

Mohar Singh
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Manoranjan Dutta *Editors*

Broadening the Genetic Base of Grain Legumes

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Preface

Most of the grain legume crop species worldwide have an intrinsically narrow genetic base that has been exploited to the maximum level of productivity. Further breakthroughs in increasing yield and improving stability in future crop cultivars will require the identification and incorporation of new sources of variation into the cultivated background. Knowledge, access, and use of diversity available in cultivated and wild relatives are essential for widening the genetic base of commercial legume crop species. In view of this need, an effort has been made to bring together the rather scattered research work done in this important area in the form of an edited collection, a compilation that should be of benefit to legume researchers across the world. The book comprises 10 chapters contributed by researchers from reputed organizations of the world. The introductory chapter presents key issues linked to domestication bottlenecks and current trends on wide hybridization. The subsequent chapters (Chaps. 2, 3, 4, 5, 6, 7, 8, 9, 10) deal with various aspects related to broadening the genetic base of grain legumes. Each chapter provides detailed information on the following aspects: crop genepool, evolutionary relationships and systematic' assessment of gene flow for crop improvement, gene flow constraints, level of diversity in crop germplasm, production related problems, traits of importance for base broadening, wide hybridization, barriers to wide hybridization, methods of wide hybridization, and genome mapping and genomics status of each grain legume. The editors are extremely thankful to all the authors for their significant contributions to this book. The entire process of preparing the manuscript was marked by cordial collegiality. We are also grateful to Prof. Kailash Chander Bansal, The Director, National Bureau of Plant Genetic Resources, New Delhi, India, for providing guidance and a supportive atmosphere for the development of this edited collection. Thanks are also due to Ms. Megha Bakshi working as project assistant with the first editor for her assistance during the preparation of this multi-authored edited book in terms of compilation, edited chapter processing, and typographical scientific work. We are also indebted to Springer India for excellent professional support in the completion of this project. Despite several rounds of proofreading and our best efforts, the book may still have some scientific, technical, and printing errors. We will appreciate it if these omissions are

brought to our notice, so that they may be rectified in future editions. Finally, we hope the book will be used and enjoyed by legume researchers and other readers across the world.

New Delhi, India

Editors

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About the Editors

Mohar Singh is presently working as a Senior Scientist (Plant Breeding) at the National Bureau of Plant Genetic Resources Pusa, New Delhi, India. Dr. Singh obtained his Doctoral degree in Plant Breeding from the Himachal Pradesh Agricultural University, Palampur, India, in 2001. He has been working on genetic and genomic resources of pulses for the last 12 years. Presently, he is working on pre-breeding and genetic enhancement for breaking yield barriers in lentil and chickpea. He has identified several useful gene sources for various traits of interest in wild *Cicer* and *Lens* species, and some of them have been introgressed into the cultivated background for widening the gene pool. Dr. Singh has published more than 50 research papers in the journals of national and international repute like *Plant Breeding*, *Crop Science*, *PLoS ONE*, *DNA Research*, *Journal of Agricultural Science*, *Journal of Genetics and Breeding*, *Journal of Genetics*, *Genetic Resources and Crop Evolution*, *Plant Genetic Resources: Characterization and Utilization*, and *Advances in Horticultural Science* and also authored two text books and edited one book published by Elsevier Insights.

Ishwari Singh Bisht is working as a Principal Scientist at the National Bureau of Plant Genetic Resources (ICAR), Pusa Campus, New Delhi. As Professor of Plant Genetic Resources (PGR) discipline of Postgraduate School, Indian Agricultural Research Institute (a deemed university), he also coordinates the postgraduate teaching and research of the discipline.

Dr. Bisht has been actively associated with various agro-biodiversity management issues being addressed at the national level including crop genetic resources exploration, collection, characterization, conservation, germplasm enhancement, etc. He has been working in the field of plant genetic resources management for over 30 years, and his academic achievements in this area have been widely recognized nationally and internationally.

Dr. Bisht's research mainly focuses on a thorough understanding of the factors that influence the level of crop genetic diversity maintained on-farm and addressing the complex range of factors shaping the conservation or erosion of genetic diversity in farmers' fields. These range from farmers' decision-making to local environmental change to interactions between and within crop populations. His research also explores modalities on mainstreaming biodiversity in production landscapes and linking biodiversity conservation to livelihood security of farmer households in smallholder subsistence farming. Dr. Bisht has also significantly contributed in

PGR education addressing country's requirement for trained manpower to carry out various biodiversity management tasks.

Dr. Bisht has published 84 research papers in peer-reviewed reputed journals. He is also the co-editor of a book titled *Genetic and Genomic Resources of Grain Legume Improvement* published by Elsevier in 2013.

