

Handbook of Plant Breeding

Antonio M. De Ron *Editor*

Grain Legumes

 Springer

Handbook of Plant Breeding

Volume 10

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ISSN 2363-8478

ISSN 2363-8486 (electronic)

Handbook of Plant Breeding

ISBN 978-1-4939-2796-8

ISBN 978-1-4939-2797-5 (eBook)

DOI 10.1007/978-1-4939-2797-5

Library of Congress Control Number: 2015942916

Springer New York Heidelberg Dordrecht London
© Springer Science+Business Media New York 2015

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Printed on acid-free paper

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(www.springer.com)

Preface

Legume species belong to the Fabaceae family and are characterized by their fruit, usually called pods. Several species of this family were domesticated by humans, such as soybean, beans, faba bean, pea, chickpea, lentil, peanut, lupine, pigeon pea, mung bean, peanut, or cowpea and many of them are of great relevance as human food and animal feed. Food legumes are typically consumed as dry seeds, which have high protein content, and in some cases as immature seeds or pods.

Members of the legume family, the Fabaceae or Leguminosae, fill critical niches in most terrestrial biomes. This is one of the few plant families whose species are capable of “fixing” nitrogen from the air, through association with specialized soil bacteria, for use as a natural fertilizer, thus reducing fertilizer requirements. The family has traditionally been divided into three subfamilies: Caesalpinioideae, Mimosoideae and Papilionoideae, this latter subfamily contains most of the major food and feed legumes.

Several grain legume crops are crucial elements of global agriculture and nutrition, both as food and feed since they are major sources of plant protein. Legumes contribute to the sustainable improvement of the environment when grown in agricultural rotations due to their ability of biological nitrogen fixation and their effects on the soil, and yield of the next crop, and the services given to other components of agroecosystems such as pollinators. Legumes play a key role in the diversification and sustainable intensification of agriculture, particularly in light of new and urgent challenges such as climate change. The overall objective is to increase the sustainability of the food and feed chain at all its steps, meet the requirements of citizens for safe, healthy and affordable food via the nutritional prevention of diet-related diseases and assure food quality and authenticity. Reducing energy and water consumption and optimizing process control contribute to making food processing and distribution more sustainable and the food sector more competitive.

The demand for plant proteins for human nutrition has increased over the past few decades in many countries due to: (i) demographic growth and urbanization, (ii) the limited land areas which can be used for production of food crops while farming systems are changing towards specialized cereal and oilseed production, (iii) a decrease in animal protein production due to shortage of irrigation and/

or rainfall especially, and (iv) deliberate reduction in red meat consumption for health reasons. Because of the high protein content of their seeds, grain legumes are attractive candidates to overcome the deficiency in plant protein production. However, in comparison to cereals, limited improvement in farming practices has been achieved over the past few decades to enhance the production of important grain legumes. A number of limiting factors affect legume yield, with water deficiency in quantity or quality being among the key ones, to obtain more stable and more reliable production. Even though these constraints have become structural in many agrosystems, very limited research and development efforts have been devoted to strategies to improve grain legume production under stress conditions to contribute to the development of sustainable agriculture worldwide.

Further, the decrease in legume cropping is linked to a heavier use of chemical fertilizers, pesticides and herbicides than in the past and an overall simplification of agricultural systems. This has reduced the level of above- and below-ground biodiversity in terms of macro- and microorganisms living in the agroecosystem and has caused an increased pollution of the environment, impairing the beneficial effects biodiversity has on crop productivity and the maintenance of agroecosystem services for future generations. In addition, the decrease in legume cropping in some agricultural areas urgently needs to be reversed as nitrogen fertilizers costs are increasing with rising energy costs, leading to high production costs for farmers, and substantial greenhouse gas emissions linked to the use of nitrogen fertilizers.

Also social and scientific issues should be considered. Interest in legumes has been decreasing among many farmers, breeders, processing sector entrepreneurs and scientists. Most worrying is the fact that knowledge on grain legumes with regard to growing legumes in rotations, appropriate harvesting, storage and preparation of the seed for further reproduction or processing have progressively been lost. In addition, the use of legumes in human diet is decreasing in many developed countries and knowledge on how to use legumes in food preparations is being lost, despite continued calls by the medical professions to include a wider range of plant proteins in the diet. To reverse these current trends, actions must be taken, to promote wider use of legumes in crop production that will enable significant benefits in economic, environmental and climate change spheres.

Approaches aimed at the improvement and exploitation of legume nutritional and technological qualities are needed and can be expected to drive consumers and farmers towards new, diverse, healthier and more sustainable choices. To contribute to the development of sustainable agriculture, special attention has to be paid to the factors limiting legume yield to obtain more consistent production and to fill the knowledge and development gap on strategies to improve grain legume production under stress conditions.

