

Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources Vegetables

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Vegetables

 Springer

Editor

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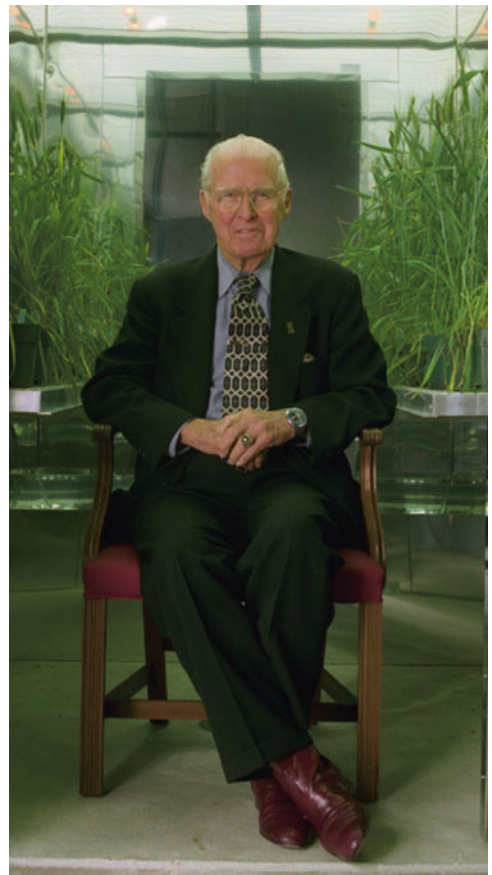
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Dedication

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 – Vegetables” includes 13 chapters dedicated to *Allium*, *Amaranthus*, *Asparagus*, *Capsicum*, *Citrulus*, *Cucumis*, *Daucus*, *Lactuca*, *Lycopersicon*, *Momordica*, *Raphanus*, *Solanum*, and *Spinacea*. The chapters of this volume were authored by 58 scientists from 12 countries of the world, namely Argentina, Australia, China, Denmark, India, Italy, Japan, Poland, South Africa, Thailand, 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 vegetable crops with an intention of serving science and society.

Clemson, USA

Chittaranjan Kole

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Abbreviations

| | |
|-----------------|--|
| 2-TD | 2-Tridecanone |
| 3G | 3-Glucoside |
| 6-PGD | 6-Phosphogluconate dehydrogenase |
| 7G | 7-Glucoside |
| <i>aadA</i> | Aldehyde–alcohol dehydrogenase gene |
| AAL | <i>Alternaria alternata</i> f. sp. <i>Lycopersici</i> |
| AB | Advanced backcross |
| <i>ABF3</i> | Gene encoding a transcription factor for expression of abscisic acid response genes |
| ABL | Advanced breeding line |
| <i>accD</i> | Acetyl-coenzyme D-subunit gene |
| ADH | Alcohol dehydrogenase |
| AFLP | Amplified fragment length polymorphism |
| <i>AG</i> | <i>AGAMOUS</i> gene |
| AIDS | Acquired immune deficiency syndrome |
| ALS | Acetolactate synthase |
| AMV | Alfalfa mosaic virus |
| Ap | Apigenin |
| ARS | Agriculture Research Service (of USDA) |
| <i>AU</i> | <i>Aurora</i> locus |
| AVGRIS | The AVRDC Vegetable Genetic Resources Information System |
| <i>Avr</i> | Avirulence gene |
| AVRDC | Asian Vegetable Research and Development Center (presently The World Vegetable Center), Taiwan |
| BAC | Bacterial artificial chromosome |
| BC | Backcross |
| BC ₁ | Backcross (first generation) |
| BCRIL | Backcross recombinant inbred line |
| BIL | Backcross inbred line |
| BWYV | Beet western yellows virus |
| CAAS | Chinese Academy of Agricultural Science |
| CAPS | Cleaved amplified polymorphic sequence |
| CATIE | Centro Agronómico Tropical de Investigación y Enseñanza (Costa Rica) |
| CC | Coiled |
| cDNA | Complementary-DNA |
| CGAA | Candidate genes associated with ascorbic acid biosynthesis |

