

Compendium of Plant Genomes  
Series Editor: Chittaranjan Kole

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N. Manikanda Boopathi  
M. Raveendran  
Chittaranjan Kole *Editors*

# The Moringa Genome

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# **Compendium of Plant Genomes**

## **Series Editor**

Chittaranjan Kole, Raja Ramanna Fellow, Government of India,  
ICAR-National Research Center on Plant Biotechnology, Pusa,  
New Delhi, India

Whole-genome sequencing is at the cutting edge of life sciences in the new millennium. Since the first genome sequencing of the model plant *Arabidopsis thaliana* in 2000, whole genomes of about 100 plant species have been sequenced and genome sequences of several other plants are in the pipeline. Research publications on these genome initiatives are scattered on dedicated web sites and in journals with all too brief descriptions. The individual volumes elucidate the background history of the national and international genome initiatives; public and private partners involved; strategies and genomic resources and tools utilized; enumeration on the sequences and their assembly; repetitive sequences; gene annotation and genome duplication. In addition, synteny with other sequences, comparison of gene families and most importantly potential of the genome sequence information for gene pool characterization and genetic improvement of crop plants are described.

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N. Manikanda Boopathi •  
M. Raveendran • Chittaranjan Kole  
Editors

# The Moringa Genome

*Editors*

N. Manikanda Boopathi  
Department of Plant Biotechnology  
Tamil Nadu Agricultural University  
Coimbatore, Tamil Nadu, India

M. Raveendran  
Department of Plant Biotechnology  
Tamil Nadu Agricultural University  
Coimbatore, Tamil Nadu, India

Chittaranjan Kole  
ICAR-National Institute for Plant  
Biotechnology  
New Delhi, India

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*This book series is dedicated to my wife Phullara  
and our children Sourav and Devleena*

*Chittaranjan Kole*

*This book is dedicated to all the forefathers who have preserved the Moringa spp., for the future.*

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## Preface to the Series

Genome sequencing has emerged as the leading discipline in the plant sciences coinciding with the start of the new century. For much of the twentieth century, plant geneticists were only successful in delineating putative chromosomal location, function, and changes in genes indirectly through the use of a number of “markers” physically linked to them. These included visible or morphological, cytological, protein, and molecular or DNA markers. Among them, the first DNA marker, the RFLPs, introduced a revolutionary change in plant genetics and breeding in the mid-1980s, mainly because of their infinite number and thus potential to cover maximum chromosomal regions, phenotypic neutrality, absence of epistasis, and codominant nature. An array of other hybridization-based markers, PCR-based markers, and markers based on both facilitated construction of genetic linkage maps, mapping of genes controlling simply inherited traits, and even gene clusters (QTLs) controlling polygenic traits in a large number of model and crop plants. During this period, a number of new mapping populations beyond F<sub>2</sub> were utilized and a number of computer programs were developed for map construction, mapping of genes, and for mapping of polygenic clusters or QTLs. Molecular markers were also used in the studies of evolution and phylogenetic relationship, genetic diversity, DNA fingerprinting, and map-based cloning. Markers tightly linked to the genes were used in crop improvement employing the so-called marker-assisted selection. These strategies of molecular genetic mapping and molecular breeding made a spectacular impact during the last one and a half decades of the twentieth century. But still, they remained “indirect” approaches for elucidation and utilization of plant genomes since much of the chromosomes remained unknown and the complete chemical depiction of them was yet to be unraveled.

Physical mapping of genomes was the obvious consequence that facilitated the development of the “genomic resources” including BAC and YAC libraries to develop physical maps in some plant genomes. Subsequently, integrated genetic–physical maps were also developed in many plants. This led to the concept of structural genomics. Later on, emphasis was laid on EST and transcriptome analysis to decipher the function of the active gene sequences leading to another concept defined as functional genomics. The advent of techniques of bacteriophage gene and DNA sequencing in the 1970s was extended to facilitate sequencing of these genomic resources in the past decade of the twentieth century.



As expected, sequencing of chromosomal regions would have led to too much data to store, characterize, and utilize with the then available computer software could handle. But the development of information technology made the life of biologists easier by leading to a swift and sweet marriage of biology and informatics, and a new subject was born—bioinformatics.

