involving QTLs with major and minor effects (Singh and Miklas 2015). More than 20 different QTLs responsible for CBB resistance have been reported across all 11 LGs of common bean (Singh and Miklas 2015; Viteri et al. 2015). Recently, Viteri et al. (2015) identified the major QTL *Xa11.4*^{OV1,OV3}, which explained up 51% of the phenotypic variance for CBB resistance in leaves. Moreover, a new isolate-specific QTL underlying CBB resistance and showing an additive effect with SU91 QTL was recently found on Pv03 (Xie et al. 2017).

Both qualitative and quantitative resistance genes have been reported for resistance to halo blight (HB), which is caused by *Pseudomonas syringae* pv. *phaseolicola* (Burkn.) Downs (Ariyarathne et al. 1999; Fourie et al. 2004; Miklas et al. 2014; Trabanco et al. 2014; González et al. 2016; Tock et al. 2017). Five dominant (*Pse-1*, *Pse-2*, *Pse-3*, *Pse-4* and *Pse-6*); one recessive (*pse-5*) gene has also been identified (Miklas et al. 2009, 2011, 2014). Furthermore, 76 main-effect QTLs were found to explain up to 41% of the phenotypic variation in HB resistance, and 101 epistatic

QTLs were identified by González et al. (2016). Moreover, Tock et al. (2017) recently found a major QTL of race-specific resistance (*HB5.1*) in cv. Rojo and a major QTL of race-nonspecific resistance (*HB4.2*) in PI 150414.

Viral Diseases

Recessive resistance to Bean common mosaic virus (BCMV) and Bean common mosaic necrosis virus (BCMNV) in common bean is controlled by four genes that include one strain-nonspecific helper gene, *bc-u*, and three strain-specific genes, *bc-1*, *bc-2*, and *bc*-3. (Drijfhout 1978). Moreover, there are two alleles each for *bc-1* (*bc-1* and *bc-1*^{2}) and *bc-2* (*bc-2* and *bc-2*^{2}). The *bc-u* and *bc-1* genes mapped at the end of Pv03; *bc-3* is located on Pv06 and belongs to the eIF4E gene family (Miklas et al. 2000; Naderpour et al. 2010; Meziadi et al. 2016). In addition, the dominant *I* gene mapping to Pv2 imparts resistance to all strains of BCMV (Drijfhout 1978). With regard to resistance to another potyvirus, Clover yellow vein virus (ClYVV), two recessive genes located on Pv06, *cyv* and *desc*, are reported to be allelic forms of *bc-3*, encoding eIF4E factors (Hart and Griffiths 2013; Meziadi et al. 2016).

Drought Resistance

Drought stress is the major limitation of common bean grown in subsistence farming systems worldwide. Several traits associated with drought tolerance have been identified, and different QTL studies have been conducted. Schneider et al. (Schneider et al. 1997) identified RAPD markers associated with yield under stress and non-stress conditions in Sierra × AC1028 and Sierra × Lef2RB populations across a broad range of environments. Additionally, Beebe et al. (2007) identified QTLs for yield under drought using an RIL population from the SEA 5 × MD 23-24 cross; this QTL also influenced yield in well-watered environments, suggesting that yield under both conditions may be influenced by the same factors. Later, Blair et al. (2012) utilized a Mesoamerican intra-gene pool RIL population derived from the cross of drought-tolerant BAT477 and drought-susceptible DOR364 to identify five QTLs associated with yield under irrigated conditions, with mapping to LGs Pv03 and Pv07 and explaining 11 and 19% of the phenotypic variance. When the same population was evaluated using mixed model analysis under eight environments differing in drought stress across Africa and South America, nine QTLs were detected for 10 drought stress tolerance mechanism traits and mapped to six of the 11 LGs (Asfaw et al. 2012a, b).

A total of 14 QTLs for performance under drought were consistently identified in different environments by Mukeshimana et al. (2014). In that study, an inter-gene pool RIL population from a cross of drought-tolerant lines SEA5 and CAL96 was evaluated for several years in Rwanda and Colombia under drought stress and nonstress. QTLs associated with phenology and seed weight traits were identified and mapped near previously reported QTL (Mukeshimana et al. 2014).

Two major QTLs, named $SY1.1^{BR}$ and $SY2.1^{BR}$, that conditioned yield in an RIL population with consistent expression across multiple drought-stress environments were identified on Pv01 and Pv02 by Trapp et al. (2015). In this study, 140 RILs from the Buster × Roza cross were tested for yield under multiple stresses (intermittent drought, compaction, and low fertility) across numerous locations and years. The $SY1.1^{BR}$ QTL explained up to 37% of the phenotypic variance for seed yield under multiple stresses and was defined by the marker SNP50809 (47.7 Mb). Moreover, when compared to QTLs identified for yield in previous studies, $SY1.1^{BR}$ and $SY2.1^{BR}$ displayed a larger effect (Asfaw et al. 2012a, b; Blair et al. 2012; Mukeshimana et al. 2014).

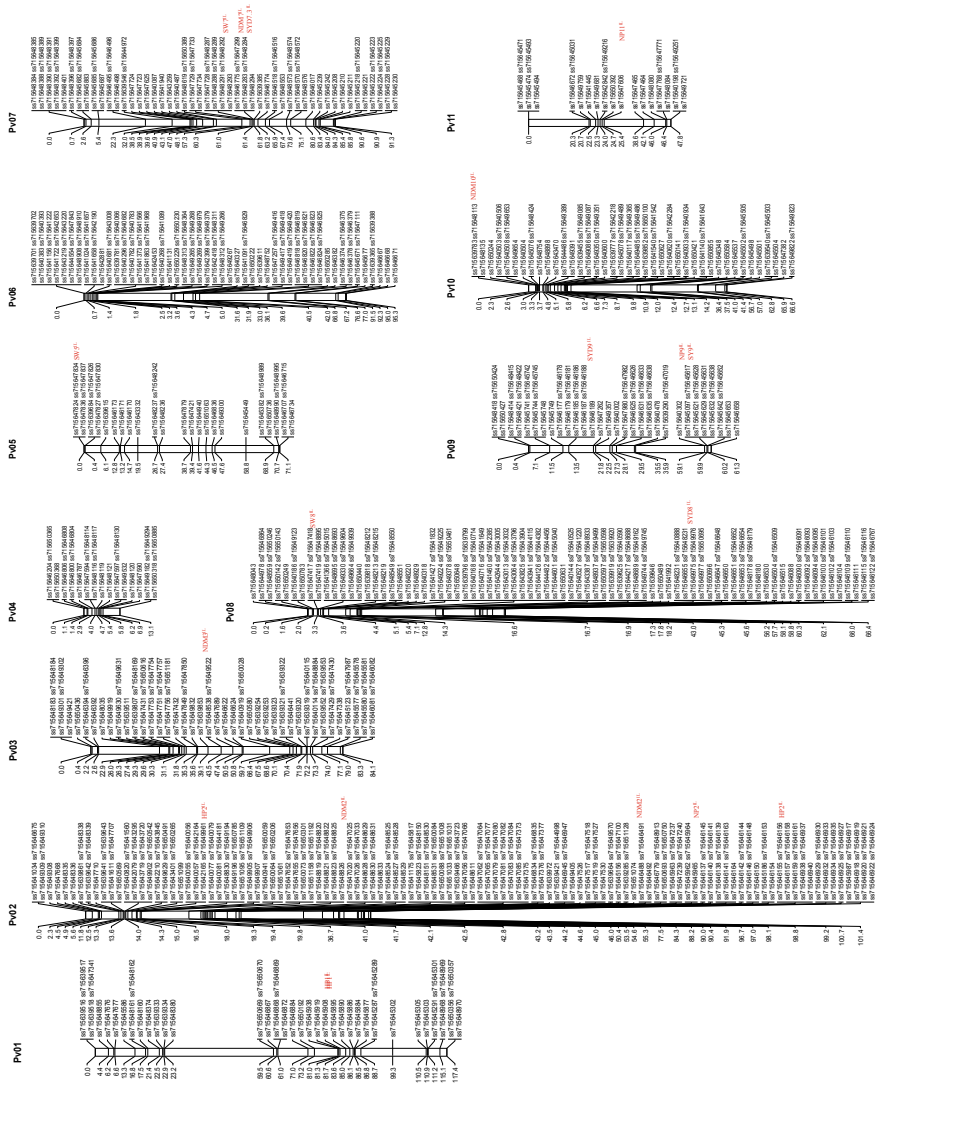
Recently, by analyzing 160 RILs derived from the cross between IAPAR 81 (drought-tolerant) and LP97-28 (susceptible to drought) under conditions of drought stress and nonstress for two years in Maringá PR, Brazil (Elias 2018), 16 QTLs were identified on five chromosomes (Pv01, Pv02, Pv07, Pv08 and Pv11) (Fig. 1.6). The author used 773 SNP markers to construct an LG covering 815.9 cM of the bean genome, with a distance of 1.34 cM between markers. The QTL $SY9^{IL}$ associated with grain yield was identified on chromosome Pv09, three QTLs for grain yield per day were mapped to Pv07, Pv08, and Pv09, and QTLs linked to seed weight were found on chromosomes Pv07 and Pv08 (Elias 2018).

