

Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources Temperate Fruits

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Temperate Fruits

 Springer

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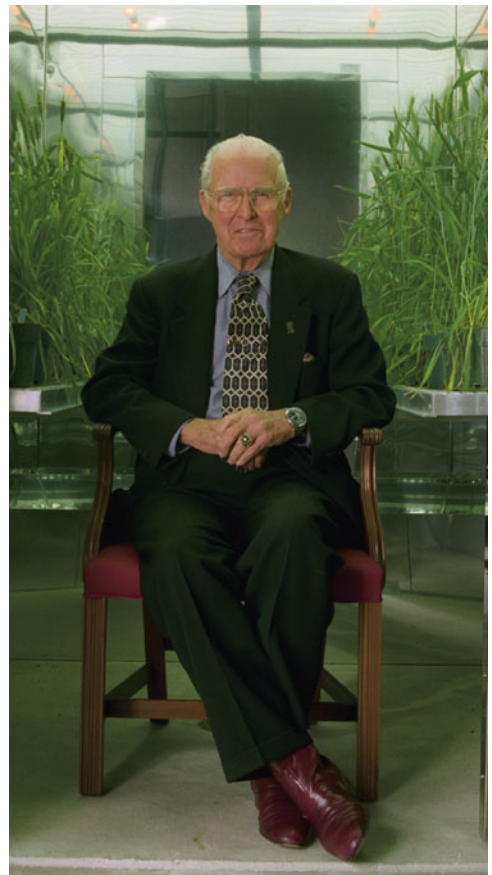
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Dedication

Dr. Norman Ernest Borlaug,¹ the Father of Green Revolution, is well respected for his contributions to science and society. There was or is not and never will be a single person on this Earth whose single-handed service to science could save millions of people from death due to starvation over a period of over four decades like Dr. Borlaug's. Even the Nobel Peace Prize he received in 1970 does not do such a great and noble person as Dr. Borlaug justice. His life and contributions are well known and will remain in the pages of history of science. I wish here only to share some facets of this elegant and ideal personality I had been blessed to observe during my personal interactions with him.

It was early 2007 while I was at the Clemson University as a visiting scientist one of my lab colleagues told me that “somebody wants to talk to you; he appears to be an old man”. I took the telephone receiver casually and said hello. The response from the other side was – “I am Norman Borlaug; am I talking to Chitta?” Even a million words would be insufficient to define and depict the exact feelings and thrills I experienced at that moment!



¹The photo of Dr. Borlaug was kindly provided by Julie Borlaug (Norman Borlaug Institute for International Agriculture, Texas A&M Agriculture) the granddaughter of Dr. Borlaug.

I had seen Dr. Borlaug only once, way back in 1983, when he came to New Delhi, India to deliver the Coromandal Lecture organized by Prof. M.S. Swaminathan on the occasion of the 15th International Genetic Congress. However, my real interaction with him began in 2004 when I had been formulating a 7-volume book series entitled *Genome Mapping and Molecular Breeding in Plants*. Initially, I was neither confident of my ability as a series/book editor nor of the quality of the contents of the book volumes. I sent an email to Dr. Borlaug attaching the table of contents and the tentative outline of the chapters along with manuscripts of only a few sample chapters, including one authored by me and others, to learn about his views as a source of inspiration (or caution!) I was almost sure that a person of his stature would have no time and purpose to get back to a small science worker like me. To my utter (and pleasant) surprise I received an email from him that read: “May all Ph.D.’s, future scientists, and students that are devoted to agriculture get an inspiration as it refers to your work or future work from the pages of this important book. My wholehearted wishes for a success on your important job”. I got a shot in my arm (and in mind for sure)! Rest is a pleasant experience – the seven volumes were published by Springer in 2006 and 2007, and were welcome and liked by students, scientists and their societies, libraries, and industries. As a token of my humble regards and gratitude, I sent Dr. Borlaug the Volume I on *Cereals and Millets* that was published in 2006. And here started my discovery of the simplest person on Earth who solved the most complex and critical problem of people on it – hunger and death.

Just one month after receiving the volume, Dr. Borlaug called me one day and said, “Chitta, you know I cannot read a lot now-a-days, but I have gone through only on the chapters on wheat, maize and rice. Please excuse me. Other chapters of this and other volumes of the series will be equally excellent, I believe”. He was highly excited to know that many other Nobel Laureates including Profs. Arthur Kornberg, Werner Arber, Phillip Sharp, Günter Blobel, and Lee Hartwell also expressed generous comments regarding the utility and impact of the book series on science and the academic society. While we were discussing many other textbooks and review book series that I was editing at that time, again in my night hours for the benefit of students, scientists, and industries, he became emotional and said to me, “Chitta, forget about your original contributions to basic and applied sciences, you deserved Nobel Prize for Peace like me for providing academic foods to millions of starving students and scientists over the world particularly in the developing countries. I will recommend your name for the World Food Prize, but it will not do enough justice to the sacrifice you are doing for science and society in your sleepless nights over so many years. Take some rest Chitta and give time to Phullara, Sourav and Devleena” (he was so particular to ask about my wife and our kids during most of our conversations). I felt honored but really very ashamed as I am aware of my almost insignificant contribution in comparison to his monumental contribution and thousands of scientists over the world are doing at least hundred-times better jobs than me as scientist or author/editor of books! So, I was unable to utter any words for a couple of minutes but realized later that he must be too affectionate to me and his huge affection is the best award for a small science worker as me!

In another occasion he wanted some documents from me. I told him that I will send them as attachments in emails. Immediately he shouted and told me: “You know, Julie (his granddaughter) is not at home now and I cannot check email myself. Julie does this for me. I can type myself in type writer but I am not good in computer. You know what, I have a xerox machine and it receives fax also. Send me

the documents by fax”. Here was the ever-present child in him. Julie emailed me later to send the documents as attachment to her as the ‘xerox machine’ of Dr. Borlaug ran out of ink!

