Genome Mapping and Molecular Breeding in Plants
Volume 4

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
Vegetables

Volume 6
Technical Crops

Volume 7
Forest Trees

Chittaranjan Kole (Ed.)

Fruits and Nuts

With 50 Illustrations, 2 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

Fruit and nut crops make perhaps the largest group of species of economic importance and they by far outnumber any other major groups of domesticated plants. However, progress of genetic or genomic researches on fruit and nut crops is indeed much slower than the pace they deserve. Relatively more importance attached to the agronomic crops might be one of the reasons. The most important reason, to our mind, however, is the constraints inherent to the long life cycle, heterozygosity, space required to raise large populations often required, and difficulty in recording phenotypic trait data for most of the fruit and nut crops. The common constraints in most of these crops include too long juvenile period, problems of sterility and incompatibility, large plant size, the randomness of artificial mutations, limitations of the sexual system to incorporate small changes, the dependence upon natural origin of variation and the exorbitant costs needed to select, detect, and evaluate desirable recombinants those lead to the difficulties for genetic analysis and breeding. Most of these crops invoke for formulating strategies specific to the above problems and limitations, employment of pseudo-testcross method and use of SDRF markers, for examples.

Appreciable progress has been made in some fruit crops, mostly temperate, including say apple, grapes, stone fruits, cherries, citrus fruits. Still many others remain neglected, particularly the tropical and subtropical fruit and nut crops grown in the developing countries, litchi, custard apple, guava to name a few. These 'orphan' fruit and nut crops are too many and deserve global attention for concerted efforts. The presentation of the chapters in this volume, therefore, has nothing to do with the production statistics and relative economic importance of the fruit and nut crops at world level, but has been done primarily envisaging the quantum of works accomplished. We have included 20 chapters in this volume including seven chapters perhaps with the first time comprehensive review such as on mango, banana, olive, pineapple, pistachio, persimmon and papaya. How we wish to have independent volumes on temperate, and tropical and subtropical fruits and nuts in near future.

Due to some unavoidable circumstances there was delay for this volume to go to press and obviously the authors had to take pain to rework on the manuscripts for updating. I remain grateful to them for their co-operations and perseverance. I am also thankful to them for presenting the most current commentary on genomic researches on fruit and nut crops.

The former three volumes of this series have earned appreciation from all levels of readers and we hope this volume also will be liked by them. In that case the credit must go to the authors and the publishers for their contributions and care. I take the sole responsibility of all the shortcomings, and look forward to the readers for their suggestions for improvement in contents and format of this volume in its future edition(s).

Pennsylvania,
15 April 2006

Chittaranjan Kole

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Abbreviations

ACC	1-Amino-Cyclopropane-1-Carboxilate
ACC	Asian Citrus Canker
AFLP	Amplified Fragment Length Polymorphism
AP	Andhra Pradesh
AP-PCR	Arbitrary Primer-PCR
ARO	Agricultural Research Organization
BA	Benzyladenosine
BAC	Bacterial Artificial Chromosome
BIBAC	Binary Bacterial Artificial Chromosome
bp	Base pair
BSA	Bulked Segregant Analysis
BSV	Banana Streak Virus
CAPS	Cleaved Amplified Polymorphism Sequence
CARBAP	Centre Africain de Recherches sur Bananiers et Plantains
cDNA	Complementary DNA
CENARGEN	Centro Nacional de Recursos Genéticos e Biotecnologia
CIRAD	Centre de Coopération Internationale en Recherche Agronomique pour le Développement
CITA	Centro de Investigación y Tecnología Agroalimentaria de Aragón
CLM	Citrus Leaf Miner
cM	centi-Morgan
CMA	Chromomycin A3
CNPMF	Centro Nacional de Pesquisa de Mandioca e Fruticultura Tropical
CP	Coat Protein
cpDNA	Chloroplast DNA
CPMR	Coat Protein Mediated Resistance
CpTi	Cowpea protease Trypsin inhibitor
CSIC	Consejo Superior de Investigaciones Científicas
CTV	Citrus Tristeza Virus
C-value	Amount of DNA contained within a haploid nucleus
CVC	Citrus Variegated Chlorosis
DAPI	4′-6-Diamidino-2-Phenylindole
DARE	Durable Apple Resistance in Europe
DNA	Deoxyribose Nucleic Acid
EAGMPP	European Apple Genome Mapping Project
ELISA	Enzyme-Linked Immunosorbent Assay
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuária
EMS	Ethyl Methane Sulfonate
EST	Expressed Sequence Tag
FAO	Food and Agriculture Organisation
FHIA	Fundacion Hondurenea de Investigacion Agricola
FISH	Fluorescent In Situ Hybridization
FPC	Fingerprinted contigs
GDR	Genome Database for Rosaceae
GFP	Green Fluorescent Protein

