

HISTORY OF THE COMMON BEAN CROP: ITS EVOLUTION BEYOND ITS AREAS OF ORIGIN AND DOMESTICATION

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HISTORIA DEL CULTIVO DE LA JUDÍA: SU EVOLUCIÓN MÁS ALLÁ DE LAS ÁREAS DE ORIGEN Y DOMESTICACIÓN

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ABSTRACT: The common bean (*Phaseolus vulgaris* L.) is the most important grain legume for direct human consumption on a global scale. Current bean germplasm collections show a wide variation of phenotypes, although genetic erosion is gradually affecting this species as in many countries local traditional varieties are being replaced by elite cultivars. This crop has spread to every continent over the past few centuries, which has resulted in a complex genetic structure of bean germplasm outside its areas of origin and domestication (South and Central America). Some evidence indicates that this germplasm is more complex than previously thought and contains additional, as yet unexplored, diversity. This is especially the case in southern Europe, particularly in the Iberian Peninsula, where it was introduced in the early sixteenth century and has been documented as a secondary focus of domestication of the species. The integration of omic data into bean germplasm documentation databases and its combination with genotypic, phenotypic and agro-ecological data is opening a new era for the enhancement and efficient use of common bean genetic resources as the main grain legume in Europe and worldwide.

KEYWORDS: biodiversity; breeding; domestication; evolution; genetics; *Phaseolus vulgaris*.

RESUMEN: La judía común (*Phaseolus vulgaris* L.) es la leguminosa de grano más relevante para el consumo humano directo en escala global. Las colecciones de germoplasma de judía actuales muestran una amplia variación de fenotipos, aunque en muchos países las variedades locales están siendo reemplazados por cultivos de élite, concentrando la producción agraria en un número cada vez más reducido de cultivos con la consecuente erosión genética o pérdida de biodiversidad. Este cultivo se ha extendido por todos los continentes durante los últimos siglos, lo que ha dado lugar a una compleja estructura genética fuera de sus áreas de origen y domesticación (Mesoamérica y Sudamérica). Diversas evidencias indican que el germoplasma europeo contiene una diversidad adicional mayor de la esperada especialmente en el Sur de Europa, y particularmente en la Península Ibérica, donde fue introducida a comienzos del siglo XVI, y que ha sido documentada como un centro de domesticación secundaria de la especie. La integración de datos ómicos en las bases de datos de documentación del germoplasma de judía y su combinación con datos genéticos, fenotípicos y agro-ecológicos está abriendo una nueva era para la valorización y el uso eficiente de los recursos genéticos de la judía común como la principal leguminosa de grano para consumo humano en Europa y globalmente.

PALABRAS CLAVE: biodiversidad; domestication; evolución; genética; mejora genética; *Phaseolus vulgaris*.

THE COMMON BEAN CROP

The common bean (*Phaseolus vulgaris* L.) is the third most important food legume crop worldwide, surpassed only by soybean (*Glycine max* (L.) Merr.) and peanut (*Arachis hypogaea* 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 preferred in many parts of Africa and Latin America (where it can be the most important source of dietary protein), as well as in traditional diets of the Middle East and the Mediterranean region (Broughton *et al.*, 2003; Casquero, Lema, Santalla and De Ron, 2006). This legume is part of the healthy diet of the Mediterranean basin and gaining importance in the USA where consumption has been increasing due to greater 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 risk of obesity, diabetes, cardiovascular diseases and colon, prostate and breast cancer (Hangen and Bennink, 2003; Thompson, Brick, McGinley and Thompson, 2009). These health benefits could be due to the fiber content in the grain but also to antioxidant compounds as the phenolic ones.

DIVERSITY IN THE BEAN GERMPASM: MARKET CLASSES

Common bean is extremely diverse crop in terms of cultivation methods, uses, range of environments to which has been adapted and morphological variability. It is found from sea-level up to 3,000 m. It is grown in monoculture, in association or rotation. It is used as green pods, green beans, and dry beans, even in places such as Africa young leaves are consumed as a source of vitamin A and in parts of South America roasted seeds are consumed, receiving the name “nuña” or popbean (González *et al.*, 2014).