Another occasion is when I was talking with him in a low voice, and he immediately chided me: “You know that I cannot hear well now-a-days; I don’t know where Julie has kept the hearing apparatus, can’t you speak louder?” Here was the fatherly figure who was eager to hear each of my words!

I still shed tears when I remember during one of our telephone conversations he asked: “You know I have never seen you, can you come to Dallas in the near future by chance?” I remember we were going through a financial paucity at that time and I could not make a visit to Dallas (Texas) to see him, though it would have been a great honor.

In late 2007, whenever I tried to talk to Dr. Borlaug, he used to beckon Julie to bring the telephone to him, and in course of time Julie used to keep alive all the communications between us when he slowly succumbed to his health problems.

The remaining volumes of the *Genome Mapping and Molecular Breeding in Plants* series were published in 2007, and I sent him all the seven volumes. I wished to learn about his views. During this period he could not speak and write well. Julie prepared a letter based on his words to her that read: “Dear Chitta, I have reviewed the seven volumes of the series on *Genome Mapping and Molecular Breeding in Plants*, which you have authored. You have brought together genetic linkage maps based on molecular markers for the most important crop species that will be a valuable guide and tool to further molecular crop improvements. Congratulations for a job well done”.

During one of our conversations in mid-2007, he asked me what other book projects I was planning for Ph.D. students and scientists (who had always been his all-time beloved folks). I told him that the wealth of wild species already utilized and to be utilized for genetic analysis and improvement of domesticated crop species have not been deliberated in any book project. He was very excited and told me to take up the book project as soon as possible. But during that period I had a huge commitment to editing a number of book volumes and could not start the series he was so interested about.

His sudden demise in September 2009 kept me so morose for a number of months that I could not even communicate my personal loss to Julie. But in the meantime, I formulated a 10-volume series on *Wild Crop Relatives: Genomic and Breeding Resources* for Springer. And whom else to dedicate this series to other than Dr. Borlaug!

I wrote to Julie for her formal permission and she immediately wrote me: “Chitta, Thank you for contacting me and yes I think my grandfather would be honored with the dedication of the series. I remember him talking of you and this undertaking quite often. Congratulations on all that you have accomplished!” This helped me a lot as I could at least feel consoled that I could do a job he wanted me to do and I will always remain grateful to Julie for this help and also for taking care of Dr. Borlaug, not only as his granddaughter but also as the representative of millions of poor people from around the world and hundreds of plant and agricultural scientists who try to follow his philosophy and worship him as a father figure.

It is another sad experience of growing older in life that we walk alone and miss the affectionate shadows, inspirations, encouragements, and blessings from the fatherly figures in our professional and personal lives. How I wish I could treat my next generations in the same way as personalities like Mother Teresa and Dr. Norman Borlaug and many other great people from around the world treated me!

During most of our conversations he used to emphasize on the immediate impact of research on the society and its people. A couple of times he even told me that my works on molecular genetics and biotechnology, particularly of 1980s and 1990s, have high fundamental importance, but I should also do some works that will benefit people immediately. This advice elicited a change in my thoughts and workplans and since then I have been devotedly endeavoring to develop crop varieties enriched with phytomedicines and nutraceuticals. Borlaug influenced both my personal and professional life, particularly my approach to science, and I dedicate this series to him in remembrance of his great contribution to science and society and for all his personal affection, love and blessings for me.

I emailed the above draft of the dedication page to Julie for her views and I wish to complete my humble dedication with great satisfaction with the words of Julie who served as the living ladder for me to reach and stay closer to such as great human being as Dr. Borlaug and express my deep regards and gratitude to her. Julie's email read: "Chitta, Thank you for sending me the draft dedication page. I really enjoyed reading it and I think you captured my grandfather's spirit wonderfully. . . . So thank you very much for your beautiful words. I know he would be and is honored".

Clemson, USA

Chittaranjan Kole

Preface

Wild crop relatives have been playing enormously important roles both in the depiction of plant genomes and the genetic improvement of their cultivated counterparts. They have contributed immensely to resolving several fundamental questions, particularly those related to the origin, evolution, phylogenetic relationship, cytological status and inheritance of genes of an array of crop plants; provided several desirable donor genes for the genetic improvement of their domesticated counterparts; and facilitated the innovation of many novel concepts and technologies while working on them directly or while using their resources. More recently, they have even been used for the verification of their potential threats of gene flow from genetically modified plants and invasive habits. Above all, some of them are contributing enormously as model plant species to the elucidation and amelioration of the genomes of crop plant species.

As a matter of fact, as a student, a teacher, and a humble science worker I was, still am and surely will remain fascinated by the wild allies of crop plants for their invaluable wealth for genetics, genomics and breeding in crop plants and as such share a deep concern for their conservation and comprehensive characterization for future utilization. It is by now a well established fact that wild crop relatives deserve serious attention for domestication, especially for the utilization of their phytomedicines and nutraceuticals, bioenergy production, soil reclamation, and the phytoremediation of ecology and environment. While these vastly positive impacts of wild crop relatives on the development and deployment of new varieties for various purposes in the major crop plants of the world agriculture, along with a few negative potential concerns, are envisaged the need for reference books with comprehensive deliberations on the wild relatives of all the major field and plantation crops and fruit and forest trees is indeed imperative. This was the driving force behind the inception and publication of this series.

Unlike the previous six book projects I have edited alone or with co-editors, this time it was very difficult to formulate uniform outlines for the chapters of this book series for several obvious reasons. Firstly, the status of the crop relatives is highly diverse. Some of them are completely wild, some are sporadically cultivated and some are at the initial stage of domestication for specific breeding objectives recently deemed essential. Secondly, the status of their conservation varies widely: some have been conserved, characterized and utilized; some have been eroded completely except for their presence in their center(s) of origin; some are at-risk or endangered due to genetic erosion, and some of them have yet to be explored. The third constraint is the variation in their relative worth, e.g. as academic model, breeding resource, and/or potential as “new crops”.