The decrease in manufacture of inorganic N fertilizers will result in reducing the emission of greenhouse gas. Nitrous oxide (N_2O) is produced naturally in the soil during the microbial processes of nitrification and denitrification; considered over a 100-year period, N_2O is a greenhouse gas with tremendous global warming potential (GWP) when compared to carbon dioxide (CO_2) since it has 310 times the ability per molecule of that gas to trap heat in the atmosphere. The decline of

soil fertility with loss of organic matter, the excessive use of chemical fertilizers, the inappropriate use of the scarce water resources and the increase in soil acidity and salinity, particularly in dry regions, all pose real threats to economic, social and environmental sustainability. Agricultural systems involving legumes represent a cheaper and more sustainable alternative to conventional practices by symbiotically capturing atmospheric N_2 , thus reducing the use of industrially produced nitrogen in the production of field crops. Improved N management is needed not only to optimize economic returns to farmers but also to minimize environmental concerns associated with N use, namely leaching problems and water pollution.

Intercropping or crop rotation including legumes is a promising strategy for more sustainable crop production in many agricultural systems through the N transfer and N release from legume residue. In crop rotation, legume crops can be used in between of cereals or other cash crops (e.g., vegetables). The final contribution of fixed N_2 to the soil depends upon the legume species N balance, environmental conditions and agricultural practices.

Globally, grain legumes are the most relevant source of plant protein, especially in many countries in Asia, Africa, and Latin America, but there are some constraints in their production, such as poor adaptation, pests and diseases, and unstable yield. Current research trends in legumes are focused on new methodologies involving genetic and -omic studies, as well as new approaches to the genetic improvement of these species, including the relationships with their symbiotic rhizobia.

The book on grain legumes includes two parts. The first one consists of eight crop-specific chapters devoted to the most produced and consumed worldwide grain legume crops covering the whole range of topics related to breeding: origin and evolution, genetic resources, breeding achievements, specific goals and techniques, including the potential and actual integration of new technologies. The second part includes five cross chapters covering topics that relate to the different crops of the general chapters. All the chapters have been written by outstanding breeders and scientists with wide experience in their crops and topics. This handbook contains all the basic and updated information on the state of the art of breeding grain legumes. The vast amount of knowledge collected in this volume should not only serve breeders but also researchers, students and academicians. It may be regarded as a scientific knowledge platform that provides practical plant breeders with new scientific information, but also to make molecular biologists more familiar with the peculiarities of breeding of the main grain legume species.

Pontevedra, Spain

Antonio M. De Ron

Acknowledgement

The editor acknowledges the excellent contributions of all the authors, as well as the support by the Springer Editorial team: Kenneth K. Teng, Hanna Smith, Elizabeth Orthmann and Megha Koirala. Special thanks to the Editors-in-Chief of this series Handbook of Plant Breeding, Jaime Prohens, Fernando Nuez and Marcelo Carena, for giving me the great opportunity to edit this Handbook on Grain Legumes.

Contents

1 Common Bean	1
Antonio M. De Ron, Roberto Papa, Elena Bitocchi, Ana M. González, Daniel G. Debouck, Mark A. Brick, Deidré Fourie, Frédéric Marsolais, James Beaver, Valérie Geffroy, Phillip McClean, Marta Santalla, Rafael Lozano, Fernando Juan Yuste-Lisbona and Pedro A. Casquero	
2 Pea	37
Thomas D. Warkentin, Petr Smýkal, Clarice J. Coyne, Norman Weeden, Claire Domoney, Deng-Jin Bing, Antonio Leonforte, Zong Xuxiao, Girish Prasad Dixit, Lech Boros, Kevin E. McPhee, Rebecca J. McGee, Judith Burstin and Thomas Henry Noel Ellis	
3 Chickpea	85
Teresa Millán, Eva Madrid, José I. Cubero, Moez Amri, Patricia Castro and Josefa Rubio	
4 Lentil	111
Thomas R. Stefaniak and Kevin E. McPhee	
5 Faba Bean	141
Gérard Duc, Jelena M. Aleksić, Pascal Marget, Aleksandar Mikić, Jeffrey Paull, Robert J. Redden, Olaf Sass, Frederick L. Stoddard, Albert Vandenberg, Margarita Vishnyakova and Ana M. Torres	
6 Lupins	179
Wojciech Świącicki, Magdalena Kroc and Katarzyna Anna Kamel	
7 Cowpea	219
Ousmane Boukar, Christian A. Fatokun, Philip A. Roberts, Michael Abberton, Bao Lam Huynh, Timothy J. Close, Stephen Kyei-Boahen, Thomas J.V. Higgins and Jeffrey D. Ehlers	

