Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources

Cereals

Springer

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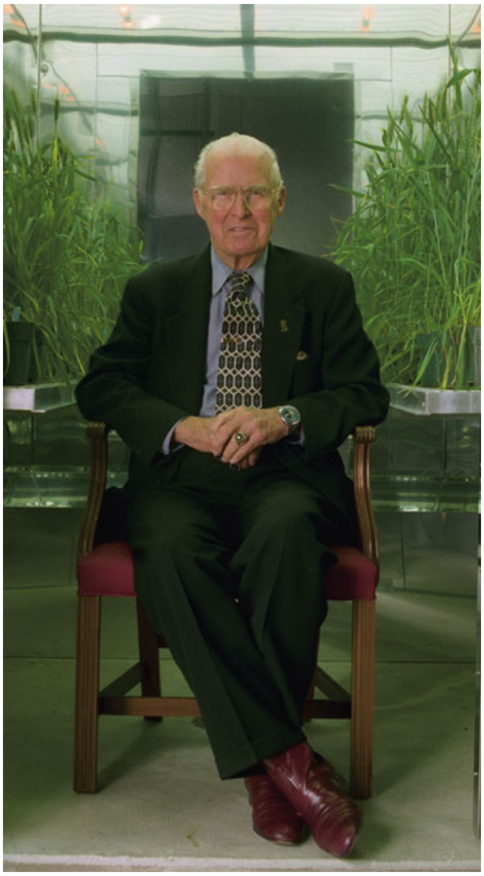
Dedication



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

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

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

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

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

In another occasion he wanted some documents from me. I told him that I will send them as attachments in emails. Immediately he shouted and told me: “You know, Julie (his granddaughter) is not at home now and I cannot check email myself. Julie does this for me. I can type myself in type writer but I am not good in computer. You know what, I have a xerox machine and it receives fax also. Send me the documents by fax". Here was the ever-present child in him. Julie emailed me later to send the documents as attachment to her as the 'xerox machine' of Dr. Borlaug ran out of ink!

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

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

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

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

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

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

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

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

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

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

Clemson, USA Chittaranjan Kole

Preface

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

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

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

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

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

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

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

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

Wild crop relatives, particularly wild allied species and subspecies, have been used since the birth of genetics in the twentieth century in several instances such as studies of inheritance, linkage, function, transmission and evolution of genes. They have been frequently used in genetic studies since the advent of molecular markers. Their involvement in molecular mapping has facilitated the development of mapping populations with optimum polymorphism to construct saturated maps and also illuminating the organization, reorganization and functional aspects of genes and genomes. Many phenomena such as genomic duplication, genome reorganization, self-incompatibility, segregation distortion, transgressive segregation and defining genes and their phenotypes have in many cases been made possible due to the utilization of wild species or subspecies. Most of the chapters contain detailed elucidations on these aspects.

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

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

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

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

I am also very pleased to present many chapters in this series authored by a large number of globally reputed leading scientists, many of whom have contributed to the development of novel concepts, strategies and tools of genetics, genomics and breeding and/or pioneered the elucidation and improvement of particular plant genomes using both traditional and molecular tools. Many of them have already retired or will be retiring soon, leaving behind their legacies and philosophies for us to follow and practice. I am saddened that a few of them have passed away during preparation of the manuscripts for this series. At the same time, I feel blessed that all of these stalwarts shared equally with me the wealth of crop relatives and contributed to their recognition and promotion through this endeavor.

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

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

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

I started editing books with the 7-volume series on Genome Mapping and Molecular Breeding in Plants with Springer way back in 2005, and I have since edited many other book series with Springer. I always feel proud and satisfied to be a member of the Springer family, particularly because of my warm and enriching working relationship with Dr. Sabine Schwarz and Dr. Jutta Lindenborn, with whom I have been working all along. My special thanks go out to them for publishing this "dream series" in an elegant form and also for appreciating my difficulties and accommodating many of my last-minute changes and updates.

