Compendium of Plant Genomes
Series Editor: Chittaranjan Kole

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The Teak Genome

Springer

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.

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The Teak Genome

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

Chittaranjan Kole

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_2 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

Foreword

Teak has global significance and needs no introduction. The recognized properties, unquestionable beauty, and noble applications of its timber make it one of the world's most valuable forest tree species. Natural teak forests have been essential to many tropical countries' forest economies. However, teak exploitation from natural forests is not sustainable and shall be further limited in the coming years. In contrast, plantation teak forests have attracted large investments from the private sector and are increasing globally.

While volumes and quality of plantation teak timber still fall short compared to those of native forests, teak growers and researchers more than ever face the challenge of making plantation timber meet the global teakwood market's expectations. When 24 renowned scientists, representing four continents, join together on a book to share their expert knowledge about teak, involving subjects as varied as economics and transcriptomics, wood chemistry, and growth modeling, it is cause for celebration to those involved with the species.

The list of subjects covered in the book is extensive and also includes silvicultural practices, teak biology and ecology, wood properties and wood genetics, seed biology and seed orchard dynamics, clonal propagation, clonal characterization and variety registration, genetic diversity and population structure, genetic improvement, teak genome, functional genomics, and molecular physiology. Authors present new strategies within the scope of modern tree improvement and planting material selection.

A few of the technologies comprehensively discussed in the book are already in practice by selected teak projects worldwide and showing very successful results, while the latest and more advanced ones shall further promote higher productivity, increased timber quality, and overall cost reduction to the next generations of plantation teak.

I am confident *The Teak Genome* will make a significant contribution to researchers, forestry companies, growers, and to all of those who already fell in love with this captivating tree species.

Fernando S. Torres
Managing Partner
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Preface

Globally, there is an unprecedented demand for timber. Booming economy and rapid urbanization in developing countries increase the consumption of timber and related products. Growing needs for timber places strains on global forests, necessitating the establishment of additional plantations and rigorous technological interventions to ensure their long-term sustainability and guaranteeing wood for the international market. The teak tree (*Tectona grandis* L.f.) is one of the world's premier tropical hardwoods native to India, Myanmar, Thailand, and Laos, but currently widely cultivated around the world. Teak has a unique place in luxury markets and is prized for its elegance, stability, strength, and natural resistance. Teakwood has a wide variety of applications, including ship building, furniture, construction industry, and magnificent carvings. Deforestation activities like shifting agriculture, population pressure, and grazing have led to a large reduction in the natural teak forest areas in all native teak-growing countries. Selective and intensive elimination of best quality mature trees has almost certainly resulted in the loss of superior germplasm in natural forests. In the past few decades, a massive growth of planted teak forests managed in shorter rotations has occurred in about 60 countries outside the natural range of teak. However, plantation harvested teakwood, unlike natural forest derived teakwood, does not yet has a high reputation in the international market. Given the diminishing supply of superior-quality teak from natural forests, plantation-grown teak has promising long-term opportunities if wood yield and quality can be increased. Like other commercial tree species, teak improvement necessitates quality planting stock, better site and clone selection, coupled with next-generation silviculture practices, and adoption of cutting-edge technologies. The timber quality of plantation-grown teakwood is primarily determined by its diameter, clear bole length, and heartwood content. Studies on wood properties have shown that the plantation-grown teakwood is no way inferior to teak from natural forests. Wood durability and aesthetic quality, the unique features of teak, are determined by the heartwood, age, color, grain pattern, and texture. Most of these wood characteristics can be influenced favorably through wise breeding strategies. Teak encompasses a wide range of diversity to successfully integrate these characteristics through breeding approaches. Further, availability of effective cloning techniques enables the production of true-to-type vegetative propagules for teak plantation programs.