Manoranjan Dutta is a well-known researcher and academician involved in teaching and research in the areas of crop improvement and genetic resource management for more than 30 years. He had a 2 years' postdoctoral research stint at the International Crops Research Institute for the Semi-Arid Tropics, India, before joining the Govind Ballabh Pant University of Agriculture and Technology where he held several important positions including Professor and Head, Department of Crop Improvement; Director, Communication and Publication among others. He was the Head, Division of Germplasm Evaluation at the National Bureau of Plant Genetic Resources, ICAR from where he retired recently. Currently, he is a consultant in the Ministry of Agriculture, Govt. of India.

During his long research career, he has developed 15 crop varieties, registered several genetic stocks, and published more than 60 research papers in reputed international and national journals, 4 books, and 17 book chapters.

Mohar Singh, Ishwari Singh Bisht,
and Manoranjan Dutta

Over the last about 60 years, the global scientific community has become increasingly aware of the implications of genetic erosion in terms of its impact on environmental and agricultural sustainability (Ford-Lloyd et al. 2008). Reductions in both the number of species and the level of intra-specific variation have resulted in crops becoming more vulnerable to unpredictable weather patterns, epidemics of pests and diseases and fluctuations in global markets. All these in combination directly affect the food availability for human consumption. The ability to respond constructively to these situations requires continuing access to a broad range of novel forms of genetic variation.

Plant breeding is one way to confront the challenge of bridging the ever-widening gap between the demand and supply of food. Despite the importance, however, plant breeding has its own negative side effects (Kenei et al. 2012). The replacement of landraces with a few genetically uniform varieties depletes genetic diversity and provides ideal conditions for diseases and insect pests, resulting in genetic vulnerability. The increasingly growing human population and the consequent rise in demand for more food, on the one hand, and the success of such efforts like the “green revolution” through adoption of genetically uniform varieties

in many parts of the world, on the other, are the main contributing factors towards the narrow genetic base of present-day crop cultivars. It is, therefore, important to understand the phenomena and adopt appropriate strategies to minimize the risks from genetic vulnerability. Under marginal conditions, where resource-poor farmers predominate, the current plant breeding strategies and variety release, registration and certification procedures leading to genetic uniformity must be reconsidered, and some level of genetic diversity should be deliberately maintained in variety development programmes. Genetic diversity can be introduced at different levels and in different ways which may include intra-varietal, inter-varietal, inter-parental and interspecific diversities. Breeding for specific adaptation instead of wide adaptation, systematic spatial and temporal gene deployment, use of inter-specific varietal mixtures and integration of horizontal and vertical resistances have been suggested as possible solutions (Kenei et al. 2012).

Crop improvement through plant breeding, like crop evolution in general, occurs through selection operating on genetic variability. Directed and intense selection by plant breeders or by farmers can be intense and has resulted in major crop improvements. However, continued success in plant breeding can only be realized in so far as new variability is available for selection to operate. Genetic diversity is therefore absolutely essential for sustained crop improvement. On the other hand, there is a perception and concern that genetic diversity is limited, both within

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production systems and in breeding programmes, and that there is a need for continuing and concerted efforts to broaden the genetic base of crops. In a wide sense, broadening the genetic base of crops can be considered at three levels: (a) increasing the extent of useful diversity available to breeders, i.e., broadening the genetic base of breeders' material through genetic enhancement or pre-breeding; (b) increasing the range of useful diversity available to farmers as planting material; and (c) increasing the diversity of crops and varieties grown in the field. All three of these areas have been critically reviewed and the main concepts related to broadening the genetic base of crops, including the greater use of participatory plant breeding and *on-farm* conservation of genetic resources, have been discussed and deliberated in greater detail by Cooper et al. (2001).

Genetic base as revealed by the pedigree records of released varieties appears to be narrow in major pulse crops, because of the frequent use of the same parents and their derivatives in breeding programmes. Pedigree analysis of 86 chickpea cultivars, for example, that have been released through hybridization in India traced back to only 95 ancestors (Kumar et al. 2004). This appears to be an insignificant part of chickpea germplasm accessions that are conserved in various gene banks across the world. Knowledge, access and use of diversity available in the cultivated and wild relatives are essential for broadening the genetic base of cultivars to sustain crop improvement. An overview of the existing level of diversity and the genetic base of major grain legumes is presented in this chapter based on the contributions made by respective crop experts collated in this book.

