Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources
Legume Crops and Forages

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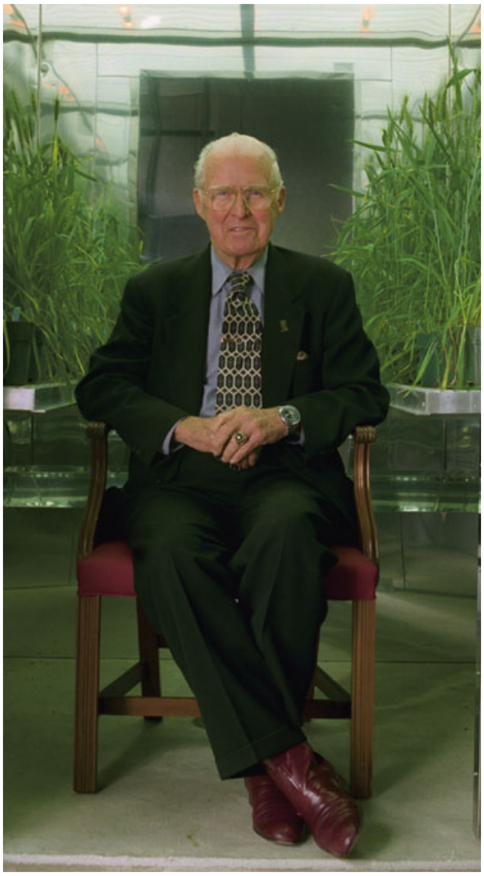
Dedication



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: Legume Crops and Forages" includes 15 chapters dedicated to *Arachis*, *Cajanus*, *Chenopodium*, *Cicer*, *Glycine*, *Lathyrus*, *Lens*, *Lotus*, *Lupinus*, *Medicago*, *Phaseolus*, *Pisum*, *Trifolium*, *Vicia*, and *Vigna*. The chapters of this volume were authored by 47 scientists from 9 countries of the world, namely Australia, Bolivia, Brazil, India, Japan, New Zealand, Poland, 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 legume crops and forages with an intention of serving science and society.

Clemson, USA — Chittaranjan Kole

Contents

Abbreviations

α-EST	α-esterase
ψleaf	Leaf water potential
1C	DNA content of the haploid genome
2C	DNA content of the diploid genome
AB	Advanced backcross
ACP	Acid phosphatase
AFLP	Amplified fragment length polymorphism
ALC	Australian Lupin Collection
AM	Association mapping
AND	Andean subregion of South America
ANF	Anti-nutritional factor
APS	Adenosine 5′ phosphosulfate
ARS	Agricultural Research Service
ASL	Apical segment length
ASPADERUC	Association for Rural Development in Cajamarca
AS-PCR	Allele-specific PCR
ATL	Atlantic subregion of South America
ATP	Adenosine triphosphate
BAC	Bacterial artificial chromosome
BBSRC	Biotechnology and Biological Sciences Research Council
BC	Backcross
BC_1F_1	First filial generation of backcross with the first parent
BES	BAC-end sequence
BGM	Botrytis gold mold
BGMV	Bean golden mosaic virus
BP	Branching pattern
BSL	Basal segment length
BYMV	Bean yellow mosaic virus
CCD	Charge coupled device
cDNA	Complementary DNA
CENARGEN	Centro Nacional de Pesquisas de Recursos Genéticos e Biotecnologia (Brazilian National Center for Genetic Resources and Biotechnology)
CEW	Corn earworm
CGIAR	Consultative Group on International Agricultural Research
CI	Centromere index