The global annual trade of teak round wood was estimated to be more than 1 million cubic meters on average during the period between 2005 and 2014 with ca. US $2,000 per cubic meter. Currently, the major teak exporting countries are Africa, Asia, and Latin America and major importing countries are India, Thailand, and China with an import value of ca. US $487 million per year. Further, it is reported that local impacts of climate change may induce shifts in natural teak distribution ranges and recommend conservation of critical teak habitats. Increased global teak plantation sector, on the other hand, is seen as a mitigation tool for reducing climate change impacts and fixing atmospheric carbon dioxide. Despite such commercial and environmental importance, unlike pulpwood trees, teak has remained less attractive for scientific research on yield improvement, genetic basis of wood traits, and functional genomics. The significance of the teak tree as a global timber crop warrants investment into genome-based technologies to strengthen the understanding of physiologies that affect wood quality, especially in secondary wood formation. Furthermore, teak genome studies would enable the development of new molecular markers to accurately differentiate the populations. Efforts have been made recently to demonstrate the bioactive compounds involved in wood durability. The teak tree has accumulated a wealth of silviculture practices for plantation spanning most of the twentieth century. Biotechnological interventions, such as micropropagation and vegetative cloning methods were employed to multiply and spread the elite selections across large fields. Since 2015, genomic approaches assisted in discovery of genes, proteins, and other regulatory elements that could be manipulated to enhance tree productivity. The first draft genome sequence of teak was published in 2018, followed by the release of chromosome scale genome assembly using advanced long read sequencing technologies.

This book has benefited from the experience of contributors from all over the world who have a diverse range of competence in different aspects of teak tree research with background in genetic and genomic technologies. The scientific expertise on teak genetics, biology, ecology, clonal propagation, morphological descriptors for clonal identification, seed biology, and seed orchards has been comprehensively compiled. Modern silvicultural aspects with special emphasis on agroforestry are deliberated in detail. Site selection for teak plantation is one of the major drivers for a financially viable endeavor. Thus, a practical and rigorous growth model and management scheme for teak plantations are prescribed in this book, including examples from financially feasible site index classes. Significance of teakwood extractives and their role in wood durability and technological properties are also systematically examined. Important and intricate features in the tree improvement of teak including variations in wood traits are discussed in depth.

The teak genetic diversity, the sequenced genome, and transcriptomes from different tissues and their implications in modern tree improvement and elite tree selections have been discussed holistically. The relevance of whole-genome information for the prospective development of markers and marker-trait association including genomic selection is presented exhaustively. Applications of transcriptome and transcriptional regulators of major metabolic pathways involved in secondary xylem formation are also included. Pervasive genome content variations will energize the research groups to conduct pan-genome analysis using several high-quality sequence assemblies and realize the full potential of teak genome for the production of superior varieties.

We acknowledge Prof. Chittaranjan Kole, the Series Editor, and the Springer team for providing us with excellent guidance and assistance for the successful achievement of this book.

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Abbreviations

a*	Color parameter of redness
A	Angstrom
AA	Accelerated aging
AARPC	Annual average rate of price change
ABA	Abscisic acid
AFLP	Amplified fragment length polymorphism
AFOCEL	Association FOrêt-CELlulose
AGB	Above-ground biomass
AID	Air dry density
AP2/ERF	Apetala2/ethylene responsive factor domain
AR	Auto-regressive
AREB	ABA responsive element-binding protein
ARF	Auxin response factor
ARW	Annual ring width
ASTM	American Society for Testing and Materials
ATF1, 2	Activating factor 1, 2
b*	Color parameter of yellowness
bHLH	Basic helix-loop-helix
BI	Bax inhibitor
BLUE	Best linear unbiased estimator
BLUP	Best linear unbiased prediction
bp	Base-pair
Ca	Calcium
CAD	Cinnamyl alcohol dehydrogenase
CaMV	Cauliflower mosaic virus
CBH	Clear bole height
CCT	Convertible clonal test
cDNA	Complementary DNA
CEN	European Committee for Standardization
CI	Consensus information
CP	Control-pollinated
CPI	Consumer price index
CPTs	Candidate plus trees
Cry	Insecticidal crystal proteins
CS	Compressive stress
CSO	Clonal seed orchard