The most perplexing problem for me was to assign the chapters each on a particular genus to different volumes dedicated to crop relatives of diverse crops grouped based on their utility. This can be exemplified with *Arabidopsis*, which has primarily benefited the Brassicaceae crops but also facilitated genetic analyses and improvement in crop plants in other distant families; or with many wild relatives of forage crops that paved the way for the genetic analyses and breeding of some major cereal and millet crops. The same is true for wild crop relatives such as *Medicago truncatula*, which has paved the way for in-depth research on two crop groups of diverse use: oilseed and pulse crops belonging to the Fabaceae family. The list is too long to enumerate. I had no other choice but to compromise and assign the genera of crop relatives in a volume on the crop group to which they are taxonomically the closest and to which they have relatively greater contributions. For example, I placed the chapter on genus *Arabidopsis* in the volume on oilseeds, which deals with the wild relatives of Brassicaceae crops amongst others.

However, we have tried to include deliberations pertinent to the individual genera of the wild crop relatives to which the chapters are devoted. Descriptions of the geographical locations of origin and genetic diversity, geographical distribution, karyotype and genome size, morphology, etc. have been included for most of them. Their current utility status – whether recognized as model species, weeds, invasive species or potentially cultivable taxa – is also delineated. The academic, agricultural, medicinal, ecological, environmental and industrial potential of both the cultivated and/or wild allied taxa are discussed.

The conservation of wild crop relatives is a much discussed yet equally neglected issue albeit the in situ and ex situ conservations of some luckier species were initiated earlier or are being initiated now. We have included discussions on what has happened and what is happening with regard to the conservation of the crop relatives, thanks to the national and international endeavors, in most of the chapters and also included what should happen for the wild relatives of the so-called new, minor, orphan or future crops.

The botanical origin, evolutionary pathway and phylogenetic relationship of crop plants have always attracted the attention of plant scientists. For these studies morphological attributes, cytological features and biochemical parameters were used individually or in combinations at different periods based on the availability of the required tools and techniques. Access to different molecular markers based on nuclear and especially cytoplasmic DNAs that emerged after 1980 refined the strategies required for precise and unequivocal conclusions regarding these aspects. Illustrations of these classical and recent tools have been included in the chapters.

Positioning genes and defining gene functions required in many cases different cytogenetic stocks, including substitution lines, addition lines, haploids, monoloids and aneuploids, particularly in polyploid crops. These aspects have been dealt in the relevant chapters. Employment of colchicoidy, fluorescent or genomic in situ hybridization and Southern hybridization have reinforced the theoretical and applied studies on these stocks. Chapters on relevant genera/species include details on these cytogenetic stocks.

Wild crop relatives, particularly wild allied species and subspecies, have been used since the birth of genetics in the twentieth century in several instances such as studies of inheritance, linkage, function, transmission and evolution of genes. They have been frequently used in genetic studies since the advent of molecular markers. Their involvement in molecular mapping has facilitated the development of mapping

populations with optimum polymorphism to construct saturated maps and also illuminating the organization, reorganization and functional aspects of genes and genomes. Many phenomena such as genomic duplication, genome reorganization, self-incompatibility, segregation distortion, transgressive segregation and defining genes and their phenotypes have in many cases been made possible due to the utilization of wild species or subspecies. Most of the chapters contain detailed elucidations on these aspects.

The richness of crop relatives with biotic and abiotic stress resistance genes was well recognized and documented with the transfer of several alien genes into their cultivated counterparts through wide or distant hybridization with or without employing embryo-rescue and mutagenesis. However, the amazing revelation that the wild relatives are also a source of yield-related genes is a development of the molecular era. Apomictic genes are another asset of many crop relatives that deserve mention. All of these past and the present factors have led to the realization that the so-called inferior species are highly superior in conserving desirable genes and can serve as a goldmine for breeding elite plant varieties. This is particularly true at a point when natural genetic variability has been depleted or exhausted in most of the major crop species, particularly due to growing and promoting only a handful of so-called high-yielding varieties while disregarding the traditional cultivars and landraces. In the era of molecular breeding, we can map desirable genes and polygenes, identify their donors and utilize tightly linked markers for gene introgression, mitigating the constraint of linkage drag, and even pyramid genes from multiple sources, cultivated or wild taxa. The evaluation of primary, secondary and tertiary gene pools and utilization of their novel genes is one of the leading strategies in present-day plant breeding. It is obvious that many wide hybridizations will never be easy and involve near-impossible constraints such as complete or partial sterility. In such cases gene cloning and gene discovery, complemented by intragenic breeding, will hopefully pave the way for success. The utilization of wild relatives through traditional and molecular breeding has been thoroughly enumerated over the chapters throughout this series.

Enormous genomic resources have been developed in the model crop relatives, for example *Arabidopsis thaliana* and *Medicago truncatula*. BAC, cDNA and EST libraries have also been developed in some other crop relatives. Transcriptomes and metabolomes have also been dissected in some of them. However, similar genomic resources are yet to be constructed in many crop relatives. Hence this section has been included only in chapters on the relevant genera.

In this book series, we have included a section on recommendations for future steps to create awareness about the wealth of wild crop relatives in society at large and also for concerns for their alarmingly rapid decrease due to genetic erosion. The authors of the chapters have also emphasized on the imperative requirement of their conservation, envisaging the importance of biodiversity. The importance of intellectual property rights and also farmers' rights as owners of local landraces, botanical varieties, wild species and subspecies has also been dealt in many of the chapters.

I feel satisfied that the authors of the chapters in this series have deliberated on all the crucial aspects relevant to a particular genus in their chapters.