CIAT	Centro Internacional de Agricultura Tropical (International Center for Tropical Agriculture)
CIP	International Potato Center
cM	Centi-Morgan
CMS	Cytoplasmic male sterility
CMV	Cucumber mosaic virus
CONDESAN	Consortium for the Sustainable Development of the Andean Ecoregion
cpDNA	Chloroplast-DNA
CSIRO	Commonwealth Scientific and Industrial Research Organization
cv.	Cultivar
CWR	Crop wild relatives
CyTed	Ibero-American Development Programme for Science and Technology
D	Nei's genetic distance
DAAL	Disomic alien addition line
DAFWA	Department of Agriculture and Food Western Australia
DAP	Days after pollination
DAPI	4′-6-Diamidino-2-phenylindole
DArT	Diversity arrays technology
DAS	Days after sowing
DE	Days to emergence
DF	Days to 50% flowering
DIA	Diafarase
DM	Days to maturity
dr	Diffusion resistance
eIF	Eukaryotic initiation factor
ELS	Early leaf spot
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuária (Brazilian Agricultural Research Corporation
EMS	Ethylmethane sulphonate
EST	Expressed sequence tag
ETS	External transcribed spacer region
F_1	First filial generation
F_2	Second filial generation
FAO	Food and Agriculture Organization
FISH	Fluorescence in situ hybridization
FLM	Flowers on main stem
FPC	Fingerprint contig
FTP	File transfer protocol
FYM	Farm yard manure
GA/ GA_3	Gibberellic acid
GH	Growth habit
GISH	Genomic in situ hybridization
GM	Genetic modification/genetically modified
GOT	Glutamic-oxaloacetic transaminase
GP	Gene pool
GRIN	Germplasm Resource Information Network
HSW	100-seed weight
HYH	Hypanthium hairiness

IAA	Indole acetic acid
IBONE	Instituto de Botánica del Nordeste (Botanical Institute of the Northeast)
IBPGR	International Board for Plant Genetic Resources (now IPGRI)
ICA	Instituto Colombiano Agropecuario (Colombian Agricultural Institute)
ICARDA	International Center for Agricultural Research in the Dry Areas
ICRISAT	International Crops Research Institute for the Semi Arid Tropics
ILDIS	International Legume Database and Information Service
IMGAG	International Medicago Genome Annotation Group
INIA	Instituto Nacional de Innovación Agraria
INIA-CGNA	Instituto Nacional de Investigación Agropecuarias – Centro de Genómica Nutricional Agro Acuícola
INIAP	Instituto Nacional de Investigación Agropecuarias
INTA	National Institute for Agricultural Technology
IPGRI	International Plant Genetic Resources Institute (Now Biodiversity International)
IPK	Leibniz Institute of Plant Genetics and Crop Plant Research
IRLC	Inverted repeat-lacking clade
ISRIC	World Soil Information
ISSR	Inter-simple sequence repeat
ITIS	International Taxonomic Identification System
ITS	Internal transcribed spacer
IUCN	International Union for Conservation of Nature
K	Number of proposed ancestral populations
KEGG	Kyoto Encyclopedia of Genes and Genomes
KN	Kinetin
KOG	EuKaryotic Orthologous Groups database
LB	Leaflet bristle
LBMSPL	Leaflet bristle on margin of main stem and primary laterals
LBPL	Leaflet bristle on primary lateral
LC	Leaflet color
LFI	Length of first isthmus
LH	Leaflet hairiness
LHMSPL	Leaflet hairiness on margin of main stem and primary laterals
LHPL	Leaflet hairiness on primary lateral
LINE	Long interspersed (repeated DNA) element
Lj	*Lotus japonicus*
*Lj*R	*Lotus japonicus* repeat region
LLAPL	Leaflet length of the apical primary lateral
LLBMS	Leaflet length on basal main stem
LLBPL	Leaflet length on basal primary lateral
LLS	Late leaf spot
LMHLMS	Leaflet midrib hairiness on lower main stem
LMHLPL	Leaflet midrib hairiness on lower primary lateral
LMHUMS	Leaflet midrib hairiness on upper main stem
LMHUPL	Leaflet midrib hairiness on upper primary lateral
LOTASSA	Lotus adaptation and sustainability in South America
LRR	Leucine-rich repeat
LSAMS	Leaflet shape on apical main stem

