

Compendium of Plant Genomes  
Series Editor: Chittaranjan Kole

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Senjuti Sinharoy  
Yun Kang  
Vagner Benedito *Editors*

# *The Medicago truncatula* Genome

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# Compendium of Plant Genomes

## **Series Editor**

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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.

**Interested in editing a volume on a crop or model plant?**

Please contact Prof. C. Kole, Series Editor, at [ckoleorg@gmail.com](mailto:ckoleorg@gmail.com)

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The *Medicago truncatula*  
Genome

 Springer

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

*Chittaranjan Kole*

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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 last 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, eight crop and model plants, eight model plants, 15 crop progenitors and relatives, and three 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, 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 beside 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

It is indisputable that *Medicago truncatula* (barrel medic) has been an invaluable model for legume species as well as to understand key plant features that are not present in the simpler model, *Arabidopsis thaliana*. Indeed, *M. truncatula* has been an essential tool to reveal the genetic, biochemical, and physiological processes of symbiotic nitrogen fixation, seed development, specialized metabolism, leaf development, and disease resistance in plants, to name a few.

This book explores the state of the art of *M. truncatula* as a model for unveiling mechanisms not only of legumes but plants in general. We start navigating the dynamics of gene expression through transcriptomics resources in Chap. 1. This chapter examines the resources available and provides a vision on how to utilize transcriptomic datasets in light of new tools, such as artificial intelligence, to discover hidden patterns to explain biological processes.

Chapter 2 explores the use of genome-wide association analyses (GWAS) to find associations between genome sequence variation and quantitative and qualitative traits. While such analyses only provide association, this approach has been uniquely useful to create strong hypotheses on gene functions to establish genetic causation of important traits.

In *M. truncatula*, the tobacco retrotransposable element *Tnt1* has been very useful in applying forward as well as reverse genetics by providing the research community with mutants from a population that virtually fully covers its genome. The *Tnt1* mutant population was extensively characterized phenotypically as well as exhaustively sequenced and deposited on a searchable database. Chapter 3 provides an update on this resource.

In the same token, Chap. 4 explores the mutant collection created via Fast Neutron Bombardment (FNB), which produces mostly deletions of varied sizes. This resource has been invaluable to understand the development of leaf complexity in legumes and the identification of key genes involved in this process.

Chapter 5 discusses the usefulness of *M. truncatula* as a reservoir for the identification of novel resistance loci for studying disease resistance in legumes, especially powdery mildew, an important fungal disease in beans that can cause significant yield losses in hot and humid climates.

As a legume model, *M. truncatula* has been uniquely positioned as a tool to study symbiotic nitrogen fixation. Chapter 6 explores the transcriptional networks during the development of the root nodule. The de novo

development of this organ upon a biotic stimulus (rhizobial infection) under a specific environmental condition (low nitrogen in the soil) and the permissive development of an intracellular symbiosis through the creation of a semi-organelle (the symbiosome) in the cortical cells of the forming nodule can be studied to understand legume biology, and they can also be further explored to understand endosymbioses and organogenesis in general.

Furthermore, Chap. 7 analyzes the dynamics of gene expression from large transcriptomic datasets in order to integrate information of nodule development through a systems biology perspective. As our knowledge of the process evolved and new tools are created to integrate different datasets, such as genetic variation, transcriptional dynamics, metabolomics, and cellular/anatomic imaging, we will be able to consolidate mechanisms of nodule development and symbiotic nitrogen fixation that will be useful to plant biologists as well as of practical use for legume breeders.

Chapters 8–10 bring textbook examples of how *M. truncatula* genetic resources, such as transcriptional databases and a mutant collection, can be used to identify novel genes involved in biological processes. Chapter 8 reveals a novel gene that is key for symbiotic nitrogen fixation in legumes. Chapter 9 shows how this model has been used to study the development of complex leaves, especially leaf blade growth patterns. Chapter 10 explores the roles that *WOX* genes play in plant development, including leaf pattern formation.