Thus, the evolution of the concepts, strategies, and tools of sequencing and bioinformatics reinforced the subject of genomics—structural and functional. Today, genome sequencing has traveled much beyond biology and involves biophysics, biochemistry, and bioinformatics!

Thanks to the efforts of both public and private agencies, genome sequencing strategies are evolving very fast, leading to cheaper, quicker, and automated techniques right from clone-by-clone and whole-genome shotgun approaches to a succession of second-generation sequencing methods. The development of software of different generations facilitated this genome sequencing. At the same time, newer concepts and strategies were emerging to handle sequencing of the complex genomes, particularly the polyploids.

It became a reality to chemically—and so directly—define plant genomes, popularly called whole-genome sequencing or simply genome sequencing.

The history of plant genome sequencing will always cite the sequencing of the genome of the model plant *Arabidopsis thaliana* in 2000 that was followed by sequencing the genome of the crop and model plant rice in 2002. Since then, the number of sequenced genomes of higher plants has been increasing exponentially, mainly due to the development of cheaper and quicker genomic techniques and, most importantly, the development of collaborative platforms such as national and international consortia involving partners from public and/or private agencies.

As I write this preface for the first volume of the new series “Compendium of Plant Genomes,” a net search tells me that complete or nearly complete whole-genome sequencing of 45 crop plants, 8 crop and model plants, 8 model plants, 15 crop progenitors and relatives, and 3 basal plants is accomplished, the majority of which are in the public domain. This means that we nowadays know many of our model and crop plants chemically, i.e., directly, and we may depict them and utilize them precisely better than ever. Genome sequencing has covered all groups of crop plants. Hence, information on the precise depiction of plant genomes and the scope of their utilization are growing rapidly every day. However, the information is scattered in research articles and review papers in journals and dedicated Web pages of the consortia and databases. There is no compilation of plant genomes and the opportunity of using the information in sequence-assisted breeding or further genomic studies. This is the underlying rationale for starting this book series, with each volume dedicated to a particular plant.

Plant genome science has emerged as an important subject in academia, and the present compendium of plant genomes will be highly useful to both students and teaching faculties. Most importantly, research scientists involved in genomics research will have access to systematic deliberations on the plant genomes of their interest. Elucidation of plant genomes is of interest not only for the geneticists and breeders, but also for practitioners of an array of plant science disciplines, such as taxonomy, evolution, cytology,

physiology, pathology, entomology, nematology, crop production, biochemistry, and obviously bioinformatics. It must be mentioned that information regarding each plant genome is ever-growing. The contents of the volumes of this compendium are, therefore, focusing on the basic aspects of the genomes and their utility. They include information on the academic and/or economic importance of the plants, a description of their genomes from a molecular genetic and cytogenetic point of view, and the genomic resources developed. Detailed deliberations focus on the background history of the national and international genome initiatives, public and private partners involved, strategies and genomic resources and tools utilized, enumeration on the sequences and their assembly, repetitive sequences, gene annotation, and genome duplication. In addition, synteny with other sequences, comparison of gene families, and, most importantly, the potential of the genome sequence information for gene pool characterization through genotyping by sequencing (GBS) and genetic improvement of crop plants have been described. As expected, there is a lot of variation of these topics in the volumes based on the information available on the crop, model, or reference plants.

I must confess that as the series editor, it has been a daunting task for me to work on such a huge and broad knowledge base that spans so many diverse plant species. However, pioneering scientists with lifetime experience and expertise on the particular crops did excellent jobs editing the respective volumes. I myself have been a small science worker on plant genomes since the mid-1980s and that provided me the opportunity to personally know several stalwarts of plant genomics from all over the globe. Most, if not all, of the volume editors are my longtime friends and colleagues. It has been highly comfortable and enriching for me to work with them on this book series. To be honest, while working on this series I have been and will remain a student first, a science worker second, and a series editor last. And I must express my gratitude to the volume editors and the chapter authors for providing me the opportunity to work with them on this compendium.

I also wish to mention here my thanks and gratitude to the Springer staff, particularly Dr. Christina Eckey and Dr. Jutta Lindenborn for the earlier set of volumes and presently Ing. Zuzana Bernhart for all their timely help and support.