CUC2	Cup-shaped cotyledon 2
CWP	Cell wall percentage
CWT	Cell wall thickness
CYP	Cytochrome P450
DBH	Diameter at breast height
DEseq	*In silico* differential gene expression
D_q	Quadratic mean diameter
DREB	Dehydration-responsive element-binding protein
DUS	Distinctness, uniformity, and stability
DW	Dry weight
ECOWAS	Economic Community of West African States
ED	Dynamic Stiffness
EIIP	Electron-ion interaction potential
ERF	Ethylene response factor
EST	Expressed sequence tag
EUTR	European Union Timber Regulations
F	Frequency
FA	Fiber angle
FA	Fixed assets
FAO	Food and Agriculture Organization
FD	Fiber diameter
FL	Fiber length
FLR	Forest and landscape restoration
FOB	Free on board
FP	Fiber percentage
FSP	Fiber saturation point
G	Basal area
Gb	Gigabytes
GCA	General combining ability
GC-MS	Gas chromatography coupled to mass spectrometry
GDP	Gross domestic product
GPa	Gigapascal
GS	Genomic selection
GS	Growth strain
GUS	β-glucuronidase
GWAS	Genome-wide association studies
H	Hardness, mechanical properties
H_c^2	Clone-mean repeatability
h^2	Narrow-sense heritability
H^2	Broad-sense heritability
H_d	Dominant height
HD	Homeodomain
HMM	Hidden Markov Model
HPLC	High performance liquid chromatography
HSP	Heat shock protein
HTS	High-throughput sequence

HW	Heartwood
HWP	Heartwood percentage
HWP/SWP	Heartwood/sapwood ratio
IP	Intellectual property
IRR	Internal rates of returns
ISM	Information-spectrum method
ISSR	Inter-simple sequence repeat
ITTO	International Tropical Timber Organization
IUCN	International Union for the Conservation of Nature
K	Potassium
Kbp	Kilo base-pair
KVTC	Kilombero valley teak company
L*	Color parameter of lightness
LEC	Lectin-like protein
LFD	Lumen fiber diameter
LMM	Linear mixed model
LS	Longitudinal shrinkage
LSM	Least-square mean
LTR	Long terminal repeat
m^3/ha	Cubic meters per hectare
MAF	Microfibrillar angle
MAS	Marker-assisted selection
Mbp	Million base-pair
MC	Moisture content
MCS	Maximum compressive stress
MET	Multi-environment trial
MFC	Minimal fungicidal concentration
Mg	Magnesium
Mha	Million hectare
MOE	Modulus of elasticity
MOR	Modulus of rupture
MP	Mate-pair
MPa	Megapascal
mRNA	Messenger RNA
N/S	Noise signal
NAC	No apical meristem
NCBI	National Center for Biotechnology Information
NGS	Next-generation sequencing
NIR	Near infrared
NIRS	Near infrared spectroscopy
NLS	Nuclear localization signal
NPV	Net present value
NSC	Non-structural carbohydrates
OP	Open-pollinated
ORF	Open reading frame
P	Phosphorous
PCIV	Principles-Criteria-Indicators-Verifiers

PCR	Polymerase chain reaction
PE	Paired-end
PIP	Plasma membrane intrinsic protein
PP	Parenchyma percentage
Py	Pilodyn penetration
qRT-PCR	Quantitative real time PCR
QTL	Quantitative trait locus
RAPD	Random amplified polymorphic DNA
RF	Ray frequency
RFLP	Restriction fragment length polymorphisms
RH	Ray height
RNA-seq	RNA-sequencing
RP	Ray percentage
rRNA	Ribosomal RNA
RS	Radial shrinkage
RW	Ray width
Ry	Rydberg
SAGE	Serial analysis of gene expression
SAMs	Shoot apical meristems
SCA	Specific combining ability
SCAR	Sequence characterized amplified region
SCW	Secondary cell wall
SG	Specific gravity
SI	Site index
SIC	Site index class
SNP	Single nucleotide polymorphism
SPA	Seed production area
Sph	Stems per hectare
SRA	Sequence read archive
SS	Shear strength
SSA	State-space approach
SSO	Seedling seed orchard
SSR	Simple sequence repeat
SWN	Secondary wall NAC
SWP	Sapwood percentage
SWV	Stress-wave velocity
t	Stand age
T/R ratio	Tangential/radial ratio
t_0	Stand base age
TAD	Transcriptional activation domain
TF	Transcription factor
TgEf-1α	*Tectona grandis* elongation factor 1-α gene
TgUbq	*Tectona grandis* ubiquitin gene
TPH	Trees per hectare
TPS	Terpene synthase
TS	Tangential shrinkage