1.1 Common Bean

The origin, domestication and organization of genetic diversity in *Phaseolus*; major production constraints and traits deficient in the common bean cultivars; sources of useful germplasm, and progress achieved in broadening the genetic base of cultivars need to be better understood. *Phaseolus* that originated in the Americas has been critically reviewed by Singh (2001). Only

five species, *P. acutifolius* A. Gray, *P. coccineus* L., *P. lunatus* L., *P. polyanthus* G. and *P. vulgaris* L., have been domesticated. The interspecies diversity in common bean is organized in primary, secondary, tertiary and quaternary gene pools. Unique among crop plants, common bean consists of two geographically distinct evolutionary lineages that predate domestication and trace back to a common, still extant ancestor. Common bean, cultivated across the world, is comprised of two major gene pools, the Andean originating from the Andes Mountains of South America and the Mesoamerican from Mexico and Central America along with well-established races. Gene flow between domesticated and wild beans led to substantial introgression of alleles from the domesticated gene pool into the wild gene pool and vice versa. Cultivars are further divided into races, each with their distinguishing characteristics. Also, cultivars of dry seed and snap bean exist. Abiotic and biotic stresses limit common bean production in most parts of the world. The genetic base of cultivars within market classes is narrow, and the level of resistance to common bacterial blight [caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye] and white mould [caused by *Sclerotinia sclerotiorum* (Lib) de Bary] is inadequate although high levels of resistance to these and other desirable traits exist in the relatives and gene pools of *P. vulgaris*. Early maturity, adaptation to higher latitude, upright plant type, high pod quality and seed yield and resistance to *bean common mosaic virus* (a potyvirus) and/or rust [caused by *Uromyces appendiculatus* (Pers.) Unger] have been bred into modern cultivars. However, most of the genetic variability available in the common bean races, gene pools and wild relatives remains to be utilized yet. Resistance to various diseases has been transferred from *P. coccineus*, *P. acutifolius* and *P. costaricensis* to *Phaseolus vulgaris*. In addition, *P. acutifolius* and *P. parvifolius* have been explored to transfer high-iron-content trait to *P. vulgaris*. In order to maximize and sustain bean production, high-yielding, high-quality cultivars that are less dependent on water, fertilizer, pesticides and manual labour should be developed. This warrants sustained, comprehensive and integrated genetic improve-

ment in which favourable alleles from cultivated and wild relatives are accumulated in superior cultivars. A three-tiered breeding approach involving (1) gene introgression from alien germplasm, (2) pyramiding favourable alleles from different sources and (3) simultaneous improvement of multiple traits for common bean cultivars would be the most appropriate strategy to meet these needs in coming future.

1.2 Chickpea

Efforts to improve the yield and quality of cultivated chickpea (*Cicer arietinum* L.) are constrained by a low level of intraspecific genetic diversity. Increased genetic diversity can, however, be achieved through hybridization of the cultivated species with the “wild” relatives from within the 43 species of the *Cicer* genus. To date, the 8 species sharing an annual growth habit and common chromosome number with *C. arietinum* have been the primary focus of screening and introgression efforts (Siddique et al. 2000). Screening of these species has uncovered novel morphological characteristics and resistance to a number of abiotic and biotic stresses that are of potential value to chickpea improvement programmes. Detailed analysis of protein and DNA, karyotyping and crossability studies have begun to elucidate the relationships between the annual *Cicer* species. In comparison, perennial species have received little attention due to difficulties in collection, propagation and evaluation. A recent review by Croser et al. (2003) discusses the progress towards an understanding of genetic relationships between the *Cicer* species and the introgression of genes from wild *Cicer* species into the cultivated background. Considerable diversity among members of the primary gene pool of the chickpea, including *C. arietinum*, *C. reticulatum* and *C. echinospermum*, has been recorded. Better understanding of the structure, diversity and relationships within and among the members of this gene pool will contribute to more efficient identification, conservation and utilization of chickpea germplasm for allele mining; association genetics; mapping and clon-

ing gene(s); and applied breeding to widen the genetic base of cultivated species, for the development of elite lines with superior yield and improved adaptation to diverse environments. Limiting factors to crop production, possible solutions and ways to overcome them, importance of wild relatives and barriers to alien gene introgression and strategies to overcome them and traits for base broadening have been discussed. It has been clearly demonstrated that resistance to major biotic and abiotic stresses can be successfully introgressed from the primary gene pool comprising progenitor species (Ahmad and Slinkard 1992). However, many desirable traits including high degree of resistance to multiple stresses are present in the species belonging to secondary and tertiary gene pools, that can also be introgressed by using special techniques to overcome pre- and post-fertilization barriers. Besides resistance to various biotic and abiotic stresses, the yield QTLs have also been introgressed from wild *Cicer* species to the cultivated varieties. Status and importance of molecular markers, genome mapping and genomic tools for chickpea improvement are duly elaborated. By using major genes for various biotic and abiotic stresses, the transfer of agronomically important traits into elite cultivars has been made easy and practical through marker-assisted selection and marker-assisted backcross breeding. Usefulness of molecular markers such as SSR and SNP for the construction of high-density genetic maps of chickpea and for identification of genes/QTLs for stress resistance, quality and yield-contributing traits has also been discussed.

