Genome Mapping and Molecular Breeding in Plants
Volume 3

Series Editor: Chittaranjan Kole

Volumes of the Series
Genome Mapping and Molecular Breeding in Plants

Volume 1
Cereals and Millets

Volume 2
Oilseeds

Volume 3
Pulses, Sugar and Tuber Crops

Volume 4
Fruits and Nuts

Volume 5
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Volume 6
Technical Crops

Volume 7
Forest Trees

Chittaranjan Kole (Ed.)

Pulses, Sugar and Tuber Crops

With 45 Illustrations, 8 in Color

Springer

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Preface to the Series

Genome science has emerged unequivocally as the leading discipline of this new millennium. Progress in molecular biology during the last century has provided critical inputs for building a solid foundation for this discipline. However, it has gained fast momentum particularly in the last two decades with the advent of genetic linkage mapping with RFLP markers in humans in 1980. Since then it has been flourishing at a stupendous pace with the development of newly emerging tools and techniques. All these events are due to the concerted global efforts directed at the delineation of genomes and their improvement.

Genetic linkage maps based on molecular markers are now available for almost all plants of significant academic and economic interest, and the list of plants is growing regularly. A large number of economic genes have been mapped, tagged, cloned, sequenced, or characterized for expression and are being used for genetic tailoring of plants through molecular breeding. An array of markers in the arsenal from RFLP to SNP; tools such as BAC, YAC, ESTs, and microarrays; local physical maps of target genomic regions; and the employment of bioinformatics contributing to all the "-omics" disciplines are making the journey more and more enriching. Most naturally, the plants we commonly grow on our farms, forests, orchards, plantations, and labs have attracted emphatic attention, and deservedly so. The two-way shuttling from phenotype to genotype (or gene) and genotypte (gene) to phenotype has made the canvas much vaster. One could have easily compiled the vital information on genome mapping in economic plants within some 50 pages in the 1980s or within 500 pages in the 1990s. In the middle of the first decade of this century, even 5,000 pages would not suffice! Clearly genome mapping is no longer a mere "promising" branch of the life science; it has emerged as a full-fledged subject in its own right with promising branches of its own. Sequencing of the *Arabidopsis* genome was complete in 2000. The early 21st century witnessed the complete genome sequence of rice. Many more plant genomes are waiting in the wings of the national and international genome initiatives on individual plants or families.

The huge volume of information generated on genome analysis and improvement is dispersed mainly throughout the pages of periodicals in the form of review papers or scientific articles. There is a need for a ready reference for students and scientists alike that could provide more than just a glimpse of the present status of genome analysis and its use for genetic improvement. I personally felt the gap sorely when I failed to suggest any reference works to students and colleagues interested in the subject. This is the primary reason I conceived of a series on genome mapping and molecular breeding in plants.

There is not a single organism on earth that has no economic worth or concern for humanity. Information on genomes of lower organisms is abundant and highly useful from academic and applied points of view. Information on higher animals including humans is vast and useful. However, we first thought to concentrate only on the plants relevant to our daily lives, the agronomic, horticultural and technical crops, and forest trees, in the present series. We will come up soon with commentaries on food and fiber animals, wildlife and companion animals, laboratory animals, fishes and aquatic animals, beneficial and harmful insects, plant- and animal-associated microbes, and primates including humans in our next "genome series" dedicated to animals and microbes. In this series, 82 chapters devoted to plants or their groups have been included. We tried to include most of the plants in which significant progress has been made. We have also included preliminary works on some so-called minor and orphan crops in this series. We would be happy to include reviews on more such crops that deserve immediate national and international attention and support. The extent of coverage in terms of the number of pages, however, has nothing to do with the relative importance of a plant or plant group. Nor does the sequence of the chapters have any correlation to the importance of the plants discussed in the volumes. A simple rule of convenience has been followed.

I feel myself fortunate to have received highly positive responses from nearly 300 scientists of some 30-plus countries who contributed the chapters for this series. Scientists actively involved in analyzing and improving particular genomes contributed each and every chapter. I thank them all profoundly. I made a conscientious effort to assemble the best possible team of authors for certain chapters devoted to the important plants. In general, the lead authors of most chapters organized their teams. I extend my gratitude to them all.

The number of plants of economic relevance is enormous. They are classified from various angles. I have presented them using the most conventional approach. The volumes thus include cereals and millets (Volume I), oilseeds (Volume II), pulse, sugar and tuber crops (Volume III), fruits and nuts (Volume IV), vegetables (Volume V), technical crops including fiber and forage crops, ornamentals, plantation crops, and medicinal and aromatic plants (Volume VI), and forest trees (Volume VII).

A significant amount of information might be duplicated across the closely related species or genera, particularly where results of comparative mapping have been discussed. However, some readers would have liked to have had a chapter on a particular plant or plant group complete in itself. I ask all the readers to bear with me for such redundancy.

Obviously the contents and coverage of different chapters will vary depending on the effort expended and progress achieved. Some plants have received more attention for advanced works. We have included only introductory reviews on fundamental aspects on them since reviews in these areas are available elsewhere. On other plants, including the "orphan" crop plants, a substantial amount of information has been included on the basic aspects. This approach will be reflected in the illustrations as well.

It is mainly my research students and professional colleagues who sparked my interest in conceptualizing and pursuing this series. If this series serves its purpose, then the major credit goes to them. I would never have ventured to take up this huge task of editing without their constant support. Working and interacting with many people, particularly at the Laboratory of Molecular Biology and Biotechnology of the Orissa University of Agriculture and Technology, Bhubaneswar, India as its founder principal investigator; the Indo-Russian Center for Biotechnology, Allahabad, India as its first project coordinator; the then-USSR Academy of Sciences in Moscow; the University of Wisconsin at Madison; and The Pennsylvania State University, among institutions, and at EMBO, EUCARPIA, and Plant and Animal Genome meetings among the scientific gatherings have also inspired me and instilled confidence in my ability to accomplish this job.