UPOV	International Union for the Protection of New Varieties of Plants
V_c	Commercial volume
VD	Vessels diameter
VF	Frequency of vessels
VL	Vessels length
V_{ob}	Over-bark volume
VP	Vessels percentage
VS	Volume shrinkage
V_{ub}	Under-bark volume
WD	Wood density
WT	Wild type

Teak: The King of Timbers

1

Sandeep Sasidharan and Yasodha Ramasamy

Abstract

Teak is regarded as the 'King of Timbers' due to its captivating wood quality and aesthetics. Because of its high durability, it can be used for a wide variety of indoor and outdoor purposes. The presence of oil in the teakwood makes it resistant to insects, fungi and termites and helps to withstand extended exposure to water as well as chemicals. The ease of workmanship is relatively high in teakwood compared to other timbers with better nail and screw holding ability, making them the best choice for furniture. It is one of the first species to be established as pure plantations for commercial purposes. Teak was once handled on 80–100-year rotations, but for commercial wood production, rotation periods have been limited to 20 or 30 years with adequate heartwood grain patterns. Heartwood in teak trees begins to develop between 4–5 years of age and the amount of heartwood produced varies with site conditions and silvicultural management. Teak plantations also contribute to climate change mitigation by sequestering carbon for longer periods and the global acceptance of teak makes it a great choice in forest landscape restoration programmes.

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1.1 Introduction

Teak (*Tectona grandis* L.f; 2n = 36) is considered as the 'King of Timbers', sharing the same position as diamond among precious stones. Teak has a unique blend of key elements to produce an unrivalled timber quality such as medium density, exceptional stability and mechanical properties, high resistance to physical and biological agents, outstanding resistance to abrasion and appealing aesthetical features. The exquisite furniture carved by the British craftsmen using teak in the eighteenth-century graces London's gardens from Hyde Park to Kew even today.

Teak has been the traditionally preferred timber for high-end engineering and construction of high-performance vessels, plywood, beams, decorative face veneer, flooring, furniture, solid fixtures, laminated panels, boards, and handicrafts. The teak timber quality has long been established to be dependent on their geographical origin and range from dark wavy brown coarse grain to straight yellow tight grain. Generally, teakwood from most geographical regions

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exhibit rich brown with dark chocolate brown streaks whereas naturally grown Burma teak usually have a uniform golden-brown colour without markings. Indian teak is characterized by straight or wavy grains with mottles, oily touch and marked with white glistening (silica deposits).

For centuries, teak has been the most preferred and potential hardwood species for large-scale plantations in the humid tropics (Bhat and Ma 2004). It has been conventionally raised in long rotations of 80–100 years. The world's first commercial teak plantation was established at Nilambur, Kerala, India in 1842. Under suitable climatic and edaphic conditions, long rotations produce relatively large-sized logs with better quality and significant amount of heartwood and thereby fetch high market prices. However, such long rotations entail long gestation periods for investments, hence short-rotation plantations of 20–30 years are now being increasingly practiced in many tropical countries for production of both veneer and sawn teakwood (Pandey and Brown 2000; Pérez 2005).

1.2 Timber Properties and Uses

Teakwood quality is generally defined by the end users based on its visual appearance, i.e. colour, grain and texture that describes the wood and its defects (Fig. 1.1). Tree size alone need not be considered as the single factor regulating wood quality, though it controls some major quality attributes such as amount of heartwood and clear wood. Though there exists a myth that faster growth would invariably lead to lower wood density, genetic studies have not established conclusively any significant relationship between rate of growth, wood density and stem diameter (Sanwo 1986). Besides density, other major structural factors influencing the market value of teakwood are its physical, mechanical, anatomical and biological properties (Bail lères and Durand 2000). The mean wood density of teak is estimated to be 650 kg/m^3 and as such maifests the wood with exceptionally high durability.