8 Grass Pea	251
Nuno Felipe Almeida, Diego Rubiales and Maria Carlota Vaz Patto	
9 The Legume–Rhizobia Symbiosis	267
Jean-Jacques Drevon, Nora Alkama, Adnane Bargaz, A. Paula Rodiño, Kiriya Sunghongwises and Mainassara Zaman-Allah	
10 Nutritional Value	291
Francesca Sparvoli, Roberto Bollini and Eleonora Cominelli	
11 Seed Physiology and Germination of Grain Legumes	327
Jaime Kigel, Leah Rosental and Aaron Fait	
12 Reproductive Biology of Grain Legumes	365
María José Suso, Penelope J. Bebeli and Reid G. Palmer	
13 Grain Legume Cropping Systems in Temperate Climates	401
Thomas F. Döring	
Index	435

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Chapter 1

Common Bean

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1 Introduction

The common bean (*Phaseolus vulgaris* L.) is a diploid annual species and is predominantly self-pollinating. Common bean consists of two major gene pools, Mesoamerican and Andean, characterized by partial reproductive isolation, that include wild populations and cultivated varieties. 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.). Among the main food crops, the common bean shows the greatest variation in growth habit, seed characteristics (size, shape and colour) and maturation time. This variability enables its production in a wide range of cropping systems and environments as diverse as the Americas, Africa, the Middle East, China and Europe (Blair et al. 2010). Despite being cultivated for its fresh pods and grains, beans are produced and consumed mainly as dry grain.

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The common bean has lately gained attention as a functional food due to its health benefits and human disease prevention. In fact, its inclusion in diets is linked to reduce risk of obesity, diabetes, cardiovascular diseases, and colon, prostate and breast cancer (Correa 1981; Hangen and Bennink 2003; Thompson et al. 2009). These health benefits may be attributed to its important fibre and starch content, ability to regulate glycaemia and gastrointestinal function, as well as to its antioxidant properties provided by the presence of phenolic compounds and proteins.

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For centuries, farmers have maintained their heirloom varieties and have exchanged their seeds with surrounding areas, mainly in local markets. It is not always easy to know the use given by farmers to their old landraces, and it must be assumed that snap and dry beans have probably been selected under dissimilar criteria and pressure. This results in a very different set of characteristics for size, shape, tenderness and cooking quality of the edible parts of plant. Therefore, the traditional varieties are a valuable source of well-adapted germplasm of common bean. The current common bean germplasm collections show a wide variation of phenotypes, although in many developed countries where landraces are being replaced by elite cultivars the genetic erosion is affecting the species. Also the traditional intercropping with maize in many countries is into abeyance, and sole cropping of bean may become unsustainable in some environments as the soil is eroded and the pressure of pests and diseases builds up (Davis and Woolley 1993).

The current integration of genomic data into gene bank documentation systems and its combination with genetic, taxonomic, agronomic, phenotypic and ecological data will usher in a new era for the valorization of the common bean genetic resources.

2 Origin and Systematics

2.1 Phylogeny

Most of the *Phaseolus* species are geographically distributed in Mesoamerica, and for this reason the genus is considered to have originated in Mesoamerica (Freytag and Debouck 2002; Delgado-Salinas et al. 2006) between 6 and 4 million years (Ma) ago (Delgado-Salinas et al. 2006). This indicates that the *Phaseolus* genus originated after the late Miocene (ca. 7 Ma ago, Coates et al. 2004) when the closure of the Isthmus of Panama allowed the connection of Mesoamerica and South America through a land bridge. Eight well-supported crown clades characterize the *Phaseolus* genus, with an average age of ca. 2 Ma, thus indicating that most of the diversity came into existence after the formation of the actual geographical and geological form of Mexico (ca. 5 Ma ago; Delgado-Salinas et al. 2006). Among the eight *Phaseolus* clades, the *vulgaris* group is the oldest, at ~4 Ma. Along with *P. vulgaris*, there are three other domesticated *Phaseolus* species that belong to this group (*P. dumosus*, *P. coccineus*, *P. acutifolius*), with the most closely related species to *P. vulgaris* being *P. coccineus* and *P. dumosus*. Gepts et al. (1999) suggested that *P. vulgaris* diverged from *P. dumosus* and *P. coccineus* some 2 Ma ago, through an analysis of the sequence data of the α -amylase inhibitor gene. The other domesticated species, *P. lunatus*, is most distantly related to *P. vulgaris* (Delgado-Salinas et al. 2006).

2.2 Origin

Wild forms of *P. vulgaris* occur from northern Mexico to northwestern Argentina, and they are characterized by three distinct gene pools (Fig. 1.1): Mesoamerica, the Andes and northern Peru–Ecuador (Debouck et al. 1993; Kami et al. 1995). The Mesoamerican and Andean are the two main gene pools, where the geographical structure is evident also for the domesticated forms, as it has been demonstrated



Fig. 1.1 Common bean gene pools

through studies based on *P. vulgaris* morphology, seed proteins, allozymes, multi-locus molecular markers and nucleotide data (Bellucci et al. 2014a). The third gene pool is constituted by wild populations that grow in a small geographical area on the western slopes of the Andes, the distinctiveness of which is the specific phaseolin (main seed-storage protein), type I ('Inca', Kami et al. 1995). This phaseolin type has not been found in the other two gene pools.

