

Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources Oilseeds

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Oilseeds

 Springer

Editor

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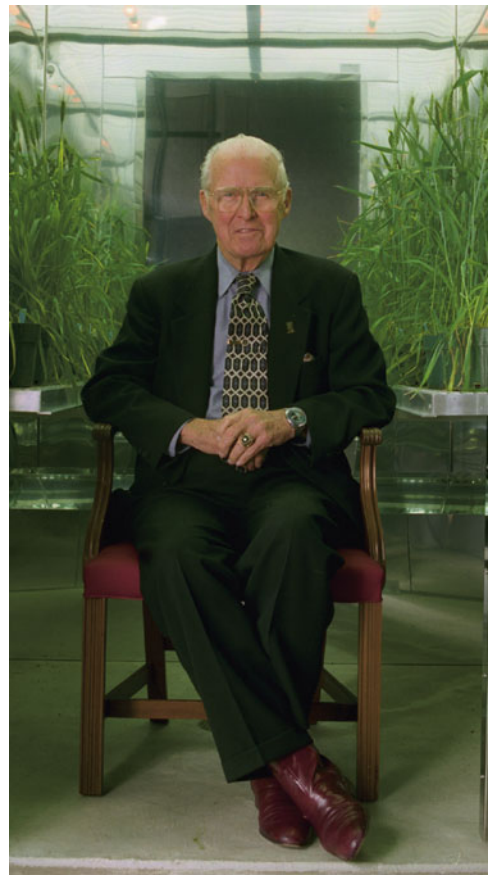
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Dedication

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

This volume “Wild Crop Relatives – Genomic and Breeding Resources: Oilseeds” includes 17 chapters dedicated to *Arabidopsis*, *Brassica*, *Capsella*, *Carthamus*, *Crambe*, *Cuphea*, *Diplotaxis*, *Eruca*, *Helianthus*, *Hirschfeldia*, *Linum*, *Moricandia*, *Orychophragmus*, *Pachycladon*, *Ricinus*, *Sesamum* and *Sinapsis*. The chapters of this volume were authored by 33 scientists from 11 countries of the world including Canada, China, France, Germany, India, Italy, New Zealand, Poland, Spain, UK and 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 oilseed crops with an intention of serving science and society.

Clemson, USA

Chittaranjan Kole

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Abbreviations

2,4-D	2,4-Dichlorophenoxyacetic acid
3MSOP	3-Methylsulfinylpropyl glucosinolate
3MTP	3-Methylthiopropyl glucosinolate
4MSOB	4-Methylsulfinylbutyl glucosinolate
7MSOH	7-Methylsulfinylheptyl glucosinolate
ACT	Acyl carrier thioesterase
ADH	Alcohol dehydrogenase
<i>Adh</i>	Alcohol dehydrogenase gene
AFLP	Amplified fragment length polymorphism
AICORPO	All India Coordinated Research Project on Oilseeds
Ala	Alanine
AMOVA	Analysis of molecular variance
<i>AOP2</i>	2-Oxoglutarate-dependent dioxygenase 2 gene
Arg	Arginine
AROS	Array-ready oligonucleotide set
ARS	Agricultural Research Service
As	Arsenic
Asp	Aspartic acid
<i>atpA</i>	Gene encoding the alpha subunit of the F(1) ATPase
<i>atpB</i>	Adenosine triphosphatase B gene
<i>atpα</i>	ATPase α gene
AWC	Allen Wilson Center
BAC	Bacterial artificial chromosome
BAP	Benzyl amino purine
BAPNA	<i>N</i> α -benzoyl-DL-arginine- <i>p</i> -nitroaniline
BC	Backcross
BCgDFS	<i>Brassica</i> C-Genome Diversity Fixed Foundation Set Resources
BEAST	A cross-platform Bayesian Markov chain Monte-Carlo sequence analysis program
BGCI	Botanic Gardens Conservation International
BGV	Banco de Germoplasma Vegetal
BLAST	Basic local alignment search tool
BolDFS	<i>Brassica oleracea</i> Crop Genepool
BoS	<i>Brassica oleracea</i> SINE
Bras-EDB	European Brassica Database
C:12	Lauric acid
C:14	Myristic acid