Fig. 1.1 The cross-sectional surface of teak with decorative streaks (growth rings). Photo © P. K. Thulasidas

As per the International Standard Classification (ASTM 1981), teakwood belongs to highly resistant class of timbers (durability class I). The synergetic effect of a large number of factors in teak enables the requisite protection from wood decaying organisms, dimensional stability and hydrophobicity. The intrinsic properties of teakwood that distinguishes it from other timbers is attributed to the presence of active extractive elements encrusted on the cell wall. These extractive elements in the heartwood vary from 10 to 19.8 percent and are poisonous to wood degrading microbes, invading termites and help repel water (Rudman and Da Costa 1959; Sandermann and Simatupang 1959, 1966; Yamamoto et al. 1998; Thulasidas and Bhat 2007). Further, polyphenols along with anthraquinone and naphthoquinone derivatives are some of the other extractives in teakwood that ensures its durability. The teak heartwood also contains ~1 percent of tectoquinone that provides termite resistance to the timber. The antioxidant caoutchouc (about 3 percent) provides teakwood with water repellence and an oily feel. These extractive contents increase with the age of teak plant and act independently or in combination to provide exceptional dimensional stability and durability to teakwood (Haupt et al. 2003; Bhat et al. 2005; Thulasidas and Bhat 2007; Sumthong et al. 2008).

In teak, immature wood referred to as juvenile wood is formed during the initial years of growth. The juvenile wood is usually lighter and spongy with relatively lesser durability and found near the pith. The physical, chemical and anatomical properties of these juvenile wood gradually change to mature characteristics in the juvenile phase itself and found to vary only moderately in the mature phase. Problems associated with juvenile wood include lower wood density, warp, excessive longitudinal shrinkage and decreased strength (Senft 1986).

Heartwood initiation starts in teak trees at 4–5 years of age and the amount of heartwood varies with site conditions, silvicultural management and the genotype–environment interactions (Hillis 1987). The heartwood percentage has been found to increase with growth rate of trees and with increasing diameter at breast height (DBH) (Moya et al. 2014). Wood from fast-grown teak is relatively paler with lesser extractives and durability than natural teak (Bhat and Florence 2003; Thulasidas et al. 2006; Kokutse et al. 2006; Moya and Berrocal 2010). However, plantation teak has an aesthetic exhibition of irregular decorative black streaks along the annual rings in the heartwood resulting in beautiful figures in the flat sawn surface (Nobuchi et al. 1996; Lukmandaru et al. 2009).

Felling ban for natural teak in Myanmar and conservation perspectives in South and South East Asia have compelled the current market demand for teakwood to be met from short-rotation plantations. As the felling age of short-rotation plantations is 20–25 years, there are chances that large proportions of timber reaching the international market may have high amounts of juvenile wood in them. However, there exists studies which refute such notions. For example, studies by Bhat (1999) show that the modulus of rupture and Young's modulus of juvenile wood phase in phenotypically superior fast-grown teak trees were lower by ~20–21% than the slow-grown ones, but the maximum crushing stress did not differ significantly between them. Enough evidence also exists to establish that short-rotation plantation-grown teak does not need to be always inferior to natural teak in terms of density, strength and shrinkage (Bhat 1999; Bhat et al. 2005; Thulasidas and Bhat 2012). Bhat et al. (2001) established that teak can attain optimum strength properties by 21 years of age and hence the fears attached with juvenile wood in logs from short-rotation plantations may be ill-founded (Fig. 1.2).

1.3 Economic Significance of Teak

Natural teak forests cover an area of ca. 29 million hectares around the world, nearly half of which grow in Myanmar. Over the years, the natural teak area has declined substantially in all major native teak-growing countries, except Thailand, mainly due to overexploitation (legal and illegal), agricultural expansion, shifting cultivation, population pressure, and grazing (Fig. 1.3). Besides reduction of natural area, targeted removal of the best quality teak trees (called 'creaming' in forestry) from the natural populations has also resulted in the genetic impoverishment of residual stands. As a consequence, the survival and sustainable use of the remaining natural teak forests is highly endangered. The decrease in availability of natural teak logs along with high market demand has placed teak as one of the few emerging valuable hardwood species that is now been increasingly grown in planted forests in about 70 countries throughout tropical Asia, Africa, Latin America and Oceania (Table 1.1 and Fig. 1.4). For most of these countries, albeit being an introduced species, teak represents a good livelihood opportunity to the dependent community and a major asset for the forestry economy attracting large investments from private sector.