1.3 Faba Bean

Broadening of the genetic base and systematic exploitation of heterosis in faba bean (*Vicia faba* L.) requires reliable information on the genetic diversity in germplasm. Three divergent groups of faba bean inbred lines were examined by molecular means, viz., European small-seeded lines, European large-seeded lines and Mediterranean lines (Link et al. 1995). The results were in harmony with published archaeobotanical findings.

Faba bean germplasm of over 38,000 accessions of landraces and varieties is conserved worldwide in at least 43 national gene banks as well as at ICARDA centre (Duc et al. 2010). The largest genetic diversity study of faba bean landraces was of 802 landraces and varieties from China, North Africa, Europe and Asia, as revealed by ISSR markers (Wang et al. 2012). The Chinese landraces were widely separated from a combined grouping of African, European and Asian (outside of China) germplasm, which were closely similar though still distinct. Further, to attain breakthrough in enhancing yield and improving stability in commercial cultivars, new sources of variation need to be incorporated from wild crop relatives for genetic base widening.

1.4 Cowpea

Cowpea (*Vigna unguiculata* L. Walp.) is a widely adapted, stress-tolerant grain legume, vegetable and fodder crop grown over seven million ha in warm to hot regions of Africa, Asia and the Americas. Major breeding achievements, current objectives and future opportunities for cowpea improvement have been reviewed by Ehlers and Hall (1997). Early maturing cultivars have been developed with regionally acceptable grain quality and resistance to some important diseases and pests including bacterial blight (*Xanthomonas campestris*), cowpea aphid-borne mosaic virus (CABMV), cowpea aphid (*Aphis craccivora*), cowpea curculio (*Chalchodermus aeneus*), root-knot nematodes (*Meloidogyne incognita* and *M. javanica*), cowpea weevil (*Callosobruchus maculatus*) and the parasitic weeds *Striga gesnerioides* and *Alectra vogelii*. Earliness is an important character in Africa and other regions because early cultivars can escape drought and some insect infestations, can provide the first food grain and marketable product and can be grown in a diverse array of cropping systems. New early maturing cultivars with indeterminate growth habits have been very effective in the extremely dry and hot environment of the Sahel. Heat-tolerant breeding lines have been developed that have markedly higher pod set than most

cultivars under high-night-temperature conditions. Development of cultivars with multiple resistance to biotic and abiotic stresses is an important current breeding objective. Earliness, delayed leaf senescence and indeterminate growth habit are characteristics, which are being combined to improve drought adaptation. In the future, high levels of resistance to important insect pests such as flower thrips (*Megalurothrips sjostedti*), maruca pod borer (*Maruca testulalis*), lygus (*Lygus hesperus*) and pod bugs (*Clavigralla tomentosicollis*) need to be identified. Introducing genes from wild cowpeas or related *Vigna* species, through genetic engineering, may be necessary to breed cultivars with high level of resistance to several of the major insect pests. A wide range of biotic (virus, bacteria, fungi, insects, nematodes and plants) and abiotic (like low phosphorus availability, soil acidity or salinity, drought and high temperature at night) factors are limiting cowpea production in different parts of the world. To overcome these constraints, diverse programmes were implemented for base broadening using interspecific hybridization between cowpea and other members of its genus with limited success because of pre- and post-zygotic barriers associated in the crop. These failures led the investigators to implement protocols to introduce foreign genes into cowpea. Currently, several genes of interest such as *herbicide imazapyr*, *α-amylase inhibitor 1* (against bruchids), *CryIAb* and *CryIAc* (against *Maruca*) have been introduced successfully into commercially important cultivars, and the genes are transmitted in Mendelian fashion. In addition, significant genomic resources and a consensus genetic map where agronomic, growth habit, disease, pest resistance and other trait loci have been placed and are ready for use in breeding programmes.