GMC	Grape Microsatellite Collection
GMO	Genetically Modified Organism
GRIN	Germplasm Resources Information Network
GSI	Gametophytic Self-Incompatibility
GUS	β-Glucuronidase
HiDRAS	High-Quality Disease Resistant Apples for a Sustainable Agriculture
HMW-DNA	High Molecular Weight DNA
HRI	Horticulture Research International
IARI	Indian Agricultural Research Institute
ICGC	International Citrus Genome Consortium
ICM	Integrated Crop Management
IGGP	International Grape Genome Program
IITA	International Institute of Tropical Agriculture
INRA	Institut National de la Recherche Agronomique
IPB	Institute for Plant Biotechnology
IPM	Integrated Pest Management
IRGC	International Rosaceae Genome Consortium
IRTA	Institut de Recerca i Tecnologia Agroalimentàries
ISSR	Inter-Simple Sequence Repeat
ITS	Internal Transcribed Spacer
IVIA	Instituto Valenciano de Investigaciones Agrarias
IWBT	Institute for Wine Biotechnology
kb	Kilobase
KUL	Katholieke Universiteit Leuven
LD	Linkage Disequilibrium
LecRK	Lectine/Kinase Receptor
LG	Linkage Group
LINE	Long Interspersed Element
LOD	Logarithm Of Odds
LRR	Leucin-Rich Repeat
LTP	Lipid Transfer Proteins
MAB	Marker-Assisted Breeding
MAS	Marker-Assisted Selection
Mb	Megabase
MBC	Map-Based Cloning
Mbp	Mega base pairs
MFLP	Microsatellite Fragment Length Polymorphisms
MS	Murashige and Skoog
MSY	Male Specific Y
mtDNA	Mitochondrial DNA
NAA	Napthalene Acetic Acid
NAD	Nicotinamide Adenine Dinucleotide
NBS	Nucleotide Binding Site
NCBI	National Center for Biotechnology Information
NIL	Near Isogenic Line
NPTII	Neomycin phosphotransferase
ORF	Open Reading Frame
OVERGO	Overlapping Oligonucleotide
PaLCuV	Papaya Leaf Curl Virus
PCA	Pollination-Constant and Astringent
PCNA	Pollination-Constant and Non-Astringent

PCR	Polymerase Chain Reaction
PD	Pierce's Disease
PDO	Protected Designation of Origin
PGI	Protected Geographical Indication
PGI	Phosphoglucoisomerase
PGM	Phosphoglucomutase
PGRI	Plant Genome Research Initiative
PPO	Polyphenol Oxidase
PPV	Plum Pox Virus
PRI	Purdue-Rutgers-Illinois
PRSV	Papaya Ring Spot Virus
PSDM	Papaya Sex Determination Marker
PTGS	Post-Transcriptional Gene Silencing
PTSL	Peach Tree Short Life syndrome
PVA	Pollination-Variant and Astringent
PVNA	Pollination-Variant and Non-Astringent
PVP	Polyvinylpyrrolidone
QTL	Quantitative Trait Loci
QUT	Queensland University of Technology
R gene	Resistance Gene
RACE	Rapid Amplification of Complementary DNA Ends
RAG	Resistance Associated Gene
RAPD	Random Amplified Polymorphic DNA
rbcL	Large subunit of riblose-1,5-bisphosphate carboxylase/oxygenase
rDNA	Ribosomal DNA
Rep	Replicase
RFLP	Restriction Fragment Length Polymorphism
RFRS	Regional Fruit Research Station
RGA	Resistance Gene Analog
RGC	Resistance Gene Candidate
RKN	Root-Knot Nematode
SAM	Sexually Ambivalent Male
SCA	Specific Combining Ability
SCAR	Sequence Characterized Amplified Region
SCRI	Scottish Crop Research Institute
SDH	Shikimate Dehydrogenase
SDRF	Single-Dose Restriction Fragment
SFB	S haplotype-Specific F-Box protein
SINE	Short Interspersed Element
SNP	Single Nucleotide Ppolymorphism
SSCP	Single-Strand Conformation Polymorphism
SSR	Simple Sequence Repeats
STMS	Sequence-Tagged Microsatellite Site
STS	Sequence Tagged Sites
TAC	Transformation-Competent Artificial Chromosome
TBLASTX	National Center for Biotechnology Information Blast Analysis
Ti	Tumor inducing
TIGR	The Institute for Genomics Research
TILLING	Targeting Local Lesions in Genomes
TIR	Toll/Interleukin-1 Receptor
TNAU	Tamil Nadu Agricultural University

