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Comparative and Evolutionary Genomics of Angiosperm Trees

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Preface

Angiosperm trees display a dizzying array of diversity in morphology, anatomy, physiology and biochemistry. This diversity has been described and catalogued by various scientific disciplines, but the molecular, genetic, and evolutionary mechanisms underlying this diversity have only recently been explored.

This book, *Comparative and Evolutionary Genomics of Angiosperm Trees* marks a change in focus of tree genomics, from single species to comparative approaches. Excitingly, advances in genomic and sequencing technologies are ushering a new era of research broadly termed comparative genomics, which simultaneously exploits and describes the evolutionary origins and genetic regulation of traits of interest. Effective comparative genomic approaches for trees are enabled by an explosion in genomic data including an increasing number of complete genome sequences available for angiosperm trees, and extensive gene expression data available for a wider array of species. We believe that there is a great potential role for comparative approaches for the study of angiosperm trees, both with regards to understanding the fundamental evolution and development, as well as addressing problems of economic or ecological importance.

This book is intended as resource to provide background on the diverse biological subject areas pertaining to comparative and evolutionary genomic approaches of angiosperm trees. We elected not to make genomic technologies (e.g. the latest sequencing technologies) or computational approaches a main focus of the book, as they are already covered by other literature, and also are rapidly changing. Instead, the chapters focus on biological, genomic, and evolutionary aspects of angiosperm trees that provide information and perspectives that will support researchers broadening the focus of their research. We hope this will provide a valuable resource, and have longevity of relevance that will outlive the particulars of current-day technical approaches.

The first section of the book provides background on the evolution and diversification of angiosperm trees, as well as description of the salient features and diversity of the unique physiology and wood anatomy of angiosperm trees. The second section describes developments in the most model advanced angiosperm tree species (poplars) as well as species that are emerging models. The third section

describes the structural features and evolutionary histories of angiosperm tree genomes, followed by a fourth section focusing on the genomics of traits of biological, ecological and economic interest.

We would like to acknowledge the significant efforts of the authors of each chapter, and the overall high quality of the writing and information contained within their chapters.

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Introduction: Comparative Genomics of Angiosperm Trees: A New Era of Tree Biology

Quentin C.B. Cronk and Andrew T. Groover

Abstract Forest tree genomics has made enormous strides in recent years, by describing the expression and function of genes influencing tree growth and development, and even sequencing the entire genomes of select “model” tree species. We believe that the next chapter of forest tree genomics will focus on cross-species comparative approaches, which will have the ability to provide fundamental new insights into the unique biology and evolutionary history of tree species. Angiosperm trees in particular are fascinating in light of evolution. Angiosperm trees represent the extensive genome evolution, including whole genome duplications, exhibited by different angiosperm lineages. Angiosperm trees also present amazing morphological, physiological and biochemical diversity, providing the opportunity to use comparative genomic approaches to understand the evolutionary origin and diversification of traits associated with trees. This book provides background on biological, genomic, and evolutionary aspects of angiosperm trees, in support of researchers exploring the use of comparative and evolutionary genomic approaches. This introduction briefly reviews the diversity of angiosperm trees and sets out the conceptual framework for comparative and evolutionary study of angiosperm tree biology using genomic tools, and highlights individual chapters within this book.

Keywords Evolution • Wood Developmental Biology • Population Genomics • Angiosperm Trees • Comparative Genomics

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A World of Trees

The carbon dioxide monitoring station at Mauna Loa, Hawaii, has revealed a steady rise of atmospheric carbon dioxide, year-on-year. However, within this rise there is strong seasonal variation. Slightly more carbon dioxide is detectable in the northern hemisphere winter and spring and slightly less in summer and fall. Allowing for a time lag of atmospheric mixing, this is attributable to the vast areas of northern hemisphere boreal and temperate forests losing biomass and releasing carbon dioxide in the fall and taking up carbon dioxide (1.5×10^{10} tons net) with new growth in the spring (Bolin and Keeling 1963). Nothing could more clearly indicate the impact of forests on the biosphere, with trees exerting an influence on atmospheric chemistry detectable half a world away in the central Pacific.