LSAPL	Leaflet shape on apical primary lateral
LSBMS	Leaflet shape on basal main stem
LSBPL	Leaflet shape on basal primary lateral
LSMS	Leaflet surface on main stem
LSPL	Leaflet surface on primary lateral
LTR	Long terminal repeat
LTSMS	Leaflet tip shape of the main stem
LTSPL	Leaflet tip shape of primary lateral
LWAMS	Leaflet width of apical main stem
LWAPL	Leaflet width of apical primary lateral
LWBMS	Leaflet width on basal main stem
LWBPL	Leaflet width on basal primary lateral
MAAL	Monosomic alien addition line
MAC	Mountain range of North and Central America
MAS	Marker-assisted selection
MFFGC	Margot Forde Forage Germplasm Centre
MFLP	Microsatellite-anchored fragment length polymorphism
MIPS	Munich Information Center for Protein Sequences
miRNA	Micro-RNA
MLG	Molecular linkage group
MS	Murashige and Skoog (medium)
MS	Mass-spectrometry
MSH	Main stem hairiness
MSHT	Main stem hair type
MSHt	Main stem height
MST	Main stem thickness
MST	Mass-spectral metabolite tag
Mt	*Medicago truncatula*
*Mt*R	*Medicago truncatula* repeat region
Mya	Million years ago
NAR	No adventitious roots
NARS	National Agricultural Research System
NBPGR	National Bureau of Plant Genetic Resources
NBRI	National Botanical Research Institute
NBS	Nucleotide-binding site
NCBI	National Center for Biotechnology Information
NIAS	National Institute of Agrobiological Sciences
NLB	Number of lateral branches
NLL	Narrow leafed lupin
NMU	N-Nitroso-N-methyl urea
NOR	Nucleolus organizer region
NPGS	National Plant Germplasm System
NPMSPL	Nature of petiole on main stem and on primary laterals
NSBP	Number of segments between pods
NSP	Non-starch polysaccharides
NSTPL	Nature of stipule on primary lateral
NTS	Non-transcribed spacer
ODAP	β-N-Oxalyl-l-α,β-diaminopropanoic acid
PAGE	Polyacrylamide gel electrophoresis

PB	Pod beak
PBMS	Petiole bristle on main stem
PBPL	Petiole bristle on primary lateral
PC	Principal component
PCGIN	Pulse Crop Genetic Improvement Network
PCR	Polymerase chain reaction
PDL	Pod length
PDR	Pea dispersed repeat
PDW	Pod width
PEBV	Pea early browning virus
PG	Peg growth
PGMS	Petiole groove on main stem
PGP	Peg pigmentation
PGPL	Petiole groove on primary lateral
PHMS	Petiole hairiness on main stem
PHPL	Petiole hairiness on primary lateral
PL	Peg length
PLMS	Petiole length on main stem
PLPL	Petiole length of primary lateral
PMS	Pigmentation on main stem
PMV	Peanut mottle virus
PPi	Pyrophosphate
PR	Pod reticulation
PRINS	Primed in situ labeling
PROINPA	Foundation for the Promotion and Investigation of Andean Products
PStV	Peanut stripe virus
QTL	Quantitative trait loci
RAPD	Random amplified polymorphic DNA
rDNA	Ribosomal DNA
RFLP	Restriction fragment length polymorphism
RG	Root growth
RGA	Resistance gene analog
RGM	Rachis groove on main stem
RGPL	Rachis groove on primary lateral
RH	Relative humidity
RI	Relative injury
RIL	Recombinant inbred line
RLMS	Rachis length of the main stem
RLPL	Rachis length of primary lateral
RNAi	RNA interference
rRNA	Ribosomal RNA
RuBisCo	Ribulose biphosphate carboxylase/oxygenase
SAGE	Serial analysis of gene expression
SALMS	Stipule adnation length on main stem
SALPLB	Stipule adnation length on primary lateral branch
SAT	Satellite chromosome
SAWMS	Stipule adnation width on main stem
SAWPLB	Stipule adnation width on primary lateral branch