TNL	TIR-NBS-LRR
TSG	Traditional Specialty Guaranteed
TSS	Total Soluble Solids
UP	Uttar Pradesh
URGV	Unité de Recherche en Génomique Végétale
USDA	United States Department of Agriculture
VMC	Vitis Microsatellite Consortium
VNTR	Variable Number Tandem Repeats
VPg	Viral Protein genome-linked
WGS	Whole-Genome Shotgun
YAC	Yeast Artificial Chromosome

1 Apple

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1.1 Introduction

1.1.1 Origin of the Domesticated Apple

The genus *Malus* belongs to the Rosaceae family and forms with its closely related fruit (*Pyrus* and *Cydonia*) and ornamental (*Amelanchier, Aronia, Chaenomeles, Cotoneaster, Crateagus, Pyracantha, Sorbus*) genera, the subfamily Maloideae (Challice 1974). This subfamily is believed to be an allopolyploid, that evolved from a hybridization between a Spiraeoidae ($x = 9$) and a Prunoidae ($x = 8$) ancestor resulting in the basic haploid number of $x = 17$ for the Pomoidae (Lespinasse et al. 1999). Most *Malus* species are diploids ($2n = 34$), but a few are triploid (e.g., *M. hupehensis* and *M. coronaria*), or tetraploid (e.g., *M. sargentii*), while some species show variable levels of ploidy (Way et al. 1989). Little information is available on the karyotype of apple. The lengths of the chromosomes in haploid *M. domestica* range from 1.5 to 3.5 µm, with 11 of them being submetacentric, and six being metacentric with respect to the position of the centromere (Bouvier et al. 2000). The longest, and possibly a second chromosome carry a satellite.

With the number ranging from eight to about 122 (Robinson et al. 2001; Harris et al. 2002), there is no agreement among taxonomists as to how many species this genus comprises. The higher estimates may also include many interspecifics, as the species are widely compatible and readily interbreed (Korban 1986). This characteristic has been deployed in apple breeding for the introgression of pest and disease resistance genes. For this reason as well as the assumed interspecific origin of the eating apple in general (Korban 1986; Korban and Chen 1992; Robinson et al. 2001), it seems appropriate to identify the domesticated apple as *M. x domestica* Borkh. However, more recently it has been argued that the correct nomenclature is *M. pumila* Mill. (Korban and Shirvin 1984), and that this species should include the wild apple identified as *M. sieversii* (Lebed.) Roem. (Mabberley et al. 2001). Vavilov (1951) also referred to the wild apple as *M. pumila* when describing the centers of origin of cultivated plant species, which is in complete opposition to the view of another well-known Russian botanist, Ponomarenko, who denied the existence of this species (Way et al. 1989). However, the relatedness of the domesticated and wild apples is strongly supported by the small degree of morphological, biochemical and molecular variation between the two species (Harris et al. 2002). The same could be said of the European wild crabapple *M. sylvestris*. This also belongs, together with *M. sieversii*, to *M. pumila* Mill. (Westwood, in Way et al. 1989), and may have been the result of a separate introduction of the wild apple into Europe. However, the UK research team has not adhered to its own recommendation in later papers and refers to the domesticated apple as *M. domestica* Borkh., while recognizing *M. sieversii* from Central Asia as a separate species (Robinson et al. 2001; Harris et al. 2002). As it suits a purpose of these reviewers, we adhere to the nomenclature according to Way et al. (1989), who identify *M. domestica* and *M. sieversii* as separate species.

