CHICAGO JOURNALS

From Nehemiah Grew to Genomics: The Emerging Field of Evo-Devo Research for Woody Plants
Author(s): Andrew Groover and Quentin Cronk
Source: *International Journal of Plant Sciences*, Vol. 174, No. 7 (September 2013), pp. 959-963
Published by: The University of Chicago Press
Stable URL: http://www.jstor.org/stable/10.1086/671569
Accessed: 26/09/2013 19:12

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *International Journal of Plant Sciences.*

http://www.jstor.org

This content downloaded from 170.144.6.61 on Thu, 26 Sep 2013 19:12:57 PM
All use subject to JSTOR Terms and Conditions

Int. J. Plant Sci. 174(7):959–963. 2013.
© 2013 by The University of Chicago. All rights reserved.
1058-5893/2013/17407-0001$15.00 DOI: 10.1086/671569

FROM NEHEMIAH GREW TO GENOMICS: THE EMERGING FIELD OF EVO-DEVO RESEARCH FOR WOODY PLANTS

Andrew Groover[1,*] and Quentin Cronk†

*USDA Forest Service Pacific Southwest Research Station and Department of Plant Biology, University of California, Davis, California 95618, USA; and †Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

Wood has played a primary role in the evolution of land plants (Spicer and Groover 2010), but our understanding of the genes and mechanisms underlying wood evolution and development has been limited until recently. Importantly, many of the fundamental questions of woody plant evolution and development are now tractable using genomics and high-capacity sequencing technologies. A major challenge is to integrate the knowledge from traditional disciplines of woody plant research (e.g., anatomy, paleobotany, physiology, and developmental biology) with genomics and sequencing-based technologies. A synthetic field of research integrating these disciplines would be well positioned to make major advances in the basic biology of plants and to address applied goals such as providing optimal biofuels feedstocks or informing conservation strategies for forests in the face of climate change. This special issue of the *International Journal of Plant Sciences* highlights some of the research opportunities, including examples of fascinating evolutionary and developmental processes associated with woody plants and new genomics-based approaches for understanding them. Interestingly, many of the outstanding questions about the evolution and development of woody plants date to the beginnings of plant science.

The Investigation of Wood: A Long and Continuing History

The first study of woody growth could be attributed to Theophrastus (a student of Aristotle), who classified plants in part on the basis of their degree of woodiness. This was a reasonable approach in early Hellenistic Greece and one that holds practical sway in modern times. The modern study of wood can be said to date from the seventeenth century and the developments in microscopy made by Robert Hooke (1635–1703) and Antonie van Leeuwenhoek (1632–1723). Although Hooke is now most famous for Hooke's law in physics, he was an adept microscopist. Hooke (1665) famously compared fossil and modern wood in his work *Micrographia* ("Observ. XVII. Of Petrify'd wood, and other Petrify'd bodies"). Hooke (1665, p. 107) realized that petrified wood was formed from mineralization of the walls of the "cells" (a Hooke coinage) of the wood. Hooke (1665, p. 97) also realized that the "pores" in wood were for transporting fluids (in his words "conveyance of appropriated juyces to particular parts") and looked in vain for anatomical structures that would control the direction of flow, analogous to the valves of the heart. Although Leeuwenhoek published little on plant anatomy, being known mainly as the founder of microbiology (with his studies of "animalcules"), he made numerous observations of wood structure in correspondence with the Royal Society (Baas 1982, 2005).

Work on plant anatomy was taken much further by two other savants of the period, Nehemiah Grew (1641–1712) and Marcello Malpighi (1628–1694), who both wrote influential treatises on the subject, which included detailed studies of the anatomy of various woods (Grew 1672, 1682; Malpighi 1675, 1679). Grew (1682) was astounded by the elaborate microscopic structure of the plant stem. As he put it, "One who walks about with the meanest stick, holds a piece of nature's handicraft which far surpasses the most elaborate woof or needle-work in the world" (Grew 1682, p. ii).

Interest in the evolution of wood began with Charles Darwin (1809–1882). Darwin, from his voyage on HMS *Beagle* and the writings of contemporaries, was fully aware of the phenomenon of island woodiness. He writes:

> Again, islands often possess trees or bushes belonging to orders which elsewhere include only herbaceous species ... an herbaceous plant, though it would have no chance of successfully competing in stature with a fully developed tree, when established on an island and having to compete with herbaceous plants alone, might readily gain an advantage by growing taller and taller and overtopping the other plants. If so, natural selection would often tend to add to the stature of herbaceous plants when growing on an island, to whatever order they belonged, and thus convert them first into bushes and ultimately into trees. (Darwin 1859, p. 172)

This phenomenon of insular woodiness (Lens et al. 2013) provides a "natural experiment" of great interest—and one that has the potential to be studied using the tools of genomics.

In the twentieth century, special mention should be made of the work of Irving W. Bailey (1884–1967), who was appointed professor of wood anatomy in Harvard's Bussey Institution in 1927 (Wetmore et al. 1974). Bailey and his coworkers not only characterized patterns of wood anatomy with great rigor and breadth but also began to put these patterns in an explicitly evolutionary context. Another towering figure of the past century in the field of vascular anatomy and development was Katherine Esau (1898–1997). Esau is well known for her textbooks of plant anatomy, and she is influential in taking a developmental approach to vascular anatomy.