Forests also have direct impacts on human lives. As producers of raw material for industrial processes they provide employment, directly or indirectly, for millions. Forests heat homes and cook food: 6.1 %, or 772 million tons of oil equivalent (MTOE), of primary global energy comes from wood (FAO 2014). This is mainly in the rural and developing world, where fuelwood is directly gathered from forests, but increasingly woody biomass is being grown as bioenergy crops.

As reservoirs of biodiversity, forests are important biomes for biodiversity conservation. More intangible but nevertheless important are the ecosystem services forests provide: climatic moderation, erosion and landslip prevention, and watershed protection, to name a few. Forests are also human habitat, providing food and shelter for many. Even in the urbanised West they are increasingly valued for recreation, and in terms of providing a “connection to nature” which is increasingly recognised as a necessary part of human development (FAO 2014). Additionally, forests and related disturbances (e.g. wildfire) directly affect an increasing number of people living at the wildland-urban interface.

Globally, natural (minimally exploited) and semi-natural (exploited but minimally managed) forests are under threat. This is mainly through conversion, by burning and logging, into agricultural landscapes (or “agrosapes”). However many

Table 1 Status of forestry plantations in 2000

Plantation type	Area (000 ha)
<i>Acacia</i> (Leguminosae)	8317
<i>Eucalyptus</i> (Myrtaceae)	17,860
<i>Hevea</i> (Euphorbiaceae)	9885
<i>Tectona</i> (Lamiaceae)	5716
Other angiosperm	33,556
Total angiosperm	75,334
Conifer(all)	58,134
Unspecified	53,618
TOTAL area (000 ha)	187,086
Rate of planting (000 ha/year)	4493

Source: The Global Forest Resources Assessment 2000 (FAO 2000)

of these agrosapes are subsequently used for the establishment of tree plantations in which intensively-managed, fast-growing, short-rotation trees are grown efficiently for industrial purposes (Table 1). Such plantations can, and should, take some of the pressure off natural forests and provide wide ranging socio-economic benefits, although their benefits are often disputed.

Angiosperm Trees as Genomic Subjects

This book deliberately focuses on angiosperm trees. Conifers, although important, are only dealt with here when appropriate to highlight the evolution of traits found in angiosperm trees. Angiosperm trees are much more diverse than conifers, as well as being the major component of most short-rotation plantation systems (FAO 2001; Table 1). While angiosperm trees present some challenges for biologists due to their large size and long generation times, modern genomic technology has done much to make them scientifically tractable and has allowed the exploitation of characteristics specific to trees that make them particularly attractive as biological subjects. First, wood itself is a globally important trait, not only economically valuable but also pivotal to the functioning of the biosphere. The enormous variety of angiosperm woody plants, and wood types, makes possible comparative and evolutionary approaches. Secondly, many trees have large populations and wide ranges, and show adaptation to diverse climates, and therefore make good subjects for the study of local adaptation. While putting trees in the laboratory is challenging, it has proved possible to take the laboratory to the tree and use wild populations as “natural breeding experiments”. Genomic characterization of natural variation grown in common gardens has allowed the molecular basis of traits to be uncovered, for instance using genome-wide association studies (GWAS).

Angiosperm Tree Diversity

There are about 369,000 species of angiosperms (RBG Kew 2016), of which between one fifth and one quarter can be considered trees (i.e. 70,000–90,000). The angiosperms, including those that are trees, display a huge amount of morphological variation, variation that makes comparative approaches particularly rewarding. Economically, there are ca. 1575 angiosperm trees with widely traded timber (Mark et al. 2014). The majority of these are tropical, reflecting the high diversity of tropical forest biomes. The most important family of tropical timber trees by far is the Leguminosae (Fabaceae), followed by the Meliaceae. A summary of some of the most important tropical tree families for forestry is given by Cronk and Forest (chapter 1: Table 4, this volume).