The domestication of the apple went hand in hand with the civilization of mankind and has been described extensively by Morgan and Richards (1993). There is evidence of fruit gathering having started as early as the Neolithic times (Juniper et al. 1999). Cultivation increased with propagation through cuttings and also with the discovery of grafting techniques (Morgan and Richards 1993). The fixing of genotypes had a long-lasting effect on apple production, enabling varieties to be grown in orchards and pro-

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viding horticulturalists with the possibility of selecting the best varieties from the many that would have only suited processing because of their bitterness and astringency. Even today, apple production is dominated by cultivars, such as McIntosh (1800s), Jonathan (1820s), Cox's Orange Pippin (1830s), Granny Smith (1860s), Delicious (1870s), Golden Delicious (1890s) and Braeburn (1940s), which were mostly selected from chance seedlings over 100 years ago. By this period, apple had reached all the corners of the world, as emigrants from the Old World introduced them into their new home countries. In Asia, these varieties often replaced the local varieties selected from the native species *M. prunifolia* and its cultivated species *M. asiatica* (Morgan and Richards 1993). It is only recently that bred cultivars developed in the 1930/40s and introduced in the 1960/70s, such as Royal Gala (Kidd's Orange Red × Golden Delicious), Jonagold (Delicious × Jonathan), Fuji (Ralls Janet × Delicious), and Elstar (Ingrid Marie × Golden Delicious), have made major inroads in some countries, even completely replacing existing cultivars. For example, China's enormous growth in apple production is entirely due to the introduction of Fuji.

1.1.2 Apple Production and Exports

With the advent of the new bred cultivars, apple production started to increase rapidly, with several Southern Hemisphere countries, into which apple was introduced, starting to develop major apple industries as they took advantage of the seasons being opposed to those in the Northern Hemisphere (Morgan and Richards 1993). Table 1 shows that in 2004, the world production of apples was an estimated 59 million metric tonnes (MT) produced on 5,280,638 ha of trees (http://faostat.fao.org). After bananas (71 million MT), grapes (65 million MT) and oranges (63 million MT), apples are the fourth biggest fruit crop in the world and production is more than three times that of pears (18 million MT). At 20.5 million MT, China produced over one third of the world production, with the USA being a distant second at 4.3 million MT (Table 1). However, many of the large producers do not export much of their crops, as they have large internal markets, with most of the fruit probably being processed. At 6.2 million MT, about 10% of the world production of apples is exported.

1.1.3 Breeding Strategy

The traditional method of apple improvement by selecting the best phenotypes from seedlings grown from open-pollinated seeds was replaced by deliberate hybridization about 200 years ago. The science of breeding started with the first controlled cross-pollinisation carried out by Thomas Knight early in the nineteenth century (Brown 1975). However, initially little progress was made in improving apple cultivars through controlled crossing, which has been attributed to poor selection of parents (Janick et al. 1996). The success of the relatively recent introductions must be attributed to the selection of parents with good fruit quality. Royal Gala, Fuji, and Jonagold were selected in the first generation from the best commercial cultivars, notably Golden Delicious and Delicious, available at the time of crossing.

Table 1. Estimated apple production (for 2004) and exports (for 2003) (× 1000 metric tonnes) by country (FAOSTAT data)

Country	Production	Export
China	20,503	609
USA	4,290	546
Poland	2,500	349
France	2,400	804
Iran	2,350	109
Turkey	2,300	19
Italy	2,012	708
Russian Federation	1,900	1
Germany	1,600	70
India	1,470	9
Argentina	1,262	200
Chile	1,100	601
Brazil	978	76
Japan	881	17
Ukraine	850	10
Romania	810	0
South Africa	701	326
Hungary	680	8
North Korea	660	0
Spain	614	73
New Zealand	550	323
Mexico	503	0
Uzbekistan	500	4
Egypt	485	0

Apple is self-incompatible and highly heterozygous, which results in very diverse progeny with only a few of them being a major improvement on the parents. As most characters are under polygenic control, low efficiency in genetic improvement of breeding lines together with a long juvenile period make breeding in this crop a slow and expensive process. Hence most apple breeders cannot afford long-term breeding strategies based on recurrent selection achieving incremental gains for a range of characters in each generation (Bringhurst 1983; Oraguzie et al. 2004). Instead, the most common breeding strategy in apple is a limited version of recurrent selection, which is applied to fewer but larger progenies derived from a limited number of parents, selected for a few characters to be improved in a new cultivar (Janick et al. 1996). As breeders cannot afford the time to develop test-crosses to assess the ability of crossing combinations to achieve the breeding goals (Bringhurst 1983), there will be an aspect of chance in the parent selection for a high specific combining ability (SCA) with regard to quantitatively inherited traits. The effect of parents with poor fruit quality is illustrated by the breeding of scab-resistant cultivars carrying the *Vf* gene from *M.* x *floribunda* 821, a crabapple with small fruit of low quality. The first cultivar, Prima (Dayton et al. 1970), is an F_4 descendant of *M.* x *floribunda* and was introduced about 30 years after the Purdue-Rutgers-Illinois (PRI) breeding program started with the specific objective of developing pest and disease resistant cultivars (Crosby et al. 1992). In spite of an "unceasing, single-minded emphasis on moving the *Vf* gene into an adapted type" (Janick et al. 1996), 35 years later there still are no cultivars that have had a considerable impact on pipfruit production by replacing major susceptible cultivars. Breeders have not been able to make the scab-resistant cultivars "catch up" with the eating quality expected of new cultivars today. Nevertheless, the program might have made still less progress if the breeders had been aiming to achieve too many breeding objectives at the same time, which creates inefficiencies as large numbers of seedlings are required to improve the chances of meeting all selection criteria (Brown 1975; Oraguzie et al. 2004).