SBMMS	Stipule bristles on margin of the main Stem
SBMPL	Stipule bristle on the margin of primary lateral
SBOMS	Stipule bristles outside of the main stem
SBOPLB	Stipule bristle outside primary lateral branch
SC	Seed color
SCAR	Sequence-characterized amplified region
SCMR	SPAD Chlorophyll meter reading
SDL	Seed length
SDS	Sodium dodecyl sulfate
SDW	Seed width
SEM	Scanning electron microscopy
SEN	Southeastern subregion of North and Central America
SHMMS	Stipule hairiness on margin of the main stem
SHMPLB	Stipule hairiness on margin of primary lateral branch
SHOMS	Stipule hairiness on outside of the main stem
SHOPL	Stipule hairiness on outside primary lateral
SLA	Specific leaf area
SLMS	Stipule length on main stem
SLPLB	Stipule length on primary lateral branch
SM	Stem modification
SMD	Sterility mosaic disease
SMP®	Solid Matrix Priming®
SNP	Single nucleotide polymorphism
SPAD	Soil plant analysis development
SPC	Standard petal color
SPL	Standard petal length
SPMBF	Standard petal markings on back face
SPMFF	Standard petal markings on front face
SPW	Standard petal width
SRAP	Sequence related amplified polymorphism
SSAP	Sequence-specific amplified polymorphism
SSR	Simple sequence repeat
STMS	Sequence tagged microsatellite site
STS	Sequence tagged site
TAC	Transformation competent artificial chromosome
TC	Tentative consensus
TIILING	Targeting induced local lesions in genomes
tr	Transpiration rate
tRNA	Transfer RNA
TSWV	Tomato spotted wilt virus
ULCL	Upper lip calyx lobation
UN	United Nations
UNALM	National Agrarian University of La Molina (Peru)
UNAP	National University of the Altiplano – Puno (Peru)
USDA	US Department of Agriculture
UV	Ultra violet light
VIGS	Virus-induced gene silencing
WPBS	Welsh Plant Breeding Station
WPC	Wing petal color

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Chapter 1
Arachis

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1.1 Introduction

Crop wild relatives (CWR) are wild plant taxa that have an indirect use derived from their relatively close genetic relationships to crops (Maxted et al. 2006). An understanding of the taxonomic and evolutionary relationships between cultigens and their wild relatives is prerequisite for the exploitation of wild relatives in crop improvement programs (Hawkes 1977). In the past, several reviews on the use of wild relatives for crop improvement have been published, which demonstrated greatest benefit towards improving the levels of resistance to pests and diseases in several crops including groundnut (Harlan 1976; Stalker 1980; Goodman et al. 1987; Lenne and Wood 1991; Hoisington et al. 1999; Dwivedi et al. 2003). Hajjar and Hodgkin (2007) documented information on the presence of genes from CWR in released cultivars of CGIAR mandate crops, demonstrating that there has been steady increase in the rate of release of cultivars containing genes from CWR. More recently, it has also been demonstrated that CWR have contributed alleles associated with increased fruit/grain yield and improved seed quality, predominantly in tomato and rice, and resistance to drought and salinity in wheat [reviewed in Dwivedi et al. (2008)].

Groundnut (*Arachis hypogaea* L.) originated in South America and is widely grown (113 countries) throughout tropical, subtropical and warm temperate regions (40°N to 40°S). Worldwide, groundnut is next in importance after soybean and rapeseed, with an annual production of 38.2 million tons and average productivity of 1.5 ton ha^{-1} (FAO 2008). The seeds are rich in oil and protein and are eaten in a variety of forms. About two-thirds of global production is crushed for extracting vegetable oil. The remaining one-third is used in the form of edible product and as seed. The cake obtained after oil extraction is used as protein-rich meal for livestock or for making other food products. The haulms are an important source of good quality animal fodder. Some of the perennial wild species, such as *A. glabrata* from the section Rhizomatosae, have been used to develop several commercial tropical forage cultivars, including the Florigraze and Arbrook in the USA that are used as an alternative to alfalfa because of their high levels of proteins and resistance to pest and diseases (Prine et al. 1981, 1986; French et al. 1994). Likewise, in Australia, *A. glabrata* is valued as high-quality forage having the ability to spread through swards of aggressive summer-growing grass species (Bowman et al. 1998). In addition, groundnut helps to improve soil fertility through biological nitrogen fixation.