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

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

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

This volume "Wild Crop Relatives – Genomic and Breeding Resources: Cereals" includes 11 chapters dedicated to *Aegilops*, *Agropyron* and *Psathyrostachys*, *Avena*, *Dasypyrum*, *Fagopyron*, *Hordeum*, *Oryza*, *Secale*, *Sorghum*, *Triticum*, and *Zea*. The chapters of this volume were authored by 43 scientists from 11 countries of the world, namely Australia, China, Germany, India, Indonesia, Israel, Italy, Philippines, Russia, Turkey, 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 Cereals with an intention of serving science and society.

Clemson, USA Chittaranjan Kole

Contents

Abbreviations

AB-QTL	Advanced backcross QTL
ACO	Aconitate hydrotase
Adh	Alcohol dehydrogenase (gene)
AFLP	Amplified fragment length polymorphism
AIL	Alien introgression line
Al	Altitude
ARN	Average repeat number
ARS	Agriculture Research Service (USDA)
BA or Ba	Basalt soil
BAC	Bacterial artificial chromosome
BARE-1	Barley retroelement 1
Bgt	*Blumeria graminis* f sp. *tritici*
BLAST	Basic alignment search tool
BSA	Bulked segregant analysis
BYDV	Barley yellow dwarf virus
CAAS	Chinese Academy of Agricultural Sciences
CAB	Chlorophyll-a/b binding protein
CAPS	Cleaved amplified polymorphic sequence
CBD	Convention on Biological Diversity
ccSSR	Consensus chloroplast simple sequence repeat
CGIAR	Consultative Group on International Agricultural Research
CIM	Composite interval mapping
CINAU	Cytogenetics Institute, Nanjing Agricultural University, China
cpDNA	Chloroplast DNA
CSSL	Chromosome segmental substutution line
CSTT	Catastrophic Sexual Transmutation Theory
CT	Chlorotolurone (herbicide)
DA	Disomic chromosome addition line
DArT	Diversity arrays technology
Db	*Dasypyrum breviaristatum*
DIA	Diaphorase
DS	Disomic chromosome substitution line
Dv	*Dasypyrum villosum*
Dw	Mean number of dew nights in summer
EADB	European *Avena* Database
ECP/GR	European Cooperative Program for Genetic Resources

ELISA	Enzyme-linked immunosorbent assay
EMS	Ethylmethane sulphonate
En/Spm	Enhancer/suppressor mutator
Est	Esterase (gene)
EST	Expressed sequence tag
EURISCO	European Network of ex situ National Inventories
Ev	Mean annual evaporation
FAL	Federal Agriculture Research Centre (Germany)
FAO	Food and Agriculture Organization (of the United Nation)
FHB	Fusarium head blight
FISH	Fluorescence in situ hybridization
G3pdh	Glyceraldehyde 3-phosphate dehydrogenase
GBIF	Global Biodiversity Information Facility
GBSS1	Granule bound starch synthase
GCA	General combining ability
GE	Genotype-environment interaction
GIS	Geographical information system
GISH	Genomic in situ hybridization
GM	Genetic modification
GMO	Genetically-modified organism
Got/GOT	Glutamate oxaloacetate transaminase
GPI	Glucose phosphate isomerase
GRASSIUS	Grass Regulatory Information Services
GRIN	Germplasm Resources Information Network (USA)
GSI	Gametophytic self-incompatibility
GSS	Genome survey sequences
GWM	Gatersleben wheat microsatellite (marker)
He	Gene diversity
Hk	Hexokinase (gene)
HMW	High molecular weight
Hu	Mean humidity
IAP	Inhibition of alien pollen
IBPGR	International Board for Plant Genetic Resources
ICARDA	International Center for Agricultural Research in the Dry Areas
IM	Interval mapping
INIBAP	International Network for the Improvement of Banana and Plantain
IPGRI	International Plant Genetic Recourses Institute
Ipol	Indophenol oxidase
IRG	International Rice Gene Bank
ISSR	Inter-simple sequence repeat
IT	International Treaty
ITS	Internal transcribed spacer
LD	Linkage disequilibrium
LMW	Low molecular weight
Ln	Longitude
LSR	Long sequence repeats
Lt	Latitude