I feel very fortunate for the inspiration and encouragement I have received from many dignified scientists from around the world, particularly Prof. Arthur

Kornberg, Prof. Franklin W. Stahl, Dr. Norman E. Borlaug, Dr. David V. Goeddel, Prof. Phillip A. Sharp, Prof. Gunter Blobel, and Prof. Lee Hartwell, who kindly opined on the utility of the series for students, academicians, and industry scientists of this and later generations. I express my deep regards and gratitude to them all for providing inspiration and extending generous comments.

I have been especially blessed by God with an affectionate student community and very cordial research students throughout my teaching career. I am thankful to all of them for their regards and feelings for me. I am grateful to all my teachers and colleagues for the blessings, assistance, and affection they showered on me throughout my career at various levels and places. I am equally indebted to the few critics who helped me to become professionally sounder and morally stronger.

My wife Phullara and our two children Sourav and Devleena have been of great help to me, as always, while I was engaged in editing this series. Phullara has taken pains ("pleasure" she would say) all along to assume most of my domestic responsibilities and to allow me to devote maximum possible time to my professional activities, including editing this series. Sourav and Devleena have always shown maturity and patience in allowing me to remain glued to my PC or "printed papers" ("P3" as they would say). For this series, they assisted me with Internet searches, maintenance of all hard and soft copies, and various timely inputs.

Some figures included by the authors in their chapters were published elsewhere previously. The authors have obtained permission from the concerned publishers or authors to use them again for their chapters and expressed due acknowledgement. However, as an editor I record my acknowledgements to all such publishers and authors for their generosity and good will.

I look forward to your valuable criticisms and feedback for further improvement of the series.

Publishing a book series like this requires diligence, patience, and understanding on the part of the publisher, and I am grateful to the people at Springer for having all these qualities in abundance and for their dedication to seeing this series through to completion. Their professionalism and attention to detail throughout the entire process of bringing this series to the reader made them a genuine pleasure to work with. Any enjoyment the reader may derive from this books is due in no small measure to their efforts.

Pennsylvania, Chittaranjan Kole
10 January 2006

Preface to the Volume

The number of "groups" of economic plant species is too many! This caused a serious problem in terms of allocating them under the seven planned volumes of the series with consideration of uniformity of size and inclusion of all relevant groups. Certain groups, for example cereals and millets, oilseeds, fruits, vegetables, and forest trees, have enough economic species those attracted the attention of molecular biologists and biotechnologists. In comparison, the number of pulse crops is too few to deserve an entire volume to itself. We had to accommodate pulse crops, sugar crops, and tuber crops together in volume 3 to maintain a more or less uniform coverage across all volumes. Except for the common bean, pea, and cowpea, most pulse crops are grown mainly in developing countries and have attracted relatively little attention of scientists from developed countries. These include the "orphan crops" such as chickpea, pigeonpea, mungbean, lentil, *Lathyrus*, etc. Thanks to certain labs in the USA and Australia, appreciable work has been done on these crops. There are still some more neglected pulse crops, we could easily ascribe the term "beggar crops" to them, such as urdbean, rice bean, adzuki bean, etc. in which almost no molecular work has been done. We must wait for future editions for their inclusion in this series. However, we have included two not-so-well-known pulse crops, quinoa and bambara groundnut, on which considerable work has been done. This volume can boast of introducing these two crops with comprehensive reviews for the first time.

Pulse crops will play a crucial role in global agriculture in the near future. Their shorter duration, docility for adaptation to several cropping schemes, tolerance to abiotic stresses particularly drought, and the preference by people in developing countries for vegetable protein to animal sources will definitely make an impact sooner rather than later. The research on these crops will fill an entire volume in a year or two!

Sugarcane has been included in this volume as well. This cash crop has generated much interest, particularly for its genomic proximity to other members of the "grass family" that comprises extensively studied crop plants like rice and maize. Sugar beet could be included here as well, but we will deal with it under beets in volume 5, which is dedicated to "vegetables".

The tuber crops included in this volume are potato, sweetpotato, cassava, and yam. Granted, potato could have been included under vegetables in volume 5, but that would have forced us to consider another "subvolume" for vegetable crops!

The contents of the chapters in this volume may appear somewhat contrasting. Crops like common bean, pea, cowpea, potato, and sugarcane contain elaborate deliberations on molecular aspects. For others, fundamental information besides preliminary molecular efforts are also discussed in depth. I hope the reader will appreciate the relative importance attached to the formulation of the contents.

In the last few years, my own research interests and research projects of my students and staff in India have mostly related to pulse crops. This gave me access to the literature accumulated on the pulse crops. For sugarcane and the tuber crops included in this volume, I had to be a student again before being an editor. The first two volumes of this series have been well received by readers. We hope this volume will also earn their appreciation.

If this volume finds favor with readers, credit must go to the authors and the publisher. The mistakes are mine alone, and I will rectify them upon the readers' welcome suggestions for improvement.

Pennsylvania, 3 March 2006 Chittaranjan Kole

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Abbreviations

ABA	Abscisic Acid
ABR	Ascochyta Blight Resistance
AFLP	Amplified Fragment Length Polymorphism
ANOVA	Analysis Of Variance
AP-PCR	Arbitrarily Primed PCR
APR	Adult Plant Resistance
ARS	Agriculture Research Service
ASAP	Allele Specific Associated Primer
AUDPC	Area Under the Disease Progress Curve
AYT	Advanced Yield Trial
BAC	Bacterial Artificial Chromosome
BAMFOOD	Increasing the productivity of Bambara Groundnut (*Vigna subterranea* L. Verdc) for sustainable food production in Semi-Arid Africa
BC	Backcross
BCMNV	Bean Common Mosaic Necrosis Virus
BCMV	Bean Common Mosaic Virus
BCTV	Beet Curly Top Virus
BGMV	Bean Golden Mosaic Virus
BGYMV	Bean Golden Yellow Mosaic Virus
BICMV	Blackeye Cowpea Mosaic Virus
BLRV	Bean Leaf Roll Virus
*Bru*1	Brassinosteroid-regulated protein
BSA	Bulked Segregant Analysis
C	Haploid Genome Content
CAPS	Cleaved Amplified Polymorphic Sequences
CC-NBS-LRR	Coiled-Coiled domain-containing NBS-LRR protein
cDNA	Complementary DNA
CIAT	Centro Internacional de Agricultura Tropical (Cali, Colombia)
CID	Carbon Isotope Discrimination
CIM	Composite Interval Mapping
cM	centi-Morgan
CMD	Cassava Mosaic Disease
CMS	Cytoplasmic Male Sterility
CPB	Colorado Potato Beetle
cpDNA	Chloroplast DNA
CRSD	Cowpea Collaborative Research Support Program
cSNP	SNP in coding region
CTCRI	Central Tuber Crops Research Institute (Trivandrum, India)
DAF	DNA Amplification Fingerprinting
DH	Doubled Haploid
DNA	Deoxyribonucleic Acid
DNC	Dry Matter Content
DR	Defense-Related
DS	Drought-Stressed
EBN	Endosperm Balance Number