In temperate regions the situation is somewhat different. There is less overall tree diversity in temperate biomes and there Fagaceae is arguably the most important forestry family (chapter 1; Table 4). When temperate forestry trees are mapped on a

summary angiosperm phylogenetic tree it can be seen that the species are highly clustered in one clade (rosid 1). When the same is done for tropical trees the spread is more even, reflecting greater tropical diversity. Genomic resources for trees are rapidly developing. Every year new genome projects are announced. Happily, any discussion in this book will quickly be out of date, which indicates the health and dynamism of the subject. Nevertheless it may be useful to make a few observations on the situation as it now exists (2016). Emerging genomes of forest trees are discussed by Sollars and Buggs (chapter 4, this volume). The best resource by far is that provided by poplar (*Populus trichocarpa*). This was the third plant genome to be completed (after *Arabidopsis* and rice) and is of high quality (Douglas, chapter 3, this volume). Many of the emerging genomes are from the same major clade (rosid 1), such as the Fagaceae genomes.

However, given the importance of the legumes in tropical forestry, the absence of a high quality tree legume genome is notable. An *Acacia* genome is nearing completion, and *Acacia* is the most important plantation legume. However a tree legume in the same clade as crop legumes like soya (*Glycine max*) would allow tremendous synergy between legume tree genomics and legume crop genomics.

The ease with which whole shot-gun sequencing can now be carried out may herald an end of the “model tree” or “model plant” paradigm. Genomic resources can now be generated for any tree, however rare or obscure. This is to be welcomed. However a note of caution should be sounded. While sequencing is easy, assembly and annotation are not. A multiplicity of poorly assembled and annotated genomes may turn out to be more trouble than they are worth.

Model Species versus Comparative Trait-Based Approaches

Woodiness is a labile trait, and it has been modified to different extents, from shrubs to forest giants, in different angiosperm lineages. It has been lost, and sometimes regained, in many lineages. The diversity of woods, from balsa to ebony and teak, differing anatomically and chemically, provide a resource for the study of the molecular basis of this trait. Trait-based approaches, i.e. choosing a trait and following it wherever it iterates in organisms, stand in opposition to the model organism-based approach in which a single organism is chosen as one in which to study many traits (or at least as many as that organism possesses). The model organism has many advantages, not least the ability to build on a growing body of organism specific protocols and resources. However the weakness of the model organism approach is the limited view of any particular trait that it offers – without examining the trait and associated regulatory mechanisms in additional species it is not possible to know if findings are unique to the model species under study, or what the evolutionary history of the trait might be. Consequently, the immense power of comparative and evolutionary approaches cannot be brought to bear when working with a single model species.

Happily the tension between the model organism approach and a comparative approach is rapidly becoming obsolete. Any organism can now be a “model” at least

in the sense that genome resources can be generated readily. Sollars and Buggs (chapter 4, this volume) detail some recent genome projects of forest trees, and, judging by the speed at which new projects are coming on stream, this is likely to be the tip of a very large iceberg. Furthermore there is the possibility of using comparisons between classic plant models such as *Arabidopsis* and emerging tree models (such as poplar). The arabidopsis-poplar comparative model approach has already proved its power in many examples (e.g. Rottmann et al. 2000; Johnson and Douglas 2007).

The huge variety of angiosperm trees provides a scientific opportunity when unleashed by genomics. Although every taxon is a potential genomics model, working with organisms that reach vast sizes and do not domesticate well in the lab has been daunting. Rather than domesticate trees to the lab, the lab has been taken to the tree. Tree biologists have learnt to use the forest as the “growth chamber” and natural populations as “breeding experiments”. Common gardens, while expensive to set up, are long lasting (if land tenure issues can be solved) and have the potential to supply large quantities of data to multiple studies over many years (Fetter, Gugger & Keller, chapter 13, this volume).