I always had to set aside additional hours to edit books besides my professional and personal commitments—hours I could and should have given to my wife, Phullara, and our kids, Sourav and Devleena. I must mention that they not only allowed me the freedom to take away those hours from them, but also offered their support in the editing job itself. I am really not sure whether my dedication of this compendium to them will suffice to do justice to their sacrifices for the interest of science and the science community.

New Delhi, India

Chittaranjan Kole

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## Preface

Moringa has long been used as a vegetable and medicine, and traditionally, people have expressed the benefits of Moringa based on their real-life experiences.

Moringa leaves are certainly worth paying special attention. Conventional medications have used these leaves over centuries in several countries to cure a range of diseases/disorders. Recent clinical experiments have also endorsed these treatments.

Further, nutritional analysis has shown that the leaves are remarkably high in protein, more importantly they contain all of the essential amino acids, including the ones that are required for lactating mothers and infants. Therefore, it is considered as rarest of rare plant food. Moringa also has a package of all essential vitamins and minerals and it is widely employed as an affordable food supplement to combat malnutrition and related diseases.

Above all, an agricultural production point of view, Moringa is a fast-growing, drought-resistant tree that can be grown in a resource-limited environment and even in barren lands.

Hence, it is no wonder to name it a miracle tree.

This book compiles all the required information on Moringa in a comprehensive style, in such a way that it will serve as a resource guide for those who are interested to evolve improved cultivars for the given environment.

Coimbatore, India  
Coimbatore, India  
New Delhi, India  
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N. Manikanda Boopathi  
M. Raveendran  
Chittaranjan Kole

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## Contributors

**Bashir Yusuf Abubakar** Department of Botany, Ahmadu Bello University, Zaria, Nigeria

**S. Amutha** Community Science College and Research Institute, Tamil Nadu Agricultural University, Madurai, India

**K. A. Apoorva** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**R. Balakumbahan** Department of Vegetable Crops, Horticultural College and Research Institute, Tamil Nadu Agricultural University (TNAU), Periyakulam, India

**A. Bharathi** Department of Plant Biotechnology, Centre for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**N. Manikanda Boopathi** Department of Plant Biotechnology, Center for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**J. Deepa** Department of Plant Biotechnology, Centre for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**J. Devi Priya** Community Science College and Research Institute, Tamil Nadu Agricultural University, Madurai, India

**M. Doddamani** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**K. Elango** Horticultural Research Station, Tamil Nadu Agricultural University, Kodaikanal, India;  
Department of Agricultural Entomology, Tamil Nadu Agricultural University, Coimbatore, India

**B. Fakrudin** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**K. Govindaraju** Centre for Ocean Research (DST-FIST Sponsored Centre), Sathyabama Institute of Science and Technology, Chennai, India

**J. D. Harshith** Department of Plant Biotechnology, Center for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**G. Hemalatha** Community Science College and Research Institute, Tamil Nadu Agricultural University, Madurai, India

**R. C. Jagadeesha** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**K. Jothilakshmi** Community Science College and Research Institute, Tamil Nadu Agricultural University, Madurai, India

**S. Kadam** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**M. Kalyanasundaram** Department of Nano Science and Technology, Tamil Nadu Agricultural University, Coimbatore, India

**Rohit Kambale** Department of Plant Biotechnology, Centre for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**M. Kannan** Department of Nano Science and Technology, Tamil Nadu Agricultural University, Coimbatore, India

**Chittaranjan Kole** Raja Ramanna Fellow, ICAR-National Institute for Plant Biotechnology, New Delhi, India

**A. Lakshmanan** Department of Nano Science and Technology, Tamil Nadu Agricultural University, Coimbatore, India

**T. N. Lakshmidhevamma** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**N. Manavalan** Government Yoga and Naturopathy Medical College, Chennai, India

**Jayakanthan Mannu** Department of Plant Molecular Biology and Bioinformatics, Centre for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**Saranya Nallusamy** Department of Plant Molecular Biology and Bioinformatics, Centre for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**R. S. Nayana** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**M. Raveendran** Department of Plant Biotechnology, Center for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**V. P. Santhanakrishnan** Department of Plant Biotechnology, Center for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**S. P. Gautham Suresh** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**J. Ugalat** Department of Biotechnology and Crop Improvement, College of Horticulture, University of Horticultural Sciences, Bengaluru, India