<i>CAD5</i>	Cinnamyl alcohol dehydrogenase 5 gene
CaMV	Cauliflower mosaic virus
CAPS	Cleaved amplified polymorphic sequence
<i>CCAI</i>	Circadian clock associated
CCP	Comparative chromosome painting
cDNA	Complementary-DNA
CGH	Comparative genomic hybridization
CGRIS	Chinese Genetic Resources Information System
Chs	Chalcone synthase
<i>CHS</i>	Chalcone synthase gene
CISS	Chromosomal in situ suppression
CMS	Cytoplasmic male sterility
CNR	National Research Council
Col-0	Columbia ecotype
CP	Chromosome painting
cpDNA	Chloroplast-DNA
CSIR	Council of Scientific and Industrial Research (New Delhi, India)
C-value	Constant value (1C = Amount of DNA within a haploid nucleus)
CWR	Crop wild relatives
Cys	Cysteine
DAMD	Direct amplification of minisatellite DNA
DBT	Department of Biotechnology (New Delhi, India)
DFS	Diversity Foundation Set
DNAML	DNA maximum likelihood program
DOG	Delay of germination
DOR	Directorate of Oilseeds Research (Rajendranagar, India)
DRDO	Defence Research and Development Organization (New Delhi, India)
DSE	Regeneration of direct organogenesis from explants
EC	European Community
ECPGR	European Cooperative Program for Crop Genetic Resources Networks
EMBL	European Molecular Biology Laboratory
EMS	Ethylmethane sulfonate
EPSPS	5-Enol acetone, acyl Shikimate-3-phosphate synthase
<i>ESM1</i>	Epithiospecifier modifier 1 gene
<i>ESP</i>	Epithiospecifier protein gene
EST	Expressed sequence tag
ETS	External transcribed sequence
EURISCO	European Network of ex situ National Inventories
F ₁	First filial (generation)
F ₂	Second filial (generation)
FA	Fatty acid
FAE	Fatty acid elongation
FISH	Fluorescence in situ hybridization
<i>FLC</i>	<i>Flowering Locus C</i> gene
<i>FMF2</i>	<i>Embryonic flower 2</i> gene
<i>FRI</i>	<i>FRIGIDA</i> gene

FSE	Farm scale evaluation
GA ₃	Gibberellic acid
<i>gapC</i>	Glyceraldehyde-3-phosphate dehydrogenase gene
<i>gdc</i>	Glycine decarboxylase gene
GDC	Glycine decarboxylase
<i>gdcP</i>	Glycine decarboxylase P gene
<i>GFP</i>	Green fluorescent protein gene
GISH	Genomic in situ hybridization
GLS	Glucosinolate compound
<i>GLS-AOP</i>	Glucosinolate 2-oxoglutarate-dependant dioxygenase gene
<i>GLS-elong</i>	Glucosinolate methylthioalkylmalate synthase gene
<i>GLS-OH</i>	Glucosinolate 2-oxoacid-dependant dioxygenase gene
<i>GLS-OX</i>	Glucosinolate flavin-monoxygenase gene
Glu	Glutamic acid
Gly	Glycine
GM	Genetic modification/ genetically modified
GMO	Genetically modified organism
GMU	Germplasm management unit
GRIN	Genetic Resources Information Network
GSL-ALK	QTL for production of alkenyl glucosinolate
HDL	High-density lipoprotein
HEA	High erucic acid
HEADE	High Erucic Acid Development Effort
His	Histidine
IBPGR	International Board for Plant Genetic Resources
Ile	Isoleucine
IO	Regeneration of explants through organogenesis from callus
IPGRI	International Plant Genetic Resources Institute
IPK	Institut für Pflanzengenetik und Kulturpflanzenforschung
ISE	Regeneration of explants through somatic embryogenesis from callus
ISSR	Inter-simple sequence repeat
ITC	Isothiocyanate
ITS	Internal transcribed spacer
IUCN	International Union for Conservation of Nature
KAS	Ketoacyl-ACPSynthase
LDL	Low-density lipoprotein
Ler	Landsberg erecta ecotype
Leu	Leucine
<i>LFY</i>	Leafy gene
LG	Linkage group
Lys	Lysine
<i>MAMI</i>	Methylthioalkylmalate synthase 1 gene
MAS	Marker-assisted selection
MatK	Maturase K
<i>matK</i>	Megakaryocyte-associated tyrosine kinase gene
MCT	Medium chain fatty acid
Met	Methionine