Evolutionary and Comparative Genomics for Angiosperm Trees

Comparative approaches to tree biology can work at many different scales (Table 2), from the comparison of different genetic individuals in the same species, to the comparison of very different tree species in different plant families. The immense

Table 2 Comparative approaches to angiosperm tree genomics

Comparison	Questions	Examples
1. Between plant families, e.g. <i>Eucalyptus</i> (Myrtaceae) vs <i>Populus</i> (Salicaceae)	Conserved pathways in major traits, e.g. wood formation	Hefer et al. (2015), He and Groover, chapter 10, this volume
2. Between related genera, e.g. <i>Populus</i> vs <i>Salix</i>	Differences in genomic architecture, e.g. differences in sex locus architecture between willows and poplars	Olson, Hamrick and Moore, chapter 7, this volume
3. Interspecific, e.g. <i>Populus deltoides</i> vs <i>Populus trichocarpa</i>	Speciation genomics, adaptive introgression	Bawa and Holliday, chapter 8, this volume
4. Interpopulation, e.g. northern vs southern or montane vs lowland	Environmental genomics, origin of adaptations	Fetter, Gugger and Keller, chapter 13, this volume
5. Intrapopulation	Allelic variation, balancing selection, gene flow/selection balance	Fetter, Gugger and Keller, chapter 13, this volume

morphological variety of angiosperm trees lends itself in particular to comparative approaches. Top level comparisons give answers to the central question of what aspects of biology are fundamental and which are special responses of a limited clade (evolutionary lineage). This approach has been used in an attempt to define core wood genes by comparing eucalyptus and poplar (Hefer et al. 2015) for instance.

Comparative approaches can also be used in a phylogenetic context to understand how key regulators were co-opted in the origin of novel traits. The moss versions of the key wood developmental regulators, NAC transcription factors, have been shown to have a conserved function, able to act as wood regulators in angiosperms, despite mosses having no wood. This is strong evidence that it is not the primary function of this gene that has changed to facilitate the origin of wood, but the downstream modules that it regulates (Xu et al. 2014).

Environmental and Population Genomics: Exploiting Genetic Diversity

Trees are generally highly outbreeding and every wild tree is generally a genetically unique individual. Every comparison between two or more trees can therefore be very revealing of the effect of their different genetic constitutions and environmental histories on phenotypes. Trees have a number of features that makes them particularly amenable for comparative biology at the population level. Some of these features are highlighted briefly here, and detailed in chapter 7 by Olson, Hamrick and Moore, and chapter 8 by Bawa and Holliday.

First, they tend to exist as large populations with a large ranges covering more than one climatic zone. They are therefore highly suitable for landscape genomics and studies of climatic adaptation. Secondly, they are generally highly outbreeding, with effective gene flow, minimising population structure. This contrasts with inbreeding herbs like *Arabidopsis thaliana* which exist as strongly structured populations (a mosaic of inbred lines). As population structure is a confounding factor in all studies of genotype:phenotype association and local adaptation, anything that reduces it is important. Additionally, hybridization among species is common in some tree genera (e.g. *Populus*, *Salix*, *Eucalyptus*), presenting intriguing questions about speciation and unique ecological attributes of hybrids in forested landscapes.

Genome-wide association studies (GWAS) using natural variation in populations have begun to disentangle the molecular basis of important tree traits such as large growth, perenniality and architecture (McKown et al. 2014) as well as wood structure and the chemistry (Porth et al. 2013). Adaptation to environment is one of the most important biological phenomena, on which much of our agricultural and forestry productivity is based. With an environment changing rapidly due to CO₂ climate forcing, it becomes more important than ever to understand.

Big Questions for Angiosperm Tree Genomics

It is difficult to predict the future but a number of big questions seem to be emerging at the intersection of genomics and tree biology. These include epigenetics, structural genome variation, the genomic basis of the origin of woodiness and the genomic basis of tree traits, such as architecture and sexuality.