Until recently, the most credited origin of the species was the northern Peru–Ecuador hypothesis, as suggested by Kami et al. (1995) who sequenced a portion of the gene coding for phaseolin and reported that the phaseolin type I gene 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).

The alternative hypothesis describes a Mesoamerican origin for *P. vulgaris*. Bitocchi et al. (2012) investigated the nucleotide diversity at five gene fragments across a wide sample of wild *P. vulgaris* accessions that were representative of the entire geographical distribution of the species. In particular, three main outcomes supported a Mesoamerican origin of the common bean. (i) A strong reduction in the genetic diversity (90%) of the Andean compared to Mesoamerican wild forms, indicating the occurrence of a bottleneck in the Andean gene pool that predates its domestication. (ii) A clear population structure is highlighted in Mesoamerica, with four different genetic groups (B1, B2, B3 and B4) that characterize the accessions from this gene pool. The B1 group included accessions distributed across all the Mesoamerica, while the other three groups were characterized by only Mexican accessions; in particular, the B2 group spread from central to southern Mexico, and the B3 and B4 being characteristic of a wide area of central Mexico. Such a population structure had not been identified before in previous studies, the main reason for which was probably related to the nature of the markers used; indeed, compared with multilocus molecular markers, sequence data are less prone to homoplasy (e.g. Wright et al. 2005; Morrell and Clegg 2007), and the assumption of no recombination is less likely to be violated, and thus, these sequence data were very useful to address evolutionary issues (Bitocchi et al. 2012, 2013). (iii) There is no clear distinction between the Mesoamerican and Andean wild gene pools, which was indicated by the phylogenetic relationships between the four different Mesoamerican genetic groups with the South American gene pools.

Considering all of these data, Bitocchi et al. (2012) suggested the Mesoamerican origin of *P. vulgaris*, with Mexico being the more likely cradle of diversity of this species, where all of the four different genetic groups are present. Moreover, they suggested that the wild common bean that grows in northern Peru and Ecuador represents a relict population that only includes a fraction of the genetic diversity of the ancestral population, with phaseolin type I appearing to be extinct in Mesoamerica. This result was recently confirmed by the resequencing of 60 wild *P. vulgaris* genotypes (Schmutz et al. 2014).

2.3 Domestication

The domesticated forms of *P. vulgaris* have important traits that distinguish them from the wild forms, such as reduced and loss of the dissemination mechanisms, loss of seed dormancy and photoperiod insensitivity, greater seed size and determinate growth habit. The main effect of domestication was a reduction in the genetic diversity in the domesticated forms that was imposed by founder effect (i.e. genetic drift) and selection at loci controlling domestication traits. This reduction has been clearly identified in the Mesoamerican domesticated gene pool in several studies (Papa et al. 2005; Papa et al. 2007; Rossi et al. 2009; Kwak and Gepts 2009; Nanni et al. 2011; Bitocchi et al. 2013). The same studies have shown that, in contrast, in the Andean gene pool, the bottleneck of domestication was less evident; in particular, Bitocchi et al. (2013) showed a reduction in the diversity that was threefold greater in Mesoamerica as compared with the Andes.

Bellucci et al. (2014b) applied next-generation sequencing technology (RNA-Seq) to investigate, not only at nucleotide but also at transcriptome level, the domestication process in Mesoamerica. They analysed nucleotide polymorphism and gene differential expression in wild and domesticated forms at 27,243 contigs, each representing a putative single gene. Their results showed that domestication not only led to a drastic reduction of diversity (~60%) but also decreased diversity of gene expression (~18%). Another important outcome of this study was the detection of ~9% of contigs being affected by selection during domestication (directly targets of selection or physically linked to the selected genes). The findings indicated that positive selection was the rule, even if, in a few cases, selection increased the nucleotide diversity in the domesticated forms at target loci associated with abiotic stress responses, flowering time and morphology.

A still open debate concerns the occurrence of single or multiple domestications within the two main gene pools, with studies suggesting both single (Papa and Gepts 2003; Kwak and Gepts 2009; Kwak et al. 2009; Rossi et al. 2009) and multiple (Singh et al. 1991a, b, c; Chacón et al. 2005) events. However, the most recent studies support a single domestication, in both Mesoamerica and the Andes (Bitocchi et al. 2013).

Mamidi et al. (2011) analysed sequence data from 13 loci and dated the domestication bottlenecks to ca. 8000 and ca. 7000 years before the present for the Mesoamerican and Andean gene pools, respectively. In Mesoamerica, two different domestication geographical areas have been suggested recently: Rio Lerma–Rio Grande de Santiago basin in west-central Mexico (Kwak et al. 2009) and in Oaxaca Valley (Bitocchi et al. 2013). Similarly, in the Andes, Chacón et al. (2005) indicated central-southern Peru as the geographical area where *P. vulgaris* was domesticated; in contrast, other studies have suggested Bolivia and northern Argentina (Beebe et al. 2001; Bitocchi et al. 2013).