Planted teak forests, according to various estimates cover between 4.35 and 6.89 million ha around the world, of which ca. 85% are in Asia, 10% in Africa, and 5% in tropical America. As per the 'State of the World's Forest Genetic Resources', teak takes the top rank in more than 20 of the listed countries in the report. Considering the declining supply from natural teak

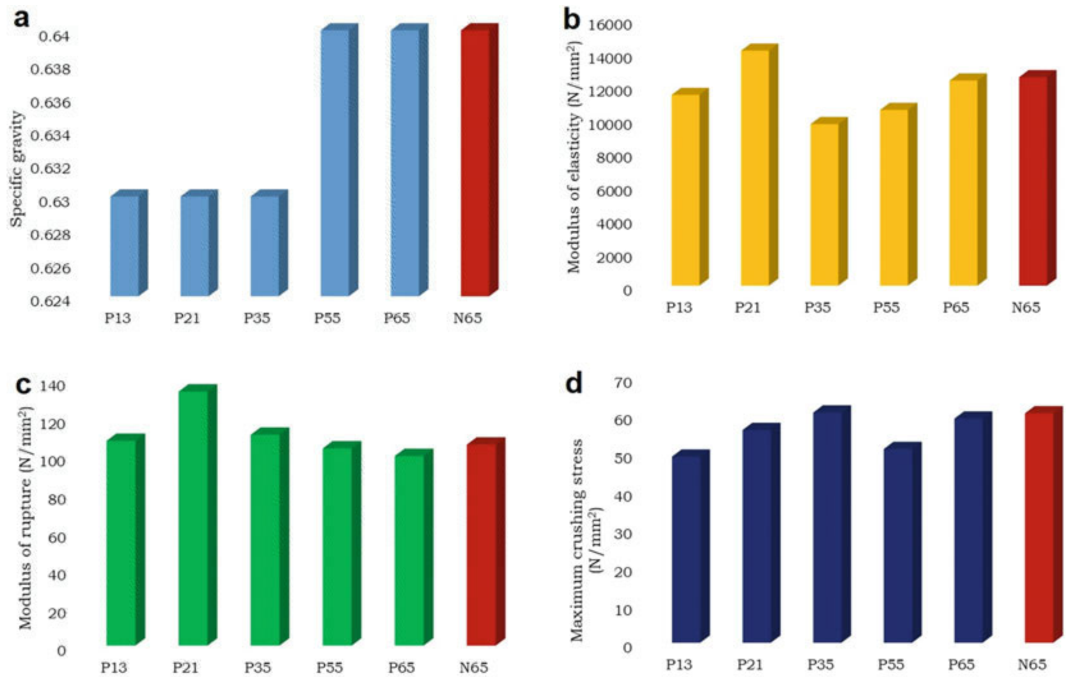

Fig. 1.2 Strength property variation among different age groups of planted teak in comparison to natural teak from Nilambur, India. **a** Specific gravity, **b** modulus of elasticity, **c** modulus of rupture, **d** maximum crushing stress. P13—Plantation of age 13 yrs; P21—Plantation of age 21 yrs; P35—Plantation of age 35 yrs; P55—Plantation of age 55 yrs; P65—Plantation of age 65 yrs; N65—Natural teak of 65 yrs. *Source* Bhat et al. (2001)