1. **Epigenetics.** Trees are long-lived organisms that cannot move to avoid environmental stress, so they have to endure it (Bräutigam et al. 2013). To what extent does environmentally-induced epigenetic regulation contribute to survival? As many trees can be cloned, it is possible to conduct what in human biology would be called “identical twin studies”, but on a vast scale.
2. **Structural genome variation.** Angiosperm tree species display the surprising history of genome duplication and rearrangements that have occurred at various points in angiosperm evolution and lineages. Structural variation in angiosperm genomes is presented in chapter 5 by Street. As discussed in chapter 6 by Hussey, Wegrzyn and Vasquez-Gross, a closely related topic is the complex evolution of gene families in angiosperm tree lineages, including how gene families undergo selection and fractionation. Additionally, angiosperm trees exist in large populations and are known to produce, at low level, structural genome variants such as triploids (Mock et al. 2012), aneuploids (with an extra copy of a particular chromosome) and segmental variants (with translocations, inversions or duplications of parts of chromosomes). Using new genomic approaches these can now be detected within populations. What is their effect on biology, speciation and genome evolution? Discussion of these and related topics is given by Bawa and Holiday (chapter 8).
3. **Woodiness** is a globally significant trait and the molecular control of its evolution is a pressing question. It is well known that various herbaceous lineages have lost woodiness only to gain it again in some clades. These clades of recently evolved woodiness provide promising experimental systems for the investigation of the evolution of woodiness itself (Moyers and Rieseberg 2013; Davin et al. 2016). Variation in wood structure and anatomy is summarized in chapter 2 by Spicer, and a discussion of the molecular regulation of wood development is presented by He and Groover in chapter 10.
4. **Genomic basis of important traits of trees**, including comparison of these traits to similar if not homologous traits in non-tree species. For example, tree architecture is tremendously complex. At its simplest, it is evident that some trees have narrow crowns whereas others are broad and spreading. Such traits are of great importance in commercial forestry and pomology (Segura et al. 2008) but are also important in the fundamental understanding of plant development. The regulation of tree architecture is presented in chapter 9 (this volume) by Hearn. Trees are also well known for the variety of sex expression from hermaphroditism to monoecy, dioecy or a mixture (polygamy). When studied in comparative framework, tree genomics may be expected to shed much light on the molecular pathways underlying such variation (Geraldes et al. 2015; Olson, Hamrick & Moore, chapter 7, this volume; Fetter, Guggen and

Keller, chapter 13, this volume). The regulation of perennial growth is fundamental to trees, and the regulation of phase change and phenology in trees is presented in chapter 11 (this volume) by Brunner, Varkonyi-Gasic, and Jones. Trees have also evolved additional strategies to deal with abiotic stress including drought, which is discussed in chapter 12 by Bastiaanse. Trees also have a variety of interactions with other organisms, including both pathogens and insect pests, as well as beneficial symbionts. Some of these interactions are described in chapter 14 by Plett and Plett.

These examples merely touch on some of the exciting basic science that will emerge from tree genomics over the next few years, and a bright future can be anticipated. However, as already alluded to, angiosperm dominated forests and plantations are of great ecological, economic and social importance. And many of these forests are in peril. Effective comparative genomic approaches can also provide new tools for applied forest management.

Conservation of Forest Biodiversity and Forest Genetic Resources

Forests, particularly tropical wet forests, are enormously rich in biodiversity. It is difficult to draw the line between trees and shrubs, but of the 369,000 species of flowering plants (RBG Kew 2016), between 70,000 and 90,000 can be regarded as trees. These are the largest organisms in terms of biomass on the planet, reaching, in the case of forest giants like *Eucalyptus regnans*, over 100 m in height. Many ordinary trees commonly reach 30 m or more. These are huge organisms by any standards. In turn trees support a pyramid of dependent organismal diversity. Erwin found 1143 beetle species on the tropical tree *Luhea seemannii*, of which an estimated 162 were only found on that tree species (Erwin 1982).