EM	Expectation Maximization (algorithm)
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuária (Goiana, Brazil)
EST	Expressed Sequence Tag
EU	European Union
FAO	Food and Agricultural Organization
FGS	Fast-Growing Salmon
FISH	Fluorescence In Situ Hybridization
Foc	Fusarium Wilt Resistance
GAT	Zentralinstitut für Genetik und Kulturpflanzenforschung (Gatersleben, Germany)
gDNA	Genomic DNA
GISH	Genomic In Situ hybridisation
GM	Genetically Modified
GMO	Genetically Modified Organism
GMS	Genetic Male Sterility
GP	Gene Pool
GP1	Primary Gene Pool
GP1A	Primary Gene Pool – Domesticated
GP2	Secondary Gene Pool
GP3	Tertiary Gene Pool
GPIB	Primary Gene Pool – Wild
GRIN	Germplasm Resources Information Network
GSIRI	Guangzhou Sugarcane Industry Research Institute (China)
Hs	Average Hardy-Weinberg expected heterozygosity per subpopulation
Ht	Hardy-Weinberg heterozygosity of the total population
ICARDA	International Center for Agriculture Research in the Dryland Areas (Aleppo, Syria)
ICRISAT	International Center of Research For Semi-Arid Tropics (Hyderabad, India)
IDS	Initial Disease Score
IITA	International Institute of Tropical Agriculture (Ibadan, Nigeria)
ILDIS	International Legume Database & Information Service
IM	Interval Mapping
indel	insertion/deletion
IPGRI	The International Plant Genetic Resources Institute (Harare, Zimbabwe)
ISSR	Inter Simple Sequence Repeat
ITS	Internal Transcribed Spacer
JIC	John Innes Center
LD	Linkage Disequilibrium
LG	Linkage Group
LOD	Logarithm Of Odds
LRR	Leucine Rich Repeat
LRS	Likelihood Ratio Statistic
LTR	Long Terminal Repeat
MAS	Marker-Assisted Selection
MDSS	Mean Disease Severity Scores
MIM	Multiple Interval Mapping
mRNA	Messenger Ribonucleic Acid
mtDNA	Mitochondrial DNA

MtGI	*Medicago truncatula* Gene Index
MYMV	Mungbean Yellow Mosaic Virus
NARS	National Agricultural Research System
NBPGR	National Bureau of Plant Genetic Resources (New Delhi, India)
NBS	Nucleotide Binding Site
NIL	Near Isogenic Lines
NOR	Nucleolar Organizer Region
NPGS	National Plant Germplasm System
NRCRI	National Root Crop Research Institute (Umuahia, Nigeria)
NS	Non-Stressed
ODAP	β-N-Oxalyl-L-α,β-DiaminoPropanoic acid
ORSTOM	Institut Français de la Recherché Scientifique pour le Développement en Coopération (now IRD; Montpellier, France)
PCN	Potato Cyst Nematode
PCR	Polymerase Chain Reaction
PEMV	Pea Enation Mosaic Virus
PI	Plant Introduction
PIs	Proteinaceous Inhibitors
PPB	Participatory Plant Breeding
PPD	Post harvest Physiological Deterioration
PPO	PolyPhenol Oxidase
PRINS	Primed In Situ (DNA Labeling)
PSbMV	Pea Seed-borne Mosaic Virus
PVX	Potato Virus X
PYT	Preliminary Yield Trial
QTA	Quantitative Trait Allele
QTL	Quantitative Trait Loci
RAF	Randomly Amplified Fragment
RAPD	Random Amplified Polymorphic DNA
rDNA	Ribosomal DNA
RFLP	Restriction Fragment Length Polymorphism
RGA	Resistant Gene Analog
RI	Recombinant Inbred
RIL	Recombinant Inbred Line
RSD	Ratoon Stunting Disease
SAM	Shoot Apical Meristem
SAT	Semi Arid Tropics
SCAR	Sequence Characterized Amplified Region
SDM	Single Dose Marker
SG	Striga Race
SGG	Slow-Growing Gray
SI	Self Incompatibility
SLA	Specific Leaf Area
SNP	Single Nucleotide Polymorphism
SPLAT	Specific Polymorphic Locus Amplification Test
SR	Specific Resistance
SSD	Single Seed Descent
SSLP	Simple Sequence Length Polymorphism
SSR	Simple Sequence Repeat
STMS	Sequence Tagged Microsatellite Site
STS	Sequence Tagged Sites

SUCEST	Sugarcane EST project
TCA	TriCarboxylic Acid
TIGR	The Institute for Genomic Research
TIR	Toll and Interleukin Receptor
UHD	Ultra-High Density
USAID	United States Agency of International Development
USDA	United States Department of Agriculture
UYT	Uniform Yield Trial
VIGS	Virus Induced Gene Silencing
WASDU	West African Seed Development Union
WHO	World Health Organization
WUE	Water Use Efficiency
YAD	Yam Anthracnose Disease
YMV	*Yam Mosaic Virus*

1 Common Bean

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1.1 Introduction

A book (Singh 1999 a), workshop proceedings (Singh 2000), and two book chapters (Singh 2001b, 2005) on the common bean (*Phaseolus vulgaris* L.) have been published within the last few years. Also, review articles are available on broadening the genetic base of cultivars (Singh 2001 a), development of integrated linkage map (Gepts 1999), and marker-assisted selection (MAS) (Kelly and Miklas 1999). More recently, Kelly et al. (2003) and Miklas et al. (2006) reviewed tagging and mapping of genes and quantitative trait loci (QTL) of economic importance and molecular MAS. Nonetheless, in this chapter we shall briefly describe the history of the crop, botanical description, economic importance, and breeding objectives and achievements of conventional breeding. The remainder of the chapter will be dedicated to the construction of linkage maps, tagging of genes and QTL of economic importance, and progress achieved by MAS.