LtTddRv	Latitude, day-night temperature, and mean relative variability of rainfall
MAAL	Monosomic alien addition line
MAS	Marker-assisted selection
MBC	Map-based cloning
Mdh/MDH	Malate dehydrogenase
MGP	Multilocus genotype pattern
MR	Multiple regression analysis
MX	Metoxuron (herbicide)
Mya	Million years ago
N5BT5D	Wheat line that is nullisomic for 5B and tetrasomic for 5D chromosomes
NAC	NAC transcription factor
NARES	National Agricultural Research and Extension Systems
NGRP	National Genetic Resources Program (USA)
NPGS	National Plant Germplasm System (USA)
NSGC	National Small Grains Collection (USA)
NSSL	National Seed Storage Laboratory (USA)
OMAP	*Oryza* Map Alignment Project
P	Proportion of polymorphic loci
PAGE	Polyacrylamide gel electrophoresis
Pc	*Puccinia coronata* Cda. f. sp. *avenae* Fraser et Led.
PCA	Principal component analysis
PCR	Polymerase chain reaction
Pept	Peptidase
Pg	*Puccinia graminis*
PGD	6-Phosphogluconate dehydrogenase
PGM	Phosphoglucomutase
PGR	Plant genetic resource
PGRC	Plant Gene Resources of Canada
Ph^I	Ph inhibitor line
POOL	Name of Pedigree of Oat Lines Database
Ppd-H1	Psuedo-response regulator
Pst	*Puccinia striiformis* f sp. *tritici*
Pt	*Puccinia triticina*
QTL	Quantitative trait loci
R^2	Coefficient of multiple determination
RAPD	Random(ly) amplified polymorphic DNA
Rd	Mean number of rainy days
RDA	Representational difference analysis
rDNA	Ribosomal DNA
Ren	Rendzina soil
RFLP	Restriction fragment length polymorphism
RIL	Recombinant inbred line
Rn	Mean annual rainfall
Rr	Mean relative interannual variability of rainfall
r_s	Spearman's rank order correlation

Rst	Inter- vs. Intra-population degree of gene differentiation among populations
RUL	Mean values for ^{22}Na uptake in *T. dicoccoides* relative to ^{22}Na uptake in Langdon control
Rv	Mean interannual rainfall variability of rainfall
SBCMV	Soil-borne cereal mosaic virus
SCAR	Sequence characterized amplified region
SDS	Sodium dodecyl sulfate
SEM	Scanning electron microscopy
SESTO	Regional (Northern) PGR Documentation System
SNB	*Stagonospora nodorum* blotch
SNP	Single nucleotide polymorphism
So	Soil type
SSR	Simple sequence repeat
STLT	Sexual Translocation Theory
STS	Sequence tagged site
Ta	Mean August temperature
TARGeT	Tree analysis of related genes and transposons
Td	Seasonal temperature difference
Tdd	Day–night temperature difference
TE	Transposable elements
TF	Transcriptional factor
TILLING	Targeting induced local lesions in genomes
Tj	Mean January temperature
Tm	Mean annual temperature
Tr/TR	Terra rossa soil
Trd	Mean number of tropical days
Tt	*Tilletia tritici*
UPGMA	Unweighted pair group method with arithmetic average
USDA	United States Department of Agriculture
VIR	N. I. Vavilov Institute of Plant Industry (Russia)
WBDC	Wild barley diversity collection
WCM	Wheat curly mite
WIEWS	World Information and Early Warning System (FAO)
WMAI	Wheat monomeric alpha amylase inhibitor gene
WSBMV	Wheat soil-borne mosaic virus
WSMV	Wheat streak mosaic virus
WSSMV	Wheat spindle streak mosaic virus
WUE	Water use efficiency
Yr	Yellow rust

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Chapter 1
Aegilops

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1.1 Introduction

The genus *Aegilops* L. belongs to the tribe Triticeae within the Pooideae subfamily of the grass family Poaceae. The tribe includes six major genera (*http://www.k-state.edu./wgrc/Taxonomy/Triticeaetax.html*), among which the important crop genera are *Triticum* (wheat), *Hordeum* (barley), and *Secale* (rye).