Rust, early leaf spot, and late leaf spot are the most common and widely distributed foliar diseases of groundnut worldwide, while leaf minor is common in South Asia; army worm (*Spodoptera*) and bacterial wilt in South-east Asia; groundnut rosette disease and termite in Africa; and nematode, corn earworm, lesser corn stock borer, and southern corn rootworm in North America. Some insects are also the vectors of important viral diseases – *Thrips palmi* for peanut bud necrosis virus, *Frankliniella occidentalis* and *F. fusca* for tomato-spotted wilt virus and *Aphis crassivora* for groundnut rosette virus. In addition to biotic stresses, the crop is also adversely affected by drought, salinity, low availability of phosphorus under acidic soils and nonavailability of iron in calcareous soils in many

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parts of the world. Aflatoxin contamination is the major problem adversely affecting the groundnut seed quality. All these factors either alone or in combination adversely affect the yield and/or quality worldwide, necessitating the identification and utilization of resistance sources to enhance and sustain groundnut production. With regard to several pests and diseases, the level of resistance required is either not present or available only at very low levels in cultivated groundnut, while very high levels of resistance to pests and diseases have been reported in many wild *Arachis* relatives [reviewed in Dwivedi et al. (2003)].

The cultivated groundnut, *A. hypogaea*, belongs to the section *Arachis*, which also contains its tetraploid progenitor *A. monticola* Krapov. and Rigoni (Favero et al. 2006), and 29 wild diploid species that are cross-compatible with *A. hypogaea*. *A. ipaënsis* and *A. duranensis* have been suggested as putative B- and A-genome donors, respectively, of the cultivated peanut (Kochert et al. 1996; Seijo et al. 2004; Favero et al. 2006). More recently, Seijo et al. (2007) used the double genomic in situ hybridization (GISH) technique on seven diploid species that harbored either the A- or B-genome, to provide further evidence that *A. duranensis* (A-genome) and *A. ipaënsis* (B-genome) are the best candidates for the genome donors of cultivated groundnut as both yielded the most intense and uniform hybridization pattern when tested against the corresponding chromosome subsets of *A. hypogaea*. Further, all the presently known subspecies and varieties of *A. hypogaea* have arisen from a unique allotetraploid plant population, or alternatively, from different tetraploid populations that originated from the same two diploid species.

Singh and Simpson (1994) have classified the genetic variability in the genus *Arachis* into four genepools: primary gene pool (landraces of *A. hypogaea* and its wild form *A. monticola*), secondary gene pool (diploid species from section *Arachis* that are cross-compatible with *A. hypogaea*), tertiary gene pool (species of section *Procumbentes* that are weekly cross-compatible with *A. hypogaea*) and the fourth gene pool (wild *Arachis* species classified into seven other sections). While interspecific crosses involving some species from secondary gene pool have been successful in groundnut, it is more difficult to cross species from tertiary and forth gene pool, for which, techniques such as in vitro culture of ovule and embryo is a must to produce viable hybrids (see Sect. 1.7).

This review is devoted to the use of wild *Arachis* for the improvement of *A. hypogaea* (cultivated groundnut) with the focus on conservation and regeneration of wild *Arachis* genetic resources; geographical distribution and the need to expedite collection of those species not present in genebanks before these are lost due to climate change or habitat disturbances in South America; differences in ploidy levels, genomes, and crossing relationships; descriptors used to characterize *Arachis* species; sources of resistance to biotic and abiotic stresses and for seed quality; barriers to interspecific hybridization; genomic resources developed to facilitate introgression of beneficial traits from wild *Arachis* to *A. hypogaea*; approaches to interspecific gene transfer and use of genetic markers to demonstrate the introgression of traits from wild *Arachis* species; the elite germplasm and cultivars developed using wild *Arachis* species; and new approaches to unlock the genetic variation from wild relatives using appropriate genetic and genomic resources.

