

Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources Forest Trees

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Forest Trees

 Springer

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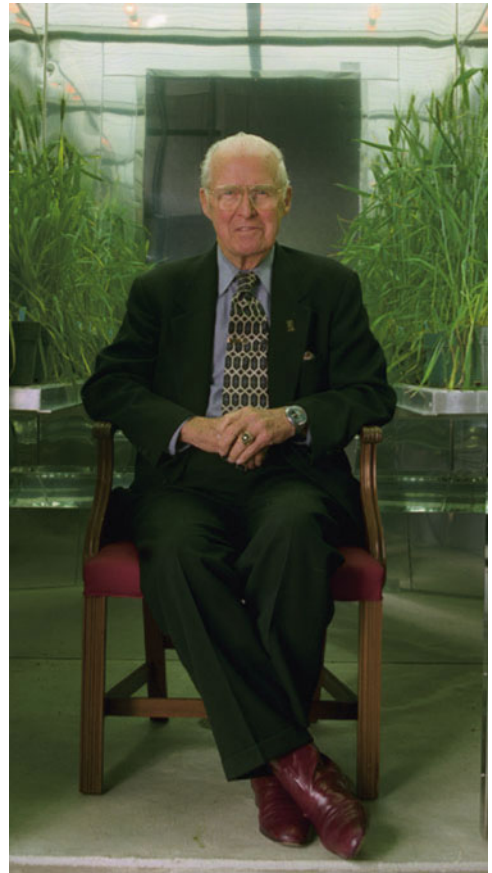
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Dedication

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 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 seven-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 volumes. 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 volumes, 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 these volumes 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 told me to forget about my original contributions and that I deserved at least the World Food Prize, if not Nobel Prize for peace like him. I felt honored but really very ashamed as I am aware of my almost insignificant contribution in comparison to his work, and was unable to utter any words for a couple of minutes!

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.

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, are you coming to Texas 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 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 communications between us when he slowly succumbed to his health problems.

The remaining volumes of the Genome Mapping and Molecular Breeding in Plants were published in 2007, and I sent him the volumes. I wished to learn about his views. During this period he could hardly speak and write. Julie prepared a letter on his behalf 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. 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. By that time I had a huge commitment to editing 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 did not even communicate my personal loss to Julie. But in the meantime, I formulated a ten-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 globe and hundreds of plant and agricultural scientists who tries 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 our next generations in the same way as personalities like Dr. Norman Borlaug did to me and many other science workers from around the world!

During most of our conversations he used to emphasize the immediate impact of research on the society. 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. This advice elicited a change in my approach to science and since then I have been devotedly endeavored to develop crop varieties enriched with phytomedicines and nutraceuticals. Inspiration, advices, and blessings of Dr. Borlaug have influenced both my personal and professional life, particularly my approach to science, and I dedicate this series to him as a token of my regards and gratitude, and in remembrance of his great contribution to science and society and above all his personal affection 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 expressing 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 phytochemicals and nutraceuticals, bioenergy production, soil reclamation, and the phytoremediation of our 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 presented, the need for reference books with comprehensive examinations of 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, etc. and/or potential as “new crops”. The most perplexing problem for me was to assign them 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 trunculata*, 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 crop relatives in a volume on the crop group to which they are taxonomically closest and to which they can make the greatest contributions. For example, I placed the chapter on *Arabidopsis* in the volume on oilseeds, which deals with the wild relatives of Brassicaceae crops.

However, we have tried to include deliberations pertinent to the individual genera or species 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 conservation 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 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 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 create 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* and *Medicago*. 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 or species.

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 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 crucial aspects relevant to a particular wild genus or species 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 roughly 150 chapters devoted to essential genera or species of wild crop relatives. However, I had to exclude a few 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 126 chapters in the ten volumes, contributed by 380 authors from 39 countries of the world. I extend my heartfelt thanks to all of 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/species. 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 offer my sincere apologies.