**R. Veera Ranjani** Department of Plant Biotechnology, Center for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**M. Williams** Department of Plant Biotechnology, Centre for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

**R. Yogeshwari** Community Science College and Research Institute, Tamil Nadu Agricultural University, Madurai, India



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## Abbreviations

18S rDNA	18 S Ribosomal DNA
AFLP	Amplified Fragment Length Polymorphism
AMOVA	Analysis Of Molecular Variance
atpB	ATP Synthase Beta Subunit
AVRDC	Asian Vegetable Research And Development Center
BA	Benzyl Adenine
BAC	Bacterial Artificial Chromosomes
BAP	6-Benzylaminopurine
BARC	Baba Atomic Research Center
BLAST	Basic Local Alignment Search Tool
BOLD	Barcode Of Life Data Systems
BUSCO	Benchmarking Universal Single-Copy Orthologs
CAPS	Cleaved Amplified Polymorphic Sequences
CBoL	Consortium For The Barcode Of Life
cDNA	Complementary DNA
CDS	Coding Sequences
CHIAS	Chromosome Image Analyzing System
CITES	Convention On International Trade In Endangered Species Of Wild Fauna And Flora
cMC	Centimcclintock
CMS	Cytoplasmic Male Sterility
CNVs	Copy Number Variations
COI	Cytochrome C Oxidase Subunit 1
COVID-19	Corona Virus Disease 2019
CRISPR/Cas	Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR-Associated Protein
CTAB	Cetyl Trimethylammonium Bromide
DBG	De Bruijn Graph
DEGs	Differentially Expressed Genes
DH	Doubled Haploids
DNA	Deoxyribonucleic Acid
EDII	Entrepreneurship Development And Innovation Institute
EST	Expressed Sequence Tags
Fe	Iron
FISH	Fluorescence In Situ Hybridization

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GISH	Genomic In Situ Hybridization
GO	Gene Ontology
GWAS	Genome-Wide Association Studies
HDL	High-Density Lipoprotein
Hi-C	High Throughput Chromatin Conformation Capture
HPLC	High-Performance Liquid Chromatography
IAA	Indole-3-Acetic Acid
IBA	Indole-3-Butyric Acid
IDA	Iron Deficiency Anaemia
IDF	International Diabetes Federation
IMGC	International Moringa Germplasm Collection
INDELS	Insertion-Deletions
IR	Inverted Repeat
IRAP	Inter-Retrotransposon Amplified Polymorphism
ISSRs	Inter Simple Sequence Repeats
ITS	Internal Transcribed Spacer (Consisting Of ITS1 And ITS2)
IYFV	International Year Of Fruits And Vegetables
KEGG	Kyoto Encyclopedia Of Genes And Genomes
LC/MS	Liquid Chromatography/Mass Spectrophotometry
LDL	Low-Density Lipoprotein
LSC	Large Single Copy
MAS	Marker Assisted Selection
matK	Maturase K
Mb	Mega Bases
McFISH	Multi-Colour FISH
MEMO	Methanolic Extract of Moringa Oleifera
M-FISH	Metaphase FISH
MFPP	Micronized Ferric Pyrophosphate
miRNA	MicroRNA
MISA	Microsatellite Identification Tool
ML	Maximum Likelihood
MS Medium	Murashige and Skoog Basal Medium
MVs	Microvesicles
NAA	1-Naphthaleneacetic Acid
NCBI	National Center For Biotechnology Information
NGO	Non-Government Organization
NGS	Next-Generation Sequencing
OLC	Overlap Layout Consensus
ONT	Oxford Nanopore Technologies
PAVs	Presence/Absence Variations
PCA	Principal Coordinate Analysis
PCR	Polymerase Chain Reaction
PEG	Polyethyleneglycol
PFGE	Pulse Field Gel Electrophoresis
pg	Pico Gram
PGRs	Plant Growth Regulators

