Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources

Tropical and Subtropical Fruits

Springer

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Editor
Prof. Chittaranjan Kole
Director of Research
Institute of Nutraceutical Research
Clemson University
109 Jordan Hall
Clemson, SC 29634
CKOLE@clemson.edu

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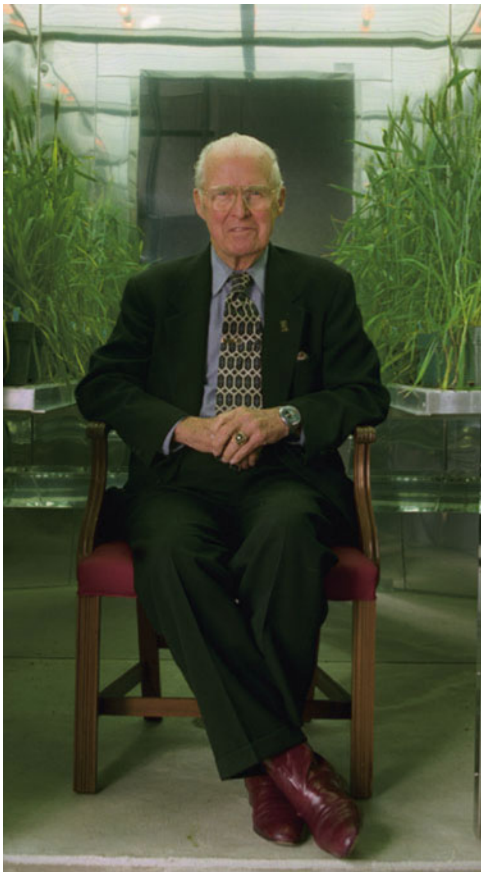
Dedication

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!

[1]The 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 been 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, monoploids and aneuploids, particularly in polyploid crops. These aspects have been dealt in the relevant chapters. Employment of colchiploidy, 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 intransgenic 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 – Tropical and Subtropical Fruits" includes 11 chapters dedicated to *Actinidia*, *Ananas*, *Citrus*, *Mangifera*, *Morus*, *Musa*, *Passiflora*, *Persea*, *Poncirus*, *Spondias*, and *Vasconcellea*. The chapters of this volume were authored by 42 scientists from 14 countries of the world, namely Australia, Brazil, Belgium, China, Columbia, France, India, Italy, New Zealand, Peru, Taiwan, Turkey, the USA and Venezuela.

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 tropical and subtropical fruit crops with an intention of serving science and society.

Clemson, USA Chittaranjan Kole

Contents

Abbreviations

2,4-D	2,4-D-dicholorphenoxy acetic acid
ACC	1-Aminocyclopropane-1-carboxylic acid
AFLP	Amplified fragment length polymorphism
AMOVA	Analysis of molecular variance
APG	Angiosperm phylogenetic group
ARS	Agriculture Research Service (of USDA)
BAC	Bacterial artificial chromosome
BAP	Benzyl amino purine
BC1	First backcross
BC2	Second backcross
BIBAC	Binary-BAC
BSA	Bulked segregant analysis
BSV	Banana streak badnavirus
CAAS	Chinese Academy of Agricultural Sciences
CABMV	Cowpea aphid-borne mosaic virus
CAPS	Cleaved amplified polymorphic sequence
CBD	Convention on Biological Diversity
CcGA20ox1	Citrus gibberellin 20-oxidase cDNA gene
cDNA	Complementary-DNA
CiMV	Citrus mosaic virus
CINVESTA	Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (Center for Research and Advanced Studies of the National Polytechnic Institute), Mexico
CIRAD	Centre de coopération Internationale en Recherche Agronomique pour le Développement (Agricultural Research Centre for International Development), France
cM	CentiMorgan
CMA	Chromomycin A 3
CMS	Carboxymethyl-Sephadex
COSEWIC	Committee on Status of Endangered Wildlife in Canada
cpDNA	Chloroplast-DNA
cpSSR	Chloroplast-SSR
CR	Critically endangered
CSGRC	Central Sericultural Germplasm Resources Centre (India)
CTV	*Citrus tristeza* clostero virus
CTV	*Citrus tristeza* virus
CVC	Citrus exocortis viriod