Mg	Magnesium
MISA	MIcroSATellite
MLO	Mycoplasma-like Organism
Mn	Manganese
MPSS	Massively parallel signature sequence
<i>MS</i>	Malate synthase gene
MS	Murashige and Skoog medium
Mt	Mountain
MTI	Mustard trypsin inhibitor
<i>MtN21</i>	<i>Medicago truncatula</i> -like nodulin 21 gene
MUFA	Mono-unsaturated fatty acid
MYA	Million years ago
N	Content of non-essential amino acid
NAA	Naphthaleneacetic acid
NAD(P)H	Nicotinamide adenine dinucleotide (phosphate) dehydrogenase
<i>nad4</i>	NADH4 gene
NADH	Nicotinamide adenine dinucleotide dehydrogenase
NBPGR	National Bureau of Plant Genetic Resources
NCBI	National Centre for Biotechnology Information
<i>ndhF</i>	NAD(P)H F gene
NeighborNet	A planar phylogenetic network construction program
NGRP	National Genetic Resources Program
NIL	Near-isogeneic lines
NMS	Nuclear male sterility
NPGS	National Plant Germplasm System
Nr	Nuclear ribosomal
Nt	Nucleotide
OIB	Outer involucral bract
<i>Orf</i>	Open reading frame
PAUP	Phylogenetic analysis using parsimony program
PCR	Polymerase chain reaction
PEG	Polyethylene glycol
PEP	Phosphoenolpyruvate
PGI	Phosphoglucose isomerase
Phe	Phenylalanine
PHYLIP	Phylogeny inference package
PhyML	Phylogenies by maximum likelihood program
<i>PI</i>	Pistillata gene
PMC	Pollen mother cell
PPT	Phosphinothricin
<i>PRK</i>	Phosphopyruvate kinase gene
Pro	Proline
PVC	Polyvinyl chloride
PVX	Potato virus X
PVY	Potato virus Y
QE II	Queen Elizabeth II
QTL	Quantitative trait loci
R&D	Research and Development