Another study of genotyping-by-sequencing analysis and 19 climatic characteristics obtained through the WorldClim site was carried out by Elias (2018), in which a set of 110 accessions of common bean previously genotyped using a sequencing genotyping methodology was evaluated, producing 28,823 SNPs. Through associative mapping, it was possible to detect loci of quantitative characteristics, for a total of 135 associations between characteristics vs. markers (Bonferroni test <0.5%). Of the 19 bioclimatic traits, eight exhibited significant associations, and associations for seasonality of temperature and precipitation in the driest quarter were found, both on Pv09, with $R^2 = 36.26$ and 36.46%, respectively. Associations between markers and climatic variables were distributed throughout common bean LGs, except for Pv08. The results show a correlation between markers and climatic characteristics on a national scale, helping to identify candidate genes for regional adaptation. These considerations are of great relevance for the conservation and exploration of genetic diversity between and within common bean accessions in Brazil (Elias 2018).

1.7 Marker-Assisted Breeding for CS Traits

1.7.1 Marker-Assisted Gene Introgression

Molecular mapping and tagging of important genes have contributed to significant advances in MAS of crop breeding. Since molecular markers are related to nucleotide sequence variations, many tags have been developed for different types of plant crops. They also have several advantages over the traditional phenotypic markers (Mohan


Pv01
Pv02
Pv03
Pv04
Pv05
Pv06
Pv07
Pv08
Pv09
Pv10
Pv11

◀**Fig. 1.6** Genetic mapping for the RIL population Iapar 81 × LP97-28 cross using 773 SNPs markers assigned to the 11 common bean linkage groups. QTL locations are mapped in the Iapar81/LP97-28 population, using the composite interval method (CIM) of the Win cartógrapher software and the LOD thresholds calculated based on 1000 permutations. A total of 16 QTLs were associated with the yield per day, weight of 100 grains, number of pods per plant, height of plant, number of days for flowering, and number of days for maturation under water stress condition

et al. 1997). In general, this method is faster, cheaper, and more accurate than traditional phenotypic assays. Consequently, it may provide higher effectiveness and efficiency in terms of time, resources, and efforts. Besides that, MAS is not affected by the environment, which allows the selection to be conducted under any environmental conditions. In traditional phenotypic selection, an individual gene or loci might be masked by the effect of others. In contrast, MAS can simultaneously identify and select single genes/QTLs in the same individuals, when traits are controlled by multiple genes/QTLs. For that reason, it is particularly feasible for gene pyramiding. The usage of MAS enables introgression of resistance genes into a cultivar and decrease of population size and time required to develop a new variety.

Methods to characterize disease-resistance genes have changed over time. Initial work with RFLP, AFLP, and RAPD markers was followed by a series of SSR, SCAR, and SNP marker systems, providing suitable markers for breeding purposes. These markers linked to single-gene traits have been successfully used in MAS (Singh and Schwartz 2010). Thus, gene introgression using MAS allowed the development of numerous common bean lines with resistance to angular leaf spot (de Oliveira et al. 2005), anthracnose (Alzate-Marin et al. 1999; Miklas et al. 2003), rust (Stavely 2000), common bacterial blight (Miklas et al. 2006b) and, bean gold yellow mosaic virus (Miklas et al. 2002). In addition, two major white mold resistance QTLs have been successfully introgressed using MAS with positive asset in the target traits (Ender et al. 2008). The use of MAS in breeding for resistance to biotic and abiotic stress in common bean has been widely reviewed by Miklas et al. (2006a, b). The latest publication about common bean reference genome (Schmutz et al. 2014) allowed mapping and comparison of several SSR, SCAR, and SNP markers' positions. Some of them were mapped in different chromosomes than the ones originally reported. In the last few years, GBS, GWAS, and WGS techniques improved plant breeding by making it quick and efficient through the use of MAS.

1.7.1.1 Common Bean Whole Genome Sequencing (WGS)

Over the past decade whole genome (re)sequencing (WGS) approach has become feasible due to its continuous cost reduction. Therefore, we currently gained a deep insight into the structure of nearly complete genomes across populations (Lobaton et al. 2018a, b). The history of common bean domestication at genomic level led to introgression of gene pools during the domestication of two independent lines (Andean and Mesoamerican) within a single species (Schmutz et al. 2014). More

recently, a large number of inter-gene pool introgressions were identified, and interspecific introgressions for disease resistance in breeding lines were also mapped (Lobaton et al. 2018a, b).

In 2014 the Joint Genome Institute, Department of Energy released the first chromosome scale version of *Phaseolus vulgaris* (v1.0) (http://www.phytozome.net/) (Schmutz et al. 2014). Interestingly, studies reported that databases like PhaseolusGenes (http://phaseolusgenes.bioinformatics.ucdavis.edu) are actually important tools to accelerate marker identification (Gonçalves-Vidigal et al. 2011; Lobaton et al. 2018a, b).

Another strategy to develop DNA markers is a combination of bulked segregant analysis (BSA) and high-throughput genotyping method. This mapping technique is able to screen many bulks with markers spread throughout the genome in a short period of time (Hyten et al. 2009). Many researchers have used the same procedures to determine the abundance of SSRs in the common bean genome and, developed candidate SSR database for common bean. The Infinium® assay is a newly developed high-throughput SNP genotyping method with higher level of capacity. Recently, the Illumina Infinium® beadchip was designed for soybean (Song et al. 2013) and, also for common bean. Illumina Infinium® beadchip (BARCBEAN 6k_3) was firstly designed for soybean and, was able to screen 5,399 SNPs (USDA-ARS, Maryland, USA). Hyten et al. (2010) developed the Illumina Golden Gate beadchip containing 1,536 SNPs. As a result, the use of Golden Gate assay successfully mapped a few SSRs linked with slow darkening trait onto bean linkage group 7 (Felicetti et al. 2012). Later, Song et al. (2015) generated a highly dense map of the common bean containing 7,040 SNP markers with BARCBean6K_1 and BARCBean6K_2 BeadChips. At the moment, common bean SNP cheap BARCBEAN6K_3 containing 5,398 SNPs (Song et al. 2015) is extensively used to develop specific molecular markers linked to resistance genes (Hurtado-Gonzales et al. 2017a, b).

The use of specific markers for population breeding through next-generation sequencing (NGS) became a common practice in plant breeding, since the development of reference genome sequences allows efficient identification of a large number of physically mapped new and/or different markers (Miller et al. 2018). Reference genomes of common bean have been recently released (Schmutz et al. 2014; Vlasova et al. 2016; http://www.beangenomics.ca/). The mentioned genomes were based on sequences of G19833 (Andean landrace), BAT93 (Mesoamerican breeding line), and OAC-Rex (Mesoamerican cultivar, introgressed with *P. acutifolius*).

The aforementioned databases provide the development of new markers for MAS use and map-based gene isolation. In addition, short genomic sequences for each breeding parent can be mapped on a reference genome and, new polymorphisms such as SSR, SNP and/or INDEL can be detected.

1.7.2 Gene Tagging and Marker-Assisted Selection for Bean Diseases

Conventional breeding methods used depend on visual to screening of genotypes to select for traits of economic importance. Nevertheless, successful using this method depends on its reproducibility and heritability of the characteristic. MAS is an excellent methodology for common bean breeders who also work to improve disease resistance. On behalf of MAS to be highly effective, a high association and tight linkage must exist between the genes for resistance to diseases and molecular markers and easy to evaluate (Yu et al. 2004). As mentioned in the previous section, associations between resistance genes and molecular markers are widely used for mapping genes to specific linkage groups. Since the last century, several studies have used molecular markers to select qualitative resistance to anthracnose (ANT), angular leaf spot (ALS), common bean mosaic virus (BCMV) and, rust diseases.

1.7.2.1 Anthracnose

Garzón et al. (2007) were the first to evaluate the efficiency of MAS to detect anthracnose resistance. For that purpose, a series of backcross plants, using PCR-based markers SAB3 and SAS13 linked to *Co-5* and *Co-4*^{2} genes were used. The authors concluded that *Co-5* is associated with SAB3, whereas *Co-4*^{2} is linked to SAS13.