| | |
|----------------|--|
| CGC | Candidate carotenoid gene |
| CGFL | Candidate gene for flowering |
| CGFSC | Candidate gene for fruit size and composition |
| CGIAR | Consultative Group on International Agricultural Research |
| Chr | Chrysoeriol |
| CHS | Chalcone synthase |
| CIP | International Center for the Potato (Peru) |
| cM | CentiMorgan |
| <i>Cm-ERS1</i> | Mutated melon ethylene receptor gene |
| Cmm | <i>Clavibacter michiganensis</i> ssp. <i>michiganensis</i> |
| CMS | Cytoplasmic male sterility |
| CMV | Cucumber mosaic virus |
| COS | Conserved ortholog set |
| COSII | Conserved ortholog set II |
| CPC | Commonwealth Potato Collection (SCRI) |
| cpDNA | Chloroplast-DNA |
| CR-EST | Candidate resistance/defense-response EST |
| cv. | Cultivar |
| CVMV | Chili veinal mottle virus |
| <i>DEF</i> | <i>DEFICIENS</i> gene |
| <i>Dm3</i> | Downy mildew resistance gene |
| EB | Early blight |
| ECPGR | European Cooperative Program for Plant Genetic Resources |
| ELISA | Enzyme-linked immunosorbent assay |
| EPSPS | 5-Enolpyruvyl-shikimate-3-phosphate synthase |
| EST | Expressed sequence tag |
| ETS | External transcribed spacer |
| EU | European Union |
| F ₁ | First filial generation |
| FAO | Food and Agriculture Organization (of the United Nations) |
| FAOSTAT | FAO Statistics |
| FISH | Fluorescence/Fluorescent in situ hybridization |
| FW | Fresh weight |
| G(M1)/G(m1) | Ganglioside |
| GBSSI | Granule-bound starch synthase |
| GDH | Glutamate dehydrogenase |
| GFP | Green fluorescent protein |
| GISH | Genomic in situ hybridization |
| <i>GLO</i> | <i>GLOBOSA</i> gene |
| GLOase | L-Gulono-gamma-lactone oxidase |
| GM | Genetically modified/modification |
| GM | Tomato gray mold |
| GRIN | Germplasm Resources Information Network (of USDA) |
| <i>gus</i> | β-Glucuronidase gene |
| HIV | Human immunodeficiency virus |
| HPT | Homogentisate phytyl transferase |
| HR | Hypersensitive response |
| IAA | Indole acetic acid |

| | |
|----------------|---|
| IBA | Indole butyric acid |
| IBC | Inbred backcross population |
| IBPGR | International Board for Plant Genetic Resources |
| IDH | Isocitrate dehydrogenase |
| IL | Introgression line |
| ILD | Incongruence length difference test |
| ILH | Introgression line hybrid |
| INIBAP | International Network for Improvement of Banana and Plantain |
| IPGRI | International Plant Genetic Resources Institute |
| ISO | Isozyme |
| ISSR | Intersimple sequence repeat |
| ITAG | The International Tomato Annotation Group |
| ITS | Internal transcribed spacer |
| IUCN | International Union for Conservation of Nature |
| Ka | Kaempferol |
| <i>KNAT1</i> | Knotted 1 gene from <i>Arabidopsis thaliana</i> |
| LA | Linoleic acid |
| LAP | Leucine amino peptidase |
| LB | Late blight |
| LBVaV | Lettuce big vein associated virus |
| LMV | Lettuce mosaic virus |
| LRR | Leucine rich repeat |
| LTB | Labile enterotoxin B |
| Lu | Luteolin |
| MAAL | Monosomic alien addition line |
| MAS | Marker-assisted selection |
| MDH | Malate dehydrogenase |
| <i>ME-4aN4</i> | Late embryogenesis abundant protein gene from <i>Brassica napus</i> |
| MH | Maleic hydrazide |
| MHa | Million hectare(s) |
| MI | First metaphase |
| MiBASE | Micro-Tom Database |
| MLBVV | Mirafiori lettuce big vein virus |
| MO | Morphological marker |
| Mpb | Million base pairs |
| MSAP | Methylation-sensitive amplified polymorphism |
| mtDNA | Mitochondrial-DNA |
| <i>MW</i> | <i>Milky Way</i> locus |
| NATP | National Agricultural Technology Project (India) |
| NBN | National Biodiversity Network |
| NBS | Nucleotide binding site |
| NCBI | National Center for Biotechnology Information |
| NCGRP | National Center for Genetic Resources Preservation |
| NIL | Near isogenic line |
| NOR | Nucleolus organizing region |
| NPGS | National Plant Germplasm System |
| <i>nptII</i> | Neomycin phosphotransferase gene |
| nrDNA | Nuclear ribosomal DNA |