RAPD	Random amplified polymorphic DNA
<i>rbcL</i>	Rubisco (Ribulose biphosphate carboxylase/oxygenase) large sub-unit gene
RCA	<i>Ricinus communis</i> agglutinin
RCP	Reverse chromosome painting
rDNA	Ribosomal DNA
RFLP	Restriction fragment length polymorphism
RIL	Recombined inbred line
rRNA	Ribosomal RNA
S	Selfing generation
SAAPLPNA	Succinyl-ala-ala-pro-leu- <i>p</i> -nitroanilide
SACPD	Stearoyl acyl carrier protein desaturase
SAGE	Serial analysis of gene expression
SAMDC	S-Adenosylmethionine decarboxylase activity
Sar	Genome of <i>Sinapis arvensis</i>
SC	Self-compatible
SCAR	Sequence-characterized amplified region
SCRI	Scottish Crop Research Institute
Ser	Serine
S-GT	S-Glucosyltransferase
SHP 1	Shatteringprof 1
SHP 2	Shatteringprof 2
SINE	Short interspersed nuclear elements
SLR	S-Locus related
SNP	Single nucleotide polymorphism
SRAP	Sequence-related amplified polymorphism
SSR	Simple sequence repeat
SSRIT	SSR identification tool
STS	Sequence tagged site
T-DNA	Transfer-DNA
TFL 1	Terminal flower
Thr	Threonine
TIGR	The Institute Genome Rresearch
<i>TOCI</i>	True oscillator component
<i>trnL-trnF</i>	Intergenic space between introns tRNA ^{Leucine} (UAA) and tRNA ^{Phenylalanine} (GAA)
Trp	Tryptophane
TuMV	Turnip mosaic virus
Tyr	Tyrosine
UPM	Universidad Politecnica de Madrid
USDA	United States Department of Agriculture
UV	Ultraviolet
Val	Valine
VAM	Vesicular–arbuscular mycorrhizae
VLCFA	Very long chained fatty acid
WinClada	A data management analysis and tree editing program
WRPIS	Western Regional Plant Introduction Station

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Chapter 1

Arabidopsis

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1.1 Introduction

Arabidopsis belongs to the family Brassicaceae, which consists of several vegetable and oilseed crops including *Brassica oleracea*, *Brassica napus*, *Brassica nigra*, *Brassica rapa* (syn. *campestris*), and *B. juncea* among others. *Arabidopsis* genus consists of several species, among which *Arabidopsis thaliana* (L.) is used extensively for research in plant biology, although it has no potential economic value as a food or fuel crop. Although it cannot be used as oilseed crop, it has been used extensively for the genetic and genomic analysis of Brassicaceae crops (Panjabi et al. 2008). Since *Brassica* species genomes are many times greater than *Arabidopsis*, it is much convenient to work in *Arabidopsis* to use the information in the *Brassica* species for crop improvement efforts. *Arabidopsis* was used extensively as a model plant species in the 1950s for mutagenesis studies (Redei 1992). *A. thaliana* is a diploid species with $n = x = 5$ chromosomes, and a total genome size of approximately 125 Mb, one of the smallest known genomes among higher plants. Its small genome size is another feature that has led to its popularity as a model species. The genome sequence of *A. thaliana* var. Columbia was completed in 2000, and now most of the genes have been annotated (The Arabidopsis Genome initiative 2000).

Besides small genome size, it has less repetitive DNA, only 28,523 genes (of which 26,772 have been sequenced and the remaining thought to be

pseudogenes) and about 50,000 proteins (Katam et al. 2010). Furthermore, microarrays were developed and are currently available for global gene profiling experiments, and data mining such as from *A. thaliana* GenExpress transcriptome database is possible. Comparison of diversion of genes between *Arabidopsis* and *Brassica* species may uncover the evolution of unique and species-specific genes that will unravel the evolution of each species in the Brassicaceae family under the presence of selective pressure (Hall et al. 2002).

Among other members of Brassicaceae, *Cardamine amara* has been estimated to have the smallest genome size of only 50 Mb (Bennett and Smith 1991). The variation in genome size among plant species, which can extend up to 120,000 Mb, have been resulted from duplication, reassembly, or by partial elimination of genes in the presence of selective pressure during plant evolution. Evolutionary trends suggest that the extant species resulted from many rounds of gene duplication, deletion, homologous recombination, unequal crossing, rearrangement, and polyploidization from their putative progenitors (Vision et al. 2000). Currently, 40% of Brassicaceae species are reported to be polyploids (Masterson 1994).