DAPI	4,6-Diamidino-2-phenylindole
DFP	DNA fingerprint
DNJ	Deoxyjirimycin
EAPV	East Asian *Passiflora* Virus
EFN	Extrafloral nectaries
ELISA	Enzyme-linked immunosorbent assay
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuária (Brazil)
EN	Endangered
EOO	Extent of occurrence
EST	Expressed sequence tag
F_1	Filial 1 (first filial generation)
F_2	Filial 2 (second filial generation)
F3	Filial 3 (third filial generation)
FAO	Food and Agriculture Organization (of the United Nation)
FHIA	Fundación Hondureña de Investigación Agrícola (Honduras Foundation for Agricultural Research), Honduras
FISH	Fluorescent/ce in situ hybridization
FocR4	Race 4 of Fusarium wilt
FPB	Farmers' participatory breeding
G3pdh	Glyceraldehyde 3-phosphate dehydrogenase
GA	Gibberellin
GA_3	Gibberellic acid 3
GCGN	Global Citrus Germplasm Network
GIS	Geographic information sysytem
GISH	Genomic in situ hybridization
GRIN	Germplasm Resources Information Network (USA)
GS	Glutamine synthetase
HAL2	Halotolerance gene
HAT-RAPD	High annealing temperature-RAPD
HBV	Hepatitis B virus
HCN	Hydrogen cyanide
hEGF	Human epidermal growth factor
IAA	Indole-3-acetic acid
IAPAR	Instituto Agronômico do Paraná (Agronomic Institute of Parana), Brazil
IBA	Indole-3-butyric acid
IEB	Institute of Experimental Botany (Czech Republic)
IGS	Ribosomal gene spacer
IIHR	Indian Institute of Horticultural Research (India)
IITA	International Institute of Tropical Agriculture (Nigeria)
INIA	Instituto Nacional de Investigaciones Agrícolas (Venezuela)
INIBAP	International Network for the Improvement of Banana and Plantain
IPGRI	International Plant Genetics Resource Institute (presently Biodiversity International), Italy
IRAP	Interretrotransposon amplified polymorphism
IRD	Institut de Recherche Pour le Développement (Institute of Research for Development), France
IRS	Intertranslation space of ribosomal-DNA

ISSR	Intersimple sequence repeat
ITC	International Transit Center (of US at Kyrgyzstan)
ITPGRFA	International Treaty on Plant Genetic Resources for Food and Agriculture
ITS	Internal transcribed spacer
IUCN	International Union for Conservation of Nature
Kn	Kinetin
LANGEBIO	Laboratorio Nacional de Genómica para la Biodiversidad (National Laboratory of Genomics for Biodiversity), Mexico
LD	Linkage disequilibrium
LG	Linkage Group
LRR	Leucine-rich repeat
LTR	Long terminal repeats
MarMV	Maracuja mosaic tobamovirus
MGIS	*Musa* Germplasm Information System
MIPS	Myo-inositol-1L-phosphate synthase
MMP-2	Metallo-proteases-2
MMP-9	Metallo-proteases-9
MS	Mono S Sepharose
MS	Murashige and Skoog (medium)
MSAP	Methylation-sensitive amplification polymorphism
MSY	Specific region of the Y chromosome
mtDNA	Mitochondrial-DNA
Mya	Million years ago
NAA	α-Naphthaleneacetic acid
NAD	Nicotinamide adenine dinucleotide
NBS-LRR	Nucleotide-binding site
NCBI	National Center for Biotechnology Information (USA)
NCEPL	National Committee on Environmental Planning and Coordination (India)
ncpGS	Nuclear copy chloroplast expressed glutamine synthase
NGO	Non-Governmental Organization
NIAS	National Institute of Agrobiological Sciences (Japan)
NISES	National Institute of Sericultural and Entomological Science (Japan)
NK	Natural killer
NT	Near threatened
nt	Nucleotides
ORF	Open reading frame
overgo	Overlapping oligonucleotide probe
PBA	P450-based analogs
PCA	Principal component analysis
PCO	Principal coordinates
PCR	Polymerase chain reaction
PE-ACS1	*Passiflora edulis* ACC synthase-1
PE-ACS2	*Passiflora edulis* ACC synthase-2
Pe-AFP1	*Passiflora edulis* antifungal peptide-1
PE-ERS1	*Passiflora edulis* ethylene receptor-1
PE-ERS2	*Passiflora edulis* ethylene receptor-2