1.5 Lentil

Cultivation of lentil (*Lens culinaris* ssp. *culinaris*) in South Asia dates back to around 2000 BC. Because of its nutritive value, soil ameliorative properties and suitability to the existing cropping systems, it attains the status of main

pulse crop in the region. Today, about half of the world's lentil is grown in South Asia for human food, animal feed and diversification and intensification of cropping systems. However, the indigenous lentils are of a specific ecotype (*pilosae*), which lack marked variability for morphological, phenological and yield related traits and resistance to key stresses. The narrow genetic base, which limited the breeding progress in the region for a long time has been widened through the introduction of exotic germplasm and their use in hybridization programmes. The progenies developed through diverse crosses have led to the selection of transgressive segregants with enormous variability for crop duration, seed traits, plant height, growth habit, biomass production, resistance to rust, *Stemphylium* blight, drought tolerance, etc. The promising progenies have led to the development of important lentil varieties in Afghanistan, Bangladesh, India, Nepal and Pakistan. Some of these cultivars with diverse genetic background are adapted to new niches emerging in the context of climate change, consumers' preference and market opportunities. Adoption and impact of these varieties have enhanced farmer's income and national production and are contributing to food and nutritional security to the people of South Asia (Sarker et al. 2010). Wild and cultivated accessions need to be further evaluated with regard to major biotic and abiotic stresses, placing emphasis on the development of more accurate screening methods. In addition, further inheritance studies of resistance/tolerance to biotic and abiotic stresses are required for a better understanding of the respective genetic systems controlling these responses. This knowledge will be useful to design appropriate breeding programmes based on regional and local requirements. There is a need to include reliable morphological and molecular markers to develop a comprehensive consensus genetic linkage map in lentil, allowing for molecular tagging of resistance genes against biotic and abiotic stresses in order to exploit them in breeding with increased selection efficiency. New molecular tools will increase the speed and precision of introgression of newly identified alleles from both the adapted and wild *Lens* species and sub-

species into advanced breeding populations. The understanding of allele values from the adapted source and the wild gene pool will definitely increase both the efficiency and worth of germplasm utilization in lentil breeding programmes.

1.6 Pigeon Pea

Pigeon pea (*Cajanus cajan* L. Millspaugh), with ample genetic and genomic information becoming available in recent times, is now considered a trendy and pace-setter crop. The results of Diversity Arrays Technology (DArT) revealed most of the diversity was among the wild relatives of pigeon pea or between the wild and cultivated pigeon pea. The genetic relationships among the accessions are consistent with the available information and systematic classification of species and the cultivated *C. cajan*. The narrow genetic base of cultivated pigeon pea is likely to represent a serious impediment to breeding progress in pigeon pea. Further, it is now possible to cross wild relatives not only from the *Cajanus* group placed in secondary and tertiary gene pool, but also the related genera placed in quaternary gene pool. The most significant achievement is the development of unique cytoplasmic male sterility systems. This is no small achievement for a legume, which is an important crop of Asia and Africa and plays a major role in the diet of majority of the people of this region. Recently, scientists from the International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, have developed interspecific crosses using *C. acutifolius* and generated recombinants for high seed weight. A good success has also been achieved while attempting interspecific crosses with *C. albicans* (Subbarao et al. 1990), *C. platycarpus* (Mallikarjuna and Moss 1995), *C. reticulatus* var. *grandifolius* (Reddy et al. 2001) and *C. acutifolius* (Mallikarjuna and Saxena 2002).

1.7 Groundnut

Groundnut (*Arachis hypogaea* L.) germplasm consists of the cultivated allotetraploid species *Arachis hypogaea* L. and a large number of wild

species, which are nearly all diploids. A very low level of genetic variability in American and other cultivars have been reported. However, in unadapted germplasm lines from various centres of origin in South America, Africa and China, considerable morphological and physiological variability has been reported to exist. Wild species of section *Arachis* were included in the evaluations since they show a high degree of variation when assayed by molecular analysis. In all cases, a very low level of variability was found in cultivated groundnut, while abundant variability was present among wild diploid species showcasing their significance to groundnut breeding (Halward et al. 1992). Cultivated groundnut contains a fraction of the genetic diversity present in their closely related wild relatives, which is not more than 13 %, due to domestication bottleneck. Closely related ones are placed in section *Arachis*, which have not been extensively utilized until now due to ploidy differences between the cultivated and wild relatives. In order to overcome *Arachis* species utilization bottleneck, a large number of tetraploid synthetics were developed at Legume Cell Biology Unit, Grain Legumes Program, ICRISAT, India. Evaluation of synthetics for some of the production constraints showed that these were good sources of multiple disease and pest resistances. Some of the synthetics were utilized by developing ABQTL mapping populations, which were further screened for important biotic and abiotic constraints. Phenotyping experiments showed ABQTL progeny lines with traits of interest were necessary for the improvement of groundnut.