Likewise, Vidigal Filho et al. (2008) evaluated backcross F_2BC_3 lines using $SAS13_{950}$ marker and observed that it was linked to *Co-4*^{2} allele. Two hundred and thirty-three BC_3F_2 near-isogenic lines containing *Co-4*^{2} resistance allele in various combinations were developed through marker-assisted selection (MAS) for the resistance genes and phenotypic selection for the anthracnose. The BC_3F_2 NILs having *Co-4*^{2} resistance allele showed a wider resistance spectrum and manifested increased levels of resistance to race 2047 of *C. lindemuthianum*. Out of the 233 BC_3F_2 lines analyzed by molecular markers, 80 of them revealed the presence of $SAS13_{950}$ linked to *Co-4*^{2} allele. Moreover, two Brazilian cultivars, both resistant to anthracnose, were obtained by five backcrossing with $SAS13_{950}$ marker through MAS (Gonçalves-Vidigal, unpublished data). These cultivars were released on the market in 2018.

1.7.2.2 Rust

On the subject of rust, the first resistance gene tagged in common bean was *Ur-4* gene (Miklas et al. 1993), using the molecular marker $OA14_{1100}$. This marker was used to perform assisted selection of plants containing *Ur-4* (Kelly et al. 1993). However, its usage is restricted to Mesoamerican cultivars, since progenies from a cross between Early Gallatin and Andean cultivar do not segregate for $OA14_{1100}$marker (Miklas et al. 1993). Previous studies reported limitations of molecular markers linked to *Ur-*

3 gene (Haley et al. 1994; Nemchinova and Stavely 1998; Stavely 2000). However, Valentini et al. (2017) developed several SSR markers linked to *Ur-3*, *Ur-4*, *Ur-5*, *Ur-11*, *Ur-14*, and *Ur-PI310762* genes. For that, accurate phenotyping for the inheritance of resistance studies, bulk segregant analysis (BSA) combined with high-throughput genotyping using the SNP chip BARCBEAN6K_3, were used. Following the same line of experiments, further SSR and SNP markers closely linked to *Ur-3* were developed based on BSA, SNP assay, and whole genome sequencing methodologies (Hurtado-Gonzales et al. 2017a, b). Interestingly, KASP SNP marker SS68 reliably distinguished cultivars containing *Ur-3* alone or in combination with other genes (Hurtado-Gonzales et al. 2017a, b). Recently, co-segregation analysis inoculating $F_{2:3}$ families from the Rudá × Ouro Negro cross with of *C. lindemuthianum* (ANT) and *U. appendiculatus* (Rust) races reported the genetic linkage between *Ur-14* and *Co-3*^{4} genes (Valentini et al. 2017). In this study, the authors did not evaluate the *P. griseola* in the $F_{2:3}$ families from the Rudá × Ouro Negro cross. A different approach was to investigate rust resistance in locus *Ur-14*, which is tightly linked to gene *Co-3*^{4} (Valentini et al. 2017b). The results allowed the construction of a genetic map linkage based on SNP, SSR and, KASP markers linked to *Ur-14*.

1.7.2.3 White Mold

QTLs for white mold on linkage groups Pv02 and Pv07 from an ICA Bunsi × Newport Middle American dry bean population were identified by Kolkman and Kelly (2003). In ICA Bunsi × Raven Middle American dry bean populations, QTLs were also detected and, mapped on linkage groups Pv02, Pv05, Pv07, and Pv08 (Ender and Kelly 2005). Later, Miklas et al. (2007) found two QTLs in a Pinto 3 navy bean (Aztec/ND88–106–04), which were mapped on linkage groups Pv02 and Pv03. Interestingly, the QTL described on Pv02 was identified previously in populations of ICA Bunsi 3 navy and ICA Bunsi 3 black bean RIL.

Further, a comparative study revealed the presence of QTLs in two separate populations, "Benton"/VA19 (BV) and "Raven"/I9365-31 (R31) crosses (Soule et al. 2011). For the first one, WM2.2 and WM8.3 were described for greenhouse straw test and field resistance. In contrast, WM2.2, WM4.2, WM5.3, WM5.4, WM6.1, WM7.3 were found in the Raven/I9365-31 (R31) for greenhouse straw test and field resistance.

In addition, two QTLs were characterized in "Tacana" × PI 318695 (linkage groups Pv04 and Pv07) and Tacana × PI 313850 (linkage groups Pv02 and Pv09) inbred backcross lines, using the greenhouse straw test (Mkwaila et al. 2011). Recently, an evaluation of RIL population from AN-37 × P02630 cross demonstrated the presence of 13 QTLs for agronomic and disease-related traits (Hoyos-Villegas et al. 2015).

1.7.2.4 Fusarium Root Rot

Resistance to FRR is quantitatively inherited and is strongly affected by environmental factors. QTLs associated with this disease varied between studies and populations. Due to limited genomic coverage of the available markers, a comparison of the physical positions of those QTLs was not suitable (Schneider et al. 2001; Chowdhury et al. 2002; Román-Avilés and Kelly 2005). In 2005, (Román-Avilés and Kelly 2005) identified nine QTLs in crosses "Negro San Luis" × "Red Hawk" and "Negro San Luis" × C97407. Later, five regions on linkage groups Pv03, Pv06, and Pv07 associated with QTL for FRR in an Eagle/Puebla 152 population were identified (Navarro et al. 2004). Most recently, two QTLs associated with FRR for greenhouse straw test and field resistance were mapped on Pv02 (Wang et al. 2018).

1.7.2.5 Common Bacterial Blight

In early 2000s, important historical research steps toward MAS were taken. PI 319443 resistance was introgressed into the common bean breeding line XAN 159. By doing that, two major QTLs for common bacterial blight resistance were defined: SCAR marker SU91 (Pedraza et al. 1997) found in Pv08, and BC420 marker detected in linkage group Pv06 (Yu et al. 2000a, b). Yu et al. (2000a, b) evaluated co-segregation of two polymorphic markers. Only $BC420_{900}$ revealed a significant association with a major QTL, which conferred resistance in HR67 to CBB. Following that, another major resistance QTL in OAC-Rex was mapped on Pv05 (Bai et al. 1997; Tar'an et al. 2001; Michaels et al. 2006). Recently was reported the full genome sequence of the common bean OAC-Rex with introgression from the tepary bean, *P. acutifolius* (Perry et al. 2013).

However, a negative association of seed yield with the SU9 marker linked with CBB resistance QTL derived from tepary bean was reported (O'Boyle et al. 2007). Furthermore, Miklas et al. (2009) addressed the presence of SH11.800, SR13.1150, and ST8.1350 markers linked to *Pse-1* and, mapped on Pv10.

1.7.2.6 Bean Common Mosaic Virus

Since BCMV resistance genes are independent in common bean, it contributes to the use of gene pyramiding as an approach for durable resistance (Tryphone et al. 2013). In 1994, Raven was released as the first common bean cultivar resistant to BCMV. The aforementioned cultivar carries two genes: one dominant hypersensitive *I* and one recessive *bc-3*, both confirmed by RAPD markers. This combination has been recognized for its durability over single-gene resistance to both BCMV and BCMNV (Kelly 1997). SCAR markers based on OC11350/420 (ROC11) and OC20460 RAPD markers linked to bc-3 gene were also developed (Johnson et al. 1997). However, the use of these markers in MAS have been limited in common bean because of a

lack of polymorphism and, reproducibility across different genetic backgrounds and gene pools (Kelly et al. 2003).

Pedigree selection through the F7 generation based on superior agronic features (early maturity, erect plant architecture, and good pod set) and commercial seed type, Bella cultivar was created. Derived from cross "Verano"//PR0003-124/"Raven," Bella combines resistance to BCMV, BCMNV, BGYMV, and web blight (Beaver et al. 2018).

1.7.3 Gene Pyramiding

The conventional breeding methods involve complex selection of several genotypes harboring different resistance genes, which can affect the accuracy and efficiency of the process. However, pyramiding gene is a good strategy for durable resistance, and it can also facilitate MAS approach. This technique is a combination of multiple desirable genes from multiple parents into a single genotype for specific trait. Thus, this methodology enhances genetic resistance into bean cultivars.

Pyramiding of different genes was developed from a single cross between lines obtained in the introgression step, using either pedigree or backcross method. Currently, several resistant common bean cultivars were developed to improve resistance level to anthracnose, angular leaf spot, rust and, BCMV (Ragagnin et al. 2009).