Chapters 11 and 12 demonstrate the usefulness of *M. truncatula* as a tool to study seed development. Chapter 11 explores the early onset of seed development from a genomic perspective, whereas Chap. 12 focuses on seed maturation and desiccation, which is fundamental for seed viability and longevity.

At last, Chap. 13 examines the genetic control of organ size development using *M. truncatula* as a model.

*In toto*, this book celebrates the humble barrel medic as a pillar of legume genomics as well as a tool that goes beyond to extend our knowledge of plant biology. The tools and resources available to the *M. truncatula* research community, allied to exquisite and talented scientists distributed worldwide that work together as an inclusive community, are expanding the knowledge and creating new challenges in this continued endeavor. We hope you enjoy reading these chapters, learn something new, and feel enthused and empowered to continue or start this journey of discoveries with us.

New Delhi, India  
Stillwater, USA  
Morgantown, USA

Senjuti Sinharoy  
Yun Kang  
Vagner Benedito

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# Contents

<b>1</b>	<b>The Model Legume, <i>Medicago truncatula</i> in the Genomic Era: Speeding Up Discoveries in Legume Biology</b> . . . . .	<b>1</b>
	Christina Laureen Wyman, Lucas Gontijo Silva Maia, Lina Yang, and Vagner Augusto Benedito	
<b>2</b>	<b>Genome-Wide Association Studies in <i>Medicago truncatula</i></b> . . . . .	<b>11</b>
	Muhammet Şakiroğlu and Yun Kang	
<b>3</b>	<b><i>Tnt1</i> Insertional Mutagenesis in <i>Medicago truncatula</i> for Gene Function Analysis</b> . . . . .	<b>23</b>
	Raja Sekhar Nandety, Jiangqi Wen, and Kirankumar S. Mysore	
<b>4</b>	<b>Fast Neutron Bombardment (FNB)-Induced Mutant Resources in <i>Medicago truncatula</i></b> . . . . .	<b>35</b>
	Yuhui Chen and Rujin Chen	
<b>5</b>	<b><i>Medicago truncatula</i> as a Model to Decipher Powdery Mildew Resistance in Legumes</b> . . . . .	<b>43</b>
	Megha Gupta, Arunima Gupta, and Divya Chandran	
<b>6</b>	<b>Transcriptional Networks in <i>Medicago truncatula</i>: Genomic and Functional Overview During Root Nodule Symbiosis</b> . . . . .	<b>71</b>
	Akanksha Bhardwaj and Senjuti Sinharoy	
<b>7</b>	<b>Understanding of Root Nodule Development at Level of System Biology as Obtained by High Throughput Transcriptomic Approach</b> . . . . .	<b>91</b>
	Akanksha Bhardwaj and Senjuti Sinharoy	
<b>8</b>	<b>Whole Genome Sequencing Identifies a <i>Medicago truncatula Tnt1</i> Insertion Mutant in the <i>VTL8</i> Gene that is Essential for Symbiotic Nitrogen Fixation</b> . . . . .	<b>103</b>
	Jingya Cai, Vijaykumar Veerappan, Taylor Troiani, Kirankumar S. Mysore, Jiangqi Wen, and Rebecca Dickstein	
<b>9</b>	<b>Regulation of Leaf Blade Development in <i>Medicago truncatula</i></b> . . . . .	<b>113</b>
	Hui Wang, Jianghua Chen, and Million Tadege	