1.8 *Vigna* species

The Asian *Vigna* species are very sensitive to photoperiod and temperatures, and these two variables have a very high bearing on the plant type and its adaptability in all these crops. Tickoo et al. (1994) elaborated the aspect in greater details in context of green gram. Jain (1975) has argued that grain legumes, as a group, are still undergoing domestication. Not long back, in the cultivation history of these crops and even today

in most areas of the growing countries, these crops are being grown under conditions, not very much different than the ones in which their wild relatives have been grown. Under conditions of low-input management, the evolution has been for the survival of the crop species itself rather than for grain yield which is important from breeders' point of view. The silver lining has been the evolution of symbiotic relationship of these crops and the nitrogen fixing *Rhizobia* and the subsequent high protein content of their seeds. However, it will always be debatable, whether the evolution of symbiosis in grain legumes is a curse or a blessing to them. Other characters like indeterminate growth habit, photo- and thermo-insensitivity, low harvest index, shattering of ripe pods, seed hardness, zero seed dormancy, etc., have all evolved more to natural than human selection (Tickoo et al. 1994). Further, information on intraspecific diversity, particularly in *mungo-radiata* complex, is lacking. This information is essential for effective use of wild species germplasm in crop improvement programmes. A wild mung bean accession, *Vigna radiata* var. *sublobata*, was reported to be highly resistant to bruchid, *Callosobruchus chinensis* (L.), a serious pest of grain legumes during storage at the AVRDC (Talekar 1994). Mung bean yellow mosaic virus (MYMV) has been a major problem in green gram. The wild species *Vigna radiata* var. *sublobata* is an important source to incorporate resistance to MYMV into cultivated varieties (Singh 1994). In addition to the landraces and cultivars, the wild species therefore needs to be collected, characterized and conserved carefully for use in crop improvement programmes.

In common with most grain legume crop species, the wild related *Vigna* species do not form a particularly extensive or accessible genetic resource. More variability in wild conspecific forms is to be exploited in addition to the fullest range of landraces and cultivars (Singh et al. 2006; Bisht and Singh 2013). Greater exploitation of the conspecific wild species with valuable characters needs to be undertaken to make extended cultivation economically attractive (Smartt 1990). Some populations of *V. mungo* var. *sylvestris*, *V. radiata* var. *sublobata* and *V. radiata* var. *setulosa*

with valuable characters like more number of pod-bearing clusters and pods per cluster have great agronomic potential for use in crop improvement programmes beside in the resistance/tolerance to biotic stresses (Bisht et al. 2005). Sources of resistance available in *Vigna radiata var. sublobata* (Singh 1994) need to be exploited more vigorously with the use of precise molecular tools.

1.9 Horse Gram

Horse gram (*Macrotyloma uniflorum*) is a dual-purpose pulse and fodder crop native to the Southeast Asia and tropical Africa. India is the only country cultivating horse gram on a large scale, where it is being used for human food purpose. About 1,161 germplasm accessions have been systematically characterized and evaluated for various stress parameters and important agromorphological traits in different research institutions of India. Disease and pest resistance and improving grain quality and protein percentage would be desirable traits for broadening the genetic base through interspecific hybridization.

There is increasing evidence that the formal breeding sector has not well served the needs of farmers in developing countries. Modern plant breeding leads inevitably to an extremely dangerous reduction of diversity in major world food crops. Indigenous locally adapted races of cultivated plants usually known as primitive cultivars are the product of agro-ecotypic differentiation during thousands of years of conscious and unconscious selection by man in the diverse conditions of cultivation in many habitats. Genetically, they are marked by high level of adaptation to climate and disease and high variability, and these factors render primitive cultivars essential in plant breeding. Unfortunately, under advanced farming systems, the essentials of *on-farm* evolution, that is, the generation of variation and its subsequent natural and farmer selection, are no longer possible. This leads to an extremely dangerous reduction of diversity in major world crops, as noted by Simmonds (1979). Successful crop breeding tends to narrow the genetic base of a crop in direct proportion to its success; in all advanced,

technology-based agriculture, few excellent varieties, themselves often interrelated, tend to cover large areas of land to the exclusion of all else (Simmonds 1979). In addition to the “bottleneck” effect during plant breeding, the diversity on which many important varieties were based was very limited, so there is also a “founder” effect. As an example, most varieties of the US soybean crop can be traced to 50 original introductions, only 10 of which contributed to 80 % of northern, and 7–80% of southern cultivars. Most introductions originated from Northeast China (Delannay et al. 1983). There is a particular danger with varieties based on limited sources of cytoplasmic male sterility—found, for example, in many food crops (Chang 1985). It has been a common consensus now that a reasonable level of genetic diversity should be deliberately maintained in variety development programmes. Farmers should be involved and get encouraged to maintain, improve and enhance the locally adapted and diverse genetic materials with appropriate technical and policy supports. In the marginal areas where problems of diseases, insects and environmental fluctuations are more and hence risks are great, we should reconsider the current breeding strategies leading to genetic uniformity. Since risk aversion strategies condition farmers’ responses to new options, technologies and policies should conform to and reinforce these strategies (Tilahun 1995).