A marker-assisted gene pyramiding approach was used to develop carioca bean elite lines harboring three different rust resistance genes (Souza et al. 2014). That was only possible because Rudá recurrent parent has a high-yield performance. On the subject of anthracnose and Pythium root rot resistance, genes were pyramided in four susceptible market class varieties using SCAR markers (Kiryowa et al. 2015). It was also shown that higher numbers of selected pyramided genes may indirectly affect yield by reducing the number of seeds per plant.

Through MAS, resistant pyramided lines to rust, anthracnose and, angular leaf spot were developed (Ragagnin et al. 2009). They showed resistance spectra equivalent to those of their respective donor parents. Besides that, yield tests showed that these lines were as productive as the best carioca-type common bean cultivar.

1.7.4 Limitations and Prospects of MAS and Marker-Assisted Backcrossing Breeding (MABCB)

MAS is an important tool to support plant breeders in crop improvement. It considerably increases the efficiency of breeding, when markers tightly linked to genes of interest are used. Despite its advantages, MAS might not be as successful as expected, when introgression of QTL is necessary (Fazio et al. 2003).

MAS is not always better or more cost-effective than direct disease resistance (DDS), especially for quantitatively inherited resistance to diseases. An efficiency comparison of these two techniques, regarding pyramiding and transfer of CBB resistance into dark red kidney bean, showed that DDS was significantly more effective than MAS (Duncan et al. 2012). Under greenhouse conditions of high disease pressure, DDS produced more resistant breeding lines with greater levels of resistance than MAS.

MAS is considered as smart breeding for different reasons. First of all, it is a non-transgenic biotechnological approach for plant improvement and is not subjected to rules/regulations that restrict its use. Second, disease-resistance selection without the use of pathogen is feasible, and off-season screening is possible. Finally, it is suitable to combine multiple sources of disease resistance for distinct pathogens.

1.8 Potential for the Role of Molecular Genetics, Transcriptomics, Epigenomics, and Bioinformatics as Tools to Address Climate Resiliency/CS Traits

1.8.1 Status of Common Bean Genomics

More than 100,000 years after the divergence of Mesoamerican and Andean gene pools a minimum of two separate domestications occurred ~8,200–8,500 years ago (Vlasova et al. 2016). The common bean (*Phaseolus vulgaris*) genome was originally released in 2014 (Schmutz et al. 2014). The Andean inbred landrace G19833 was used for this sequence. The second version of this genome is currently available (*Phaseolus vulgaris* v2.1, DOE-JGI, and USDA-NIFA, http://phytozome.jgi.doe.gov/). Approximately 537.2 Mb of the genome is arranged in 478 scaffolds. An estimated 99.1% of the genome is contained within 87 scaffolds of >50 kb in size. There are 27,433 coding sequence loci and 36,995 protein-coding transcripts; thus, there are 9,562 alternatively spliced variants. A second sequence was released two years after the G198333 genome was released for the Mesoamerican breeding line BAT93 (Vlasova et al. 2016). The Mesoamerican genome was found to be approximately 549.6 Mb, of which 81% is anchored within eleven linkage groups. The BAT93 genome was found to have 30,491 coding sequence loci, with 66,634 protein-coding transcripts that encode for 53,904 unique proteins (Vlasova et al. 2016).

The Mesoamerican genotype BAT93 has been identified to be more resistant to some diseases, including anthracnose, angular leaf spot, and bean common mosaic virus, and rust (Vlasova et al. 2016). Despite its decreased susceptibility, BAT93 was found to have fewer cytoplasmic NBS-LRR class resistance genes (234), than G19833 (376) (Vlasova et al. 2016). Functional enrichment analysis showed that BAT93 has undergone the largest gene expansion in genes related to cellular receptors

with extracellular domains. Genes related to seed development and the ubiquitin pathway were also enriched in BAT93, compared to G19833 (Vlasova et al. 2016).

In the BAT93 genome, 35% was found to be composed of transposable elements (Vlasova et al. 2016). The G19833 genome is approximately 41% of transposable elements (*Phaseolus vulgaris* v2.1, DOE-JGI, and USDA-NIFA, http://phytozome.jgi.doe.gov/). Long noncoding RNAs (lncRNAs) were highly conserved between the two genotypes, with 94% of Mesoamerican lncRNAs also contained within the Andean genome (Vlasova et al. 2016). lncRNAs appear not to be highly conserved within legumes, as only a third were found to be conserved past soybean (*Glycine max*) (Vlasova et al. 2016).

Since the sequencing of the common bean genomes, numerous resequencing, transcriptomic, epigenomic, proteomic, and metabolomic projects have been conducted. A recent resequencing project identified introgression within the Mesoamerican and Andean common bean gene pools (Lobaton et al. 2018a, b). This project undertook sequencing of 35 common bean, 22 Mesoamerican and 13 Andean, accessions and one genotype each of the closely related species *P. acutifolius* and *P. coccineus* (Lobaton et al. 2018a, b). These lines were selected based on agriculturally significant traits, including resistance to a variety of biotic and abiotic stresses. The other *Phaseolus spp.* were selected as they have introgressed into some common bean cultivars (Lobaton et al. 2018a, b). A total of 203 possible introgression events were detected (Lobaton et al. 2018a, b). Surprisingly, it was determined that the Andean reference genome, G19833, contained a large Mesoamerican introgression on chromosome Pv08, which spans 24 Mbp. Additionally, there were three other Andean-derived genotypes that contained this same introgression. Other introgressions of over 1 Mbp were identified in other chromosomes (Lobaton et al. 2018a, b). Due to self-fertilization, heterozygosity rates were low, averaging 0.17% in Andean and 0.46% in Mesoamerican genotypes.

1.8.2 Gene, Genome, and Comparative Genome Databases (Phytozome, NCBI, LIS, EBI, CoGe, DAVID)

Phaseolus spp has been proposed to serve as a model for understanding crop evolution due to the multiple domestication events in Mesoamerica and South America and other characteristics (Bitocchi et al. 2017; Rendón-Anaya et al. 2017).

1.8.2.1 Databases

Vast information on common bean genes, genomes, and comparative genomics are widely publicly available. Phytozome is the "Plant Comparative Genomics portal of the Department of Energy's Joint Genome Institute" (Goodstein et al. 2012). Currently, the *Phaseolus vulgaris* version 2.1 genome is the most recent release. Previous

versions of released genomes can be found at the "Download" section of Phytozome's dropdown menus. Genome v2.1 combined an 83.2x sequence coverage PacBio-based assembly that is annotated with their proprietary Gene Model Improvement (GMI) pipeline. Genes can be searched for via running a BLAST search or keyword search. The output yields genes and ontologies with a direct link to PANTHER. The gene section reveals the functional annotation, view in a genome browser (JBrowse), genomic, transcript, and coding sequences, protein homologs, gene ancestry, and gene expression and co-expression in various tissue types. PhytoMine allows users to search for information of genomics, transcripts, proteins, comparative species, and expression based on a variety of input identifiers; which includes gene IDs, GO terms, and panther terms.

The National Center for Biotechnology Information (NCBI) is a repository for several different data types. NCBI hosts categories of information classified as Literature (books, journal articles, and reports), Genes (ESTs, genes, homologs, phylogenetics, unigenes, functional genomics), Genetics (clinical, genotype/phenotype, human-related), Proteins (conserved domains, sequences, clusters, structure), Genomes (genome assembly, biosamples/projects, SRA, nucleotide sequences, proves, taxonomy, and Chemicals (molecular pathways, screening, deposited information). The current genome data was supplied by the Joint Genome Institute. NCBI's Sequence Read Archive hosts user-supplied next-generation sequencing data for public availability ("National Center for Biotechnology Information" n.d.).

The Legume Federation also serves as an information and tool repository to "facilitate collaborative development of software, methods, and standards…to help build a healthy research ecosystem." Tools that are offered or linked to include Legume Mines, Data Store at CyVerse, Transcript annotation, Genomic Context Viewer, Data Store at Legumeinfo, and upcoming CMap-js ("Legume Federation" n.d.). Legume Mines-BeanMine is a common bean database that provides gene expression, QTL, gene ontology (GO) terms, and QTL marker resources. Annotation data are available to download at the National Science Foundation-funded CyVerse ("CyVerse" n.d.) database and at the Legume Information System (LIS) ("Legume Information System" n.d.). CMap-js is a comparative genome software in alpha testing, which upon release will allow users to compare biological maps, which includes genetic, physical, cytogenetic, genomic, linkage groups, chromosomes, and scaffolds ("Legume Federation" n.d.).