1.1.1 History of the Crop

The common bean is among the five domesticated *Phaseolus* species that are native to the Americas (Gepts and Debouck 1991). From its origin and domestication regions in the Andean South America, Central America, and Mexico, the common bean has expanded into other parts of the Americas (from about 35°S to >50°N latitude and from sea level to >3000 m altitude) (Gepts et al. 1988; Singh 1992). Subsequently, it was introduced into Africa, Asia, Europe, and Oceania (Gepts and Bliss 1988).

Wild populations of common bean are distributed from northern Mexico (Chihuahua) to northeastern Argentina (San Luis) (Gepts et al. 1986). The common bean is a noncentric crop that had multiple domestications throughout the range of its wild populations (Harlan 1975; Gepts et al. 1986). Hybrids between wild and cultivated beans are fully fertile and no major barriers exist for introgression and exchange of favorable alleles and QTL (Singh et al. 1995; Koinange et al. 1996; Zizumbo-Villarreal et al. 2005).

Through domestication the common bean shifted from extreme indeterminate climbing to determinate bush types; from sensitivity to insensitivity to long photoperiod; from small to large leaves, pods, and seeds; and from a few gray, brown, beige, and cream colored spotted and speckled seeds that mimicked surroundings in wild grassland and oak-pine forest habitats to highly attractive and showy colors except blue and green with solid as well as stripes, spots, speckles, etc. Similarly, the common bean has evolved from having an impermeable to a water-permeable seed coat, and from types that shatter due to highly fibrous and parchmented pod walls to forms with less fiber that are less subject to shattering (Gepts and Debouck 1991; Gepts 1998). Major alleles and QTLs that influenced common bean domestication have been identified and mapped (Koinange et al. 1996; Freyre et al. 1998; Gepts 1999). These traits are growth habit (*fin*), photoperiod insensitivity (*ppd, hr*), pod fiber (*St*), seed dormancy, and seed size, color, and shape. Existence of a considerably larger variation in the evolutionary marker, phaseolin types (Gepts 1988 a), in wild bean populations compared to cultivars suggests that not all wild beans were domesticated and cultivars may have reduced genetic diversity (Koenig et al. 1990; Gepts 1998; Zizumbo-Villarreal et al. 2005). The Andean South American wild and cultivated common beans differ from those of Central America and Mexico. These differences occur in seed size and other mor-

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phological (Singh et al. 1991 c), isozyme (Koenig and Gepts 1989; Singh et al. 1991 b), physiological (White et al. 1992), molecular (Becerra-Velásquez and Gepts 1994; Haley et al. 1994 c), and adaptive traits (Singh 1989). Also, there are occasional incompatibilities between the two groups of wild (Koinange and Gepts 1992) and cultivated (Singh and Gutiérrez 1984; Gepts and Bliss 1985) germplasm such that they are considered two distinct gene pools. Singh et al. (1991 a) further divided the Andean and Middle American gene pools into six races: three Andean gene pool (all large-seeded) = Chile, Nueva Granada, and Peru races; and three Middle American gene pool = Durango (medium-seeded semiclimber), Jalisco (medium-seeded climber), and Mesoamerica (all small-seeded) races. Beebe et al. (2000) reported the existence of additional diversity within the Middle American gene pool, especially within a group of Guatemalan climbing bean accessions that were distinct from previously defined races.

1.1.2 Botanical Description

Freytag and Debouck (2002) described in considerable detail the taxonomy, distribution, and ecology of over 25 *Phaseolus* species, including *P. vulgaris*, that are native to North America, Mexico, and Central America. Cultivated and wild *P. vulgaris* (Brücher 1988) and other *Phaseolus* species (Debouck 1999) are also native to Andean South America. The natural habitat of wild common bean ranges between ca. 800 to 2750 m elevations. Indeterminate climbing populations have a perennial tendency in the wild, but when planted in the field they may behave as an annual similar to most cultivated types.

The genus *Phaseolus* belongs to family Leguminosae, subfamily Papilionoideae. *P. vulgaris* belongs to its section Phaseoli. There is continuous variation in growth habit from determinate bush to indeterminate climbing cultivars. Singh (1982), however, classified growth habits into four major classes using the type of terminal bud (vegetative vs. reproductive), stem strength (weak vs. strong), climbing ability (nonclimber vs. strong climber), and fruiting patterns (mostly basal vs. along entire stem length or only in the upper part). These are the Type I = determinate upright bush, Type II = indeterminate upright bush, Type III = indeterminate, prostate, nonclimbing or semiclimbing, and Type IV = indeterminate, strong climbers. Roots are generally fibrous with a marked tap or main root. Under most field conditions, especially in cool subtropical and temperate environments, they may bear nitrogen-fixing nodules from a few weeks after emergence through flowering. The main stem derives from the axis of the seed embryo. The number of branches and branching pattern may vary greatly depending upon the genotype and environment. Often more than 50% of the pods are borne on branches. The two unifoliolate leaves borne above the cotyledonary node are opposite to each other followed by one trifoliolate leaf at each node in an alternate phyllotaxy. The fully developed trifoliolate leaf has a long (> 7 cm) petiole, a small (< 3 cm) petiolule, very small pulvini, and three leaflets of which the central one is often symmetrical and chordate, ovate, or lanceolate. The inflorescence is a pseudoraceme often with several flowers of which only the basal few bear pods; an exception are small-diameter snap bean that bear a profusion of pods. Also, dry bean of outrigger types bearing six or more pods can be rarely found. Papilionaceous flowers can be pink, purple, white, or bicolor with or without stripes at the outer base of a very pronounced standard. Sessile bracteoles often are larger in Middle American compared to Andean genotypes and may be chordate, ovate, or lanceolate. Bilabiate calyx is small (< 5 mm) with the upper two teeth united. The two keels may be coiled up to two times. There is a single vexillary stamen on the upper side and nine stamen united into a long sheath or tube around the style. The introrse stigma tends to extend around the tip of the style. Flowers are cleistogamous and normally are highly self-pollinated (< 1% outcrossing). Nonetheless, Ibarra-Pérez et al. (1997) reported outcrossing rates ranging from 0.0 to 78% for individual families with a mean rate for six dry bean genotypes ranging from 4.4 to 10.2% in California. Anthesis occurs in early morning hours, and crosses are made with or without emasculation of anthers prior to anthesis. Mature pods are straight to slightly curved with five to eight seeds. There is considerable variation in size, shape, and color of pods and seeds. Germination is epigeal with cotyledons dropping off a couple of weeks after emergence.