1.2 Species of *Arabidopsis*

Advances in molecular methods have enhanced our ability to better understand the function and evolution of genes that regulate during high temperature, drought, pathogens, insects, and other environmental challenges. Although no single model system can address the diverse range of ecological and evolutionary questions of interest, *A. thaliana* and its wild relatives

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1.2.1 Origin of New Species Through Polyploidy

Although comparative genomics can detect more ancient events than classical cytology, all events may not be detected. It has long been recognized that polyploidy has played an important role in speciation, especially in plants (Stebbins 1971). The new species will, therefore, evolve independently of its parental species, and if the polyploidization occurs only once, there will be no additional gene-flow into the species once it is formed. Even if it occurs several times, different polyploid lineages may well be isolated because of the rapid chromosome rearrangements (Pontes et al. 2004) and changes in gene expression (Osborn et al. 2003) that may accompany polyploidization. If polyploid species become diploidized over time, all plant species will have polyploid ancestors (Ku et al. 2000). *A. suecica* (Fr.) was first described as an allotetraploid ($2n = 26$), which has *A. thaliana* and *Arabidopsis* (*Cardaminopsis*) *arenosa* as its parental species, a suggestion supported by molecular phylogenetics (O’Kane and Al-shehbaz 1997). It is diploid ($2n = 10$), although tetraploid *A. thaliana* individuals are occasionally found. *A. arenosa* is a European species, which is tetraploid ($2n = 4x = 32$) in most of its range and reportedly diploid ($2n = 2x = 16$) in a small area in eastern Europe (Mesicek 1970). cpDNA sequencing confirmed that *A. thaliana* is the maternal parent of *A. suecica* (Säll et al. 2003). Furthermore, when producing artificial *A. suecica* through crosses, viable offsprings were produced from *A. thaliana* maternal parent (Comai et al. 2000). An important aspect of the formation of a polyploid species is the number of independent origins. Many allopolyploid species are believed to have multiple origins (Soltis and Soltis 1993). If all the polyploids form a single branch within the tree, there is evidence of a single origin, whereas if the allopolyploids appear at different positions relative to the parent, there is evidence of multiple origins. This method was used to analyze cpDNA from *A. suecica*, and the results indicated a single origin.

Speciation by polyploidization is instantaneous, which is the result of a well defined, discrete event (s). The new polyploid species is expected to be isolated from its parental species because crosses between a polyploid and its parental species are most

likely infertile. However, repeated polyploidization events may result in a polyploid species with multiple origins. More than one polyploidization event of genetically very closely related parental individuals results in polyploidy species. The observation of monophyly at one or a small number of loci with respect to the parental species does not imply a single origin. Alleles in the polyploid species could be monophyletic with respect to the parental species since they coalesce more recently than the origins of the species (Rosenberg and Nordborg 2002).

1.2.2 Genome Differentiation in Closely Related Species

The phenomenon of heterosis or hybrid vigor is poorly understood despite its perceived importance in evolution and its practical significance in breeding programs that aim to increase yield of crop plants. The identification of positively selected chromosomal segments that increase the fitness of backcross progeny (Rieseberg et al. 1999) would provide a basis for the study of heterosis. Several models have been proposed to explain the genetic basis of heterosis, including the masking of deleterious alleles, complementation of allelic variants, and epistasis (Rieseberg et al. 2000). The interspecific hybrid system has a potential to facilitate progress to analyze biological processes that do not exist such as self-incompatibility and perennial growth habit and cannot be studied in *A. thaliana*. The interspecific hybrid system facilitates evaluation of the genetic basis of heterosis and understanding of genome evolution, specifically as a complement to the commonly used strategy of comparative mapping of the differentiated genomes of related species. However, the few molecular marker studies that have addressed this issue led to conflicting conclusions regarding the primary cause of heterosis possibly because a combination of causes might produce heterotic effects (Monforte and Tanksley 2000). Backcross populations of *A. thaliana*–*A. lyrata* hybrids may be used to investigate the extent of chromosome differentiation between *A. thaliana* and *A. lyrata* and the degree to which it might interfere with chromosome pairing and gene flow between the two species. It is critical to determine whether the backcross plants incur differential inheritance of different