Another unique feature of this series is that the authors of chapters dedicated to some genera/species have dedicated their chapters to scientists who pioneered the exploration, description and utilization of those wild genera/species. 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 seven-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 graciously tolerating my sparing some time rightly deserved by them and constantly supporting me in the publication of this series.

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 Forage 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 – Forest Trees” includes 8 chapters dedicated to *Alnus*, *Corylus*, *Cryptomeria*, *Eucalyptus*, *Juglans*, *Quercus*, *Santalum*, and *Trigonobalanus*. The chapters of this volume were authored by 16 scientists from 4 countries of the world, namely Australia, India, Japan, 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 forest trees with an intention of serving science and society.

Clemson, USA

Chittaranjan Kole

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Abbreviations

ABA	Abscisic acid
AFLP	Amplified fragment length polymorphism
AMOVA	Analysis of molecular variance
ARS	Agriculture Research Service (USDA)
ATSC	Australian Tree Seed Centre
BGCI	Botanic Gardens Conservation International
BTS	Big-tree structure
CAPS	Cleaved amplified polymorphic sequence
CDF	Co-dominant forest
cpDNA	Chloroplast DNA
ECM	Ectomycorrhizal
ECP/GR	European Cooperative Program on Plant Genetic Resources
EFB	Eastern filbert blight
EST	Expressed sequence tag
ETS	External transcribed spacer
EUCAGEN	Eucalyptus Genome Network
EUFORGEN	European Forest Genetics Resources Programme
FFI	Forest Frontiers Initiative
FFPRI	Forestry and Forest Products Research Institute
FISH	Fluorescence in situ hybridization
FTGRFCF	Forest Tree Genetic Resources Conservation Forest
FTSGCS	Forest Tree Superior Gene Conservation Stand
GIS	Geographical information systems
HAD	Heavily disturbed by human activities
HJG	Hydrojugloneglucoside
HTIRC	Hardwood Tree Improvement and Regeneration Center
HTS	Huge-tree structure
IAA	Indole-3-acetic acid
IBPGR	International Board of Plant Genetic Resources
IEA	International Energy Agency
INRA	French National Institute for Agricultural Research
ISSR	Inter-simple sequence repeat
ITS	Internal transcribed spacer
LD	Linkage disequilibrium
MAS	Marker-assisted selection
MDF	Mono-dominant Forest
MDS	Mono-dominant structure

MDSD	Mono-dominant structure in developing
ML	Maximum likelihood
MOE	Module of elasticity
MP	Maximum parsimony
Mya	Million years ago
Mybp	Million years before present
NALB	North Atlantic Land Bridges
NCGR	National Clonal Germplasm Repository
NJ	Neighbor joining
<i>nptII</i>	Neomycin phosphotransferase II gene
OSU	Oregon State University
PCR	Polymerase chain reaction
PICME	Platform for integrated clone management
PR	Population in recovery
PRP	Proline rich protein
QTL	Quantitative trait loci
RAPD	Random amplified polymorphic DNA
<i>rbcL</i>	Ribulose-bisphosphate carboxylase-L (gene)
RBS	Relatively balanced structure
rDNA	Ribosomal DNA
RFLP	Restriction fragment length polymorphism
RNAi	RNA interference
rRNA	Ribosomal RNA
RT-PCR	Real-time PCR
RT-PCR	Reverse transcription PCR
rubisCO	Ribulose-1,5-bisphosphate carboxylase oxygenase
SCAR	Sequence characterized amplified region
SMP	Supplemental mass pollination
SNP	Single nucleotide polymorphism
SSCP	Single-stranded DNA conformation polymorphism
SSR	Simple sequence repeat
STS	Sequence tagged site
SW	Sprouting woods
TPS	Terpene synthases
UCD	University of California, Davis
<i>uidA</i>	β -glucuronidase A gene
UPGMA	Unweighted pair group method of arithmetic average
USD	Unstable structure in developing
USDA	United States Department of Agriculture
USDA	United States Department of Agriculture
VAM	Vesicular arbuscular
ybp	Years before present