I am also very pleased to present many chapters in this series authored by a large number of globally reputed leading scientists, many of whom have contributed to the development of novel concepts, strategies and tools of genetics, genomics and breeding and/or pioneered the elucidation and improvement of particular plant

genomes using both traditional and molecular tools. Many of them have already retired or will be retiring soon, leaving behind their legacies and philosophies for us to follow and practice. I am saddened that a few of them have passed away during preparation of the manuscripts for this series. At the same time, I feel blessed that all of these stalwarts shared equally with me the wealth of crop relatives and contributed to their recognition and promotion through this endeavor.

I would also like to be candid with regard to my own limitations. Initially I planned for about 150 chapters devoted to the essential genera of wild crop relatives. However, I had to exclude some of them either due to insignificant progress made on them during the preparation of this series, my failure to identify interested authors willing to produce acceptable manuscripts in time or authors' backing out in the last minute, leaving no time to find replacements. I console myself for this lapse with the rationale that it is simply too large a series to achieve complete satisfaction on the contents. Still I was able to arrange about 125 chapters in the ten volumes, contributed by nearly 400 authors from over 40 countries of the world. I extend my heartfelt thanks to all these scientists, who have cooperated with me since the inception of this series not only with their contributions, but also in some cases by suggesting suitable authors for chapters on other genera. As happens with a mega-series, a few authors had delays for personal or professional reasons, and in a few cases, for no reason at all. This caused delays in the publication of some of the volumes and forced the remaining authors to update their manuscripts and wait too long to see their manuscripts in published form. I do shoulder all the responsibilities for this myself and tender my sincere apologies.

Another unique feature of this series is that the authors of chapters dedicated to some genera have dedicated their chapters to scientists who pioneered the exploration, description and utilization of the wild species of those genera. We have duly honored their sincere decision with equal respect for the scientists they rightly reminded us to commemorate.

Editing this series was, to be honest, very taxing and painstaking, as my own expertise is limited to a few cereal, oilseed, pulse, vegetable, and fruit crops, and some medicinal and aromatic plants. I spent innumerable nights studying to attain the minimum eligibility to edit the manuscripts authored by experts with even life-time contributions on the concerned genera or species. However, this indirectly awakened the "student-for-life" within me and enriched my arsenal with so many new concepts, strategies, tools, techniques and even new terminologies! Above all, this helped me to realize that individually we know almost nothing about the plants on this planet! And this realization strikingly reminded me of the affectionate and sincere advice of Dr. Norman Borlaug to keep abreast with what is happening in the crop sciences, which he used to do himself even when he had been advised to strictly limit himself to bed rest. He was always enthusiastic about this series and inspired me to take up this huge task. This is one of the personal and professional reasons I dedicated this book series to him with a hope that the present and future generations of plant scientists will share the similar feelings of love and respect for all plants around us for the sake of meeting our never-ending needs for food, shelter, clothing, medicines, and all other items used for our basic requirements and comfort. I am also grateful to his granddaughter, Julie Borlaug, for kindly extending her permission to dedicate this series to him.

I started editing books with the 7-volume series on Genome Mapping and Molecular Breeding in Plants with Springer way back in 2005, and I have since

edited many other book series with Springer. I always feel proud and satisfied to be a member of the Springer family, particularly because of my warm and enriching working relationship with Dr. Sabine Schwarz and Dr. Jutta Lindenborn, with whom I have been working all along. My special thanks go out to them for publishing this “dream series” in an elegant form and also for appreciating my difficulties and accommodating many of my last-minute changes and updates.

I would be remiss in my duties if I failed to mention the contributions of Phullara – my wife, friend, philosopher and guide – who has always shared with me a love of the collection, conservation, evaluation, and utilization of wild crop relatives and has enormously supported me in the translation of these priorities in my own research endeavors – for her assistance in formulating the contents of this series, for monitoring its progress and above all for taking care of all the domestic and personal responsibilities I am supposed to shoulder. I feel myself alien to the digital world that is the sine qua non today for maintaining constant communication and ensuring the preparation of manuscripts in a desirable format. Our son Sourav and daughter Devleena made my life easier by balancing out my limitations and also by willingly sacrificing the spare amount of time I ought to spend with them. Editing of this series would not be possible without their unwavering support.

I take the responsibility for any lapses in content, format and approach of the series and individual volumes and also for any other errors, either scientific or linguistic, and will look forward to receiving readers’ corrections or suggestions for improvement.

As I mentioned earlier this series consists of ten volumes. These volumes are dedicated to wild relatives of Cereals, Millets and Grasses, Oilseeds, Legume Crops and Forages, Vegetables, Temperate Fruits, Tropical and Subtropical Fruits, Industrial Crops, Plantation and Ornamental Crops, and Forest Trees.

This volume “Wild Crop Relatives – Genomic and Breeding Resources: Temperate Fruits” includes 11 chapters dedicated to *Cydonia*, *Fragaria*, *Malus*, *Muscadiniana*, *Olea*, *Pistacia*, *Prunus*, *Pyrus*, *Rubus*, *Vaccinium*, and *Vitis*. The chapters of this volume were authored by 27 scientists from 8 countries of the world, namely India, Italy, Japan, Portugal, Russia, Spain, UK, and the USA.

It is my sincere hope that this volume and the series as a whole will serve the requirements of students, scientists and industries involved in studies, teaching, research and the extension of temperate fruit crops with an intention of serving science and society.