1.1.4 Breeding Objectives

The principal breeding objective for apple is to increase the marketability of the fruit (Janick et al. 1996). As most breeding programs aim to develop new cultivars for the fresh market, the emphasis is on appearance and eating quality meeting the consumers' expectation of pleasurable fruit consumption, linked with storability to extend the market window. Selection criteria for external quality mostly pertain to skin color, the pattern and amount of fruit covered with color, and the size and shape of the fruit, while internal quality is predominantly determined by flesh texture and flavor (Janick et al. 1996). However, selection criteria may differ in accent, as different breeders aim to develop new cultivars specific to the particular market they target (Laurens 1999) and long-term breeding goals are being increasingly determined by consumer preference research. For example, in reply to an increased consumer interest in the nutritional value of fruit and vegetables, apple is currently being investigated particularly as a source of antioxidants (Davey and Keulemans 2004; Thielen et al. 2004; Lichtenthaler and Marx 2005), which may help prevent diseases and ageing (Raskin and Ripoll 2004; Graziani et al. 2005). On the other hand, a health concern is that apple is a well-known source of allergens. Genetic markers have been identified for genes controlling development of allergens in apple (Gao et al. 2005a, b) (see also Sect. 1.3.2.5.6) and ways are being sought to reduce their negative effect (Hoffman-Sommergruber and the SAFE consortium 2005).

Breeding for pest and disease resistance comes a close second as a major objective (Laurens 1999). Apple is host to a wide range of pests and diseases (Way et al. 1989), many of which need to be controlled in order for commercial production to be profitable. The use of plant resistance is widely regarded as the preferred means of controlling pests and diseases. There are major socio-economic advantages in using resistant cultivars, because they help reduce production costs and diminish the effects on the users and environment because of the reduced requirements for equipment, labour, and fossil fuels (Way et al. 1989; Hogenboom 1993). However, while the potential benefits of resistance breeding are large with regard to the wider impact of pesticide use, the savings to the grower in the direct costs of disease protection are only about 4% of the value of the annual crop (Merwin et al. 1994). The savings also may easily be offset by

market fluctuations and may be reduced by the emergence of other diseases requiring additional control (Merwin et al. 1994). Consumer objection to the use of pesticides was a significant driver for apple breeders to include resistance breeding as a major objective in the development of new cultivars (Laurens 1999), but this to date has not translated into consumers showing a preference for resistant varieties. Although new resistant selections with improved fruit quality are available (Crosby et al. 1992; Fischer et al. 1999), their success in the market place is determined foremost by their ability to differentiate themselves based on appearance and texture in direct competition with the current susceptible cultivars (Murphy and Schertz Willet 1991; Merwin et al. 1994). Therefore, the value of disease resistance to the marketers may prove to be only incremental, until resistant varieties provide an opportunity to rapidly reap the financial benefits of increased demand for fruit produced with reduced chemical inputs, e.g. in organic production systems. These gains will be realised in the long-term only if resistances are durable.

Climatic adaptation is a general breeding objective that ensures trees are productive, bear regularly, and produce fruit with minimal defects, and is achieved by selecting for tree habit, vigor, duration of the juvenile period, and flowering season (Janick et al. 1996). A few breeding programs have more specific objectives to meet the needs of their industries, e.g. adaptation to cold hardiness for climates with severe winters, or low chilling requirements for some subtropical climates. New cultivars often are selected to replace cultivars occupying certain market windows, but in some cases the aim is to extend the marketing period by selecting for very early, or very late maturing cultivars (Laurens 1999).