The Legume Information Systems (LIS) is a legume-specific database with the intention of building on traits for crop improvement. LIS hosts unique tools for QTLs, germplasm resources, genetic maps, physical maps, and molecular markers. Some of these tools are accessible through the Legume Federation website. The Transcript Annotation tool allows the user to upload nucleotide or protein sequences and run the sequences. The Genomic Context Viewer is a comparative genome viewer that allows the user to input a variety of gene identifiers and the output includes "Macro-Synteny" and "Micro-Synteny" tracks to visualize chromosomal patterns or conserved gene function-specific functions (Cleary and Farmer 2018). Phylotree is a gene family search tool allowing users to search gene family IDs, gene descriptions, or by count, the results for each of the legumes are displayed. A "list" of genes can be built for

users to save for future analysis; which serves as a convenient organizational tool for complicated data analysis.

The European Bioinformatics Institute (EBI) and the Wellcome Trust Sanger Institute jointly host plant-specific information and tools including pHMMER, BLAST, comparative genomics, variant effect predictor (VEP), assembly converter, and ID history converter. The user can search the database for genomes and metagenomes, nucleotide and protein sequences, macromolecular structures, bioactive molecules, gene and protein expression, molecular interactions, reactions and pathways, protein families, enzymes, literature, and samples and ontologies, which totals over 1.3 million results.

CoGe is a comparative genomics platform, containing over 47,000 genomes from over 18,000 organisms. Genomes can be viewed in a browser with GC content, coding sequence (CDS), gene annotations, rRNA, and tRNA. Features unique to CoGe, which are not included in JBrowse include: filter track list by name, data type, manage experiments, export track data, search features by name, search tracks, combine tracks by dragging and dropping, convert search results into marker tracks, and save search results as new experiments in CoGe. CoGeBlast allows the user to perform a BLAST search against selected genomes. Multiple common bean genomes are available to search in this database. SynMap is a tool that allows the user to find homologs among two or more species.

1.8.2.2 Diversity Panels and Seed Banks

Common bean diversity panels are assemblies of germplasm for breeding and crop improvement purposes (Cichy et al. 2015a, b). Domesticated Andean bean genotypes have less genetic diversity than domesticated Mesoamerican genotypes due to a bottleneck event that occurred before domestication events (Cichy et al. 2015a, b). Because of the lack of diversity in Andean genotypes, breeding among this gene pool is limited in comparison to progress made in Mesoamerican genotypes (Cichy et al. 2015a, b).

An Andean diversity panel (ADP) was developed in 2015, consisting of 396 accessions; 349 Andean, 21 Mesoamerican, and 26 admixed accessions collected globally. Information can be accessed about this diversity panel at http://arsftfbean.uprm.edu/bean/ (accessed 15 May 2015). Diversity panels have been used in many types of studies, including those screening for flooding tolerance (Soltani et al. 2018), drought tolerance (Asfaw et al. 2017), resistance to root rot (Binagwa et al. 2016), population structure in Uganda (Okii et al. 2014), cooking time (Cichy et al. 2015a, b), gene-based microsatellites (Blair et al. 2009), SNPs between common bean and tepary bean (Gujaria-Verma et al. 2016), and agronomic traits (Moghaddam et al. 2016). A Middle American diversity panel was developed to include 280 Middle American cultivars from the BeanCAP diversity panel (Moghaddam et al. 2016).

The Consultative Group on International Agricultural Research (CGIAR) hosts an international database, Genebank Platform, which allows researchers to request 750,000 accessions of various plant species ("Genebank Platform" n.d.). CGIAR

partners with AfricaRice, Bioversity International, International Center for Tropical Agriculture (CIAT), International Maize and Wheat Improvement Center CIMMYT, International Potato Center, Crop Trust, International Center for Agricultural Research in the Dry Areas (ICARDA), International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), International Institute of Tropical Agriculture (IITA), International Livestock Research Institute (ILRI), International Rice Research Institute (IRRI), and the World Agroforestry Center. CIAT's missions are to develop crops for food security and improved nutrition, profits for small-scale farmers and food accessibility, and developing resilient crops. CIAT currently contains nearly 38,000 *Phaseolus spp.* accessions, 32,375 of which are common bean genotypes. Accessions can be searched by species, location and collection features, characterization features (growth habit, seed color, shape, brightness, and weight, days to flowering, first and last harvest, and use), reactions to biotic and abiotic stresses, and/or nutritional and technological traits. CIAT scientists and collaborations have led to the development and release of more than 550 bean varieties, beans that are tolerant to $\geq$3 °C higher average temperatures, 3× higher yielding climbing beans, and beans that accumulate higher iron.

The IITA's research programs are based in four areas, mainly impacting natural resources in Africa: 1. biotechnology and genetic improvement, 2. natural resource management, 3. Social science and agribusiness, and 4. Plant production, plant health, nutrition, and food technology ("International Institute of Tropical Agriculture" n.d.). The Genesys Plant Genetic Resources (PGR) database was created by Bioversity International and is the largest plant genetic resource repository, containing more than 2.8 million accessions, more than 54,000 are common bean accessions. Bioversity International's goal is to establish community seed banks to benefit small-scale farmers ("Genesys Plant Genetic Resources" n.d.).

Crop Trust was also developed by Bioversity International on behalf of CGIAR and the UN Food and Agriculture Organization (FAO). The goal of this initiative is to conserve diverse crop genetic material for food security ("Crop Trust" n.d.). The Svalbard Global Seed Vault contains nearly 1 million seed samples, from almost 6,000 species ("Svalbard Global Seed Vault" n.d.). National Plant Germplasm System (NPGS) is a collaborative initiative of the United States Department of Agriculture Agricultural Research Service (USDA-ARS) to protect genetic diversity ("National Plant Germplasm System" n.d.).

The National Agricultural Research Organisation (NARO) organizes agricultural research in Uganda, which includes the National Agricultural Research System (NARS) ("National Agricultural Research Organisation" n.d.). The National Bureau of Plant Genetic Resources (NBPGR) is headquartered in New Delhi, India, where researchers work toward conserving germplasm and to provide tools for breeders ("National Bureau of Plant Genetic Resources" n.d.). Some web application tools that are provided by the NBPGR include the PGR portal for information on germplasm, PGR searchable map, an herbarium, intellectual property, Cryo database, crop wild relatives portal, genebank, climate smart management, and genetic resources.

The European Cooperative Programme for Plant Genetic Resources (ECPGR) which aims to conserve germplasm for breeding purposes and functions under

Bioversity International ("European Cooperative Programme for Plant Genetic Resources" n.d.). The germplasm repository, the European Search Catalogue for Plant Genetic Resources (EURISCO), contains more than 52,000 accessions in the *Phaseolus* genus, more than 46,000 accessions are common bean. ECPGR provides a platform to acquire accessions by allowing requests to be directed to institutions that are associated with the accession.

The Genetic Resources Center, National Agriculture and Food Research Organization (NARO) Genebank Project is a conservation effort coordinated in Japan ("NARO Genebank Project" n.d.). This database contains 915 germplasm accessions (accessed July 25, 2018) which can be searched/filtered by many physical characteristics. There are other international crop resources including the Australian Temperate and Field Crops Collection, the Chinese Crop Germplasm Information System (CGRIS), Leibniz Institute of Plant Genetics and Crop Plant Research, the National Institute of Agrobiological Sciences Genebank, and the Asian Vegetable Research and Development Center.

1.8.3 Gene Expression Databases

Many databases that were described previously, in Sect. 13.2.1 are used by researchers who perform high-throughput RNA sequencing methodologies. Some of these databases allow users to upload their generated data, among the most frequently used is NCBI's Short Read Archive (SRA) hosts many user-supplied gene expression data, which can be openly downloaded by other users. The SRA Toolkit includes many free programs that can be used for analyzing sequencing data. Similarly, to NCBI, EBI allows users to submit high-throughput sequencing data to the database as well as searching existing projects and downloading previously submitted data.

Phytozome released the common bean genome, which also contains gene expression data on many tissue types, reported as fragments per kilobase of transcript per million mapped reads (FPKM). Phytozome also contains gene ancestry and co-expression. This information is useful in determining whether selected genes are expressed in target tissues, which can serve as a confirmation for RNA sequencing data. The *Phaseolus vulgaris* Gene Expression Atlas (PvGEA) database hosts downloadable data for common bean tissues harvested at several developmental stages. Expression data for roots, nodules, leaves, stems, flowers, seeds, and pods are available. The user can download normalized and/or raw data or view gene expression data by performing a keyword or sequence search ("PvGEA" n.d.).