Common bean is a short-day crop (White and Laing 1989). Cultivars adapted to higher latitudes either have evolved during dissemination from the primary centers of domestication or have been developed by breeding. Mildly cool environments favor growth and development. Thus, under nonstressed environments with 18 to 22 °C mean growing temperatures and about 12-h day-length, most cultivars complete their growing cycle from germination to seed maturity in 70 to 120 d. In the highlands (above 2000 m elevation) of Bolivia, Colombia, Ecuador, and Peru, climbing cultivars often require more than 250 d to mature. In the humid highlands of Guatemala and Mexico and in Principado de Asturias, Spain, climbing cultivars require ca. 150 d to mature.

At higher latitudes in temperate climates, dry bean cultivars of growth habit Types I, II, and III predominate. These are harvested within 90 to 120 d of planting. Cultivars of growth habit Types I, II, and III are grown in monoculture as well as under different relay, strip, and intercropping systems throughout the world (Singh 1992). Type IV cultivars always require support. Thus, these are grown in either association with maize (*Zea mays* L.) and other crops or on trellises or stakes. Although dry bean is grown in a wide range of soil types, light loamy soils with pH 7.0 and rich in organic matter are more suitable for production. A 90- to 120-d crop with a yield of 2500 kg ha^{-1} will usually remove 60 to 80 kg of soil nitrogen and 40 kg of phosphorus.

P. vulgaris and a great majority of other cultivated and wild *Phaseolus* species have $2n = 2x = 22$ chromosomes. The *P. vulgaris* chromosomes are extremely small, and all 11 chromosomes have been identified (Mok and Mok 1977; Cheng and Bassett 1981). They were also recently assigned to the respective linkage groups (LGs) (Table 1) using the fluorescence in situ hybridization (FISH) (Pedrosa et al. 2003). However, they have been of little or no use in breeding. The common bean has one of the smallest genomes in the legume family with 0.65 pg/haploid genome or 635 mbp (Arumuganathan and Earle 1991).

Table 1. Integration of common bean (*Phaseolus vulgaris* L.) linkage and chromosome maps

Chromosome	Linkage group	
	Florida	Davis (BJ)
1	G	B6
2	H	B1
3	F	B8
4	A	B7
5	C	B3
6	J	B11
7	E	B5
8	I	B10
9	D	B2
10	B	B4
11	K	B9

1.1.3 Economic Importance

The common bean is the most important of over 30 *Phaseolus* species native to the Americas, occupying more than 85% of areas sown to these species worldwide. There are two principal types of common bean: snap and dry. Fully developed green pods of snap bean harvested for fresh-market or processing purposes have reduced fiber in the pod walls and sutures. The USA, Europe, and China are the largest producers of snap bean. Although exact area planted to snap bean is not known, it is estimated to be <3 million ha. For further details on snap bean, the reader should refer to Myers and Baggett (1999) and Myers (2000).

Dry bean is grown in more than 14 million ha in the world. The Americas are the largest dry bean producing regions (6.7 million MT), and Brazil (2.5 million MT) is the largest producer and consumer (Singh 1999b). Asia (2.2 million MT), Africa (2.1 million MT), and Europe (~1 million MT) follow the lead of the Americas in dry bean production in the world. The USA (1.3 million MT) and Mexico (0.98 million MT) follow Brazil as leading dry bean producers. Production has increased substantially in the last 50 years in Argentina, Bolivia, Brazil, Canada, and the USA. Consumer preferences for dry bean size, color, shape, and brilliance vary a great deal (Singh 1992; Voysest 2000). In Latin America, the highest per-capita consumption of dry bean is in Brazil and Mexico (>10 kg per year). In Rwanda and Burundi, per-capita consumption is over 40 kg per year. Dry, green-shelled, and snap bean have high nutritional value, especially in conjunction with cereals and other carbohydrate-rich foods, and can reduce cholesterol and cancer risks (Andersen et al. 1999; Myers 2000). Dry bean (average of 22% protein) dishes range from simply beans boiled in water to more sophisticated preparations of baked beans, cakes, chips, creams, pastes, salads, soups, and stews (Hosfield et al. 2000).

1.1.4 Objectives and Achievements of Classical Breeding

Nearly a century of organized genetics and breeding of common bean has been carried out in the USA and elsewhere in the world. Early efforts emphasized breeding for disease resistance, early maturity, and upright determinate bush growth habit Type I to facilitate mechanical harvest, especially in snap bean. Initially, selection within and between landraces followed by pedigree, mass-pedigree, and recurrent backcrossing were used. Common bean breeding accelerated in the second half of the 20th century in the Americas and Europe. Improved germplasm and cultivars were developed using recurrent backcross (Pompeu 1982), pedigree (Kelly et al. 1994 a), and mass-pedigree (Singh et al. 1989) methods and their modifications. Congruity backcrossing (Mejía-Jiménez et al. 1994; Urrea and Singh 1995), single-seed descent (SSD) (Kelly et al. 1989; Urrea and Singh 1994), recurrent (Kelly and Adams 1987; Beaver and Kelly 1994; Singh et al. 1999), and gamete (Singh 1994; Singh et al. 1998) selection methods have been used more recently.