PEG	Polyethylene glycol
Pf-AOS	*Passiflora* allene oxide synthase
PLV	*Passiflora* latent virus
PPO	Polyphenol oxidase
PRI	Pineapple Research Institute (USA)
PRSV	Papaya ringspot virus
prsv-1	Single resistant gene for *PRSV*
PRSV-P	Papaya ringspot virus type P
PWV	Passion fruit woodiness virus
QDPI	Queensland Department of Primary Industries and Fisheries
QRL	Quantitative resistance loci
QTL	Quantitative trait loci
RAF	Randomly amplified DNA fingerprint
RAPD	Random(ly) amplified polymorphic DNA
rDNA	Ribosomal DNA
REMERFI	Red Mesoamericana de Recursos Fitogeneticos [Mesoamerican Network of Plant Genetic Resources]
RFLP	Restriction fragment length polymorphism
RGA	Resistance gene analog
RT	Reverse transcriptase
SAGE	Serial analysis of gene expression
SAMPL	Selective amplification of microsatellite polymorphic loci
SCAR	Sequence characterized amplified region
SD-AFLP	Secondary digest-AFLP
SES	Sericulture Experiment Station (Bulgaria)
SMTA	Standard material transfer agreement
SNP	Single nucleotide polymorphism
SSR	Simple sequence repeat
STMS	Sequence-tagged microsatellite site
STS	Sequence tagged site
tRNA-Leu	Leucine Transfer-RNA
tRNA-Lys	Lysine Transfer-RNA
tRNA-Phe	Phenylalanine Transfer-RNA
UC	University of California
UNDP	United Nations Development Program
UNESCO	United Nations Educational, Scientific and Cultural Oraganization
USDA	United States Department of Agriculture
UTR	Untranslated region
VNTRS	Variable number tandem repeats
VU	Vulnerable
WGS	Whole genome shotgun
WWF	World Wide Fund
Ω	Omega

List of Contributors

Q. Ali Department of Horticulture, University of Agricultural Sciences, GKVK Campus, Bangalore 560 065, India, algabal_9@hotmail.com

Vanessa E.T.M. Ashworth Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697–2525, USA, ashworth@ucr.edu

Sheikh M. Basha Plant Biotechnology Laboratory, Center for Viticulture and Small Fruit Research, Florida A & M University, 6505 Mahan Drive, Tallahassee, FL 32317, USA, mehboob.sheikh@famu.edu

Haofeng Chen Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA, haofengc@nmsu.edu

Michael T. Clegg Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697, USA, mclegg@uci.edu

Geo Coppens d'Eeckenbrugge CIRAD, UMR 5175 CEFE, 1919 Route de Mende, 34293 Montpellier, France, geo.coppens@cirad.fr

Paul M. Datson The New Zealand Institute for Plant & Food Research Ltd, Private Bag 92 169, Auckland, New Zealand, paul.datson@plantandfood.co.nz

M.R. Dinesh Division of Fruit Crops, Indian Institute of Horticultural Research, Hessarghatta Lake post, Bangalore 560089, Karnataka, India, mrdinesh@iihr.ernet.in

Rod Drew School of Biological and Physical Sciences, Griffith University, Nathan, QLD 4111, Australia, r.drew@griffith.edu.au

Marie-France Duval CIRAD, UPR Multiplication Végétative, Avenue Agropolis, TA A-75/03, 34398 Montpellier, France, marie-france.duval@cirad.fr

Sezai Ercisli Faculty of Agriculture, Department of Horticulture, Ataturk University, Erzurum 25240, Turkey, sercisli@hotmail.com

A. Ross Ferguson The New Zealand Institute for Plant & Food Research Ltd, Private Bag 92 169, Auckland, New Zealand, ross.ferguson@plantandfood.co.nz

Patricia Gutiérrez-Pesce Dipartimento di Produzione Vegetale, Università degli Studi della Tuscia, Via S.C. de Lellis, Viterbo 01100, Italy, patgut65@hotmail.com

Devaiah Kambiranda Plant Biotechnology Laboratory, Center for Viticulture and Small Fruit Research, Florida A & M University, 6505 Mahan Drive, Tallahassee, FL 32317, USA, devaiah29@gmail.com

Chittaranjan Kole Department of Genetics and Biochemistry, Institute of Nutraceutical Research, Clemson University, 109 Jordan Hall, Clemson, SC 29634, USA, ckole@clemson.edu

Tina Kyndt Department of Molecular Biotechnology, Faculty of Bioscience Engineering, Ghent University (UGent), Coupure links 653, 9000 Ghent, Belgium, tina.kyndt@ugent.be

Freddy Leal Facultad de Agronomía, Maracay, Universidad Central de Venezuela, Aragua 2101A, Venezuela, flealpinto@hotmail.com

Allison Miller Department of Biology, Saint Louis University, 3507 Laclede Avenue, St. Louis, MO 63103-2010, USA, amille75@slu.edu