1.1.5 Molecular Markers and Genetic Maps

Most of the molecular research to date has focused on identifying genetic markers for pest and disease resistance genes, as apple has proved to be a rich source of simply inherited resistance genes with major effects (Table 2). Initially, isoenzymes were used, but they were rapidly superseded by DNA-based markers (see Sect. 1.2). Many different types of markers are available to breeders now, but it has become clear that highly informative markers, such as microsatellite (SSR) and single nucleotide polymorphism (SNP) markers are required to identify resistance genes that are linked or residing in clusters (e.g. Bus et al. 2005b). To date, the primary use of genetic markers in resistance breeding has been in the application of marker-assisted selection (MAS) for pyramided resistance genes in seedling progenies, but they also are an important tool for germplasm screening for sources of resistance (see Sect. 1.5), in host-pathogen interaction research, and map-based cloning of resistance genes (see Sect. 1.6). The mapping of resistance gene loci increasingly shows that they are often linked (Hemmat et al. 2003; Bus et al. 2005a, b), or form part of a gene cluster (Vinatzer et al. 2001; Xu and Korban 2002b). Recent research has also shown that quantitative trait loci (QTL), e.g. for scab resistance, map to the same chromosomal regions as major genes (Durel et al. 2003; Calenge et al. 2004), which suggests that these QTLs probably include residual resistance of "defeated" major effect genes (Pedersen and Leath 1988). The same research has shown that some QTLs are isolate-specific, which suggests that they conform to a gene-for-gene relationship and therefore are subjected to the same risk of resistance "breakdown" as major effect genes (see Sect. 1.4). In apple, gene-for-gene relationships have been demonstrated for *Venturia inaequalis* (Boone and Keitt 1957; Williams and Shay 1957; Bagga and Boone 1968a, b); and apple-cedar rust *Gymnosporangium juniperi-virginianae* (McNew 1938; Niederhauser and Whetzell 1940; Aldwinckle 1975b). The presence of biotypes overcoming major resistance genes suggests that gene-for-gene interactions exist for woolly apple aphid (*Eriosoma lanigerum* Hausm.) (Giliomee et al. 1968; Sandanayaka et al. 2003) and the rosy leaf curling aphid (*Dysaphis devecta* Wlk.) (Alston and Briggs 1968, 1977). Major gene resistances against powdery mildew are also common, while resistance to diseases, such as fire blight and crown rot are predominantly under polygenic control. The same applies to polyphagous insect species, such as leafrollers, although it recently was shown that the resistance to the New Zealand native leafroller species *Ctenopseustis obliquana* Walk. in Prima is controlled by a major gene (Wearing et al. 2003).

QTL mapping is becoming more important in apple breeding as more QTLs are detected not only for pest and disease resistance characters, but increasingly for fruit and tree characters as well (King et al. 2000, 2001; Durel et al. 2003; Liebhard et al. 2003a, c; Calenge et al. 2004; Stankiewicz-Kosyl et al. 2005). Successful mapping of QTL for use by breeders re-