Bean markets and consumers in different countries and regions show particular preferences for grain size, shape, color and cooking time. Among some 600 bean varieties grown in the world, 62 dry bean market classes are recognized (FAO, 2002) according to consumer preferences, production and market price. Some authors have described the major worldwide market classes (Voysset, 2000; Santalla, De Ron and Voysset, 2001) according to con-

sumer preferences, production and market price. The main international market classes are displayed in the table 1, including some local types. Market classes usually include improved germplasm and thus tend to show a low level of variability. Breeding for commercial varieties in common bean usually occurs within each market class in order to retain their preferred seed size, shape, color, and pattern. However, the range of commercially available bean cultivars and varieties in different market classes is constantly changing. New cultivars are being released for their increased yield potential, disease resistance and improved grain.

The polymorphism of common bean is so great that, in each region, and even in each locality, different varieties with similar characteristics correspond to different names. There are several ethnic varieties or “heirloom” varieties, which are characteristic of an area or region, and they can be designated with different names. This germplasm has derived from ancient types by conscious or unconscious selection by farmers and are currently adapted to the agro-ecological conditions under which they have been grown for centuries.

ORIGIN AND DOMESTICATION OF THE SPECIES

Understanding the effects of domestication on genetic diversity of common bean 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 generalised 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 centres of domestication to other areas. The reduction of genetic diversity is usually more drastic in autogamous species as common bean, which have restricted genetic recombination and present a higher population structure as compared with allogamous species (Jarvis and Hodgkin, 1999). This reduction is caused by both stochastic events (for example, a bottleneck and genetic drift due to a reduction in the population size) and selection (for example, for adaptation to a novel cultivated environment) (Vigouroux *et al.*, 2002).

European arrival to the Americas, from the 15th century, marked the entry into Europe of a number of plant species such as common bean (*Phaseolus vulgaris* L.), peanuts (*Arachis hypogaea* L.), cocoa (*Theo-*

broma cacao L.), corn (*Zea mays* L.), potato (*Solanum tuberosum* L.) and tomato (*Solanum lycopersicum* L.), previously unknown in the Old World. The introduction of 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.

The taxonomic enclave of the common bean is (Sitte *et al.*, 2004):

- Class: Dicotyledoneae
- Subclass: Rosidae
- Superorder: Fabanae
- Order: Fabales
- Family: Fabaceae
- Subfamily: Papilionoideae
- Tribe: Phaseoleae
- Subtribe: Phaseolinae
- Genus: *Phaseolus*

Until now, over 400 species have been described in the genus *Phaseolus* (Freytag and Debouck, 2002) of which five have been domesticated and are being currently cultivated: *Phaseolus vulgaris* L. (common bean), *P. lunatus* L. (lima bean), *P. coccineus* L. (runner or scarlet bean), *P. acutifolius* A. Gray (tepariy bean), and *P. polyanthus* Greenman (year bean). These species have genetic and phenotypic differences, particularly the reproductive system, which could be self-pollinated or outcrossed based.

Within the genus *Phaseolus* there are different groups or natural gene pools (Gepts and Debouck, 1991). The primary gene pool of the common bean includes the wild populations and the cultivated varieties of the species, which can intersect each other and recombine without any genetic barrier. The secondary gene pool includes the runner bean and the year bean. The crossing between common bean and the species of the secondary gene pool is easily done without embryo rescue, although using runner bean as female parent requires usually in vitro embryo rescue techniques (Bannerot, 1979). The tertiary gene pool includes the tepary bean and the crosses with common bean require techniques “in vitro. Lima bean belongs to the quaternary gene pool, and no successful crosses between the two species have been reported.