1.8.4 Protein and Metabolome Databases (NCBI, EBI, UniProt, PvTFDB, KEGG)

1.8.4.1 Protein

The integration of proteomic and genomic approaches, termed "proteogenomics," has been developing into a powerful tool to better understand the molecular mechanisms that are activated in plants during stress (Zargar et al. 2017). However, proteome studies in common bean are lacking and underrepresented among other legumes (Zargar et al. 2017). These types of studies are important for determining genes as related to stress tolerance, and growth and development of plants and seed (Zargar et al. 2017). To date, most studies on legume proteomics have involved gel-based approaches, which are considered to be low-throughput (Zargar et al. 2017).

Posttranslational modifications are yet another factor in proteomics, for example, phosphorylation of a dehydrin in responding to and recovering from osmotic stress (Zargar et al. 2015). Changes in phosphorylation of phaseolin proteins were found to be implicated in seed dormancy transition to germination (Zargar et al. 2015). Developing a "proteome atlas" to detect rare proteins may prove to be a powerful identification tool to target pathways involved in response to specific stresses (Zargar et al. 2015).

Biotic and abiotic stresses can cause changes in plant protein expression (Zargar et al. 2017)

Databases like NCBI and EBI contain information and tools to search protein sequences, but there are some databases that provide more insight into common bean-specific protein structure and function; including UniProt and PvTFDB. UniProt is a protein database, which contains more than 32,000 protein entries for common bean, 159 of which have been manually annotated and reviewed (accessed July 17, 2018). UniProt provides information on function (catalytic activity, cofactors, enzyme regulation, binding and active sites, gene ontology (GO) molecular functions, and links to other enzyme databases), taxonomy/aliases, subcellular location, pathology, post-translational modifications/processing, interactions, and structure ("UniProt" n.d.).

PvTFDB is a database that houses information on 2,370 putative transcription factors (TFs) in common bean ("Phaseolus Vulgaris Transcription Factor Database" n.d.). The authors of this database suggested that transcription factors are the most important target in terms of developing stress-tolerant crops (Bhawna et al. 2016). PvTFDB also provides other useful data on these TFs including tissue-specific gene expression, *cis*-regulatory elements, phylogeny, gene ontology, and functional annotations (Bhawna et al. 2016). This database has downloadable information for each transcription factor family, which includes the DNA sequence, coding sequence (CDS), primary transcript, amino acid sequence, and the 2 kb region upstream from the transcription start site (Bhawna et al. 2016).

1.8.4.2 Metabolome

An estimated 100,000 to 1 million metabolites are present in all plants, of which 5,000 or more are unique to each species (Alseekh et al. 2018). The most widely used tools to study metabolomics are nuclear magnetic resonance (NMR), gas chromatography mass spectrometry (GC-MS), and liquid chromatography mass spectrometry (LC-MS) (Alseekh et al. 2018). Each methodology comes with positives and pitfalls. NMR is limited by its ability to only detect abundant metabolites, or those extracted from copious amounts of tissue. LC-MS requires samples to be treated prior to testing. GC-MS analytes are largely unannotated (Alseekh et al. 2018).

The Kyoto Encyclopedia of Genes and Genomes (KEGG) database models signaling pathways in biological systems. For common bean, KEGG currently has 134 pathways available (accessed June 25, 2018), which are mostly related to metabolism, but other pathways are represented as well ("Kyoto Encyclopedia of Genes and Genomes" n.d.). It is established that symbiotic relationships with microbes can change the physiology of the host common bean plant (Figueiredo et al. 2008; Mwenda et al. 2018; Sánchez et al. 2014).

Nitrogen fixation is a metabolic process that is characteristic of legumes (Ramalingam et al. 2015). Common bean was crossed with *Phaseolus acutifolius* yielded a common bacterial blight resistant genotype; this consequently led to decreased ability to form symbiotic relationships with bacteria (Farid et al. 2017). Rhizobia are the microbes responsible for establishing the symbiosis of fixing nitrogen in the soil. Due to pleiotropic effects, tracking many phenotypes and physical characteristics will be an important component of breeding studies moving forward as crop improvement projects continue.

Another important group of compounds is phytochemicals, which have positive health benefits for humans (Thompson et al. 2017). A study conducted in rats with cancer showed that triacylglycerol (TAG) precursors were reduced in the mammary glands of the bean-fed rats compared to the control group (Mensack et al. 2012). The results of this study suggest that lipid metabolism is a target of bioactive chemicals in dry beans (Mensack et al. 2012). However, the lack of plant metabolome coverage continues to be a challenge in this area of study, as well as annotation of metabolites (Alseekh et al. 2018).

1.8.4.3 Role of Microbial Interactions

In addition to resources specifically involving common bean, genomes and resources of symbionts may prove to be useful as well. There are distinct differences in the interaction between allowing symbiotic relationships with some microbes versus defense mechanisms against potentially pathogenic microbes. A recent study showed that increased disease resistance in common bean showed a decreased ability to form symbiotic relationships (Farid et al. 2017).

Rhizobium spp. are gram-negative bacteria that form symbiotic relationships with legumes (Carrasco-Castilla et al. 2018). Common bean is a promiscuous host, mean-

ing it can form nodules with multiple species of rhizobia. Currently, it is known that common bean can be nodulated by at least 27 rhizobia species (Mwenda et al. 2018). Plant growth-promoting rhizobacteria (PGPR) are thought to play a role on plant growth by different mechanisms, including alteration of hormones within the plant, increasing solubilization of nutrients and nitrogen uptake, iron chelation, and negative effects on plant pathogens (Figueiredo et al. 2008; Sánchez et al. 2014). The third mechanism may prove to be a promising disease management practice to increase yield (Figueiredo et al. 2008). Beans co-inoculated with nonpathogenic *Rhizobium tropici* (CIAT 899) and *Paenibacillus polymyxa* (DSM36) were found to form more efficient symbiotic associations (Figueiredo et al. 2008). This study examined co-inoculation of CIAT 899 with other PGPRs and the results showed significant differences in phytohormone activity and cytokinin content in the host.

Another recent study described the relationship between rhizobial infection, nodulation, and bean expression of annexin (Carrasco-Castilla et al. 2018). Rhizobia secrete lipo-chitooligosaccharides, or nod factors, which are detected by bean root hairs to induce the formation of the infection thread. This thread is a channel that allows the rhizobia to cross the root hair cell to ultimately lead to nodulation and nitrogen fixation (Carrasco-Castilla et al. 2018). Bean annexins have been shown to play wide-ranging roles, including abiotic stress, biotic stress, growth and development, immunity, and symbiotic microbial relationships (Carrasco-Castilla et al. 2018).

Complete genome sequences of eight *Rhizobium* symbionts associated with common bean (Santamaría et al. 2017). Interestingly, the *Rhizobium etli* and *Rhizobium phaseoli* isolates were found to be rather different in their genomic lineages, despite all being associated with common bean nodules and nitrogen fixation. Beneficial microbes are able to establish symbiotic relationships by secretion of effector molecules that interact with the host, which can lead to downregulation of plant immunity genes (Seidl and Thomma 2017).

Coevolution with pathogens has been noted in several studies including the fungal pathogens *Colletotrichum lindemuthianum* (Geffroy et al. 1999; Luana et al. 2017), *Colletotrichum lindemuthianum* (Padder et al. 2017) *Uromyces appendiculatus* (Cooper and Campbell 2017; Odogwu et al. 2016), *Pseudocercospora griseola* (Ddamulira et al. 2014; Chilagane et al. 2016), and bacterial pathogen *Pseudomonas syringae* (O'Leary et al. 2016), (Vlasova et al. 2016). Transposable elements (TEs) are one of the major contributing factors to coevolution of plants and pathogens (Seidl and Thomma 2017). TEs provide opportunities to substantially impact the structure of the host's genome and this is discussed in more detail in other section.

1.8.5 History of Epigenetics/Epigenomics

The idea of epigenetics is considered to have started in the 1930s, by Waddington, who was interested in embryology. He wanted to determine what happens during development to allow an adult to form from an embryo (Nicoglou and Merlin

2017). In the 1940s and 1950s, McClintock observed "coordinated transposition" in maize and chromatin organization effects on gene expression. "Cellular memory" was introduced by Nanney in the 1950s, which was described as mitotically stable phenomenon; meaning that the same genotype can display different phenotypes. In 1961, the operon model of gene expression was introduced by Jacob and Monod. This model describes the induction of enzymes when a substrate is present. Britten and Davidson introduced the gene-batter model in 1969, which stated that noncoding sequences regulate gene expression. In the 1970s, Riggs and Holliday independently hypothesized about DNA methylation affecting gene expression. DNA experiments in methylation and histone modifications and their effect on gene expression started to appear in the 1990s (Nicoglou and Merlin 2017). Presently, it is widely known that there are several epigenetic mechanisms that contribute to control of gene expression, which include DNA methylation, histone modifications, and noncoding RNAs. Plants, including common bean, have the relatively unique capability to have widespread, extensive DNA methylation in three different motifs, CG, CHG, and CHH (Crampton et al. 2016; Kim et al. 2015).