2.4 Diffusion and Evolution Out of the Americas

The diffusion of *P. vulgaris* out of the American domestication centres appears to have been very complex and to have involved numerous introductions into different

continents and countries. Several of these have been proposed as secondary centres of diversification, such as Europe (Santalla et al. 2002; Angioi et al. 2010; Gioia et al. 2013), central-eastern and southern Africa, Brazil and China (Bellucci et al. 2014a). In particular, *P. vulgaris* from Europe is characterized by a higher frequency of the Andean (ca. 70%) as compared to Mesoamerican types (Gepts and Bliss 1988; Gil and De Ron 1992; Logozzo et al. 2007; Angioi et al. 2010). In Brazil, Burle et al. (2010) reported that the Mesoamerican types are fourfold more frequent than the Andean. In Africa, there is an equal frequency of the two types (Gepts and Bliss 1988; Asfaw et al. 2009; Blair et al. 2010), while China shows a predominance of the Mesoamerican types (Zhang et al. 2008).

Moreover, once out of the Americas, the spatial isolation between the Mesoamerican and Andean gene pools was not maintained, which provided increased potential for their hybridization and introgression. In Europe, this aspect is very important for breeding; indeed, their hybridization has led to the recombination of the Mesoamerican and Andean traits that has resulted in the production of novel and useful genotypes and phenotypes (i.e. resistance to biotic and abiotic stress; Rodiño et al. 2006; Angioi et al. 2010; Blair et al. 2010; Santalla et al. 2010). However, various studies suggest that in other continents, the introgression between these gene pools appears not to be as relevant as it has been in Europe.

3 Genetic Resources and Utilization

Somewhere in Central America during the Pliocene and for 4 Ma (Delgado-Salinas et al. 2006), a group of legumes evolved in what is today the section Phaseoli of the *Phaseolus* genus (Freytag and Debouck 2002). One of them, *P. vulgaris* L., migrated northwards and to the Andes and has survived as wild in montane forests to this date. When humans crossing Beringia during the last Ice Age colonized the Americas, they found common beans growing wild from Mexico down to Argentina. Genetic studies with the help of molecular markers have shown these beans to be diverse though grouped in 2–3 pools (Tohme et al. 1996). For reasons possibly linked to food shortages, about 8000 years ago (Mamidi et al. 2011), Amerindians started planting beans, that is, initiated a domestication process. This happened independently in western Mexico (Kwak et al. 2009) and in the central Andes (Chacón et al. 2005), possibly at the same time or slightly earlier in the Andes. Beans planted with corn were a basic staple for all New World civilizations from the Carolinas (USA) down to Jujuy (Argentina). In 1493, the Spanish galleons brought common beans to the Old World where new processes of selection and recombination resumed. Not surprisingly, new landraces and some recombinants occurred in these new lands of adoption such as Spain, Italy, eastern Africa and China. If time correlates with the piling up of genetic diversity, useful sources are clearly in the secondary gene pool of Phaseoli and in the wild forms (Porch et al. 2013).

Bean breeding has often focused first on transfer of resistances to diseases and pests because of the imperative to secure the ‘meat of the poor’ throughout Latin America and Africa (where the highest consumption per capita is registered). Yield per se, tolerance to drought, adaptation to low phosphorus soils and nutritional qual-

ity are priorities of bean breeders since the 1990s (Broughton et al. 2003). Although not the entire germplasm has been collected nor evaluated, many interesting traits have been disclosed in ex situ collections (Table 1.1) and have been used to get yield gain close to 20% over the past 50 years (Singh et al. 2007). While many landraces were topping at 400 kg/ha, yields of 2900 kg/ha are no longer the exception. Growth habit from a vine liana has been ‘domesticated’ too, namely with the selection of type II, for mechanical harvesting, and changing the original poor root system is coming into the horizon, by using the secondary gene pool (Porch et al. 2013). Although current ex situ collections harbour diversity (Table 1.2, where the top five gene banks have 34% of total accessions worldwide), wild species and secondary gene pools are not yet fully represented nor evaluated, an obvious and timely priority.