| | |
|-------------|---|
| <i>Nv</i> | Non-virion gene |
| ODO | Overdominant |
| <i>OR</i> | <i>Orion</i> locus |
| <i>OxdC</i> | Decarboxylase gene |
| PA | Petroselinic acid |
| PBMC | Peripheral blood mononuclear cells |
| PCN | Potato cyst nematode |
| PCR | Polymerase chain reaction |
| PEG | Polyethylene glycol |
| PepMoV | Pepper mottle virus |
| PGI | Phosphoglucose isomerase |
| PGM | Phosphoglucomutase |
| PGRU | Plant Genetic Resources Unit |
| PM | Powdery mildew |
| pMAC | Hybrid promoter of cauliflower mosaic virus 35S protein and the Ti plasmid mannopine synthase gene promoter |
| PMC | Pollen mother cell |
| PPO | Protoporphyrinogen oxidase |
| PPX2 | Allelic form of protoporphyrinogen oxidase |
| PRV | Papaya ringspot virus |
| PSII | Photosystem II |
| PVY | Potato virus Y |
| QAL | Queen Anne's lace |
| QTL | Quantitative trait loci |
| Qu | Quercetin |
| RAPD | Random amplified polymorphic DNA |
| RDA | Recommended dietary allowances |
| rDNA | Ribosomal DNA |
| RFLP | Restriction fragment length polymorphism |
| <i>RG</i> | Resistance gene |
| RGA | Resistance gene analog |
| RIL | Recombinant inbred line |
| RNAi | RNA interference |
| RS | Reproductive stage |
| RT-PCR | Reverse transcriptase-PCR |
| SAMPL | Selectively amplified microsatellite polygenic loci |
| SC | Self-compatibility/Self-compatible |
| SCAR | Sequence characterized amplified region |
| SCRI | Scottish Crop Research Institute |
| sCTB | Synthetic cholera toxin B subunit |
| SG | Seed germination |
| SGe | Selective genotyping |
| SGN | SOL Genomics Network |
| SI | Self-Incompatibility or Self-Incompatible |
| SINGER | System-wide Information Exchange Network (of CGIAR) |
| SNP | Single nucleotide polymorphism |
| SOL | International Solanaceae Genome Project |
| SSC | Soluble solids content |

| | |
|-----------|--|
| SSR | Simple sequence repeat |
| ST | Salt tolerance |
| STS | Sequence tagged site |
| TC | Test cross |
| TC | Tocopherol cyclase |
| TED | Tomato Expression Database |
| TEI | Tomato EST-derived intronic polymorphism |
| TES | Tomato EST-derived SSR |
| TEV | Tobacco etch virus |
| TGRC | Tomato Genetics Resource Center |
| TGS | Tomato genome-derived SSR |
| TILLING | Targeting induced local lesions in genomes |
| TIR | Tol interleukin receptor homology |
| TL | Tocopherol cyclase |
| TMRD | Tomato Mapping Resource Database |
| TMV/ToMV | Tobacco mosaic/mottle virus |
| t-NBS-LRR | Tomato-nucleotide binding site-leucine rich repeat |
| TPI | Triose phosphate isomerase |
| TRAP | Target region amplification polymorphism |
| TSED | Tomato Stress EST Database |
| TSWV | Tomato spotted wilt virus |
| TYLCV | Tomato yellow leaf curl virus |
| UI | Unilateral incongruity |
| UNU | United Nations University |
| UPGMA | Unweighted pair group method |
| USDA | United States Department of Agriculture |
| USFWS | United States Fish and Wildlife Service |
| VG | Vegetative growth |
| VIGS | Virus induced gene silencing |
| WHO | World Health Organization |
| WMV | Watermelon mosaic virus |
| WUE | Water use efficiency |
| YAC | Yeast artificial chromosome |
| ZYMV | Zucchini yellow mosaic virus |