---

<b>10</b>	<b>Function of <i>Medicago</i> WOX Genes and their Diversity . . . . .</b>	<b>123</b>
	Hao Lin, Yingying Meng, Million Tadege, and Lifang Niu	
<b>11</b>	<b>Early Stages of Seed Development in <i>Medicago truncatula</i>: Lessons from Genomic Studies . . . . .</b>	<b>131</b>
	Garima Chauhan, Prashant Yadav, Jaiana Malabarba, Jerome Verdier, and Kaustav Bandyopadhyay	
<b>12</b>	<b>Seed Maturation Events in <i>Medicago truncatula</i>: Focus on Desiccation Tolerance . . . . .</b>	<b>139</b>
	Jaiana Malabarba, Kaustav Bandyopadhyay, and Jerome Verdier	
<b>13</b>	<b>Functional Genomic and Genetic Studies of Organ Size Control in <i>Medicago truncatula</i>: An Overview . . . . .</b>	<b>153</b>
	Zeyong Zhang and Rujin Chen	

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## Abbreviations

$\delta^{13}\text{C}$	Carbon-13 isotope discrimination
ABA	Abscisic acid
ABI	Abscisic acid insensitive
ABRE	ABA response element
Ac/Ds	Activator–dissociator
aCGH	Array-based comparative genomic hybridization
AD	Arbitrary degenerate
AGLF	AGAMOUS-like flower
AI	Artificial intelligence
AM	Arbuscular mycorrhiza
AON	Autoregulation of nodulation
ARF	Auxin response factor
ARP	Actin-related Protein
AS	Asymmetric leaves
ASL18	Asymmetric leaves 2-like
BC	Back crossed
BOP	Blade on petiole
BR	Brassinosteroid
BRI	Brassinosteroid receptor
BS	Big seed
BZR	Brassinazole resistant
C <sub>2</sub> H <sub>2</sub>	Cystine-2/ histidine-2
CAPS	Cleaved amplified polymorphic sequences
CBS	Cystathionine- $\beta$ -Synthase-like
CC	Coiled-coil
CCaMK	Calcium calmodulin-dependent protein kinase
CE	Cytokinin response elements
CEP	C-terminally encoded peptide
ChIP	Chromatin immunoprecipitation
CHS	Chalcone synthase
CK	Cytokinin
CKX	Cytokinin oxidase/dehydrogenase enzymes
CLE	CLAVATA3/embryo surrounding region related
CLV	CLAVATA
CMLM	Compressed MLM
CNVs	Copy number variations
CO	Cortex-specific transcript

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CoGe	Comparative genomics
CRA	Compact root architecture
CRE	Cytokinin response
CSSP	Common symbiosis signaling pathway
CYC	CYCLIN
CYC-box	CYC-RE contains a palindromic sequence
CYC-RE	Cyclops responsive cis element
DAP	Days after pollination
DASH	DOF acting in seed embryogenesis and hormone accumulation
DIB	Dwarf and increased branching
DMI	Does not make infections
DNF	Defective in nitrogen fixation
dNod <sup>+/-</sup> , Fix <sup>+</sup>	Delayed nodule formation and effective nitrogen fixation
DS	Desiccation sensitive
DT	Desiccation tolerance
EDS	Enhanced disease susceptibility
EFD	Ethylene response factor required for nodule differentiation
EMS	Ethyl methane sulfonate
ENOD	Early nodulin
EOD	Enhancer of DA1
ERN	Ethylene response factor required for nodulation
EST	Expressed sequence tags
ET	Ethylene
ETI	Effector-triggered immunity
EXO	Exocyst
EXP	Expansin
FAO	Food and Agriculture Organization
FCL	Fused compound leaf
Fix-	N-fixation defective
Fix-	Non-functional
FLOT	Flotillin
FNB	Fast neutron bombardment
FST	Flanking sequencing tags
FUS3	FUSCA 3
GA	Gibberellin
GAN	Generative adversarial network
GID	Gibberellin insensitive dwarf
GIF	GRF-interacting factor
GIF/AN	GRFs-ANGUSTIFOLIA
GL	Glabra
GLM	General linear model
GPARG	Genetic profile-activity relationship
GRF	Growth-regulating factor
gRNA	Guide RNA
GWAS	Genome-wide association studies
HAN	HANABA TARANU