Crop production characterized by genetic diversity is normally stable as compared to those characterized by genetic uniformity (Simmonds 1979; de Boef et al. 1996) for a number of reasons. The problem with narrow genetic base is particularly aggravated by the widespread use of one or a few genetically uniform varieties over a large hectarage (spatial dominance), which is considered the other prerequisite for the widespread of disease and insect pests as it provides ideal condition and creates vulnerability (Simmonds 1979; Sharma 2001; Rubenstein et al. 2005; Smolders 2006). The continuous production of a single variety of the same crop year after year will facilitate disease epidemics particularly when host plant resistance is defeated by the counteractive mutation of disease pests and pathogens (Marshall 1977; Wolfe and Barrett 1977; Agrios 1978;

Simmonds 1979; de Boef et al. 1996; Rubenstein et al. 2005; Smolders 2006).

Conventional breeding will continue to have a valuable role in providing resistance to biotic and abiotic stresses. Nevertheless, it appears that in some systems there will continue to be barriers to achieving resistance using this approach (Edwards and Singh 2006). Molecular tools give us an opportunity to develop genotypes that carry resistance genes, and these tools have been utilized in DNA fingerprinting for identification of cultivars, marker-assisted selection and, to a limited level, genetic modification in breeding for resistance (Acosta-Gallegos et al. 2008). Problems associated with the need for long backcrossing cycles, gene pyramiding and the difficulties of crossing heterozygous clonally propagated crops with the conventional breeding method have already been resolved with the use of modern biotechnological tools to a great extent (Higgins et al. 1998; Witcombe and Hash 2000).

The habit of pushing varieties for release under marginal situations to a state of extreme uniformity by modern plant breeding has been criticized by several researchers (Marshall 1977; Wolfe and Barrett 1977; Simmonds 1979; de Boef et al. 1996). Under such situations, it is rather believed that uniformity is not biologically necessary or even desired, but diversity can, at least sometimes, enhance performance and stability (Simmonds 1979). Traits of interest to the resource-poor farmers in the marginal areas include yield stability; resistance to diseases, insects and abiotic calamities; and low dependence on external inputs (de Boef et al. 1996). Farmers achieve these by deliberately creating genetic diversity at intra-varietal and/or interspecific levels (Weltzien and Fischebeck 1990; Broerse and Visser 1996; de Boef et al. 1996). Breeding activities to address this group of farmers should, therefore, build on farmers' practices to complement them and not to substitute their practices (Bundlers et al. 1996). The physical environment and price ratios between external inputs and farm outputs do not allow the use of large quantities of purchased inputs, especially agrochemicals in large parts of the tropics and

subtropics (de Boef et al. 1996) and which are also not ecofriendly.

Several co-workers have suggested that emphasis should be given to the maintenance of diversity in some planned fashion (Marshall 1977; Wolfe and Barrett 1977; Simmonds 1979; de Boef et al. 1996) for sustainability. The dangers of genetic uniformity can also largely be avoided if plant breeders use different sources of genes (inter-parental diversity) in their breeding material, and it would certainly be dangerous to rely too much on any one individual source of resistance (Russell 1978). There are also speculations that crosses between parents with high inter-parental divergence would not only be more responsive to improvement since they are likely to produce higher heterosis and desirable genetic recombination and segregation in their progenies (Wallace and Yan 1998; Chahal and Gosal 2002) but also help to develop varieties with broad genetic base (Russell 1978; Chandel and Joshi 1983) that are not liable to genetic vulnerability (Chandel and Joshi 1983). There is a possibility that, like many other traits including grain yield, heterosis may be manifested through diseases and insect pest resistance (Singh 2002) and climatic resilience.

Farmers, particularly in the tropics and subtropics, have been employing interspecific varietal mixtures not only as a yield maximization and diversification but also as risk aversion strategies since time immemorial (Weltzien and Fischebeck 1990; Broerse and Visser 1996; de Boef et al. 1996). In marginal areas where resource-poor farmers dominate and environments are highly variable, the initiation and enhancement of local breeding should be thought as one of the best strategies to overcome problems associated with genetic vulnerability of modern crop cultivars (Smolders 2006). Farmers have been breeders since time immemorial, and the key feature in local crop development has been its maintenance of genetic diversity, both between and within species (de Boef et al. 1996). Local breeding involves the maintenance of local varieties (conservation through utilization), their enhancement (through selection and enrichment with exotic materials) and the seed system (production, selection, treatment, storage and exchange).