Favorable alleles and QTLs have been introgressed from the tepary bean (*P. acutifolius* A. Gray) for common bacterial blight [caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye] resistance (Scott and Michaels 1992; Singh and Muñoz 1999), from runner bean (*P. coccineus* L.) for common bacterial blight (Miklas et al. 1994) and white mold [caused by *Sclerotinia sclerotiorum* (Lib.) de Bary] resistance (Miklas et al. 1998 a), and from wild common bean for the bean weevil (*Zabrotes subfasciatus* Boheman) resistance (Cardona et al. 1990). Singh and Muñoz (1999), while introgressing common bacterial blight resistance from the tepary bean (VAX 1 and VAX 2), also pyramided the highest level of common bacterial blight resistance to develop breeding lines VAX 3 to VAX 6. Nonetheless, most breeding has largely utilized favorable alleles and QTLs available between and within cultivated common bean market classes, races, and gene pools. The major breeding achievements in the Americas include introgression of upright growth habit Type II from race Mesoamerica into traditional Type III cultivars of race Durango using phenotypic recurrent selection (Kelly and Adams 1987) and other breeding methods (Coyne et al. 2000; Kelly et al. 2000). Recently developed cultivars also carry resistance to *Bean common mosaic virus* (BCMV, a potyvirus), *Bean common mosaic necrosis virus* (BCMNV, a potyvirus), and rust [caused by *Uromyces appendiculatus* (Pers.) Ung.]. Adams (1982) and Grafton et al. (1993) used Type II cultivars to change Type I growth habit of navy and small white cultivars into more stable high-yielding Type II. Similarly, cream-striped carioca beans (traditionally a Type III) with growth habit Type II and resistance to leafhopper (*Empoasca kraemeri* Ross & Moore) and five diseases were developed using gamete selection (Singh et al. 1998). Seed yield was improved using mass-pedigree (Singh et al. 1993) and recurrent (Singh et al. 1999) selection methods from interracial populations within the Middle American gene pool and from Andean×Middle American intergene pool crosses using recurrent selection (Beaver and Kelly 1994; Singh et al. 1999). Pereira et al. (1993) increased nodule number and weight after three cycles of recurrent selection. Bliss et al. (1989) developed five high N_2-fixing genotypes.

Schneider et al. (1997 a, b) and Rosales-Serna et al. (2000) developed drought-resistant breeding lines from biparental populations using seed yield and/or random amplification of polymorphic DNA (RAPD) markers as selection criteria. Singh (1995) and Terán and Singh (2002) developed drought-resistant breeding lines from double-cross interracial and intergene pool populations using a bulk-pedigree method. Similarly, breeding lines such as A 321, A 445, and A 744 resistant to low soil fertility were developed from interracial populations within Middle American gene pool (Singh et al. 2003 b).

Kelly et al. (1994 b) developed anthracnose [caused by *Colletotrichum lindemuthianum* (Sacc. and Magn.) Bri. & Cav.], BCMV, BCMNV, and rust-resistant black-seeded cultivar Raven, which was then used to develop Phantom with similar resistance (Kelly et al. 2000). Kelly et al. (1999 c) also combined good canning quality, BCMV resistance, and the Andean *Co-1* and Middle American *Co-2* alleles for anthracnose resistance in a large-seeded light red kidney bean Chinook 2000. Both anthracnose resistance alleles were also combined with BCMV and rust resistance in small black cultivar Jaguar (Kelly et al. 2001). Good canning quality and resistance to anthracnose, BCMV, *Beet curly top virus* (BCTV, a leafhopper vectored geminivirus), and rust, either singly or in various combinations, have also been bred into dark and light red kidney, red mottled, white kidney, and cranberry beans for North America (Miklas and Kelly 2002; Miklas et al. 2002 a) and for the tropics and subtropics (Beaver et al. 2003). Singh et al. (2003 a) developed angular leaf spot [caused by *Phaeoisariopsis griseola* (Sacc.) Ferr.], anthracnose, BCMV, rust, and halo blight [caused by *Pseudomonas syringae* pv. *phaseolicola* (Burkh.) Young] resistant breeding lines A 339, MAR 1, MAR 2, and MAR 3 from interracial populations between the three Middle American races.

Acosta-Gallegos et al. (1995), Ibarra-Pérez et al. (2004), and Sanchez-Valdez et al. (2004) combined resistance to angular leaf spot, anthracnose, BCMV, and rust into high-yielding "bayo," black, "flor de mayo," ojo de cabra, pinto, and shiny black bean cultivars for Mexican highlands. Kelly et al. (1999 a, b), Coyne et al. (2000), and Brick et al. (2001), among others (see Brick and Grafton 1999; Singh 2001 a; Beaver et al. 2003), combined BCMV and rust resistance into great northern and pinto beans. Resistance to BCMV and BCMNV and rust resistance were combined into pinto Kodiak (Kelly et al. 1999 a) and great northern UI98-209G (Stewart-Williams et al. 2003). Pinto germplasm 92US-1006 (Silbernagel 1994) and cultivar Quincy (synonymous with USPT-73) (Hang et al. 2005) carry *I* and $bc\text{-}2^2$ resistance alleles for BCMV and BCMNV. The *I* and *bc-3* alleles imparting resistance to all known strains of BCMV and BCMNV were combined with four to six rust resistance alleles into great northern BelMiNeb-RMR-6 to 13 and pinto BelDakMi-RMR-14 to 23 beans (Pastor-Corrales 2003; Pastor-Corrales et al. 2001).