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Chapter 1

Allium

Damaris A. Odeny and Satya S. Narina

1.1 Introduction

The word “*Allium*” comes from the Greek word “aloe,” which means to avoid, and was given to the genus because of the characteristic offensive smell of its members. The genus *Allium* is one of the largest plant genera and includes about 780 species. Cultivation of *Allium* species is reportedly very old and as extensive as civilization itself (Block 2010). The wealth of *Allium* species was mentioned in the ancient civilizations both as flavorful foods and healing herbs.

Allium is a genus within the family Alliaceae and belongs to the order Asparagales of the monocot division. Asparagales and the Poales (which includes the grasses) are two well-supported monophyletic orders within the monocots (Rudall et al. 1997). The genus *Allium* is mainly restricted to the regions that are seasonally dry, with centers of diversity in Southwest/Central Asia, eastern Asia, and in North America. Members of the genus *Allium* include many economically important crops such as onions (*Allium cepa*), shallots (*Allium oschaninii*), leeks (*Allium ampeloprasum* var. *porrum*), scallions (*Allium ascalonicum*), garlic (*Allium sativum*), chives (*Allium schoenoprasum*), Japanese bunching onions (*A. fistulosum*), rakkyo (*A. chinense*) and Chinese chives (*A. tuberosum*). Others such as *A. karataviense* and *A. christophii* are cultivated as ornamentals (Huxley et al. 1992).

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Different communities use several wild *Allium* species for different purposes while breeders use them as sources of economically important traits for improving the cultivated species. Many wild *Allium* species are believed to have significant potential contribution to the *Allium* breeding community and to the global food and health needs. Despite the importance of these species, there are very few studies and research investments on them. The taxonomy is not extensive and conservation efforts have been limited. The limited extent of genomic tools within the genus as a whole has further limited research focus to cultivated species. We provide here a brief review on wild *Allium* species including basic botany, conservation initiatives, contribution toward the development of cytogenetic stocks, genetic tools, and improvement of the cultivated species. The potential for more domestication and commercialization of wild *Allium* species as a source of income, nutrition, and medicinal remedy are also mentioned.

1.2 Basic Botany of the Species

The taxonomy of *Allium* has been described as complicated with a great number of synonyms and intra-generic groupings (Klaas 1998). The genus comprises either short- or long-lived perennials (Brewster 1998) with characteristic storage organs (Fritsch and Friesen 2002). The typical storage organs are rhizomes, roots, or bulbs.

The bulbs are generally enclosed in membranous tunics, free or almost free tepals, and often in a subgynobasic style (Friesen et al. 2006). The bulbs can be large and single, or small, forming clusters (Le Guen-

Le Saos et al. 2002) and range in size from 2–3 mm to 8–10 cm in diameter.

The leaves are tubular (as in onions) or flat arising from the underground stem with long sheathing base, which can give the appearance of a stem (Block 2010). Many *Allium* species have basal leaves that wither away from the tips downward before or while the plant is flowering (<http://www.absoluteastronomy.com/topics/Allium>). The inflorescence can be fasciculate, umbel or head like, few to many, and loose to dense flowers have been reported (Fritsch and Friesen 2002). Flowering time varies with various *Allium* species. Flowering has been recorded in spring, summer, or autumn (Brewster 1998). A majority of *Allium* species are outbreeders, but the occurrence of both outbreeding and inbreeding forms in the same species has been reported (Brat 1965).