Table 2. Major genes for resistance or susceptibility[z] in apple

Gene	Species	*Malus* source	Reference
Apple scab			
Va	*Venturia inaequalis*	Antonovka PI172623	(Hough et al. 1970)
Vb	*Venturia inaequalis*	Hansen's baccata #2	(Dayton and Williams 1968)
Vc	*Venturia inaequalis*	Cathay	(Korban and Chen 1992)
Vbj	*Venturia inaequalis*	*Malus baccata jackii*	(Dayton and Williams 1968)
Vd	*Venturia inaequalis*	Durello di Forlí	(Tartarini et al. 2004)
Vf	*Venturia inaequalis*	*M. floribunda* 821	(Hough et al. 1953)
Vfh	*Venturia inaequalis*	*M. floribunda* 821	(Bénaouf and Parisi 2000)
Vg	*Venturia inaequalis*	Golden Delicious	(Bénaouf et al. 1997)
Vh8	*Venturia inaequalis*	*M. sieversii* W193B	(Bus et al. 2005a)
Vj	*Venturia inaequalis*	Jonsib	(Korban and Chen 1992)
Vm	*Venturia inaequalis*	*M. micromalus* 245-38	(Dayton et al. 1970a)
Vh2	*Venturia inaequalis*	Russian apple R12740-7A	(Bus et al. 2005b)
Vr2	*Venturia inaequalis*	Russian apple R12740-7A	(Patocchi et al. 2003)
Vh4	*Venturia inaequalis*	Russian apple R12740-7A	(Bus et al. 2005b)
Powdery mildew			
Pl-1	*Podosphaera leucotricha*	*M.* x *robusta* OP 3762	(Knight and Alston 1968)
Pl-2	*Podosphaera leucotricha*	*M.* x *zumi* OP 3752	(Knight and Alston 1968)
Pl-8	*Podosphaera leucotricha*	*M. sargenti* 843	(Korban and Dayton 1983)
Pl-d	*Podosphaera leucotricha*	D12	(Visser and Verhaegh 1980)
Pl-m	*Podosphaera leucotricha*	Mildew Immune Selection	(Dayton 1977)
Pl-w	*Podosphaera leucotricha*	White Angel	(Batlle and Alston 1996)
Aphids			
Er-1	*Eriosoma lanigerum*	Northern Spy	(Knight et al. 1962)
Er-2	*Eriosoma lanigerum*	*M.* x *robusta*	(King et al. 1991)
Er-3	*Eriosoma lanigerum*	Aotea	(Bus et al. 2000)
Sd-1	*Dysaphis devecta*	Cox's Orange Pippin	(Alston and Briggs 1968)
Sd-2	*Dysaphis devecta*	Northern Spy	(Alston and Briggs 1977)
Sd-3	*Dysaphis devecta*	*M.* x *robusta* OP MAL59/9	(Alston and Briggs 1977)
Sm-h	*Dysaphis plantaginea*	*M.* x *robusta* OP MAL59/9	(Alston and Briggs 1970)
Miscellaneous pests and diseases			
Cob-1	*Ctenopseustis obliquana*	Prima	(Wearing et al. 2003)
Gb[z]	*Glomerella cingulata*	Golden Delicious	(Thompson and Taylor 1971)
Gy-a	*Gymnosporangium juniperi-virginianae*	Spartan	(Aldwinckle et al. 1977)
Gy-b	*Gymnosporangium juniperi-virginianae*	Spartan	(Aldwinckle et al. 1977)
Pc	*Phytophthora cactorum*	Northern Spy	(Alston 1970)
Ps-1[z]	*Phyllosticta solitaria*	Jonathan	(Mowry and Dayton 1964)
Ps-2[z]	*Phyllosticta solitaria*	Idared	(Mowry and Dayton 1964)

quires appropriate and rigorous phenotyping techniques, as well as maps saturated with markers that are transportable across genetic backgrounds. The development of the genetic marker maps, e.g. Liebhard et al. (2002, 2003b), perhaps is the easier task, as the meaningful measurement of some quantitatively inherited characters, such as fruit texture (King et al. 2001), is difficult and further complicated by environmental factors (Kearsey and Luo 2003).

In this chapter we describe the advances made in the development and application of molecular techniques in apple breeding to date. We cover the areas of genetic map construction, gene mapping, identification of QTLs, the application of MAS and map-based cloning, following the gene annotation of Alston et al. (2000). Finally, we will discuss the most advanced technologies that are being developed, and future directions of cultivar improvement.

1.2 Construction of Genetic Maps

1.2.1 Brief History of Genetic Mapping in Apple

The earliest genetic maps of apple were developed in the USA and took advantage of the ready availability of Random Amplified Polymorphic DNA (RAPD) markers during the nineties. They also included a small number of isoenzyme markers (Hemmat et al. 1994; Conner et al. 1997). These maps were specific to the genetic background of the mapping parents because of the poor transferability of RAPD markers. For that reason, an international initiative based in Europe developed a genetic map with a number of codominant transportable markers. These were mostly Restriction Fragment Length Polymorphisms (RFLPs) plus a few microsatellite markers (Maliepaard et al. 1998). The most complete map to date is constructed with 129 microsatellites, as well as larger numbers of dominant Amplified Fragment Length Polymorphisms (AFLPs) and RAPDs to assist in filling in gaps (Liebhard et al. 2003b). Such robust polymerase chain reaction (PCR)-based saturated reference maps are essential for whole genome scanning and for understanding complex traits controlled by several Quantitative Trait Loci (QTLs). Several groups worldwide are currently developing transportable genetic maps for apple and a fully saturated consensus map of apple is still required.

1.2.2 First-Generation Maps

Progress in construction of apple genetic maps is summarized in Table 3. The first map (Hemmat et al. 1994) exhibits isoenzyme, RFLP and RAPD markers distributed over 21 and 24 linkage groups, for the cultivars Rome Beauty and White Angel, respectively. Neither of these cultivars was being used in the Cornell University breeding program at the time. However, the second set of maps, for accessions Wijcik McIntosh, NY 75441-67 and NY 75441-58, that were being used in that breeding program, also relied heavily on the contribution of RAPD markers, limiting their usefulness in other progenies. The number of linkage groups (19, 16 and 18 respectively) had been reduced to a number closer to that of the chromosome number of *Malus* ($n = 17$), indicating that these maps were more saturated than previous ones (Conner et al. 1997).