The recessive resistance allele *bgm-1* for leaf chlorosis induced by *Bean golden mosaic virus* (BGMV, a geminivirus) and *Bean golden yellow mosaic virus* (BGYMV, a geminivirus) from the landrace Garrapato (synonymous with G 2402) was inadvertently transferred into breeding line A 429 (Morales and Singh 1993). A 429 was subsequently used to develop highly resistant small red, black, and carioca bean cultivars for Central America and Brazil, using pedigree, mass-pedigree, or gamete-selection methods. Beaver et al. (1999) were the first to develop BGYMV (*bgm-1* allele), BCMV, common bacterial blight, and rust-resistant large-seeded light red kidney bean breeding line PR9443-4 for the Caribbean. Singh et al. (2000) pyramided a high level of BGYMV resistance in different dry beans using direct disease screening that was subsequently verified by the presence of molecular markers. In the tropics and subtropics of Latin America, resistance to bean pod weevil (*Apion godmani* Wagner), angular leaf spot, anthracnose, BCMV, BGYMV, bruchid, common bacterial blight, and leafhopper, and upright plant type in beige, black, cream, cream-striped, and red beans were incorporated (Singh et al. 1998; Beaver et al. 2003). Silva et al. (2003) in Brazil in 1984 released the first cultivar, EMGOPA-Ouro-201 (synonymous with A 295), that combined angular leaf spot, anthracnose, BCMV, common bacterial blight, halo blight, powdery mildew (caused by *Erysiphe polygoni* DC), and rust resistance.

1.2 Genetic Linkage Maps

1.2.1 Linkage Mapping Prior to 1990

Lamprecht (1961) published the first genetic linkage map for common bean, which summarized previous linkage reports. This map comprised 26 naturally occurring traits. Most of the genes controlled the color of the flower or seed or affected pod traits. The Lamprecht map was extended with additional isozymes, seed proteins, and induced mutations (Bassett 1988; Gepts 1988 b; Arndt and Gepts 1989; Koenig and Gepts 1989; Vallejos and Chase 1991 b). These early maps were extensively reviewed by Bassett (1988, 1991) and culminated in a revised linkage map for common bean consisting of 13 LGs and 47 marker genes that included his own mapping of four recessive marker genes and three recessive induced mutants. For example, Nagata and Bassett (1984) mapped dark green savoy leaf (*dgs*), dwarf seed (*ds*), stipelless lanceolate leaf (*sl*), and round leaf (*rnd*) on LG VII, and spindly branch (*sb*), diamond leaf (*dia*), and progressive chlorosis (*prc*) on LG IX. He also discussed some of the less defined associations that had not yet been mapped. For example, Kyle and Dickson (1988) reported a tight linkage or pleiotropy of the dominant *I* allele imparting resistance to all known strains of the BCMV, and resistance to four related potyviruses. The *I* allele was also linked with seed coat (Temple and Morales 1986; Kyle and Dickson 1988) and hilum-region-darkening allele *B* (Park and Tu 1986). Deakin and Dukes (1975) and Dickson and Petzoldt

(1986) observed linkage of colored seed coat with resistance to Pythium and/or Rhizoctonia root rots. Coyne et al. (1973) found association between resistance to common bacterial blight and late flowering. Valladares-Sanchez et al. (1979) reported linkage between late maturity and indeterminate growth habit, Stavely (1984) among genes for rust resistance, and Osborn et al. (1986) between arcelin and lectin genes. Association of isozyme EST-2 with white flower (Weeden and Liang 1985) and white seed coat color (Weeden 1984) was also reported. These early "classical" maps were rudimentary, providing very little genomic coverage and utility for marker-assisted selections (MAS), but they did provide a point of reference for subsequently developed DNA-based linkage maps.

Bassett (1991) noted in revising the classical map that many previously described mutants lacked a seed source and therefore could not be tested. The renewed *Phaseolus* Genetics Committee in 1987 (Gepts 1988 c) advocated for a repository for genetic stocks that Bassett established and is currently maintained by the USDA-ARS, NPGS (National Plant Germplasm System) at the Western Regional Plant Introduction (PI) Station in Pullman, WA, USA (http://www.ars-grin.gov/cgi-bin/npgs/html/desc.pl?83034).

Another problem encountered in establishing the classical maps was the use of different gene symbols by different researchers for the same gene (Bassett 1991). A subcommittee of the *Phaseolus* Genetics Committee addressed this lack of coordination among geneticists for naming genes and formulated guidelines for gene designation and nomenclature (Myers and Weeden 1988; Bassett and Myers 1999). Bassett (2004) updated the list of genes for *P. vulgaris*.

1.2.2 Linkage Mapping After 1990

Availability of DNA-based markers in the mid-1980s aroused great interest and facilitated development of common bean linkage maps within the last 15 years. Vallejos et al. (1992) and Nodari et al. (1993 a) were among the first to develop molecular linkage maps of common bean, which subsequently evolved into the two major bean-mapping populations. For both maps, widely divergent parents were chosen to maximize (i) polymorphism at the nucleotide level, (ii) phenotypic diversity, and (iii) variability for disease resistance and other traits. Vallejos et al. (1992) developed a backcross (BC_1) population (Florida map) from diverse parents XR-235-1-1 (recurrent parent) and DIACOL Calima, representatives of the Middle American and Andean gene pools, respectively (Table 2). The Florida BC_1 map consisted of the pigmentation gene *P*, 224 restriction fragment length polymorphisms (RFLPs) (from *Pst*I genomic clones), 9 seed proteins, and 9 isozyme marker loci, which sorted into 11 LGs labeled in descending order of length from A to K. This map covered 963 cM of the estimated 1200 cM of the bean genome. Gepts et al. (1993), using the same prediction model of Hulbert et al. (1988), estimated the genome length to be 1250 cM. Seven additional markers added 17 cM of coverage (980 cM) (Vallejos 1994). To date the Florida map consists of 294 markers, including the addition of RFLP probes from synteny studies (Boutin et al. 1995), and covers 900 cM (Vallejos et al. 2001), which is less than previous reports because of an increased stringency (LOD >2.0) for placement of markers on the map.