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PIC	Polymorphic Information Content
PKM	Periyakulam
ppm	Parts Per Million
PTC	Plant Tissue Culture
qRT-PCR	Quantitative Real Time PCR
QTL	Quantitative Trait Loci
RAMP	Randomly Amplified Microsatellite Polymorphism
RAPD	Random Amplified Polymorphic DNA
rbcl	Ribulose-1,5-Bisphosphate Carboxylase Large Subunit
RBIP	Retrotransposon-Based Insertion Polymorphism
RDA	Recommended Dietary Allowances
rDNA	Recombinant DNA
REM-AP	Retrotransposon-Microsatellite Amplified Polymorphism
RFLP	Restriction Fragment Length Polymorphism
RNA	Ribonucleic Acid
ROS	Reactive Oxygen Species
RSM	Response Surface Methodology
RT-PCR	Reverse Transcription Polymerase Chain Reaction
SCAR	Sequence Characterized Amplified Regions
SCOT	Start Codon Targeted Marker
smRNA-FISH	Single-Molecule RNA-FISH
SMRT	Single Molecule Real Time
SNP	Single Nucleotide Polymorphism
SRAP	Sequence-Related Amplified Polymorphism
SSC	Small Single Copy
SSCP	Single-Strand Conformation Polymorphism
SSDs	Small-Scale Duplications
SSR	Simple Sequence Repeat
TE	Transposable Elements
TGS	Third-Generation Sequencing
TRAP	Target Region Amplification Polymorphism
UN-FAO	United Nation's-Food And Agriculture Organization
UNAM	Universidad Nacional Autónoma De México
UPLC-ESI-MS/MS	Ultra-Performance Liquid Chromatography-Electrospray Tandem Mass Spectrometry/Mass Spectrometry
v/v	Volume By Volume
w/v	Weight By Volume
WGD	Whole Genome Duplication
WGS	Whole-Genome Shotgun Sequencing
YAC	Yeast Artificial Chromosomes
ZMW	Zero-Mode Waveguide



# Moringa and Its Importance

1

N. Manikanda Boopathi and M. Raveendran

## Abstract

In the recent past, *Moringa oleifera* Lam (Moringaceae) has been recognized as an economically and nutritionally important crop owing to its health benefits. Moringa is widespread and found in all tropical and subtropical climates. As this crop is grown by different groups of people, it is known by several regional names such as drumstick tree, sajiwan, kelor, murungai, marango, mlonge, mulangay, saijhan, ben oil tree and sajna. Moringa is valued for its high nutritional value and medicinally important phytochemicals. Edible parts of this plant are found to contain necessary nutritional compounds such as proteins, essential and non-essential amino acids, vitamins, minerals, antioxidants and other phenolic compounds. They have been historically consumed over centuries and have been employed in the indigenous system of medicine for the treatment of different maladies or disorders. Leaves, roots, seed, bark, fruit, flowers and immature pods of Moringa were found to have antioxidant, antidiabetic, antibacterial, antifungal, antitumour, anti-inflammatory, antiulcer, antispasmodic, diuretic antihypertensive, hep-

atoprotective, antipyretic, antiepileptic, cardiac and cholesterol-lowering activities. This chapter focuses on the nutritional and medicinal values of Moringa, their application in medicine along with their pharmacological properties besides providing an overview of promising cultivars and their cultivation.

## 1.1 Introduction

Universally, policy makers and scientists are always looking for alternative crops and strategies to increase food productions as the productivity of agricultural and horticultural crops is threatened by continuous climate change. It is imperative to double the production by 2050 to ensure the food and energy supply to the growing world population (Ray et al. 2013).

The FAO has projected that between 2005 and 2050, the area under cropland must be increased to a minimum of 69 million ha (Alexandratos and Bruinsma 2012) to meet the food demand in 2050. Such effort is considered as a gigantic challenge, owing to unpredictable weather conditions (including erratic precipitations and temperatures besides alterations in CO<sub>2</sub> levels; Gruda et al. 2019). This implies that we need to look for alternative crops, which can thrive well in these unpredictable harsh environments.

Moreover, ~95% of the human calories are supplied by only 30 crop species, of which wheat, maize, and rice are considered as staple foods.

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N. M. Boopathi (✉) · M. Raveendran  
Department of Plant Biotechnology, Center for Plant  
Molecular Biology and Biotechnology, Tamil Nadu  
Agricultural University, Coimbatore, India  
e-mail: [nmboopathi@tnau.ac.in](mailto:nmboopathi@tnau.ac.in)