Allium species contain nectaries, which are located between the base of the ovary and the flattened widened base of the inner whorl of stamen and filaments (Peumans et al. 1997). The ovaries are largely trilocular and the styles are single and slender (Fritsch and Friesen 2002). The seeds can be angular or globular (Fritsch and Friesen 2002). Polyembryony (the development of multiple seedlings from a single seed) has been observed in several *Allium* species within the subgenus *Rhizirideum* (Specht et al. 2001).

1.3 Conservation Initiatives

As in many other crop species, there is evidence of genetic erosion in *Allium* species (Mingochi and Swai 1994). Goodding's onion (*Allium gooddingii*), a delicate perennial with reddish-purple flowers and a pungent onion aroma, was listed as a candidate for federal endangered/threatened status (<http://www.fws.gov/southwest/es/Arizona/Goodings.htm>). *Allium roseum* var. *odoratissimum*, which is harvested from roadsides during spring in Tunisia, is marketed very cheaply creating the risk of genetic erosion. *Allium roylei*, one of the most important sources of disease resistance genes in the genus *Allium* (Kofoet et al. 1990), is also a threatened species (Araki et al. 2010) and an urgent plea for its conservation has been made (Kohli and Gohil 2009). The need for protection of *A. gooddingii* was recognized in 1998 by the Forest Service

and the Environmental Protection Agency of the United States of America, which helped considerably toward the protection of this species against erosion (USFWS 2000). Ghrabi (2010) describes the need to protect and domesticate *A. roseum* as an urgent necessity.

Global networks have, therefore, been formed to coordinate the collection, conservation, and utilization of the genetic resources within the genus *Allium*. Examples include the European Cooperative Program for Plant Genetic Resources (ECPGR) *Allium* Working Group, the United Kingdom Natural Resources Institute Onion Newsletter for the Tropics network, and the *Allium* Improvement Newsletter (Astley 1994). The *Allium* working group (<http://www.ecpgr.cgiar.org/Workgroups/Allium/Allium.htm>) established in 1982 in Europe is one of the original six working groups constituted during the first phase of ECPGR. The work of the ECPGR *Allium* working group benefited significantly from the work program of the European Genetic Resources *Allium* project (ended 31 Mar 2000), and the research projects FAIR (1996–2001) and “Garlic and Health” (1998–2003). In the framework of the European Genetic Resources 20 Project, over 200 accessions of wild taxa belonging to 35 species were collected and preserved in Greek gene Bank, Greece (Samaras 2001).

In India, the National Bureau of Plant Genetic Resources (NBPGR) conducted extensive plant exploration in different *Allium*-growing states resulting in the collection of over 2,200 accessions of *Allium* species including wild relatives such as *A. ampeloprasum*, *A. auriculatum*, *A. ascalonicum*, *A. carolinianum*, *A. chinensis*, *A. wallachi*, *A. tuberosum*, and *A. rubellum* (Singh and Rana 1994). NBPGR also introduced over 1,100 accessions of *Allium* germplasm from over 40 countries (Singh and Rana 1994). In Tunisia, the Medenine Institut des Regions Arides has recently developed a research program to protect, conserve, and domesticate *A. roseum* (<http://www.uicnmed.org/nabp/database/HTM/PDF/p5.pdf>).

Given the outbreeding nature of most *Allium* species, cryopreservation has been suggested as a viable method of conservation (Volk et al. 2004) but this will need to be combined with traditional field maintenance, pollen storage, and in vitro culture (Working Group on Allium 2009). Cryopreservation should be done carefully due to the high risk of contamination and virus infection.

1.4 Role in Elucidation of Origin and Evolution of Cultivated *Allium* Species

The genus *Allium* is one of the largest genera of perennial bulbous plants on earth. The use of internal transcribed spacer (ITS) region of ribosomal DNA recently classified the genus into 780 species, 56 sections, and 15 subgenera (Friesen et al. 2006). Earlier molecular comparisons recognized 67 sections and 14 subgenera (Fritsch and Friesen 2002). The fact that so many species exist suggests that a lot of evolutionary differentiation has occurred (Stevenson et al. 1999).