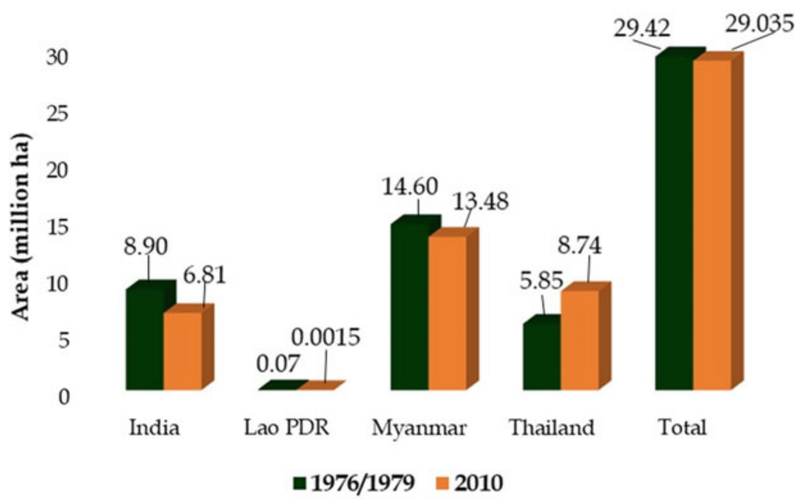

Fig. 1.3 Changes in area of natural teak forest during 1976–79 to 2010. *Source* Kollert and Cherubini (2012)

forests, the long-term prospects for plantation-grown teak appear promising, and demand is likely to increase in the future. Investments in teak plantations growing under suitable site conditions with genetically superior planting material and good management practices can yield attractive and robust financial returns. For example, large-scale private teak plantation developers in Ghana have reported to achieve internal rates of return (IRR) of more than 10%.

Table 1.1 Changes in area of planted teak by region during 1970–2000

Continent/region	Plantations (m ha)		
	1970	1995	2000
Africa	0.099	0.109	0.469
Asia	1.185	2.108	3.598
Carribbean	0.010	0.008	0.015
Central America	0.002	0.023	0.132
Oceania	0.002	0.003	0.008
South America	0.001	0.003	0.122
Total	1.299	2.254	5.346

Source Keogh (1979), Pandey and Brown (2000), Kollert and Cherubini (2012)

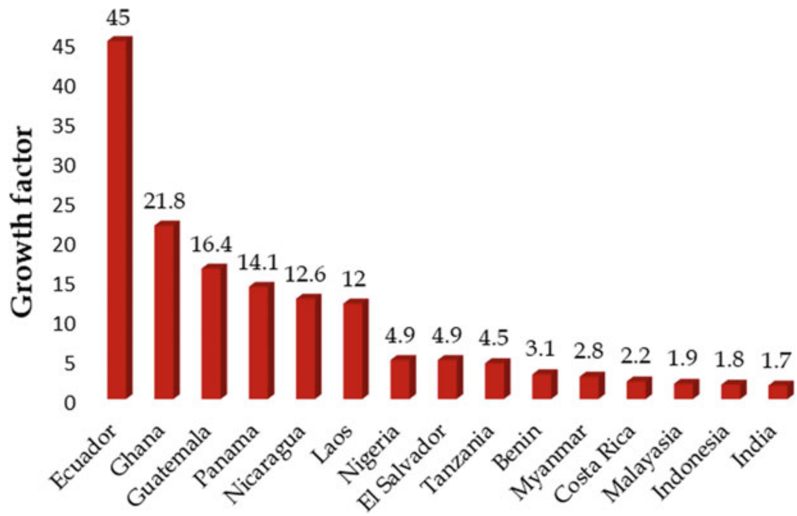

Fig. 1.4 Growth in area of planted teak (1995–2010). *Source* Pandey and Brown (2000), Kollert and Cherubini (2012)

As investors often look for quicker returns, teak from plantations of short rotations (20–25 years) will lead the international market in future and make the luxury items from long-rotation plantations a rare commodity.

Global teak imports (avg. 2005–2014) stands at 1.07 million m^3/yr worth 487 million US $/yr. The major teak trade flows worldwide are directed mainly towards India followed by China and these two countries together accounts for more than two-thirds of the global teak imports (Fig. 1.5). Thus, the global teak market is governed by trends in the Asian market that holds more than 90% of the world's teak resources. Since 2000, the global trade in teak logs of the major importing countries (India and China) has more than doubled in terms of volume and more than quadrupled in terms of value. Among the different teak-growing countries, Myanmar remains the dominant supplier of teakwood to global market even though the teak supplier base has broadened manifold outside the traditional natural forests in Asia. The non-traditional areas in Ghana, Tanzania, Ecuador, Costa Rica, Panama, Colombia and Brazil have continuously expanded their trade volumes since 2000, reaching a peak in recent years, a trend likely to continue in the future. However, lack of uniform grading rules, standards and consistency in measurements and quality assessment for teak logs results in widespread uncertainty and confusion around teak trade and investments.