To conclude that, narrow genetic base of crops and less use of germplasm are the prime factors limiting grain legume production and productivity worldwide. Therefore, exploitation of diverse sources of variability is required through pre-breeding for the genetic enhancement of grain legumes. It also further necessitates the identification and use of wild germplasm resources to develop new high-yielding cultivars with a broad genetic base.

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Abstract

The chapter on the common bean reviews the origin and domestication, gene pool organization and their evolutionary relationship, genetic diversity and gene flow assessment, production constraints, crop production-limiting factors, and crop improvement strategies. While the common bean originated in the Americas, it is now widely grown in all continents of the world. Several bean germplasm banks have been established and contain diverse genetic resources comprising five domesticated and wild *Phaseolus* species, as well as an incipient stock collection. Unique among crop plants, the common bean consists of two geographically distinct evolutionary lineages that predate domestication and trace back to a common, still extant ancestor. The common bean cultivated across the world comprises of two major gene pools: the Andean originating from the Andes mountains of South America and the Mesoamerican from Mexico and Central America along with well-established races. Gene flow between domesticated and wild beans led to substantial introgression of alleles from the domesticated gene pool into the wild gene pool and vice versa. Like other crops, the common bean also suffers from various biotic and abiotic stresses; however, these constraints vary with the agroecological regions experiencing tropical to temperate environments. The important biotic and abiotic constraints limiting bean production are bean anthracnose, angular leaf spot, bean common mosaic and necrosis virus, bean golden mosaic virus, bacterial blights, drought, and phosphorus deficiency. The common bean improvement program in Europe and the USA is mainly focused on biotic and abiotic factors, mainly diseases, drought, and biofortification involving intra- and interspecific hybridization programs.

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Various breeding methods, namely, recurrent backcrossing, congruity backcrossing, inbred backcross line and gamete selection using multiple-parent crosses, and recurrent selection, have been used to transfer the trait of interest from related species. Resistance to various diseases has been transferred from *P. coccineus*, *P. acutifolius*, *P. costaricensis* to *Phaseolus vulgaris*. In addition, *P. acutifolius* and *P. parvifolius* have been explored to transfer high iron content to *P. vulgaris*. The crop improvement program over the last two decades involves the use of a marker-assisted selection strategy as a number of useful genes vis-à-vis molecular markers linked to them have been identified. In addition, bean transformation protocols have also been developed to facilitate introgression of alien genes. The sequencing of whole common bean genome is going to open an era of functional genomics to understand, identify, and overcome the constraints experienced by researchers across the world.

2.1 Introduction

The common bean (*Phaseolus vulgaris* L.) is one of the most important legume crops grown in all continents of the world except Antarctica, because of its high protein, fiber, and complex carbohydrate content. Beans (*Phaseolus* spp.) are extremely diverse crops in terms of cultivation methods, in diverse environments and elevations ranging from sea level to 3,000 m height, morphological variability, and utilities (dry as pulse and green as vegetable). The tremendous variability for plant types and growth behavior makes beans part of the most diverse production systems of the world (Broughton et al. 2003). They are cultivated in monoculture, in associations, or in rotations. Dry beans are consumed both as pulse and vegetable (both leaves and pods). Their genetic resources exist as a complex array of major and minor gene pools, races, and intermediate types, with occasional introgression between wild and domesticated types. Beans are thus a crop that is adapted to many niches, both in terms of agronomic and consumer preference. While its production is mainly centered on small holdings, beans are grown in monoculture bush beans to a complex association of indeterminate or climbing beans with maize, sugarcane, and other cereals or fruit crops. Short bush growth habits offer minimal competition and permit interplanting with other species, for example, in

reforestation projects or among fruit trees or coffee plantations during the early years until the main crop can be exploited. At the other extreme, aggressive climbers are found at higher altitudes on subsistence farms where a few plants are maintained as a sort of insurance and are continually harvested for about 6 months. Over the past 20 years, beans have also been increasingly cultivated on a commercial scale and are now offered in national, regional, and international markets. The common bean regarded as a “grain of hope” is an important component of subsistence agriculture grown worldwide over an area of about 28.78 million hectares with an annual production of 23.14 million tonnes (FAO 2013), and feeds about 300 million people in the tropics and 100 million people in Africa alone. Besides it is emerging as an important income generation especially in Central America where beans have top ranking as income generators among field crops. In terms of global pulse production, the common bean alone with 23 million tonnes accounts for about half of the total pulse production (FAO 2012). However, this number is an overestimate as FAO does not report data for *Phaseolus* and non-*Phaseolus* species separately. Many comprehensive reviews on the different aspects of the common bean like origin and evolution (Gepts 1998), genetic diversity (Singh et al. 1991a, b, c; Blair et al. 2012a, b), population structure and evolutionary dynamics (Zizumbo-Villarreal et al.