Clemson, USA

Chittaranjan Kole

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Abbreviations

2,4-D	2,4-Dichlorophenoxyacetic acid
AAMTR	Average annual minimum temperature range
AAT	Alcohol transferase
AAT	Aspartate aminotransferase
ACC	1-Aminocyclopropane-1-carboxylate
ADH	Alcohol dehydrogenase
AMOVA	Analysis of molecular variance
Ana	Allele for susceptibility to <i>Alternaria alternata</i>
Ani	Allele for susceptibility to <i>Alternaria alternata</i>
AQP	Aquaporin
ARS	Agricultural Research Service (of USDA)
AVG	Aminoethoxyvinyl glycine
BA	Benzyladenine
BAC	Bacterial artificial chromosome
BBDG	The Blueberry Genomics Database
BC ₁	First backcross generation
BS	Baron Solemacher
BSA	Bulk segregant analysis
CAPS	Cleaved amplified polymorphic sequence
CATCN-PGR	Central Asian and Transcaucasian Network on Plant Genetic Resources
cDNA	Complementary DNA
cM	Centi-Morgan
<i>CoTFL1</i>	<i>Cydonia oblonga</i> homolog of terminal flower gene 1
<i>CoTFL2</i>	<i>Cydonia oblonga</i> homolog of terminal flower gene 2
COX	Cytochrome-C oxidase
cpDNA	Chloroplast DNA
DAPI	4'-6-Diamidino-2-phenylindole
DGAT	Diacylglycerol acyltransferase
DHAR	Dehydroascorbate reductase
DHFR	Dihydroflavonol reductase
DIA	Diaphorase
DN	Day-neutral
Dp-1	Dominant allele for resistance to <i>Dysaphis pyri</i>
EMBL	European Molecular Biology Laboratory
EMR	East Malling Research
ENP	Endopeptidase

EST	Expressed sequence tag
EUCPPGR	European Cooperative Program for Plant Genetic Resources
EURISCO	European Network of ex situ National Plant Germplasm Inventories
F ₁	First filial generation
F ₂	Second filial generation
F ₃	Third filial generation
FAO	Food and Agriculture Organization of the United Nations
FAOSTAT	FAO Statistics
FB	<i>Fragaria bucharica</i>
Fe(III)EDTA	Ferric ethylenediaminetetraacetic acid
FV	<i>Fragaria vesca</i>
FWt	Fresh weight
GA ₃	Gibberellic acid-3
GBSSI	Granule-bound starch synthase I
<i>gbsl/GBSSI</i>	Granule bound starch synthase gene I
GDR	Genome Database for Rosaceae
Gfp	Green fluorescent protein
GM	Genetic modification
GOT	Glutamate oxaloacetate transaminase
GPH	Gene pair haplotype
GRIN	Germplasm Resources Information Network (USA)
GSA	Genome scanning approach
GSI	Gametophytic self-incompatibility
GSS	Genome survey sequences
Gus/GUS	β-Glucuronidase
H	Hapil
Ha	Hectare
HiDRAS	High-quality disease resistant apples
HPLC	High performance liquid chromatography
HR	Hypersensitive reaction
<i>I</i>	Russet-inhibiting gene in <i>Pyrus pyrifolia</i>
IBA	Indole butyric acid
IBPGR	International Board for Plant Genetic Resources
IDH	Isocitrate dehydrogenase
INRA	Institut National de la Recherché Agronomique
ISSR	Inter-simple sequence repeat
ITS	Internal transcribed spacer
ITSR	Internal transcribed spacer region
IUCN	International Union for the Conservation of Nature
LAP	Leucine aminopeptidase
LD	Linkage disequilibrium
<i>LFY</i>	Leafy gene
LG	Linkage group
LTR	Long terminal repeat
<i>M</i>	Russet-modifying gene
MAS	Marker-assisted selection
MAT	Multi-auto-transformation
matK	Megakaryocyte-associated tyrosine kinase K

Mbp	Mega base pairs
MFLP	Microsatellite-anchored fragment length polymorphism
mRNA	Messenger RNA
MT	Million tons
NAA	α -Naphthaleneacetic acid
NAD(P)H	Nicotinamide dinucleotide phosphate (reduced)
NCBI	National Center for Biotechnology Information
ndhF	NAD(P)H dehydrogenase F
NPGS	National Plant Germplasm System
nptII	Neomycin phosphotransferase II
NrITS	Nuclear internal transcribed spacer
ORAC	Oxygen radical absorbance capacity
PAT	Phosphoinositricine acetyl transferase
PCR	Polymerase chain reaction
PGD	6-Phosphogluconate dehydrogenase
PGI	Phosphoglucoisomerase
Pgip	Polygalacturonase-inhibiting protein
PGM	Phosphoglucomutase
PIP	Plasma membrane intrinsic protein
PpACS	ACC synthase locus from <i>Pyrus pyrifolia</i>
PPFD	Photosynthetic photon flux density
PPO	Polyphenol oxidase
PpSFBB	S-locus F-Box brother from <i>Pyrus pyrifolia</i>
PRX/PX	Peroxidase
QTL	Quantitative trait loci
R	Dominant allele for fruit russet in <i>Pyrus pyrifolia</i>
RAPD	Random(ly) amplified polymorphic DNA
Rbc	Ribulose 1,5-bisphosphate carboxylase large subunit
<i>rbcL</i>	Rubisco large subunit
RefSeq	NCBI Reference Sequence database
RFLP	Restriction fragment length polymorphism
RG	Red Gauntlet
RGA	Resistance gene analog
RGAP	RGA polymorphism
Ri	Root-inducing plasmid
Rol	Root loci
<i>rolB</i>	Root locus gene B of <i>Agrobacterium rhizogenes</i>
<i>rolC</i>	Root locus gene C of <i>Agrobacterium rhizogenes</i>
RS	Russian seedling
Rs-AFP2	Antifungal peptide 2 from <i>Raphanus sativus</i>
RT-PCR	Reverse transcriptase PCR
SCAR	Sequence-characterized amplified region
SD	Short-day
Sdh	Shikimate dehydrogenase
SE	Somatic embryogenesis
SFBB	S-locus F-box brothers
S-genotype	Self-incompatibility genotype
S-locus	Self-incompatibility locus