1.2 Wild *Arachis* Species

1.2.1 Geographical Distribution

Arachis is exclusively a genus of South America and consists of nine sections that comprise 80 annual and perennial species (Krapovickas and Gregory 1994; Valls and Simpson 2005). It belongs to the family Leguminosae-Papilionoideae, tribe Aeschynomeneae and subtribe Stylosanthinae, and is restricted to Argentina, Bolivia, Paraguay and Uruguay. The *Arachis* section species occur in Brazil (mostly in the west central region) followed by Paraguay, Argentina and Uruguay. Wild *Arachis* species occur both in open and shaded areas, ranging from near to the equator to 34°S and from sea level to an attitude of almost 1,600 m. Because of the geocarpic nature of the fruit, species distribution generally follows major river valleys. Infrageneric groups may be closely associated with specific drainage basins, such as members of the section Triseminatae are found in the São Francisco, while species of the section *Arachis* in the drainage basin of the river Paraguay and also in the Amazon drainage basin. Some overlap in distribution does occur for the sections Arachis, Erectoides, Rhizomatosae and Extranervosae (Gregory et al. 1973; Valls 1983; Valls et al. 1985). Species in the section Arachis are distributed in Argentina, Bolivia, Brazil, Uruguay and Paraguay, from the southern extreme of the genus along the river Uruguay to the eastern most extreme of the genus in Bolivia and Argentina and north-eastwards across the Brazilian Highlands. Section Heteranthae contains six species and is endemic to the north-eastern highlands of Brazil, while section *Trierectoides* contains two species, *A. guaranitica* and *A. tuberosa*, and is geographically restricted to a narrow distribution range in Brazil (one population of *A. guaranitica* is also reported from Paraguay). Species in section *Caulorhizae* including *A. pintoi* and *A. repens* are endemic to Brazil and centered in the eastern Brazilian highlands with scattered populations found towards the highlands of Mato Grosso do Sul. Section *Procumbentes* species are distributed where the borders of Paraguay, Bolivia and Brazil come together, near an area known as Pantanal while Erectoides section species are restricted largely in the Brazilian Province of Mato Grosso do Sul stretching southwards in Paraguay. Section *Extranervosae* species are also endemic to Brazil, inhabiting the Brazilian Highlands north and west of Mato Grosso do Sul, spreading across the Brazilian Plateau as far as 5°S. Section *Triseminatae* is endemic to the north-eastern Brazilian Highlands, while section *Rhizomatosae* species inhabit areas surrounding the Parana basin, and southwards through Paraguay, Argentina and into Uruguay, following the Rio Paraguay and meeting the Rio Uruguay (Ferguson et al. 2005).

1.2.2 *Ex Situ Conservation of Wild* Arachis *Genetic Resources and Priority Areas for Future Collection*

The major centers of conservation of wild *Arachis* species are in India, Brazil, USA, Argentina and Columbia, together holding ~2,800 accessions (Table 1.1). ICRISAT developed *Arachis* house, an open space fixed with a large cylindrical concrete structure (75 cm high, 90 cm in inner ring diameter, and of 5 cm ring thickness) with a ring-to-ring distance of 52.5 cm, for regenerating the seeds of wild *Arachis* species (Fig. 1.1). These rings are filled with about 0.5 m^3 pasteurized [3 cycles of 1 h each at 82°C and 34.5×10^3 Pa (5 psi)] soil mixture (soil, sand and FYM in 3:2:1 ratio). Five to six plants can be accommodated in one ring. After harvesting the pods at maturity, the remnant pods/seeds are visually collected and destroyed to avoid contamination with the next seed lot. The rings are kept fallow for 2–3 months and 2–3 irrigations are provided to allow remnant seeds, if any, to germinate, which are destroyed before the next seed lot is sown.

Preservation of wild *Arachis* species, in general, is difficult, particularly for accessions that produce a few seeds, and especially the section *Rhizomatosae* species, which are maintained as vegetative materials in greenhouse (Stalker and Simpson 1995). An international cooperative effort is underway to ensure that these vegetatively propagated species are maintained in multiple environments for conservation to minimize their loss (Singh and Simpson 1994). This effort involves the cooperation of USDA, North Carolina State University, Texas A&M University, ICRISAT, the Brazilian Corporation for Agricultural Research

Table 1.1 Major holdings of wild *Arachis* species accessions in genebank

Country	Institute	# Accessions
Argentina	Instituto Botánico del Nordeste, Universidad Nacional de Nordeste (IBONE)	109
Australia	Australian Tropical Crops and Forages Genetic Resources Centre	65
Brazil	Embrapa Recursos Geneticos e Biotecnologia (CENARGEN) Instituto AgronOmico de Campinas	450
Colombia	Centro Internacional de Agricultura Tropical (CIAT)	243
	Centro de Investigaciones de Nataima, Instituto Colombiano Agropecuario (ICA)	225
India	International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Hyderabad	453
USA	USDA, Griffin, USA	498
	Texas A&M University, USA	798