Because of the low transferability of RAPD markers between different cultivars and laboratories, several groups have developed more specific microsatellite markers (also called SSRs or Simple Sequence Repeats). These highly polymorphic and transferable markers proved to be the marker of choice. The first microsatellite markers mapped in apple included some of those identified by Guilford et al. (1997) and Hemmat et al. (1997), as well as four developed by Horticulture Research International (HRI), Wellesbourne, UK. The use of these markers, plus a number of codominantly segregating isoenzymes and RFLPs in a Prima × Fiesta population of 152 seedlings, permitted alignment of the 17 linkage groups and construction of the first integrated apple map (Maliepaard et al. 1998). This initial apple reference map utilized a small number of AFLP markers as well as RAPDs to assist in filling the longer intervals. The cultivars Prima and Fiesta are used in European breeding programs and as such are central to the succession of research programs on genetic mapping in apple situated there: European Apple Genome Mapping Project (EAGMP), Durable Apple Resistance in Europe (DARE) (Lespinasse and Durel 1999) and High-Quality Disease Resistant Apples for a Sustainable Agriculture (HiDRAS). Information from this collaboration, plus that from the mapping of 41 microsatellite markers in the White Angel × Rome Beauty population (Hemmat et al. 2003) enabled cross-referencing of US linkage group numbering with that adopted in Europe. This Prima × Fiesta population has been used to map QTL for apple scab (Durel et al. 2003) and fireblight (Calenge et al. 2005b) (see Sect. 1.4.2).

The genetic map constructed in a Fiesta × Discovery population of 267 individuals (Liebhard et al. 2003b) contains the largest core of robust PCR based markers to date, namely 129 microsatellites, including loci identified by Gianfranceschi et al. (1998) and Liebhard et al. (2002). These markers are supplemented by 710 dominant RAPDs and AFLPs, enabling a good coverage of the 17 linkage groups. The construction of this map was aided by the use of a robotic workstation to set up the large number of PCR reactions required. This reference map has already been used as the framework for mapping QTL (Liebhard et al. 2003a, c; Calenge et al. 2005a, b) – (see Sect. 1.4 below) and Resistance gene analogs (RGAs) that are homologues of nucleotide binding-site (NBS)/leucine-rich repeat resistance genes (LRRs)

Table 3. Genetic maps of apple

Cross	Pop size	Number of markers		Marker Type						Length of map	Reference	Traits
		Female parent	Male parent	Isoen-zyme	RFLPs	RAPD	AFLP	Micro-satellite	Others	cM (female, male)		
Rome Beauty × White Angel	56	156	253	34	8	367	–	–	–	–, 950	Hemmat et al. 1994	*Pl-w*
Wijcik McIntosh × NY 75441-67	114	238	110	6	–	138	–	–	–	1206 (integrated WM), 692	Connor et al. 1997	Skin color, *Vf*, columnar habit, juice pH
Wijcik McIntosh × NY 75441-58	172	181	183	6	–	266	–	–	–	1206, 898	–	
Prima × Fiesta	152	194	163	17	124	133	9	10	SCAR = 1 *Rf*, BC226	842, 984	Maliepaard et al. 1998	*Vf*, *Sd-1*, *Ma*, *SI*
Fiesta × Discovery	112	202	227	–	–	217		118		914, 1015	Liebhard et al. 2002	–
Fiesta × Discovery.	267	439	499	–	–	235	475	129	SCAR = 1 *Rf*, BC226	1144, 1455 (F × D integrated 1371)	Liebhard et al. 2003b	–
	–	–	–	–	–	–	–	–				–
Fiesta × Discovery	44 (subset of 112)	–	–	–	–	–	–	–	18 RGAs (NBS LRR)	Partial map, based on Liebhard et al. 2003b	Baldi et al. 2004	RGAs
Discovery × TN10-8	149	–	–	13	–	–	102	62	22 RGAs (43 bands generated by NBS profiling mapped)	1,219 (integrated map)	Calenge et al. 2004, 2005	*Vg*, scab QTL, RGAS
Telamon × Braeburn	257	259	264	–	–	–	463	20		1039, 1245	Kenis and Keulemans 2005	For QTL analysis growth habit and fruit quality