Table 1. Main international common bean market classes (adapted from Santalla *et al.*, 2001)

<i>White seed</i>	<i>Yellow seed</i>
Small white	Small yellow
Navy	Garbancillo
Great Northern	Canario bola
Marrow	Azufrado
Large Great Northern	<i>Brown seed</i>
Hook	Chumbinho
Canellini	Brown Marrow
White kidney	Brown garbanzo
Favada	Brown mottled
<i>White (bi-coloured) seed</i>	Manteca
Hen eye	<i>Pink seed</i>
Rounded Caparron	Rosada
Red Caparron	Light red kidney
Kidney Caparron	<i>Red seed</i>
Favada pinto	Small red
<i>Cream seed</i>	Sangretoro
Carioca	Guernikesa
Mulatihno	Dark red kidney
Dark garbanzo	Red Pinto
Sargaço	Large red mottled
Mottled Canellini	<i>Purple seed</i>
Viscado	Morado
Pinto	Purple Caparron
Ojo de Cabra	<i>Black seed</i>
Bayo Gordo	Black Turtle
Cranberry	Negro brillante
Canela	Black Canellini
Large Cranberry	Black mottled

The distribution of wild common bean from northern Mexico to northwestern Argentina encompasses over 8000 km (Toro, Tohme and Debouck, 1990; Freytag and Debouck, 2002). Two major ecogeographical gene pools with partial reproductive isolation between them are recognized: Mesoamerica (from northern Mexico to Colombia) and the Andes (from southern Peru to northwestern Argentina). Additional structure within each of these gene pools accounts for ecogeographic races in each gene pool (Singh, Gepts and Debouck, 1991; Díaz and Blair, 2006). Until recently, the most credited origin of the species was the northern Peru-Ecuador hypothesis (Kami, Becerra Velásquez, Dbouck and Gepts, 1995). Based on a DNA sequence analysis of the genes for phaseolin seed protein the authors reported that the phaseolin type I gene found in this area does not have the tandem direct repeats that are, instead, characteristic of the Mesoamerican and Andean phaseolin types. Considering that duplications, which generate tandem direct repeats, are more likely to occur than deletions, which specifically eliminate a member of a tandem direct repeat, Kami *et al.* (1995) suggested that *P. vulgaris* originated from the wild populations of northern Peru and Ecuador, and subsequently spread northwards (from Colombia to northern Mexico) and southwards (from southern Peru to Argentina).

One recent alternative hypothesis for the origin of the common bean defended a Mesoamerican origin (Bitochi *et al.*, 2012; Bitochi *et al.*, 2013). This was mainly based on the extensive diversity and population structure within the Mesoamerican gene pool, and the signature of predomestication bottlenecks in the south of the Andes detected in five gene fragments across 102 wild 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 re-sequencing of the genome of the common bean by Schmutz *et al.* (2014) recently confirmed this hypothesis.

Domestication took place after the formation of these gene pools, and thus their structure is evident in both the wild and the domesticated forms (Papa and Gepts, 2003; Papa, Acosta, Delgado-Salinas and Gepts, 2005; Papa *et al.*, 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; Bitocchi *et al.*, 2013). However, the number of domestication events within each pool is still debated. Bitochi *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.

EVOLUTION OF THE CROP BEYOND ITS AREAS OF ORIGIN AND DOMESTICATION

The review of many herbaria and germplasm collections showed that so much variability exists in the genus *Phaseolus*. For centuries farmers have maintained their traditional or heirloom varieties and have exchanged their seeds with surrounding areas, mainly in local markets, and among themselves also. This results in a very different set of characteristics for size, shape, tenderness and cooking quality of the edible parts of the plant (pod and grain). Therefore, the traditional varieties are a valuable source of well adapted germplasm of common bean as displayed in the current common bean germplasm collections that show a wide phenotypic, although in developed countries the traditional varieties are being replaced by improved cultivars, therefore the genetic erosion is affecting the species. Deepening the phenotypic and genotypic characteristics of the different varieties in collections and genebanks is a first step to understand the variability that is currently available. This is essential to carry out breeding programs in kind, to obtain new improved varieties with desirable traits in terms of quality and production, as well as resistance to abiotic and biotic stresses.

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 (Ortwin-Sauer, 1966) and from the southern Andes after 1532, through sailors and traders who brought with them the nicely coloured and easily transportable seeds as a curiosity (Brücher and Brücher, 1976; Debouck and Smartt, 1995).