SNP	Single nucleotide polymorphism
SOD	Superoxide dismutase
SRAP	Sequence-related amplified polymorphism
S-RNase	Self-incompatibility RNase
SSR	Simple sequence repeat
STS	Sequence tagged site
TACy	Total anthocyanin content
TC	Tentative consensus
T-DNA	Tumor-inducing (plasmid Ti)
TDZ	Thidiazuron
TE	Transposable element
tfGDR	Tree fruit Genome Database Resources
<i>TFL1</i>	Terminal flower gene 1
TIGR	The Institute for Genomic Research
TIP	Tonoplast intrinsic protein
<i>trnF</i>	Transfer RNA pseudogene F
<i>trnL</i>	Transfer RNA pseudogene L
uidA	β -Galacturonidase enzyme A
USDA	United States Department of Agriculture
VIVC	<i>Vitis</i> International Variety Catalog
<i>Vn</i>	Dominant allele for resistance to <i>Venturia nashicola</i>
<i>Vnk</i>	Dominant allele from the cultivar “Kinchaku” for resistance to <i>Venturia nashicola</i>
VNTR	Variable number tandem repeat

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Chapter 1

Cydonia

Richard L. Bell and José Manuel Leitão

1.1 Introduction

The genus *Cydonia* is commonly known as quince, and the fruits are pomes, as the species is closely related to apples (*Malus*), pears (*Pyrus*), and Japanese quince (*Chaenomeles*). The name is derived from the name of a Greek city on the island of Crete, Cydonea, now called Canea (Sykes 1972). Quinces have been grown for their fruit for over 2,000 years, as Pliny the Elder described several cultivars in *Historia Naturalis* in 77 CE, and they are thought to have been cultivated in Mesopotamia (Webster 2008). The genus *Cydonia* is monospecific, that is, it is comprised of a single species, *Cydonia oblonga* Mill., and thus, almost all genomic and breeding resources are to be found in existing wild populations and cultivar forms. The exceptions are artificial intergeneric hybrids with apple (*Malus* × *domestica* Borkh.) and Japanese pear (*Pyrus pyrifolia* [Burm. F.] Nakai). Therefore, much of the discussion of the role of crop relatives in the genomics, genetics, and breeding of quince will deal with these hybrids rather than intra-specific hybridization using *Cydonia* germplasm.

1.2 Basic Botany of the Genus *Cydonia*

1.2.1 Distribution and Geographic Locations of Genetic Diversity

The genus is thought to have originated in northern Iran, Turkmenistan, and the Caucasus, including the

countries of Armenia, Azerbaijan, and the Russian Federation. The current distribution includes the warm, temperate areas of central Asia, including the Kopet Dag and Gissar-Darvaz mountain ranges (Vavilov 1930, 1935; Bakhridinov 1985), the Transcaucasus from Daghestan to Talysh, the Caucasus region, and throughout the Middle East, being particularly abundant and diverse in Iran (Khoshbakht and Hammer 2006; Amiri 2008) and Turkey (Ercisli 2004), with populations also in Syria (Thompson 1986), Turkmenistan, and Afghanistan (Frantskevich 1978; Büttner 2001; Webster 2008). It is naturalized and cultivated elsewhere in western Asia and southern Europe, and is cultivated as far north as England, but is particularly well-adapted to the Mediterranean climate and can be found up to 2,500 m above sea level (Bakhridinov 1985). It is adapted to regions with an annual rainfall of more than 800 mm, with regular summer rains, being somewhat drought-sensitive because of a shallow root system. Optimum mean temperature should be about 15°C. The chilling requirement for bud-break is relatively low, ranging from 100 to 500 h. The species is moderately to highly tolerant of low soil pH, but high pH causes chlorosis due to poor uptake of iron.

1.2.2 Taxonomic Position

Cydonia is a member of the subtribe Pyrinae, tribe Pyreae, subfamily Spiraeoideae (formerly Maloideae), family Rosaceae, order Rosales, class Magnoliopsida, and division Magnoliophyta. Sax (1931) concluded that the genera of the Maloideae form a closely related group based on the chromosome number and the presence of intergeneric hybrids. The species was formerly

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Table 1.1 Subspecies, botanical varieties and forma of *Cydonia oblonga* Mill

<i>Cydonia oblonga</i> subsp. <i>oblonga</i>
<i>Cydonia oblonga</i> subsp. <i>integerrima</i> Lobachev
<i>Cydonia oblonga</i> subsp. <i>maliformis</i> (Mill.) Thell.
<i>Cydonia oblonga</i> subsp. <i>pyriformis</i> Medik. ex Thell.
<i>Cydonia oblonga</i> var. <i>oblonga</i>
<i>Cydonia oblonga</i> var. <i>biserrulata</i> Kakhadze
<i>Cydonia oblonga</i> var. <i>integerrima</i>
<i>Cydonia oblonga</i> var. <i>integerrimo-sepala</i> Lobachev
<i>Cydonia oblonga</i> var. <i>integerrimoespala</i> Kakhadze
<i>Cydonia oblonga</i> var. <i>lusitanica</i> (Mill.) C. K. Schneid.
<i>Cydonia oblonga</i> var. <i>maliformis</i> (Mill.) Rehder
<i>Cydonia oblonga</i> var. <i>obpyricarpa</i> Lobachev
<i>Cydonia oblonga</i> var. <i>obpyriformis</i> Lobachev
<i>Cydonia oblonga</i> var. <i>orbiculato-complanata</i> Lobachev
<i>Cydonia oblonga</i> var. <i>ovalicarpa</i> Lobachev
<i>Cydonia oblonga</i> var. <i>ovalis</i> Lobachev
<i>Cydonia oblonga</i> var. <i>plano-cyclocarpa</i> Lobachev
<i>Cydonia oblonga</i> var. <i>pomiformis</i> Lobachev
<i>Cydonia oblonga</i> var. <i>rotundata</i> Kakhadze
<i>Cydonia oblonga</i> var. <i>serrulata</i> C. K. Schneid.
<i>Cydonia oblonga</i> var. <i>typica</i> Kakhadze
<i>Cydonia oblonga</i> var. <i>urceolata</i> Lobachev
<i>Cydonia oblonga</i> forma <i>lusitanica</i> (Mill.) Rehder
<i>Cydonia oblonga</i> forma <i>marmorata</i> (Dippel) C. K. Schneid.
<i>Cydonia oblonga</i> forma <i>pyramidalis</i> (Dippel) Rehder
<i>Cydonia oblonga</i> forma <i>pyriformis</i> (Dierb.) Rehder