Table 1.1 Some bean germplasm used to overcome limiting factors in bean production

Trait looked for	Material used ^a
<i>Abiotic stresses</i>	
Aluminium toxicity	G35346 (<i>P. coccineus</i> , from Oaxaca)
Drought	Common red Mexican G11212; G21212 landrace from Colombia
Low phosphorus	G19227A; Chaucha Chuga G19833
<i>Diseases</i>	
Angular leaf spot	Interspecific hybrids with <i>P. coccineus</i> ; Bolivian G8719; Mexican G2726
Anthraxnose	Aliya G02333; Kaboon G1588; Cornell 49–242 G5694
Anthraxnose	Interspecific hybrids with <i>P. coccineus</i>
Ascochyta blight	<i>P. dumosus</i> G35182 from Guatemala
BGYMV	Royal Red G04450; <i>coccineus</i> G35172 from Rwanda
BCMV	Porillo Sintético G4495, Royal Red G04450
Beet curly top virus	California Pink G06222, Red Mexican G05507
Beet curly top virus	Porillo Sintético G04495, Burtner, Tio Canela 75
Common bacterial blight	Interspecific hybrids with <i>P. acutifolius</i> VAX4, MBE7
Common bacterial blight	Montana No. 5; PI 207262
Halo blight	Montcalm G06416, ICA Tundama G14016
Halo blight	Pinto US 14 G18105
Halo blight	Wis HBR 72 G03954
Fusarium root rot	Porillo Sintético G04495; wild <i>P. vulgaris</i> G12947
Pythium root rot	PI 311987 G02323

Table 1.1 (continued)

Trait looked for	Material used ^a
<i>Rhizoctonia solani</i>	N203 G00881
Rot	
Rust	Compuesto Negro Chimaltenango G05711
Rust	Redlands Pioneer G05747
Rust	PI 260418
Web blight	BAT 93; Flor de Mayo G14241
White mould	Interspecific hybrids with <i>P. coccineus</i> G35172
White mould	Interspecific hybrids with <i>P. costaricensis</i> G40604
<i>Pests</i>	
<i>Acanthoscelides weevil</i>	Wild <i>P. vulgaris</i> from western Mexico G12952, G2771
<i>Apion godmani</i> pod weevil	Amarillo 154 G03982; G03578
<i>Empoasca</i> leafhoppers	California dark red kidney, from USA G17638
<i>Ophiomyia</i> bean fly	<i>P. coccineus</i> G35023 and G35075, and inter-specific hybrids
Whiteflies Aleyrodidae	DOR 303
<i>Zabrotes</i> weevil	Wild <i>P. vulgaris</i> from Chiapas, Mexico G24582
<i>Nitrogen fixation</i>	
N ₂ fixation under low P	Bituyano from Cajamarca, Peru, G19348
<i>Yield</i>	
Favourable QTLs	Wild <i>P. vulgaris</i> from Colombia G24423
Favourable QTLs	Wild <i>P. vulgaris</i> from Colombia G24404
<i>Nutritional traits</i>	
Seed protein quantity	PI 229815
High zinc content	Peruvian landrace G23823
High iron content	Peruvian landrace G23823
Polyphenols	Wild <i>P. vulgaris</i> from Mexico G11025

^a G numbers refer to the International Center for Tropical Agriculture (CIAT) genebank, while PI numbers refer to the Western Regional Plant Introduction Station at Pullman, Washington, USA. *BCMV* bean common mosaic virus, *BGYMV* bean golden yellow mosaic virus, *QTLs* quantitative trait loci

Table 1.2 Major germplasm collections of *Phaseolus* beans, and type of accessions. FAO (2010)

Gene bank	Accessions (%)	Landraces (%)	Wild species (%)
CIAT, Colombia	35,891 (14)	30,507 (85)	2153 (6)
USDA, USA	14,674 (6)	9832 (67)	880 (6)
Embrapa, Brazil	14,460 (6)	5784 (40)	–
INIFAP, Mexico	12,752 (5)	7014 (55)	2168 (17)
IPK, Germany	8680 (3)	5729 (66)	87 (1)

4 Varietal Groups: Market Classes

Bean consumers of different countries and regions show specific preferences for various combinations of seed size, shape, colour, cooking time, broth appearance and storability (De Ron et al. 2000). Therefore, a classification often used for common bean is the one into commercial types, which is based predominantly on characteristics of grain colour and size, and is related to market preferences. The wide range of seed characteristics has been formalized in the bean world into distinct commercial or market classes. Among the bean varieties grown in the world, 62 dry bean market classes are recognized (Santalla et al. 2001; FAO 2002) according to consumer preferences, production and market price (Fig. 1.2). Dry bean market classes are produced under recommended agronomic practices and traded according to the defined class attributes. Thus, classes must be segregated throughout production and distribution.

Increased diversity of commercial market classes has been achieved to meet market and consumer interests. Among the Durango beans, the most important market classes are ‘great northern’ and ‘pinto’. The most abundant market classes that represent race ‘Nueva Granada’ are ‘dark red kidney’, ‘white kidney’, ‘calima’ and ‘large cranberry’ beans. Regarding the race Mesoamerica, the most popular bean market classes are ‘navy’, ‘small white’, ‘mulatinho’, ‘carioca’ and the classes of small black seed. The Chilean market classes most accepted and consumed are ‘tortola’ and ‘coscorrón’. In addition, other minor market classes, such as ‘manteca’, ‘sapito’ and ‘cuyano’, are also consumed in more specific areas. Race Peru is char-