Ray Ming Department of Plant Biology, University of Illinois at Urbana-Champaign, 1201W Gregory Drive, Urbana, IL 61801, USA, rming@life.illinois.edu

Paul H. Moore Hawaii Agriculture Research Center, 92–1770 Kunia Road, Kunia, HI 96759, USA, pmoore@harc-hspa.com

Chirakkara Venugopalan Nair SeriBiotech Research Laboratory, Kodathi, Carmeleram, Bangalore 560035, India, cvgn_2000@yahoo.com

P. Narayanaswamy Department of Horticulture, University of Agricultural Sciences, GKVK Campus, Bangalore 560 065, India, swamy.papanna@gmail.com

Rodomiro Ortiz Department of Plant Breeding and Biotechnology, Swedish University of Agricultural Sciences, P.O. Box 101, SE-230 53 Alnarp, Sweden, rodomiroortiz@gmail.com

Jogeswar Panigrahi Department of School Life Sciences, Sambalpur University, Jyoti Vihar, Burla, Orissa 768 019, India, hodbiotech_mits@yahoo.co.in

Madhugiri Nageswara Rao Citrus Research & Education Center, University of Florida, IFAS, 700 Experiment Station Road, Lake Alfred, FL 33850, USA, mnrbhav@yahoo.com

K.V. Ravishankar Division of Biotechnology, Indian Institute of Horticultural Research, Hessarghatta Lake post, Bangalore 560089, Karnataka, India, kv_ravishankar@yahoo.co.in

Eddo Rugini Dipartimento di Produzione Vegetale, Università degli Studi della Tuscia, Via S.C. de Lellis, Viterbo 01100, Italy, rugini@unitus.it

Leela Sahijram Division of Biotechnology, Indian Institute of Horticultural Research, Hessaraghatta Lake Post, Bangalore 560089, India, leelas@iihr.ernet.in

Garth M. Sanewski Department of Primary Industries and Fisheries, PO Box 5083 SCMC, Nambour, QLD 4560, Australia, garth.sanewski@dpi.qld.gov.au

Xavier Scheldeman Regional Office for the Americas, Bioversity International, PO Box 6713, Cali, Colombia, xschelde@gmail.com

Mike K. Smith Department of Primary Industries and Fisheries, PO Box 5083 SCMC, Nambour, QLD 4560, Australia, mike.smith@dpi.qld.gov.au

Jaya R. Soneji Citrus Research & Education Center, University of Florida, IFAS, 700 Experiment Station Road, Lake Alfred, FL 33850, USA, jayasoneji@yahoo.co.in

Tatiana T. Souza-Chies Departamento de Botânica, Instituto de Biociëncias, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS 91501–970, Brazil, tatiana.chies@ufrgs.br

Devarajan Thangadurai Molecular Breeding Laboratory, Department of Botany, Karnatak University, Dharwad 580003, Karnataka, India, drdthangadurai@gmail.com

Amalendu Tikader Central Sericultural Germplasm and Resources Centre, Thally Raod, Hosur, Tamil Nadu 635 109, India, atikader_csgrc@yahoo.co.in

Chi-Hua Tsou Institute of Plant and Microbial Biology, Academia Sinica, Taipei 11529, Taiwan, ROC, chtsou@gate.sinica.edu.tw

Patrick Van Damme Laboratory for Tropical and Subtropical Agriculture and Ethnobotany, Department of Plant Production, Faculty of Bioscience Engineering, Ghent University (UGent), Coupure links 653 9000 Ghent, Belgium, patrick.vandamme@ugent.be

Bart Van Droogenbroeck Unit Technology and Food, Institute for Agricultural and Fisheries Research (ILVO), Burg. Van Gansberghelaan 115, 9820 Merelbeke, Belgium, bart.vandroogenbroeck@ilvo.vlaanderen.be

Hemanth K. N. Vasanthaiah Plant Biotechnology Laboratory, Center for Viticulture and Small Fruit Research, Florida A&M University, 6505 Mahan Drive, Tallahassee, FL 32317, USA, hemanth.vasanthaiah@gmail.com

Kunjupillai Vijayan Institute of Plant and Microbial Biology, Academia Sinica, Taipei 11529, Taiwan, ROC, kvijayan01@yahoo.com

Zhao Weiguo Jiangsu University of Science and Technology, Sericultural Research Institute, Chinese Academy of Agricultural Sciences, Jiangsu province 212018, China, wgzsri@126.com

Roxana Yockteng Origine, Structure et Evolution de la Biodiversité, UMR 7205, Muséum National d´Histoire Naturelle, 16 rue Buffon CP 39, 75005 Paris, France, yockteng@mnhn.fr

Chapter 1
Actinidia

P.M. Datson and A.R. Ferguson

1.1 Introduction

Kiwifruit in comparison with most other crop plants have a very short history of cultivation.