The phylogenetic relationships and evolution within the Triticeae are of great interest due to potentially favorable alleles to be discovered in wild wheat relatives and to be transferred to bread wheat. However, especially the relationships within and between *Aegilops* and *Triticum* in the subtribe Triticinae are a matter of ongoing discussion, and the relationships among the taxa are far from being completely understood. This is also documented in various classification systems, as presented for *Aegilops* in Table 1.1. Most researchers currently follow the latest monograph of van Slageren (1994). However, new data have been recently produced and some aspects have to be reconsidered. New molecular data are urgently needed to provide more insights in the Triticeae phylogeny.

Tables 1.1 and 1.2 report the *Aegilops* taxa considered in this chapter. The genus *Aegilops* comprises 23 annual species, of which 11 are diploids and 12 are allopolyploids (see Table 1.2 and the species descriptions for synonyms).

Some *Aegilops* species participated in wheat evolution and played a major role in wheat domestication. Thus, the genus *Aegilops* represents the largest part of the secondary gene pool of wheat, and several species have been used in crop improvement programs.

The latest revision of *Aegilops* by van Slageren (1994) is based on morphological studies. Van Slageren conducted field trips in the years 1988–1994 and examined about 20,000 herbarium specimens representing, in van Slageren's opinion, an estimated 75–85% of all *Aegilops* material available. In this chapter, we therefore refer to van Slageren (1994) and Hammer (1980a, b) for morphological descriptions and history of the genera *Aegilops* and nomenclature.

For wheat, the latest comprehensive, systematic overview was completed in 1979 by Dorofeev and colleagues. In this chapter, the nomenclature and the genome formula given for *Triticum* by Dorofeev et al. (1979) is mainly followed (exception e.g., *T. dicoccon* Schrank). Other concise comparisons of the main wheat classifications are also available (Hanelt 2001; Mac Key 2005; Hammer et al. 2011).

This chapter is an introduction and an overview on *Aegilops*. A key and a brief botanical description are presented, together with ear morphology and distribution maps, and cytological and molecular data for each species.

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"For the sake of future generations, we MUST collect and study wild and weedy relatives of our cultivated plants as well as the domesticated races. These sources of germplasm have been dangerously neglected in the past, but the future may not be so tolerant. In the plant breeding programs of tomorrow we cannot afford to ignore *any* source of useable genes." Harlan (1970)

C. Kole (ed.), *Wild Crop Relatives: Genomic and Breeding Resources, Cereals*,
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Table 1.1 Overview of selected *Aegilops* classifications