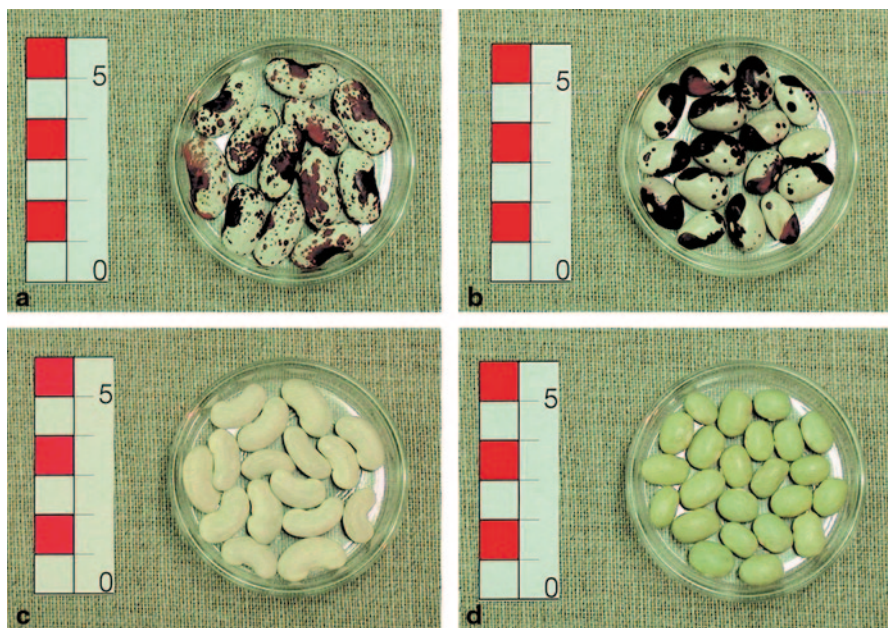


Fig. 1.2 Common bean international market classes. **a** Favada Pinto (race Nueva Granada). **b** Red Caparron (race Peru). **c** Hook (race Durango). **d** Small Yellow (race Mesoamerica)

acterized by large seeds which are often round or oval but can also be elongated. Its most popular types are ‘yellow canario’ and ‘azufrado’ beans.

Market classes usually include improved germplasm and thus tend to show a low level of variability. However, the range of commercially available bean cultivars and varieties in different market classes is constantly changing. New cultivars are released for their increased yield potential, pest and disease resistance, full-season and early double-cropped growth potential and improved market quality. Public and private plant breeders develop new varieties by adding desirable features to old cultivars or create new and better cultivars by recombining the best traits from available germplasm.

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. These landraces evolved from ancient types by conscious or unconscious selection and are currently well adapted to the agroecological conditions under which they have been grown for centuries. In Europe, the high appreciation by consumers of these ‘heirloom’ varieties is recognized by the attribution of the protected geographical indication (PGI), one of the European Union marks attributable to traditional foods. With the increased interest in ‘heirloom’ varieties (seeds passed down from generation to generation), many fine old-fashioned varieties have been reintroduced recently by various seed companies.

5 Major Breeding Achievements and Specific Goals in Current Breeding

5.1 Achievements in Dry Bean Breeding in the USA

Along with corn (*Zea mays* L.) and squash (*Cucurbita* spp.), dry bean was among the earliest crops domesticated in the Americas (Kaplan 1956). Native Americans commonly grew beans as a companion crop with corn and squash in what is termed the ‘three sisters’ or milpa method that originated in Mesoamerica and spread northward into Mexico and the southwestern USA. Some of the old landraces were eventually selected and produced by the New World settlers for local consumption. Beans were also introduced into Europe from the New World as early as AD 1500 by the early explorers (Zeven 1997). Subsequently, they were reintroduced into the eastern USA by Europeans that migrated from Europe to the USA. The first large-scale commercial production of dry edible beans in the USA occurred in Orleans County, New York in 1839. New York became one of the first important producers of dry beans and maintained its dominance until the early 1900s when Michigan became the leading producer.

A significant change in dry bean production occurred in 1917, when seed production began shifting from the central and the eastern USA to the semiarid western USA, where today most commercial bean seed is produced (Brick and Lowry

2000). This shift initially occurred because seed-borne pathogens, such as anthracnose (ANT; *Colletotrichum lindemuthianum* (Sacc et Magn.) Scrib.) and common bacterial blight (*Xanthomonas axonopodis* pv. *phaseoli* (Smith) Dye), became serious problems in commercial production fields (Adams 1996). Idaho was among the first states to produce large quantities of commercial dry bean seed and still produces more certified bean seed than any other state.