The two commercially important kiwifruit species are *Actinidia deliciosa* and *A. chinensis*. These are sometimes combined as varieties of the same species (Li et al. 2007a, b), but we retain them here as distinct species. *A. deliciosa* was introduced into cultivation toward the end of the nineteenth century (Ferguson and Huang 2007) and the first commercial orchards were established in New Zealand around 1930. *A. chinensis*, a species closely related to *A. deliciosa*, was successfully introduced into cultivation in China as recently as 1961 (Zhang et al. 1983) and it has been grown commercially in other countries and its fruits have been traded internationally for little more than a decade. At present, *A. deliciosa* provides about 85% of the kiwifruit produced commercially worldwide and *A. chinensis* about 15%. A few other *Actinidia* species are also cultivated, *A. arguta*, *A. eriantha*, *A. kolomikta*, and *A. polygama*, but these are of very minor commercial importance.

Almost all current kiwifruit cultivars are either direct selections from the wild or only a few generations removed from the wild (Ferguson and Huang 2007; Ferguson and Seal 2008; Ferguson 2009; Li et al. 2010). All the early New Zealand cultivars of *A. deliciosa*, including the main commercial cultivar 'Hayward', are selections descended from a very small number of seedlings grown from a single seed introduction into New Zealand from China at the beginning of the twentieth century (Ferguson and Bollard 1990). Very few cultivars of *A. deliciosa* have yet emerged from systematic breeding programs and there are only small commercial plantings of them (Testolin and Ferguson 2009). Only one commercially important cultivar of *A. chinensis* has so far resulted from a controlled hybridization. 'Hort16A' came from the cross of a female, the product of open-pollination of seedlings from a seed accession from the wild, and a male raised from seed collected in the wild (Muggleston et al. 1998; Ferguson et al. 1999).

- Cultivated kiwifruit are, therefore, generally not greatly different from those in the wild. Some wild individuals of *A. deliciosa* and *A. chinensis* contained genes suitable for domestication and selection has involved recognition of plants with fruit having commercial potential. Comparison of the plants that have been selected with those remaining in the wild contributes to our understanding of the kiwifruit we now grow and the potential for their improvement. We describe studies using both cultivated plants and their wild allies on the origin, evolution, phylogenetic relationships, cytogenetics, and the genetic improvement of kiwifruit employing both classical strategies and advanced tools of genomics and biotechnology.

1.2 Basic Botany

1.2.1 *The Genus* Actinidia

Kiwifruit belong to the genus *Actinidia* Lindl. Currently, 55 species and about 76 taxa are recognized

P.M. Datson (✉)
The New Zealand Institute for Plant & Food Research Ltd. (Plant & Food Research), Private Bag 92 169, Auckland, New Zealand
e-mail: Paul.Datson@plantandfood.co.nz

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within the genus, with the most recent revision (Li et al. 2007a, b, 2009) having relegated about 25% of the species and 40% of all taxa previously described (Ferguson and Huang 2007). Further changes seem inevitable as many taxa are not well known, and transitional forms, sometimes formally described, suggest considerable hybridization between taxa with overlapping geographical distributions (Liang 1983; Ferguson 1990a, b; Chat et al. 2004; Li et al. 2009).

Female flowers of the genus have a characteristic radiating arrangement of styles, like the spokes of the wheel. This is the basis for Lindley's generic name *Actinidia* from aktis (Greek), ray. In China, the name mihoutao [monkey peach] is used for the whole genus and individual species are now distinguished such as zhonghua [Chinese] mihoutao for *A. chinensis* and meiwei [delicious] mihoutao for *A. deliciosa* (Cui et al. 2002; Li et al. 2007a). In older literature, these two species were usually distinguished by the hairs on the fruit, ruanmao for soft-haired [*A. chinensis*] and yingmao [*A. deliciosa*] for stiff-haired. A variety of names were used traditionally, yangtao [sun peach] being one of the most common (Ferguson 1990c). Outside China, "Chinese gooseberry" became the most popular name (or translations such as groseille de Chine) until it was replaced in New Zealand by kiwifruit (Ferguson and Bollard 1990). This is the most widely used name today, even in China, although in Italy, "actinidia" is often used. Kiwifruit is sometimes incorrectly shortened to "kiwi" or wrongly separated into two words.