As well as the organismal diversity there is the genetic diversity of the trees themselves, which is essential to maintaining vigorous, well-adapted tree populations. Genomic tools are hugely powerful in characterising this genetic diversity (e.g. Geraldès et al. 2014; Fetter, Gugger and Keller, chapter 13, this volume) and in relating it to adaptation and the environment, whether through phenology (Brunner, Varkonyi-Gasic and Jones, chapter 11, this volume), abiotic stress (Bastiaanse, Theroux-Rancourt and Tixier, chapter 12, this volume) or species interactions (Plett and Platt, chapter 14, this volume).

Protection of Forests against Emerging Pests, Pathogens and Environmental Stressors Including Climate Change

Trees are large, long-lived resources that cannot move, and as such they are “sitting ducks” for pathologies of various sorts. Past epidemics such as Dutch elm disease and chestnut blight have been devastating. Plantation trees of a single genotype are

particularly vulnerable during their multi-decadal lifespan. The arrival of a new pest or pathogen, which may have multiple generations per year, is a real possibility during the relatively long rotation age. Resistance breeding, as well as planting of mixed genotypes, can mitigate risk on landscape scales. Genomics can help by permitting a gene-based understanding of resistance (Plett and Plett, chapter 14), and by providing breeding tools, as in “genomic selection” (Denis and Bouvet 2011). On the other hand, we are increasingly realising the beneficial role that fungal and bacterial endophytes in roots and leaves can play in pest and pathogen resistance. Such endophytes are very difficult to characterize by traditional means but lend themselves to metagenomic approaches.

Climate change is a major threat to forests, particularly as it now appears that the pace of change may exceed the ability of adapted genotypes to migrate to new climatic optima. Assisted migration (including planting trees that are adapted not to the present climate, but to future climate) is likely to emerge as a very important, and hotly debated, issue. Again, genomics has a role to play. Chapter 12 (Bastiaanse, Theroux-Rancourt and Aude Tixier) highlights our current understanding of how trees respond to drought stress and how genomics may aid in identifying genes and genotypes conferring resistance to drought and other abiotic stress.

The Future of Angiosperm Tree Genomics

The scientific issues highlighted in this introduction, and the other chapters in this book, indicate the health and excitement of the subject. Trees have traditionally been difficult to study and genomic tools now permit a catch-up. Much work needs to be done however. Despite the enormous importance of forests and forestry, this sector has fewer resources than the health and agriculture sectors that have already been deeply impacted by genomic technology.

The biology of trees provides many important problems that are unique to, or characteristic of, trees as opposed to other plants. For instance, most tree species are highly outbred and suffer from inbreeding depression. Hybrids, on the other hand, can show significant hybrid vigour. Indeed the highest yielding plantation crop in the world is a hybrid eucalyptus (*E. grandis* × *E. urophylla*) in Brazil. One explanation for hybrid vigour may be that trees carry a large genetic load of sublethal alleles, as suggested by genetic studies (Bradshaw and Stettler 1994). Surprisingly however, recent functional genomic work in poplar showed that most of the genome can be reduced to a haploid state without lethality (Henry et al. 2015). The interplay of inbreeding depression and hybrid vigour is just one example of many opportunities for new genomic studies in angiosperm trees. The size and genetic basis of load in trees has been a big unknown but genomic techniques offer potential solutions to this important problem. This is just one example of many opportunities for new genomic studies in angiosperm trees. As the chapters in this book will show, with powerful genomic tools at hand the solution to these and other problems in tree biology are within grasp.

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Postscript While this book was in preparation, but after the manuscript of his chapter was submitted, we received the news of the tragic death of Carl Douglas in a climbing accident in the mountains of British Columbia. We have lost a great colleague and trusted friend. Carl was a true leader in the field of the genomics of angiosperm trees and will be greatly missed. We dedicate this volume as a small tribute to his memory.

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