Source: Encyclopedia of Life (2009)

named *Cydonia vulgaris* Pers. and *Pyrus cydonia* L. Within the species, various botanical varieties, subspecies, or forma have been described (Table 1.1). Many of these subspecies, botanical varieties, and forma should probably not be considered as formal taxa but merely represent genetic variation within the species. Lobachev and Korovina (1981) divided the genus into two subspecies, *C. oblonga* subsp. *oblonga* and *C. oblonga* subsp. *integerrima*.

1.2.3 Cytology, Karyotype, and Genome Size

Like apple and pear, quince is a diploid with $2n = 34$. The nuclear DNA content is 0.73 pg (Dickson et al. 1992). The basic number ($n = 17$) of *Cydonia* is considered to be a secondary unbalanced number, and the genus is probably a secondary polyploid (Blando et al. 1992).

1.2.4 Morphology

Botanical descriptions are found in Webster (2008) and the Encyclopedia of Life (2009). Quince forms a small tree or shrub, up to 8 m in height, with dense, spreading, and often pendulous tree architecture. Shoots are purplish-red when young, turning purplish-brown when mature, terete, initially densely tomentose when young but turning glabrous. Vegetative and flower buds are also purplish-brown and tomentose. Stipules are caduceous, ovate, and the petioles are 0.8–1.5 cm long and tomentose. Leaf blades are ovate to oblong 5–10 cm long and 3–5 cm wide, with veins conspicuous on the abaxial side. The adaxial side is glabrous or sparsely pubescent when young, and the abaxial side is pubescent. The leaf base is round or subcordate, with entire margins, and the apex is acute or emarginated. The flowers are 4–5 cm in diameter with caduceous, ovate bracts. They possess five styles, which are free and pubescent below, and 20 stamens, with the styles nearly as long as the stamens. The hypanthium is campanulate and abaxially tomentose. The nectaries are large in comparison with other closely related genera of the Pomoideae and possess the thickest epidermis and cuticle (Weryszko-Chmiellewska and Konarska 1995). Sepals are ovate or broadly lanceolate. The petals are white or pinkish and about 1.8 cm long. The ovary is inferior and has five carpels. Floral initiation takes place immediately prior to anthesis (Webster 2008). The flowers are single and on the apices of current season shoots. The fruits are yellow when mature, densely tomentose, with persistent reflexed calyces, and can weigh over 0.5 kg. The pedicel tends to be about 5 cm long, thick, and also tomentose. The fruit is aromatic and the flesh is firm, containing many grit cells (i.e., sclerenchyma), which are large and irregular, similar to *Pyrus* (Aldasoro et al. 1998). Fruit shape can be either pyriform, globose, or maliform, with a ribbed contour in some genotypes.

1.2.5 Agricultural Status

Quince is cultivated for fruit production all over the world. Nevertheless, most of the production is in the region where this fruit crop is supposed to have originated. In 2008, world production of quince totaled

478,813 metric tons (FAO 2010). Turkey was the most important producer, with 95,395 metric tons/year, followed by Uzbekistan (50,000), Iran (34,115), Morocco (33,133) Argentina (27,000), and Azerbaijan (26,990). Quince production is also considerable in the West Mediterranean region, where Spain (12,098) is the largest producer. This fruit crop is also produced in Mexico 6,473 mt.

Compared with apples and pears, there are fewer documented cultivars (Yamamoto et al. 2004). Quinces are grown for their fruits, which need to be cooked to attain suitable texture for consumption. They have been made into marmalade, jelly, or conserves with various spices (Webster 2008). Liquors and wines can also be made. A major use for some quinces is as a rootstock for pear scion cultivars. Selected quince rootstocks impart size control, with a 40–50% reduction in tree size, precocious bearing, and improved productivity when compared to seedling and clonal pear (*Pyrus communis* L.) rootstocks (Lombard and Westwood 1987).

1.3 Conservation Initiatives

1.3.1 Evaluation of Genetic Erosion

Cydonia has not been evaluated for inclusion on the International Union for the Conservation of Nature (IUCN) Red List. However, like most wild populations of fruit crops of the Rosaceae, it can be assumed that habitat destruction and development have caused some loss of these native populations. Avanzato and Raparelli (2005) analyzed genetic erosion of crop species as a function of the disappearance from nursery catalogs. Although the number of quince cultivars cultivated for their fruit is relatively small when compared with apples and pears, a comparatively high percentage (28%) of cultivars have apparently remained in the nursery trade during the period of 1897–2005. A relative dearth of modernization of quince cultivation, reflected in a low level of breeding activity, probably accounts for the relatively low level of genetic loss in production agriculture.

1.3.2 In Situ and Ex Situ Conservation

Ex situ conservation of wild crop relative conservation has received much more emphasis than in situ

conservation, except in a general sense of preservation of natural habitat for plants and animals. A 1989 survey listed 26 ex situ collections in 16 countries (International Board for Plant Genetic Resources 1989). Major ex situ germplasm collections resulting from plant exploration and exchange have been established in several countries, including Italy (Ianni and Mariotti 2005). USA (Postman 2008; USDA 2009), Italy (Ianni and Mariotti 2005) and UK (University of Reading 2009). Coordinated documentation of 11 collections in Italy, France, Spain, and Greece has been initiated (European Cooperative for Plant Genetic Resources 2009) as part of a European project on under-utilized fruit crop species (Bellini and Giordani 2000; European Commission 2007). At least 86% of the accessions in European collections have complete passport data and some characterization data. Ex situ collections in countries with native populations include those in India (Dhillon and Rana 2004), Iran (Amiri 2008), Turkey (Sykes 1972; Küden 2001; Küden and Küden 2008), Turkmenistan (Vitkovskii and Denisov 1991), and Ukraine (Yezhov et al. 2005).