The common bean germplasm currently grown in the Iberian Peninsula suggests interesting questions about the nature of the variation observed, as well as the evolutionary forces affecting the current European germ-

plasm of this crop. The Mesoamerican beans arrived in the Iberian Peninsula probably displayed limited genetic variation, represented by a small population size (population bottlenecks), and further establishment of new populations were based on a few individuals (founding events) based on farmers preferences, that could have increased genetic drift. However, later germplasm introductions from the southern Andes after around 1532, principally from Peru, could have broadened the genetic diversity (Brücher and Brücher, 1976). 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, Rodiño and De Ron, 2002).

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 in Europe. 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 (e.g. favada, hook and large-great-northern class cultivars) could have arose from recombination events between Mesoamerican and Andean gene pools, better adapted to the conditions of the new agrosystems (Santalla *et al.*, 2001). Evidence of this phenomenon has been detected using phaseolins, allozymes and morphological data (Santalla *et al.*, 2002; Rodiño, Santalla, González, De Ron and Singh, 2006), and ISSRs and SSRs from both the chloroplast and nuclear genomes (Sicard, Nanni, Porfiri, Bulfon and Papa, 2005; Angioi *et al.*, 2009). Gene flow between both gene pools appears to be relatively common in the Andean (Debouck, Araya Vilalobos, Ocampo Sánchez and González, 1989; Paredes and Gepts, 1995; Beebe, Toro, González, Chacón and Debouck, 1997; Chacón, Pickersgill and Debouck,

2005) and European zones (Santalla *et al.*, 2002; Sicard *et al.*, 2005; Piergiovanni, Taranto, Losavio and Pignone, 2006; Rodiño *et al.*, 2006; Sánchez, Sifres, Casañas and Nuez, 2008).

These new forms could have subsequently been disseminated to other parts of Europe, contributing to much-wider variation observed in the current European germplasm (Lioi, 1989; Gil and De Ron, 1992; Escribano, De Ron and Amurrio, 1994; Limongelli, Laghetti, Perrino, and Piergiovanni, 1996; Zeven, 1997; González, Monteagudo, Casquero, De Ron and Santalla, 2006). Therefore, the Iberian Peninsula, mainly the north and northwest regions, could be considered as a secondary center of genetic diversity for the common bean crop, especially regarding the large white-seeded cultivars (Santalla *et al.*, 2002; Rodiño *et al.*, 2006).

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, Rodiño, Santalla and De Ron (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 semi-arid regions, and from drought periods to more wet conditions.

In the case of rhizobia symbiotic system, it is possible that migration of the species had not been parallel, so additional efforts are under way to achieve efficient symbiotic genotypes of common bean and rhizobia (Rodiño *et al.*, 2011). As a result of plant-rhizobia co-evolution, a spectrum of compatible rhizobia has developed each specific for one or more given legume species.

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; Rodiño, Riveiro, Santalla and De Ron, 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, Kelly, Beebe and Blair, 2006). The disease resistance in common bean is crucial to adapt this species to new zones. The most important diseases that constrain common bean production worldwide, particularly in Europe, are anthracnose (caused by *Colletotrichum lindemuthianum*), rust (caused by *Uromyces appendiculatus*), common bacterial blight (caused by *Xanthomonas axonopodis* pv. *phaseoli*), halo blight (caused by *Pseudomonas syringae* pv. *phaseolicola*), bean common mosaic virus and bean common mosaic necrosis virus (Monteagudo *et al.*, 2006). Pathogens causing anthracnose (Pastor-Corrales, Otoyá, Molina and Singh, 1995) and rust (Sandlin, Steadman, Araya and Coyne, 1999) have co-evolved with common bean, thereby forming clearly distinct Andean and Middle American populations. Geographic divergence between both gene pools has led to co-adaptation of the two host gene pools and their respective pathogens, such that Andean isolates are more virulent on average on Andean hosts, and vice-versa. As a consequence, breeders have sought to identify resistance for Andean host lines in the Mesoamerican host gene pool and vice versa.