The link between evolution and the development of organisms is abbreviated as "evo-devo." This was essentially the 1990 s-2000 s version of the "epigenetics" concept, particularly in explaining differences in phenotypic variation and maps (Abouheif et al. 2014; Nicoglou and Merlin 2017). "Eco-evo-devo" incorporates ecological/environmental impact on an organism's genes and development (Abouheif et al. 2014).

Plants are unique as they comprise the highest number of polyploid/alloploid species found in nature. Polyploidy events can cause gene silencing, loss of redundant genes, chromosomal recombination, and TE bursts (Wendel et al. 2018). Genome fractionation and chromosomal restructuring can occur following a polyploidy/whole genome duplication event. Ancient genome duplications and fractionation have led to the current status of the common bean genome (Schmutz et al. 2014). Gene and genome duplications are a major driver of species evolution. Whole genome duplication events can cause other downstream functions to occur that further the evolution of genes and genomes (Wendel et al. 2018). Genome duplications can cause transposable element (TE) bursts, which is the unpredictable mobilization of TEs (Galindo-González et al. 2017; Wendel et al. 2018). This event can cause major mutagenesis leading to chromosome rearrangements (Wendel et al. 2018). Mechanisms that control chromosome conformation and gene expression are affected by genome duplication, specifically, these are small RNAs and DNA and histone modifications (Wendel et al. 2018).

Transposable elements used to be thought of as almost exclusively parasitic DNA in genomes (Galindo-González et al. 2017). TEs are present in significant proportions in plant genomes, from 14% in *Arabidopsis thaliana*, 41% in *Phaseolus vulgaris*, to 80% in *Zea mays* (DOE-JGI 2018; Galindo-González et al. 2017). TEs are classified as type/class 1 (retrotransposons), which spread via "copy-and-paste" and type/class 2 (DNA transposons), which move via "cut-and-paste" (Paszkowski 2015; Gao et al. 2016). Within type/class 1 TEs there are long terminal repeats (LTRs) and non-LTRs (Paszkowski 2015). LTRs are further categorized as Ty1-*copia* and Ty3-*gypsy* (Gao

et al. 2014). Non-LTR retrotransposons are categorized as either short interspersed nuclear elements (SINEs) or long interspersed elements (LINES) (Gao et al. 2014). The most prevalent TEs in common bean genome are retrotransposons, which comprise 35% of the total genome (DOE-JGI 2018). DNA transposons comprise about 5.3% of the genome, with 0.7% as "unclassified transposons" (DOE-JGI 2018).

1.8.6 Integration of "Omic" Datasets

Because gene and protein expression are complicated processes, the integration of multiple "omic" analyses has proven to be a powerful tool. There are many recent studies that involve the integration of multiple "omic" datasets; such as histone modifications (Ayyappan et al. 2015), proteomics, metabolomics, genome resequencing (Vlasova et al. 2016), DNA methylation, and small RNA sequencing, which are combined with mRNA sequencing.

Before the release of the reference genome, a multi-omics study was conducted on navy bean and white kidney genotypes from both centers of domestication (Mensack et al. 2010). The combination of transcriptomics, proteomics, and metabolomics allowed the authors to classify the cultivars to the correct center of domestication, which also suggests inherent differences in gene expression, protein expression, and metabolism (Mensack et al. 2010).

Omics approaches have also been useful in biotic stress when looking at the host and pathogen. The microbial–host interaction is complex, as common bean plants must make a differentiation between friend and foe. Since there is coevolution between pathogens and common bean, integrated omics studies are even more appealing.

1.9 Social, Political, and Regulatory Issues

This section of the chapter addresses social, political, and regulatory issues related to common bean genetic resources and associated traditional knowledge.

The importance of plant genetic resources for food and agriculture (PGRFA) for achieving food security worldwide and for sustainable development of agriculture in the context of poverty alleviation and climate change is widely recognized. PGRFA are maintained in situ, on farm, and ex situ.

PGRFA have been used and exchanged since the beginnings of agriculture, some 10,000 years ago. Consequently, nowadays all countries depend to some extent on genetic diversity that originated elsewhere. There is a continued need for exchange of PGRFA for research, breeding and conservation for ensuring continued ability to adapt to climatic changes, pest and disease resistance, reduced soil fertility, and ultimately, food security. In fact, while studies suggest that the average degree of genetic interdependence among countries for their most important crops is around

70% (Palacios 1998), in the light of climate change, it is expected that this interdependency will increase considerably. Awareness about the importance of continuous access to PGRFA led to the creation during the last few decades of different international instruments, agreements, and institutions to ensure its management, especially in those aspects related to PGRFA shared use (Chiarolla et al. 2012; Esquinas-Alcázar et al. 2012; Halewood 2014). Some examples of these include the Convention on Biological Diversity (CBD), its Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from the Utilization (hereinafter referred to as the Nagoya Protocol), the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) and different forms of intellectual property rights.

The CBD, adopted in 1992, is the first legally binding international instrument that recognized the sovereignty of the States over their genetic resources regarding their conservation and sustainable use, the traditional knowledge of the indigenous and local communities and the distribution of benefits derived from their use with these communities. The Nagoya Protocol, adopted in 2010, established a legal framework for the implementation of the third objective of the CBD: the fair and equitable sharing of benefits arising out of the utilization of genetic resources and associated traditional knowledge, including by appropriate access to them. Implementing this third objective should contribute to the conservation of biological diversity and the sustainable use of its components, the other two objectives of the CBD. The ITPGRFA, adopted in 2001, established an international legal framework, in harmony with the CBD, for the conservation and sustainable use of plant genetic resources for food and agriculture and the fair and equitable sharing of the benefits arising from their use. Both international agreements are meant to be implemented in complementarity. That is, the Nagoya Protocol does not apply for the Parties to the ITPGRFA in respect of the PGRFA covered by and for the purpose of the Treaty. The Nagoya Protocol and the ITPGRFA are, however, based on two different models of access and benefit sharing systems. On the one hand, the Nagoya Protocol establishes that, in accordance with national legislation, access to genetic resources and to its associated traditional knowledge for their utilization is subject to obtaining the prior informed consent (PIC) from the provider and to the establishment of mutually agreed terms (MAT), which are to be agreed between the user and the provider. The ITPRFA, on the other hand, creates a "multilateral system of access and benefit sharing" whereby countries agree to virtually pool and grant facilitated access to "all PGRFA listed in Annex I of the Treaty that are under the management and control of the Contracting Parties and in the public domain." The Treaty's Annex I includes 64 crops and forages that were selected according to criteria of food security and interdependence. This facilitated access under the ITPGRFA is provided under the terms and conditions of the Standard Material Transfer Agreement (SMTA) when the intended use of the genetic resource is its conservation and sustainable use for research, breeding, and training for food and agriculture. Common bean is part of the crops listed in Annex I of the ITPGRFA. Therefore, access to common bean genetic resources by any legal or private person from any Contracting Party to the ITPGRFA should be facilitated

under the conditions established in the SMTA when the intended uses are those cover by the ITPGRFA.

Indigenous and local communities, farmers, researchers, and breeders worldwide have all contributed throughout history to the range of crop diversity that is currently the base of the world's production systems. The development of new varieties is in general a costly and time-consuming process. As a result, intellectual property rights were created as a mean to promote investments in knowledge creation and business innovation by granting exclusive rights to right-holders to prevent others from using newly developed technologies, goods, and services without their permission.

The Agreement on Trade Related Aspects of Intellectual Property Rights (TRIPS), binding on all the members of the World Trade Organization, is a multilateral agreement on intellectual property. TRIPS establishes that plant varieties must be provided with some form of intellectual property system, either patents or an effective sui generis system (a system especially designed for its purposes). As a result, countries worldwide are progressively adopting a plant variety protection law in line with the regulations established by the International Convention for the Protection of New Varieties of Plants (hereinafter referred to as the UPOV Convention). The UPOV Convention is a sui generis system designed specifically to protect the rights of plant breeders over new plant varieties. Its first Act was drafted in 1961 and was later revised in 1972, 1978 and 1991. As of July 2018, 73 countries (plus the African Intellectual Property Organization and the European Union) were members of this organization (www.upov.int). The UPOV Convention offers protection to the breeder of a plant variety (according to the definition established by the UPOV Convention), in the form of a "breeder's right," if his plant variety satisfies the conditions set out in the UPOV Convention (i.e., novelty, distinctness, uniformity, and stability).