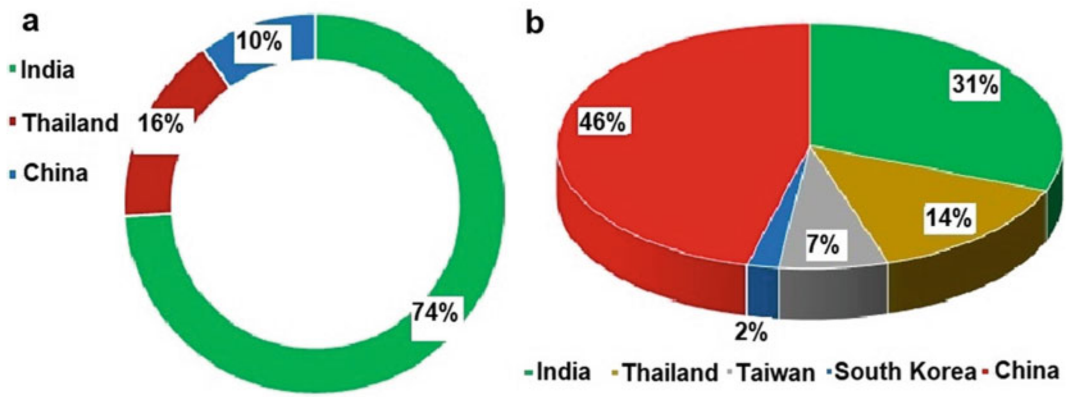

Fig. 1.5 Global teakwood imports (Avg. for 2005–2014 is 1.07 million m^3/year; **a**. round wood imports **b**. sawn wood. *Source* Kollert and Cherubini (2012)

1.4 Genetic Resources and Management

Teak has a geographically separated and environmentally diverse range of natural distribution, covering India, Thailand, Myanmar and Laos. A genetic analysis of 29 provenances of teak across their natural distribution (India, Myanmar, Laos and Thailand) found three main clusters of diversity each with two sub-clusters: (i) Interior and Western India (sub-clusters: Dry Interior India and Moist Western India); (ii) Eastern India and Myanmar (sub-clusters: Northern Myanmar and Semi Moist East India/Southern Myanmar) and (iii) Thailand and Laos (sub-clusters: West to Northwest Thailand and East Northwest Thailand and Laos) (Hansen et al. 2015). The high adaptability, ease of plantation establishment and value of teak timber have made it an important tree species even outside its natural distribution area (Kaosaard 1981; Keogh 1996; Kollert and Cherubini 2012; Midgley et al. 2015). However, changes in geographical regions and environmental conditions bring about subtle changes in their leaf morphology, stem form, branch characteristics, growth increment, heartwood proportion, wood quality, wood extractives, mineral contents, soil preferences, and pest and drought resistance. These variations can be attributed to a combination of differences in genetic structure (between populations and between individuals within populations) and growing environments (soils, climate and silvicultural practices).

For establishing plantations outside the natural areas, seeds were transferred worldwide primarily from Myanmar and India and has been continuing for decades (Koskela et al. 2014). In some of these introduced areas, such as Java, it has naturalized over the last two centuries (Verhaegen et al. 2010). Studies show that teak was introduced before 1900 in Nigeria (Egenti 1978), Papua New Guinea (Cameron 1968), West Indies and Trinidad (Keogh 1979). The early decades of the twentieth century saw teak being introduced to more countries such as Ghana (Chollet 1958) Tanzania (Wood 1967), Côte d'Ivoire (Tariel 1966), Togo (Chollet 1958), Sudan (Hall and Williams 1956) and by the final decades of the century it had expanded to a large number of additional countries in Central and South America (Keogh 1979, 1980, 1981). The early introductions were relatively small and served to verify the suitability of the species at these new sites and as seed sources for future expansion (Kjær and Graudal 2010; Koskela et al. 2010, 2014). The transferred seeds during these phases originated from multiple sources and has led to the development of landraces in Africa and America over the years. Though the origins of these landraces are not well documented, available historical records and genetic studies have reconstructed some of the possible germplasm sources and introduction routes (Koskela et al.