In the Mediterranean basin can be clearly differentiated populations probably descendants of populations of the Iberian Peninsula where there was gene flow between Mesoamerican and Andean (Santalla *et al.*, 2002). Gene flow between both gene pools appears to be relatively common in the Andean (Debouck *et al.*, 1989; Paredes and Gepts, 1995; 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). Evidence of hybridisation due to the presence of morphological intermediate plants is relatively weak, since it may result from either a phenotypic plasticity or a convergent evolution rather than from a gene flow. The presence of crop-specific alleles in morphologically intermediate landraces can help to provide strong evidence for a history of hybridisation. Molecular analyses in conjunction with phenotypic studies of germplasm are recommended because they provide

complementary information and increase the resolving power of the genetic diversity (Singh, Gutiérrez, Molina, Urrea, and Gepts, 1991). In the Mediterranean basin the Andean populations appear to have experienced major phenomena of evolution and adaptation, as clear differences between them appear. A particular case is the white seed beans types from Turkey that seem to be phylogenetically distant from the rest of the European beans varieties, probably due to their introduction into this country through East Asia via the Silk Route (De la Fuente, De Ron, Rodiño and Santalla, 2010).

After the initial domestication process, the common bean crop spread across Mesoamerica and South America and, after the European exploration of the Americas, to Europe and Africa (Gepts and Bliss, 1988; Gepts, Osborn, Rashka and Bliss, 1986; Gepts, 1988) where it was cultivated under diverse agrosystems, environmental conditions and farmer preferences.

In Asia, China is a large producer of dry beans, and is the most important producer of snap beans in the world. An analysis of 229 landraces revealed higher prevalence of the Mesoamerican type (Zhang, Blair and Wang, 2008). At present, it is believed that there were only a limited number of introductions of the common bean ("caidou") into China, which were biased towards the Mesoamerican type. In Africa, the Mesoamerican and Andean gene pools are approximately equal in frequency (Asfaw, Blair and Almekinders, 2009; Blair, González, Kimani and Butare, 2010), even if there are striking differences between different countries due to different farmer selection preferences and the input of germplasm from national programs. In Japan, the common bean is usually called "ingen mame" and "sasage" in the Tohoku district (the northeastern parts of Japan). The crop is considered to have been introduced into Japan in the 16th century (Hoshikawa, 1981), maybe from China, and now is grown widely as a garden crop, being Hokkaido (the northernmost parts of Japan) the main area of commercial production.

Portuguese and Spanish traders probably introduced common bean to Africa from the 16th century through Sofala (Mozambique), Zanzibar and Mombasa, from where it was carried to higher altitude areas of the interior by slave trading caravans and merchants (Greenway, 1945). Common bean became well established as a pulse crop in parts of Africa before the colonial era. Genetic diversity of common bean and its pathogens and linguistic evidence indicate that it became a major crop in Central African highland ar-

eas (e.g. in Rwanda and Burundi) earlier than in other parts of Africa. The crop is of significance in many African countries and most intensively grown in the Great Lakes areas of Central Africa (Wortmann, 2006). Many varieties of beans are grown in Africa, with wide diversity in seed types and adaptation to climatic and agronomic very different. Additionally, the consumer and market preferences have produced a high phenotypic diversity in this species. For these reasons, Africa highlands are proposed as a secondary center of diversity for the species by Asfaw *et al.* (2009) and Blair *et al.*, (2010). Blair *et al.* (2010) identified Andean and Mesoamerican distinct genotypes and landraces intermediate between the gene pools and representing inter-gene pool introgression in terms of phenotypic characteristics and alleles.

BREEDING PERSPECTIVES

Common bean has become, over the last twenty 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.

An important long-term challenge is the discovery of the gene(s) that control important production traits. This will need to be a cooperative world-wide 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.

To date, considerable efforts have been made towards 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 re-sequencing 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 HiSeq2000 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 under the framework of the Phaseolus consortium within the Project "Sequencing of the common bean genome (*Phaseolus vulgaris* L.) for the rational exploitation of the natural resources of Iberoamerica" funded by the Ibero-American Programme for Science, Technology and Development (CYTED). The genome sequence has an immediate application by providing a reference from which new markers can be developed.

Currently new technologies built around the recently released common bean genome sequence (Schmutz *et al.*, 2014) 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, Comai, Greene and Henikoff, 2000). TILLING has gained popularity as a reverse genetic approach because it can produce 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

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