The breeder's right is granted for a period of not less than 20 years from the date of grant or, in the case of trees and vines, for not less than 25 years. An authorization of the breeder is therefore needed for the use of the reproduction or multiplication material. The breeder's right under the UPOV Convention, however, does not extend to acts done privately and for noncommercial purposes, acts done for experimental purposes and acts done for the purpose of breeding other varieties and, for the purpose of exploiting these new varieties provided the new variety is not a variety essentially derived from another protected variety (UPOV 1991).

Common bean is a self-pollinated crop or, in other words, it is easily copied. Therefore, there are no great incentives for farmers to buy seeds from the breeder (or the producer under contract). Nonetheless, common bean was among the 13 botanical genera included in the first list to which the UPOV procedures were to be applied. As of August 2018, 11.492 varieties of genus Phaseolus had been included in the UPOV PLUTO database, including information provided by 61 countries, the African Intellectual Property Organization and the European Union (last accessed in July 2018—available at http://www.upov.int/pluto/en/).

Under the formal seed sector, breeding programs are usually focused on producing plant varieties for high-input commercial agriculture that perform well in uniform environments. As a consequence, these varieties are usually not suitable for the nonuniform conditions typical of marginal areas or for those farmers who can-

not afford to purchase additional inputs (Ceccarelli and Grando 2007; Assefa et al. 2005). In many developing countries, common bean constitutes the staple food and it is mainly produced by smallholder farmers who grow the crop in small areas. In fact, in many of these countries, both the production and the market for certified seed under the responsibility of the formal sector is still limited. Depending on the crop and country, between 60 and 90% of the seed sown comes from the informal system (Almekinders and Louwaars 2002). Studies show that technologies developed for smallholder farmers without their own participation or without taking into account their own knowledge are rarely adopted (Trutmann et al. 1996). As a result, there is an increasing number of initiatives aiming at creating linkages between the formal and informal seed systems through collective initiatives such as participatory plant breeding and participatory variety selection. These approaches join farmers and professional breeders, local and formal conditions, and the rural communities' experience and traditional knowledge to identify varieties that perform well in specific agroecological systems and that are attractive to farmers. Some examples of participatory breeding in common bean have been carried out in Rwanda (Waldman et al. 2014; Isaacs et al. 2016), Kenya (Ojwang et al. 2009), Central Africa (Trutmann et al. 1996) and in Ethiopia (Asfaw et al. 2012a, b; Balcha and Tigabu 2015). The involvement of farmers can take place during the definition of breeding objectives and priorities. These include hosting trials on their land, contributing during the selection of lines for further crossing or in the planning for the following year's activities, etc.

In the same lines, the potential of community seed banks for both contributing to link in situ and ex situ conservation and to the interaction and integration of the informal and formal seed systems is increasingly being recognized. Defined as "locally governed and managed, mostly informal, institutions whose core function is to maintain seeds for local use" (Sthapit 2013), community seed banks play different functions in the community. Examples of these are preserving seeds, providing seed access for members of the community, and generating a degree of food security and food sovereignty (Vernooy et al. 2015), contributing at the same time to the implementation of farmers' rights through the recognition of farmers' knowledge of local biodiversity, their participation in decision-making for its conservation and benefit sharing (Sthapit 2013).

The importance of involving farmers in conservation and breeding activities also relies on the internationally recognized contribution made by local and indigenous communities and farmers to the conservation, management, and development of plant genetic resources for food and agriculture. This international recognition has led to the relatively recent appearance of different tools aiming at supporting the implementation at the local level of the international agreements on access and benefit sharing of genetic resources and its associated traditional knowledge. An example of these instruments are the so-called biocultural community protocols, which are formally recognized by the Nagoya Protocol, whereby Parties committed to take into account community protocols and other community rules and procedures where traditional knowledge associated with genetic resources is concerned. When driven and designed by the communities, the development of these documents has the potential

to strengthen community cohesion and the capacity to make visible their connection with the agrobiodiversity of their surroundings. Moreover, these protocols have the potential to simultaneously advance the communities' interests in both obtaining an equitable share of benefits when their genetic resources are accessed and used, and gaining access to, and being able to use genetic diversity from elsewhere (by taking, for example, advantage of the multilateral system of the ITPGRFA when PGRFA are concerned) for use in their own agricultural production systems.

In addition, there is an increasing number of efforts and initiatives worldwide aiming at compiling traditional knowledge related to genetic resources. In Spain, for example, where the traditional agricultural practices have almost completely disappeared, a national inventory of traditional knowledge related to biodiversity has been currently developed (Pardo de Santayana et al. 2014) focused on wild diversity of plant, animal, and fungus.

1.10 Future Perspectives

Common bean has become, over the last 20 years, in a competitive crop in national, regional, and international markets. This situation presents a dynamic environment for producers and researchers of this crop and requires a rethinking of current strategies against research and production needs, the opportunities, and challenges of the future.

The secondary diversification of the common bean and the existence of new recombinant types between the Andean and Mesoamerican genetic pools open the door for new opportunities for the genetic improvement of the species. Breeders can cross between Mesoamerican and Andean gene pools, as well among races, although it is well known that there are constraints to the crosses between Mesoamerican and Andean germplasm due to genetic barriers [blocked cotyledon lethal (BCL), crinkle leaf dwarf (CLD) and dwarf lethal (DL)] (Singh and Gutierrez 1984; Hannah et al. 2007). González et al. (2009) reported successful interracial and interpool crosses for the development of new common bean varieties in Europe. Since the Mesoamerican germplasm usually display resistance to pathogens and some Andean varieties have high seed quality, the use of the European recombinant germplasm as bridge parents in interpool crosses to overcome the interpool genetic barriers provides an interesting opportunity for introgression of relevant genes in the common bean varieties currently grown in Europe. Breeding can also involve gene introgression from additional genes pools, such as the secondary and tertiary gene pools, covering a range of environments from cool moist highlands to hot semiarid regions, and from drought periods to more wet conditions.

An important long-term challenge is the discovery of the gene(s) that control important production traits. This will need to be a cooperative worldwide effort that involves breeders, geneticists, and genomic and bioinformatics experts. Breeders provide the essential skills of phenotyping and the identification and development of genetic populations. Connecting phenotyping with the functional gene requires

the skills of pathologists, physiologists, and those with a deep knowledge of plant anatomy. Those skilled with genomics and bioinformatics provide the expertise to link the phenotypic and genotypic data with candidate genes. Once a candidate gene is defined and the causative mutation is discovered, breeders will then have access to best possible marker, one that is in the gene controlling the important phenotype.

Currently, new technologies built around the recently released common bean genome sequence (Schmutz et al. 2014; Vlasova et al. 2016) are now being developed. Regarding the new breeding technologies, genetic transformation causes some public concern in many countries, but novel breeding material obtained by mutagens are more acceptable to consumers, breeders, and governments. In this context, Targeting Induced Local Lesions in Genome (TILLING) technology has been developed as a new powerful breeding methodology (De Ron et al. 2015). TILLING is a non-transgenic method that uses gene-specific primers for the identification of mutants of a gene of interest from a large mutagenesis population (McCallum et al. 2000). TILLING has gained popularity as a reverse genetic approach because it can produce a series of mutants, including knockouts, and it does not rely on the transformation method for gene discovery and verification. Significant advances have been made in the development of a TILLING platform in common bean, but the protocol for this crop has yet to be optimized. Induced mutation breeding is an effective method to increase the common bean genetic variability available to the plant breeders. Additionally, renewed interest is being generated in induced mutations since the sequence of the common bean genome is already available and it will bring new opportunities for functional genomics research. Therefore, induced mutagenesis will probably become a powerful tool for the isolation and functional characterization of interesting genes, which can be used in common bean genetic improvement.

Improvement of the common bean means possessing in-depth knowledge of its genetic diversity, the genome and gene functions, to enable the analysis of pathways and networks in response to fluctuating environmental conditions. Various genomic resources for common bean are available and include physical maps, bacterial artificial chromosome libraries, anchored physical and genetic maps, expressed sequence tags, and the recently published complete genome sequence (Schmutz et al. 2014; Vlasova et al. 2016). However, these approaches require precise phenotypic data. Complex interactions between the crop genotype, environmental factors in combination with plant population dynamics and crop management greatly affect plant phenotypes in field experiments. Hence, novel techniques should be kept cost-effective and robust under varying field conditions and should allow for the monitoring of various and complex traits.

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