Both morphological and molecular data have been used to study evolution of the genus *Allium*. Wendelbo (1969) initially suggested that all other groups in *Allium* might be derived from rhizomatous species without bulbs. Rhizomes are a distinct feature within the subgenus *Rhizirideum*. More recent reports indicate that rhizomes have evolved from an ancestral bulbous life form that was subsequently lost at least twice independently (Ricroch et al. 2005). Other *Allium* species (*A. caeruleum*, *A. proliferum*, *A. vineale*, *A. carinatum*, and *A. scorodoprasum*) have been grouped as viviparous due to the development of topsets instead of flowers or intermingle with flowers in the florescence (Kamenetsky and Rabinowitch 2001).

More molecular studies of the genus have given insight into evolution of the cultivated *Allium* species. Amplified fragment length polymorphism (AFLP) studies in garlic clustered garlic clones very closely with *A. longicuspis* suggesting that the two species are not genetically distinct (Ipek and Simon 2001). *A. longicuspis* and *A. tuncelianum* are genetically identical to garlic and therefore, were earlier suggested as possible ancestors of garlic (Block 2010). However, DNA analysis indicated that neither *A. longicuspis* nor *A. tuncelianum* are ancestor species of garlic (Block 2010).

In the subgenus *Cepa*, section *Cepa*, the closest wild relative of *A. cepa* and *A. fistulosum* has been identified as *A. vavilovii* and *A. attaicium*, respectively (Klaas and Friesen 2002). *A. oschaninii*, on the other hand, appears to be a sister group to *A. cepa*/*A. vavilovii* evolutionary line (Friesen and Klaas 1998). *A. ampeloprasum* is thought to be the ancestor species of leek and kurrat (*A. ampeloprasum* var. *kurrat*) (Block 2010).

The use of nuclear ribosomal DNA [ITS and external transcribed spacer (ETS)] has been suggested to provide sufficient resolution for investigating evolutionary relationships within *Allium* (Nguyen et al. 2008). Nguyen et al. (2008) used combined sequences from 39 native Californian *Allium* species with 154 ITS sequences available on GenBank to develop a global *Allium* phylogeny with the simultaneous goals of investigating the evolutionary history of *Allium* in the Californian center of diversity and exploring patterns of adaptation to serpentine soils (Nguyen et al. 2008). The ITS region alone was sufficient to resolve the deeper relationships in North American species.

1.5 Role in Development of Cytogenetic Stocks and Their Utility

Allium species show variation in several cytogenetic characters such as basic chromosome number, ploidy level, and genome size. *Allium* species are identified by their symmetrical and uniform karyotypes, which can often make chromosome identification difficult (Stevenson et al. 1999). The somatic chromosome number ranges from $2n = 16-40$ with basic chromosome numbers of $x = 7, 8,$ and 9 (Karpaviciene 2007).

The ploidy level varies from $2x$ to $16x$ (De Sarker et al. 1997; Klaas 1998; Bennett et al. 2000) while the 2C DNA amounts per genome ranges from 16.93 to 63.57 pg (Ricrocha and Brown 1997). In a study of 25 *Allium* species, Jones and Rees (1968) found considerable differences among 2C-values measured by Feulgen densitometry. Ohri et al. (1998) confirmed this in a survey of 86 *Allium* species (representing all six subgenera), measured in 4C nuclei by Feulgen densitometry. The same conclusions were drawn from the study of genome size in 28 *Allium* species (Baranyi and Greilhuber 1999).

To study chromosome organization within *Allium* species, an integrated map of *Allium cepa* \times (*A. roylei* \times *A. fistulosum*) was used (Khrustaleva et al. 2005), which showed that *Allium* species recombination predominantly occurs in the proximal half of chromosome arms. Cytological analysis in populations of *A. roylei* has reportedly revealed presence of complex chromosomal configurations during male meiosis and chromosomal heteromorphicity in somatic metaphase spreads (Kohli and Gohil 2009). Unstable