This chapter	van Slageren (1994)	Kimber et Sears (1983)	Whitcombe (1983)	Hammer (1980a, b)	Kihara (1954)	Eig (1929)	Zhukovsky (1928)
Section *Aegilops*							
1 *Ae. biuncialis* Vis.	*Ae. biuncialis* Vis.	*Triticum macrochaetum* (Shuttl. et Huet) Richter	*Ae. lorentii* Hochst.	*Ae. lorentii* Hochst.	*Ae. biuncialis* Vis.	*Ae. biuncialis* Vis.	*Ae. biuncialis* Vis.
2 *Ae. columnaris* Zhuk.	*Ae. columnaris* Zhuk.	*Triticum columnare* (Zhuk.) Morris et Sears	*Ae. columnaris* Zhuk.	*Ae. columnaris* Zhuk.	*Ae. columnaris* Zhuk.	*Ae. columnaris* Zhuk.	*Ae. columnaris* Zhuk.
3 *Ae. geniculata* Roth	*Ae. geniculata* Roth	*Triticum ovatum* (L.) Raspail	*Ae. ovata* L.	*Ae. geniculata* Roth	*Ae. ovata* L.	*Ae. ovata* L.	*Ae. ovata* L.
ssp. *geniculata*							
ssp. *gibberosa* (Zhuk.) Hammer							
4 *Ae. kotschyi* Boiss.	*Ae. kotschyi* Boiss.	*Triticum kotschyi* (Boiss.) Bowden	*Ae. kotschyi* Boiss.	*Ae. kotschyi* Boiss.	*Ae. kotschyi* Boiss.	*Ae. kotschyi* Boiss.	
5 *Ae. neglecta* Req. ex Bertol.	*Ae. neglecta* Req. ex Bertol. (4x and 6x)	*Triticum triaristatum* (Willd.) Godr. et Gren. (4x and 6x)	*Ae. triaristata* Willd. (4x and 6x)	*Ae. neglecta* Req. ex Bertol.	*Ae. triaristata* Willd. (4x and 6x)	*Ae. triaristata* Willd. (4x and 6x)	*Ae. triaristata* Willd. (4x and 6x)
ssp. *neglecta* (4x)				ssp. *neglecta* (4x)			
ssp. *recta* (Zhuk.) Hammer (6x)				ssp. *recta* (Zhuk.) Hammer (6x)			
6 *Ae. peregrina* (Hackel) Maire et Weiller	*Ae. peregrina* (Hack. in J.Fraser) Maire et Weiller	*Triticum kotschyi* (Boiss) Bowden	*Ae. peregrina* (Hackel) Maire et Weiller	*Ae. peregrina* (Hackel) Maire et Weiller	*Ae. variabilis* Eig	*Ae. variabilis* Eig	
ssp. *peregrina*	var. *peregrina*			ssp. *peregrina*			
	var. *brachyathera* (Boiss.) Maire et Weiller			ssp. *cylindrostachys* (Eig et Feinbrun) Maire et Weiller			
7 *Ae. triuncialis* L.	*Ae. triuncialis* L.	*Triticum triunciale* (L.) Raspail	*Ae. triuncialis* L.	*Ae. triuncialis* L.	*Ae. triuncialis* L.	*Ae. triuncialis* L.	*Ae. triuncialis* L.
ssp. *triuncialis*	var. *triuncialis*			ssp. *triuncialis*			
ssp. *persica* (Boiss.) Zhuk.	var. *persica* (Boiss.) Eig			ssp. *persica* (Boiss.) Zhuk.			
8 *Ae. umbellulata* Zhuk.	*Ae. umbellulata* Zhuk.	*Triticum umbellulatum* (Zhuk.) Bowden	*Ae. umbellulata* Zhuk.	*Ae. umbellulata* Zhuk.	*Ae.*		*umbellulata* Zhuk.
Ae. umbellulata Zhuk.	*Ae. umbellulata* Zhuk.						
ssp. *umbellulata*							
ssp. *transcaucasia* Dorof. et Migusch.				ssp. *transcaucasia* Dorof. et Migusch.			

(*continued*)

Table 1.1 (continued)