Earlier, the Florida BC_1 population and an F_2 population from the same cross were used to map isozymes, seed proteins, and the *P* locus controlling pigmentation (Vallejos and Chase 1991 b), which resulted in the combination and extension of LGs X and XIII of the classical map (Bassett 1991). In a companion study (Vallejos and Chase 1991 a), a linked pair of isozyme markers *Adh-1* and *Got2* was significantly associated with seed size, which in effect identified a QTL. Sax (1923) was the first to note a linkage association between a morphological marker (seed pigmentation) and quantitative trait (seed size) in bean. Johnson et al. (1996) speculated that the phaseolin locus, *Phs*, was the candidate gene underlying the QTL for seed size, and its linkage with *P* was the morphological locus for seed color that Sax (1923) had identified. This mapping population was later used directly to identify QTL for common bacterial blight resistance (Yu et al. 1998).

The Davis map (Table 2), based on an F_2 population, was obtained from the wide cross between BAT 93 of the Middle American and Jalo EEP558 of Andean gene pool (Nodari et al. 1993 a). The map, with 143 markers, consisted of three genes (*I* for resistance to BCMV, *Cor* for seed color pattern, and an unknown gene for flower color), 108 RFLP (primarily *Pst*I clones), 7 isozyme, 7 RAPD, and 18

Table 2. Common bean (*Phaseolus vulgaris* L.) populations used for tagging and mapping genes and quantitative trait loci between 1992 and 2004.

Parents	Source	Abbre-viation	Map size	Predominant marker	Traits mapped	References
BAT 93/Jalo EEP558 (F_2 and RI)	Davis	BJ, core	1226 cM	RFLP, mix	ALS, anthracnose, CBB, Rhizobium	Nodari et al. 1993a,b; Freyre et al. 1998; Gepts 1999
XR235-1-1/DIACOL Calima (BC)	Florida	XD	900 cM	RFLP, mix	Seed size, CBB	Vallejos et al. 1992; Yu et al. 1998
Corel/Ms8EO2 (BC)	Paris	CE	567 cM	RAPD, mix	Anthracnose	Adam-Blondon et al. 1994 a
DOR 364/G 19833	CIAT	DG	Full	RFLP, SSR	BGYMV, low P, root traits, ALS, Anthracnose	Beebe et al. 1998; Blair et al. 2003; López et al. 2003
Midas/G 12873	Davis	MG		RFLP	Domestication traits	Koinange et al. 1996
BAC 6/HT 7719	NE	BH	545 cM	RAPD	CBB, web blight, rust	Jung et al. 1996
Olathe/Sierra	ID, ND	OS	Partial	RAPD	BCMV, rust	Strausbaugh et al. 1999; Kalavacharla et al. 2000
DOR 364/XAN 176	PR, ARS	DX	930 cM	RAPD	ASB, BGYMV, CBB, rust	Miklas et al. 1996 b, 1998 b, 2000 a
PC-50/XAN 159	NE	PX	404 cM	RAPD	CBB, rust, white mold	Jung et al. 1997; Park et al. 2001
CDRK/Yolano	Davis	CY	1487 cM	AFLP	Seed yield	Johnson and Gepts 1999
A 55/G 122	Harris Moran, Davis	AG	1631 cM	AFLP	Seed yield, white mold, heat tolerance	Johnson and Gepts 1999; Miklas et al. 2001; Porch 2001
Eagle/Puebla 152	WI	EP	825 cM	RAPD	Root rot	Vallejos et al. 2001; Navarro et al. 2003
Jamapa/DIACOL Calima	Florida	JC	950 cM	Mix	RGA	Rivkin et al. 1999; Vallejos et al. 2001
Benton/NY6020-4	ARS	BN	Partial	RAPD	White mold	Miklas et al. 2003 b
OAC Seaforth/OAC 95-4	Guelph	S95	1717 cM	Mix	CBB, agronomic traits	Tar'an et al. 2001, 2002
BelNeb-RR-1/A 55	NE	BA	755 cM	RAPD	BBS, HBB, BCMV, Fusarium wilt	Ariyarathne et al. 1999; Fall et al. 2001; Jung et al. 2003; Fourie et al. 2004
Sierra/Lef-2RB	MI		Partial	RAPD	Drought, Fusarium wilt	Schneider et al. 1997 a, b; Brick et al. 2004
Sierra/AC1028	MI		Partial	RAPD	Drought	Schneider et al. 1997 a, b
Isles/FR266	MI		Partial	RAPD	Fusarium root rot	Schneider et al. 2001
Montcalm/FR266	MI	MF	Partial	RAPD	Fusarium root rot	Schneider et al. 2001
Bunsi/Huron	MI	BH	Partial	AFLP	White mold	Kolkman and Kelly 2003
Bunsi/Newport	MI	BN	Partial	AFLP	White mold	Kolkman and Kelly 2003
Montcalm/CDRK-82	ARS, MI, ND		Partial	RAPD	Canning quality	Posa-Macalincag et al. 2002
Montcalm/CELRK	ARS, MI, ND		Partial	RAPD	Canning quality	Posa-Macalincag et al. 2002
Berna/EMP 419	Guelph		Partial	Mix	Leafhopper, seed size	Murray et al. 2004
Bayo Baranda/G 22837 (F_2)	Mexico		497 cM	AFLP	Seed Ca, Fe, Zn, tannin, mass	Guzmán-Maldonado et al. 2003
Moncayo/Primo	ARS	MP	Partial	RAPD	BCTV	Larsen and Miklas 2004
Minnuette/OSU 5630	OR		Full	Mix	Snap bean traits	Myers et al. 2004
Aztec/ND88-106-04	ND, ARS	AN	Partial	Mix	White mold, rust, zinc	Miklas et al. 2005 a
Bunsi/Raven	MI	BR	Partial	Mix	White mold, BCMV	Ender and Kelly 2005
HR67/OAC 95	Harrow	H95	Partial	Mix	CBB	Yu et al. 2004
Red Hawk/Negro San Luis	MI	RN	Parital	Mix	Root rot	Román-Avilés and Kelly 2005

Abbreviations: ALS: angular leaf spot, ASB: ashy stem blight, BBS: bacterial brown spot, BCMV: bean common mosaic virus, BCTV: beet curly top virus, BGYMV: bean golden yellow mosaic virus, CBB: common bacterial blight, HBB: halo bacterial blight, RGA: resistance gene analog