A regional strategy for in situ and ex situ conservation and use of plant genetic resources for countries of central Asia and the Caucasus has been put forward (CATCN-PGR 2008). Similar plans have been devised for countries in eastern and central Europe (Alexanian 2001). The challenges of in situ conservation of wild crop relatives in general, either in protected or unprotected areas, have been discussed in detail by Heywood (2008).

1.3.3 Modes of Preservation and Maintenance

Most ex situ preservation is in the form of clonally propagated trees. Clones preserved for their edible fruit are usually propagated by budding or grafting onto clonal quince rootstocks. The rootstocks can be also propagated onto specific clonal rootstocks, maintained in stool beds as self-rooted plants, or planted as self-rooted trees.

In vitro methods of preservation are intended as secondary or back-up collections, established as a safeguard against loss of trees in nursery or orchard plantings due to disease, insect, or climatic hazards, e.g., due to low winter temperature. Medium-term storage of clonal propagules has been attained through

in vitro culture of shoots, and long-term storage has been achieved through cryopreservation of in vitro cultured apical meristems in liquid nitrogen. Medium-term storage involves slowing growth through low temperature and medium manipulations. Viable cultures can be maintained for 12–18 months at 4°C with a 16-h photoperiod, and storage for over 2 years can be achieved using gas-permeable bags instead of glass culture tubes. Defoliated shoots have been stored for up to 4 years at 2°C on an agar medium without growth regulators (Druart 1985). The three major techniques of cryopreservation are slow freezing, vitrification, and encapsulation-dehydration (Reed and Chang 1997). Pre-treatment with cold-acclimation and abscisic acid has been shown to be very important for pear genotypes (Bell and Reed 2002), and the same is likely to be true for quince.

1.4 Elucidation of Origin and Evolution of *Cydonia*

The most closely related genera and intergeneric hybrids are listed in Table 1.2. All species of *Chaenomeles* were once classified as species of *Cydonia*, as was *Pseudocydonia sinensis* and \times *Pyronia*. Classification is based on morphological and molecular genetic traits. Styles of *Cydonia* are free, and those of *Docynia* and *Chaenomeles* are connate; leaves are entire, as opposed to sometimes serrate.

A study of pollen morphology detected considerable variation in number of pores, pollen grain shape, and exine structure, in addition to various abnormalities that were associated with fertility (Romanova et al. 1988). Pollen size, shape, and sculptural features may be useful in taxonomic studies within the Maloideae (Zhou et al. 2000).

There are a few chemotaxonomic studies. Phenolic profiles for nine compounds for 36 genotypes from three geographical regions of Portugal did not reveal much polymorphism within the genus. Significant differences were found in 3-*O*-caffeoylquinic and 3,5-*O*-dicaffeoylquinic acids among geographical provenance and date of leaf harvest (Oliveira et al. 2008).

Within the species, early attempts at classification were strictly based on morphological traits, such as fruit shape (Hedrick 1925), or in the case of those

Table 1.2 Related crop and other plant genera and species

Scientific Name	Comment
<i>Chaenomeles cathayensis</i> (Hemsl.) C. K. Schneid.	–
<i>Chaenomeles japonica</i> (Thunb.) Lindl. Ex Spach	–
<i>Chaenomeles japonica</i> f. <i>alba</i> (Nakai) Ohwi	–
<i>Chaenomeles speciosa</i> (Sweet) Nakai	–
<i>Chaenomeles</i> \times <i>suberba</i> (Frahm) Rehder	<i>C. japonica</i> \times <i>C. speciosa</i> artificial hybrid
\times <i>Cydomalus</i> (syn. <i>Cydolus</i>)	<i>Cydonia</i> \times <i>Malus pumila</i> artificial hybrid (Rudenko 1989)
<i>Docynia delavayi</i> (Franch.) C. K. Schneid.	Native to China
<i>Docynia indica</i> (Wall.) Decne.	Native to China, Indo- China, and South Asia
<i>Pseudocydonia sinensis</i> (Thouin) C. K. Schneid.	–
\times <i>Pyronia veitchii</i> (Trab.) Guillaumin	<i>Pyrus pyrifolia</i> \times <i>Cydonia</i> <i>oblonga</i> artificial hybrid
\times <i>Pyronia veitchii</i> var. <i>luxemburgiana</i>	–

genotypes used as rootstocks, on the basis of plant growth habit (Tukey 1964). As with apple, pear, and other crops, early molecular studies of genetic diversity focused on isoenzyme polymorphisms. Isoenzyme analysis of acid phosphatase, esterase, peroxidase, and Polyphenol oxidase was successful in distinguishing 11 groups of *Cydonia* and two groups of \times *Pyronia*, but the diversity was much less than previously seen in *Malus* and *Pyrus* (Sanchez et al. 1988). Peroxidases have also been implicated in graft incompatibility between quince rootstocks and certain pear scion cultivars. Gulen et al. (2002) predicted that matching of isoperoxidase “A” in quince rootstocks in the graft-compatible “Beurre Hardy” scion may be associated with a compatible graft combination, and that the presence of isoperoxidase “A” and “B” in graft union tissues predicts compatibility between quince and “Bartlett” scions. Later, an association between rootstock/cultivar compatibility and a specific anodal isoperoxidase marker was identified by Gulen et al. (2005). Esterases and malate dehydrogenases were used by Hudina et al. (1999) to discriminate between eight European pear cultivars and the quince rootstock cultivars “Malling Quince A” and “BA29”. The authors speculate that an esterase band, common to