This chapter	van Slageren (1994)	Kimber et Sears (1983)	Whitcombe (1983)	Hammer (1980a, b)	Kihara (1954)	Eig (1929)	Zhukovsky (1928)
Section *Comopyrum*							
9 *Ae. comosa* Sibth. et Sm.	*Ae. comosa* Sm. in Sibth. et Sm.	*Triticum comosum* (Sibth. et Sm.) Richter	*Ae. comosa* Sibth. et Sm.	*Ae. comosa* Sibth. et Sm.	*Ae. comosa* Sibth. et Sm.	*Ae. comosa* Sibth. et Sm.	*Ae. comosa* Sibth. et Sm.
ssp. *comosa*	var. *comosa*			ssp. comosa			
ssp. *heldreichii* (Boiss.) Eig (syn.: var. *subventricosa* Boiss.)	var. *subventricosa* Boiss.			ssp. *heldreichii* (Boiss.) Eig		ssp. *heldreichii* (Holzm.) Eig	
10 *Ae. uniaristata* Vis.	*Ae. uniaristata* Vis.	*Triticum uniaristatum* (Vis.) Richter	*Ae. uniaristata* Vis.	*Ae. uniaristata* Vis.	*Ae. uniaristata* Vis.	*Ae. uniaristata* Vis.	*Ae. uniaristata* Vis.
Section *Cylindropyrum*							
11 *Ae. cylindrica* Host	*Ae. cylindrica* Host	*Triticum cylindricum* Ces.	*Ae. cylindrica* Host	*Ae. cylindrica* Host	*Ae. cylindrica* Host	*Ae. cylindrica* Host	*Ae. cylindrica* Host
12 *Ae. markgrafii* (Greuter) Hammer	*Ae. caudata* L.	*Triticum dichasians* (Zhuk.) Bowden	*Ae. caudata* L.	*Ae. markgrafii* (Greuter) Hammer	*Ae. caudata* L.	*Ae. caudata* L.	*Ae. caudata* L.
Section *Sitopsis*							
13 *Ae. bicornis* (Forssk.) Jaub. et Sp.	*Ae. bicornis* (Forssk.) Jaub. et Spach	*Triticum bicorne* Forssk.	*Ae. bicornis* (Forssk.) Jaub. et Spach	*Ae. bicornis* (Forssk.) Jaub. et Spach	*Ae. bicornis* (Forssk.) Jaub. et Spach	*Ae. bicornis* (Forssk.) Jaub. et Spach	*Ae. bicornis* (Forssk.) Jaub. et Spach
	var. *bicornis*						
	var. *anathera* Eig						
14 *Ae. longissima* Schweinf. et Muschl.	*Ae. longissima* Schweinf. et Muschl.	*Triticum longissimum* (Schweinf. et Muschl.) Bowden	*Ae. longissima* Schweinf. et Muschl.	*Ae. longissima* Schweinf. et Muschl. emend. Eig s.l.	*Ae. longissima* Schweinf. et Muschl.	*Ae. longissima* Schweinf. et Muschl.	*Ae. longissima* (Schweinf. et Muschl.) Eig
				ssp. *longissima*			
15 *Ae. sharonensis* Eig	*Ae. sharonensis* Eig		*Ae. sharonensis* Eig	ssp. *sharonensis* (Eig) Hammer		*Ae.*	*sharonensis* Eig
16 *Ae. searsii* Feldman et Kislev ex Hammer	*Ae. searsii* Feldman et Kislev ex Hammer	*Triticum searsii* (Feldman et Kislev) Feldman	*Ae. searsii* Feldman et Kislev	*Ae. searsii* Feldman et Kislev ex Hammer			
17 *Ae. speltoides* Tausch	*Ae. speltoides* Tausch	*Triticum speltoides* (Tausch) Gren. ex Richter	*Ae. speltoides* Tausch	*Ae. speltoides* Tausch	*Ae. speltoides* Tausch	*Ae. speltoides* Tausch	*Ae. speltoides* Tausch
ssp. *speltoides*	var. *speltoides*			ssp. *speltoides*			
ssp. *ligustica* (Savign.) Zhuk.	var. *ligustica* (Savign.) Fiori		*Ae. ligustica* (Savign.) Coss.	ssp. *ligustica* (Savign.) Zhuk.		*Ae. ligustica* (Savign.) Coss.	

(*continued*)

Table 1.1 (continued)

This chapter	van Slageren (1994)	Kimber et Sears (1983)	Whitcombe (1983)	Hammer (1980a, b)	Kihara (1954)	Eig (1929)	Zhukovsky (1928)
Section *Vertebrata*							
18 *Ae. crassa* Boiss. (4x and 6x)	*Ae. crassa* Boiss. (4x and 6x)	*Triticum crassum* (Boiss.) Aitch. et Hemsl. (4x and 6x)	*Ae. crassa* Boiss. (4x and 6x)	*Ae. crassa* Boiss. (4x and 6x)	*Ae. crassa* Boiss. (4x and 6x)	*Ae. crassa* Boiss. (4x and 6x)	*Ae. crassa* Boiss. (4x and 6x)
				ssp. *crassa*			
19 *Ae. vavilovii* (Zhuk.) Chennav. (6x)	*Ae. vavilovii* (Zhuk.) Chennav.	*Triticum syriacum* Bowden	*Ae. vavilovii* (Zhuk.) Chennav.	ssp. *vavilovii* Zhuk. (6x)			
20 *Ae. juvenalis* (Thell.) Eig	*Ae. juvenalis* (Thell.) Eig	*Triticum juvenale* Thell.	*Ae. juvenalis* (Thell.) Eig	*Ae. juvenalis* (Thell.) Eig	*Ae. juvenalis* (Thell.) Eig	*Ae. juvenalis* (Thell.) Eig	*Ae. turcomanica* Roshev.
				Ae. turcomanica Roshev.			
21 *Ae. tauschii* Coss.	*Ae. tauschii* Coss.	*Triticum tauschii* (Coss.) Schmalh.	*Ae. squarrosa* L.	*Ae. tauschii* Coss.	*Ae. squarrosa* L.	*Ae. squarrosa* L.	*Ae. squarrosa* L.
ssp. *tauschii*							
ssp. *strangulata* (Eig) Tzvel.							
22 *Ae. ventricosa* Tausch	*Ae. ventricosa* Ces.	*Triticum ventricosum* Tausch	*Ae. ventricosa* Tausch	*Ae. ventricosa* Tausch	*Ae. ventricosa* Tausch	*Ae. ventricosa* Tausch	*Ae. ventricosa* Tausch
Subgenus *Ambylopyrum*							
23 *Ae. mutica* Boiss.	*Ambylopyrum muticum* (Boiss.) Eig	*Triticum tripsacoides* (Jaub. et Spach) Bowden	*Ae. mutica* Boiss.	*Ae. mutica* Boiss.	*Ae. mutica* Boiss.	*Ae. mutica* Boiss.	*Ae. mutica* Boiss.
ssp. *mutica*	var. *muticum*			var. *muticum*			
ssp. *loliacea* (Jaub et Spach) Zhuk.	var. *loliaceum* (Jaub. et Spach) Eig			var. *loliacea* (Jaub. et Spach) Eig			