1.2.2 Geographic Distribution

Nearly all *Actinidia* species (52 of 55) and taxa (73 of 76) occur in China (Li et al. 2007a) and some extend to adjoining countries, but only three species occur exclusively outside China: *A. strigosa* from Nepal, *A. petelotii* from Vietnam, and *A. hypoleuca* from Japan. The genus has a wide geographic distribution in eastern Asia, from just south of the Equator, to as far north as latitude 50°, with most taxa occurring in south-central and south-west China between the Yangzi (Chang Jiang) and Pearl (Zhu Jiang) Rivers, in a belt between approximately 25 and 30°N (Fig. 1.1). Most *Actinidia* grow best in warm, moist, and sheltered environments; cold, dry conditions are unsuitable. Hence, the northernmost boundary of the area of greatest abundance corresponds to the Qin Ling Mountains in southern Shaanxi, the western boundary, the lower mountains of the eastern border of the Tibetan plateau, the Hengduan Shan (Hengduan Mountains) to the west of Yunnan and Sichuan, and the southernmost, the isotherm that corresponds to a mean annual temperature between 20°C and 22°C (Ferguson and Huang 2007). This area is considered to be the center of diversity of *Actinidia* as well as the center of current evolution (Liang 1983). Taxa tend to vary little in their relative vertical distributions, but the altitude at which a particular *Actinidia* taxon occurs is not absolute but decreases with increasing latitude (Ferguson and Huang 2007). Thus, taxa that grow high in the mountains of southern China can be found at sea level in Siberia.

1.2.3 Vegetative Morphology

All *Actinidia* are climbing plants and under most conditions are deciduous. Vines can be extraordinarily robust and vigorous, capable of smothering large trees (Li 1952), but high in the mountains or in cold, northernmost regions, plants may be reduced to scrambling thickets rather like brambles (Berestova 1970). In cultivation, vine vigor will depend on local growing conditions and genotype, but commercial vines are usually very vigorous and require strong and expensive support structures.

Actinidia species are often very variable in vegetative structures. Even individual plants can show variation in the leaves produced at different times of year or on different types of wood (Dunn 1911). This can cause confusion when single specimens are used to describe taxa. Differences in vegetative morphology between staminate and pistillate plants can also be misleading (Cuong et al. 2007). Widespread species have often been divided into morphologically distinct varieties, which sometimes, but not always, occupy discrete geographical areas. Broader taxonomic concepts with more intrataxal variation seem more realistic, and further collections, especially of taxa based on only a few specimens, are needed (Li et al. 2009).

Key	Taxa
F	1-5
E	6-10
D	11-15
C	16-20
B	21-30
A	31-40

Countries	Taxa
Bhutan	2
Cambodia	1
India	2
Indonesia	1
Japan	5
Korea	4
Laos	1
Malaysia	1
Myanmar	2
Nepal	2
Russia	3
Thailand	2
Vietnam	6

Fig. 1.1 Geographic distribution of *Actinidia* taxa

1.2.4 Flower Morphology and Sex Determination

All *Actinidia* species appear to be dioecious, although functional dioecy has been confirmed in only *A. deliciosa* and *A. polygama* (McNeilage 1991a; Kawagoe and Suzuki 2004). *Actinidia* are cryptically dioecious: female plants produce morphologically perfect flowers with well-developed pistils and stamens, but their stamens produce non-viable pollen; flowers of male plants have small, rudimentary ovaries without viable ovules, but their stamens release viable pollen (Rizet 1945; Schmid 1978; White 1990) (see Fig. 1.2). Failure of pollen maturation or of pistil growth occurs late in flower bud development (Brundell 1975; Schmid 1978; Messina 1993). Dioecy creates problems in commercial cultivation: part of the orchard area (usually about 10%) must be dedicated to pollenizer vines, male and female vines must flower at the same time, and there must be efficient transfer of pollen as fruit size in kiwifruit is largely dependent on the number of seed set. Orchard layout must also encourage honeybee activity to facilitate pollination. Some of these problems are overcome by mechanical pollination of fruiting vines by harvested pollen; a better solution might be the development of hermaphrodite, self-setting vines.

Fig. 1.2 Flowers of female (*left*) and male (*right*) *Actinidia eriantha*

There is an active-Y sex determination system (X_nX/X_nY) in *Actinidia* with the plants that contain