5.2 Genetic Improvement

Several books have been published that address dry bean improvement, production challenges and genetic resources in the USA and the Europe: *Genetic Resources of Phaseolus Beans* by P. Gepts (ed) in 1988; *Common Bean Production Problems in the Tropics* by H. F. Schwartz and T. Pastor-Corrales (eds) in 1989; *Common Beans: Common Beans: Research for Crop Improvement* by A. van Schoonhoven and O. Voysest (eds) in 1991; *Phaseolus spp: Bean Science* by R. Maiti (ed) in 1997; *Common Bean Improvement in the Twenty-First Century* by S. P. Singh (ed) in 1999; *Catalogue of Bean Genetic Resources* by J. M. Amurrio, M. Santalla and A. M. De Ron (eds) in 2001; *Handbook on Evaluation of Phaseolus Germplasm* by C. De la Cuadra, A. M. De Ron and R. Schachl (eds) in 2001; and *Compendium of Bean Diseases* (2nd edn) by H. F. Schwartz, J. R. Steadman, R. Hall and R. L. Forster (eds) in 2005.

Early breeding efforts primarily focused on improved disease resistance and adaptation to local environments, later efforts also focused on improved seed quality, improved plant architecture and breeding for yield. Among the early bean researchers, R. A. Emerson, renowned for his research on maize genetics, worked on beans at the University of Nebraska from 1898 until 1912. The Michigan Agricultural College (currently Michigan State University) was among the first institutions in the USA to employ a full-time dry bean breeder in 1906 followed by the University of Idaho in 1925 (Singh et al. 2007). Michigan State University released the first USA navy bean cultivar 'Robust' in 1915 as a selection from locally grown landraces. In the early twentieth century, breeding programmes at Cornell University and Michigan Agricultural College focused on disease resistance, primarily resistance to ANT (Burkholder 1930) and common bacterial blight (Adams 1996). Additional research in the western USA focused on developing resistance to a range of pathogens, including rust (*Uromyces appendiculatus* Pers: Unger.), white mould (caused by *Sclerotinia sclerotiorum* (Lib.) DeBary), bacterial blights, viruses, root pathogens and *beet curly top virus* (BCTV) transmitted by the beet leafhopper (*Circulifer tenellus* (Baker)).

5.3 Seed Yield

Many review papers and chapters have been published that summarize breeding strategies to increase yield in dry bean (Beaver 1999; Brick and Grafton 1999; Singh 1999a,

1999b; Urrea and Singh 1994; Kelly 2004; Kelly and Cichy 2012; Vandemark et al. 2014). Some strategies employed by dry bean breeders to improve yield include interracial and interspecific crosses, gamete selection, early generation testing, recurrent selection, ideotype breeding and selection for physiological efficiency.

To ensure that breeding programmes have optimum genetic diversity for yield improvement, Kelly et al. (1998) suggested a 'three-tiered' pyramidal breeding strategy to manage germplasm in a breeding programme. The three tiers were composed of three levels of germplasm improvement/advancement in the breeding programme and included types of crossing protocols to use in each tier. The apex of the pyramid consisted of elite, agronomically acceptable germplasm within the target market class and the use of single-seed descent to advanced lines and testing of advanced lines. Germplasm in this tier would be used to develop cultivars that are commercially acceptable to the industry and have high yield. The intermediate tier of the pyramid has diverse germplasm outside of the market class and includes the use of interracial material, and pedigree and inbred backcross breeding methods. The base tier places no restrictions on germplasm, including interspecific and interracial material, and no restriction on breeding methods employed including gamete selection, congruity backcrosses and conical crossing. This system would advance germplasm up the tiers or maintain them as they became more adapted to optimize improvement at each tier of the breeding pyramid.

Improvements in yield have also been achieved in some cases by selection for yield components. However, because seed size is a descriptor of market class, only the yield components pod number and seed number can be exploited to increase yield. Selection of hybrid populations was especially relevant to crosses between small-seeded Mesoamerican and large-seeded Andean germplasm because it prevented breeders from combining the high pod load potential of small-seeded navy beans with very large seed size of a kidney bean (White and Gonzales 1990), even though maximum genetic diversity could be attained by crosses between the Middle American and the Andean gene pools (Becerra-Velásquez and Gepts 1994). Studies with interracial crosses have shown mixed results to improve yield (Singh and Urrea 1994; Singh et al. 2002; González et al. 2009). Interracial hybridization between beans from races Durango and Mesoamerica has been used to improve pinto, great northern, small red and pink beans (Singh et al. 1993). Urrea and Singh (1994) compared breeding methods in interracial crosses for beans and suggested that early generation testing and selection should be used to more efficiently manage populations from interracial crosses. Singh and Urrea (1994) made crosses between races of Andean and Middle American origin and found that on average mean yield was higher in the interracial crosses than within race crosses. It is known that epistasis can play a role in the performance of progeny that result from interracial crosses (Johnson and Gepts 2002; Moreto et al. 2012).

During the early development of some market classes, yield gains were achieved by selection for a more vigorous vine that produced higher biomass than traditional landraces. However, cultivars developed by selection for more vigorous vine growth had increased risk of white mould disease due to denser plant canopies that retained canopy humidity. Subsequently, breeders developed cultivars with semi-vine habit