Table 1.2 Sections and species of *Aegilops*. Genomic formulas of tetraploids and hexaploids are cited as "female × male parent." Underlining indicates modification of the same genome as present in the diploid species. Genome (G) and cytoplasm (C) symbols are according to Kimber and Tsunewaki (1988). Mean nuclear DNA content (Mean 1C) in pg of *Aegilops* species according to Eilam et al. (2007, 2008). nd – not determined

Aegilops section	Diploid				Tetraploid				Hexaploid			
	Species	G	C	Mean 1C	Species	G	C	Mean 1C	Species	G	C	Mean 1C
Aegilops L.	*Ae. umbellulata*	U	U	5.38	*Ae. biuncialis*	$\mathrm{U\underline{M}}$	U	10.37				
					Ae. columnaris	$\mathrm{U\underline{M}}$	U^2	10.86				
					Ae. geniculata	$\mathrm{\underline{M}U}$	M^o	10.29				
					Ae. kotschyi	$\mathrm{\underline{S}U}$	S^2	12.64				
					Ae. neglecta ssp. *neglecta*	$\mathrm{U\underline{M}}$	U	10.64	*Ae. neglecta* ssp. *recta*	$\mathrm{\underline{UMN}}$	U	16.22
					Ae. peregrina	$\mathrm{\underline{S}U}$	S^s	12.52				
					Ae. triuncialis	$\mathrm{U\underline{C}}$, $\mathrm{C\underline{U}}$	C,U	9.93				
Comopyrum (Jaub. et Spach) Zhuk.	*Ae. comosa*	M	M	5.53								
	Ae. uniaristata	N	N	5.82								
Cylindropyron (Jaub. et Spach) Zhuk.	*Ae. markgrafii*	C	C	4.84	*Ae. cylindrica*	DC	D	9.59				
Sitopsis (Jaub. et Spach) Zhuk	*Ae. bicornis*	S^b	S^b	6.84								
	Ae. longissima	S^l	S^l	7.48								
	Ae. sharonensis	S^{sh}	S^l	7.52								
	Ae. searsii	S^s	S^s	6.65								
	Ae. speltoides	S	S	5.81								
Vertebrata Zhuk. emend. Kihara	*Ae. tauschii*	D	D	5.17	*Ae. crassa* ssp. *crassa* (4x)	$\mathrm{D\underline{M}}$	D^2	10.86	*Ae. crassa* ssp. *crassa* (6x)	$\mathrm{\underline{DDM}}$	D^2	nd
									Ae. vavilovii	$\mathrm{\underline{DMS}}$	D^2	17.13
					Ae. ventricosa	DN	D	10.64	*Ae. juvenalis*	$\mathrm{\underline{DMU}}$	D^2	nd
Subgenus *Amblyopyrum*	*Ae. mutica*	T	nd	nd								