This brief and partial history illustrates that the study of woody tissues has an extraordinary depth of resources, partly as a consequence of its long history. As work on the evolution and development of woody tissues continues, it is already clear that the combination of wood anatomy, paleobotany, physi-

* Author for correspondence; e-mail: agroover@fs.fed.us.

This content downloaded from 170.144.6.61 on Thu, 26 Sep 2013 19:12:57 PM
All use subject to JSTOR Terms and Conditions

ology, molecular biology, and genomics could support a new age of discovery exploring the origin of wood and its evolutionary diversification.

The Woody Lifestyle

Woody plants can be defined as those that have a mechanism for secondary growth of the stem or root by which tissue is produced radially, in contrast to the elongation phase of primary growth. In the seed plants, this is usually achieved by the presence of a single bifacial lateral meristem, the vascular cambium (Larson 1994). The cambium produces cells that are incorporated into the secondary xylem, or wood, to the inside of the stem. To the outside, this same meristem produces cells that become the inner bark. There is a great deal of variation among species and in response to environmental conditions in wood anatomy, and wood anatomy has been an area of intense study from the earliest days of plant biology, as previously mentioned.

When, why, and how did the innovation of wood evolve, and what are the relationships among woody taxa? Trees have evolved independently in two lineages, the euphyllophyte clade, which contains the seed plants, and the lycophyte clade, which produced the arboreous fossil lycopsids, a key component of the Carboniferous coal swamps. Although functionally equivalent to euphyllophyte trees, tree lycopsids have a number of important differences in trunk anatomy (Green 2010), the most obvious being that the cambium is unifacial only. No arboreous lycopsids are now extant, but their closest living relative, the wetland plant genus *Isoetes*, does have the capacity for some secondary growth. In the euphyllophyte clade, the tree habit predates seed plants, with the first "modern tree" being the progymnosperm *Archaeopteris* (Meyer-Berthaud et al. 1999).

Water transport is key to understanding the evolution of wood, as illustrated by diminutive plants of the early Devonian presenting the first known appearance of wood (Gerrienne et al. 2011). While these plants had little advantage in height over herbaceous neighbors, they possessed greater water conductance that may have been of especial importance as dropping CO_2 levels in the Early Devonian led to increased gas exchange and water loss to transportation. Indeed, radial production of wood underlies myriad adaptive traits, and wood has supported an explosion of body plans such as trees with towering height unparalleled in the competition for light (e.g., the tallest plants, coast redwood, *Sequoia sempervirens*) and persistent woody bodies capable of producing gametes over hundreds or even thousands of years (e.g., individual bristlecone pine, *Pinus longaeva*, can grow for nearly 5000 years). For seed plants, woody habit was likely the ancestral state (although this is not fully resolved; discussed in Spicer and Groover 2010).

The strategies afforded by woody growth are believed to be a major factor in the founding and diversification of the angiosperms, which show numerous transitions between woody and herbaceous extremes in various taxa (Carlquist 2013). While monocots have lost the ability to produce typical wood from a single vascular cambium, there are arboreous monocots such as palms (Arecaceae) that produce large stems from primary thickening meristems at the growing apex of the plant, which in some cases is supplemented by a "monocot cambium" that can produce new vascular bundles radially (Carlquist 2012). Other woody plants, such as the gnetalean gymnosperm *Welwitschia* (Carlquist and Gowans 1995) and many angiosperms (Carlquist 2007; Pace and Angyalossy 2013), produce a succession of cambia. Curiously, all extant gymnosperms are woody (some *Ephedra* species come closest to being exceptions), which raises the question of what developmental or evolutionary restraints in gymnosperms have curtailed the emergence of herbaceous forms (or, conversely, what angiosperm developmental characteristics have facilitated the emergence of herbaceous forms).

The ecological importance and evolutionary significance of the woody habit is underscored by the fact that although it is frequently lost, it is also frequently regained, as is seen conspicuously on oceanic islands. In angiosperms there are numerous herbaceous lineages with little or no capacity for secondary growth, but in many cases these lineages contain secondarily woody members (Lens et al. 2013). Further evidence of the importance of the tree habit comes from the convergent attainment of a treelike form by means other than secondary growth, such as the massive primary stems of bamboo (Poaceae) and the false stem (made up of overlapping leaf petioles) in banana (*Musa*).

Major Questions in the Evolution of Woodiness

We list here but a few examples of outstanding questions regarding the evolution and development of woody plants. While previously largely intractable, each of these examples is now readily available to exploration using sequencing and genomics-based approaches.

The earliest land plants were not woody, and subsequent to the colonization of the land by plants, there has been a progressive elaboration of woody tissue associated with greater stature as seen (and well documented thanks to the favorable preservation of lignified woody tissues) in the fossil record. This has involved innovations at various levels: biochemical, anatomical (new cell types), and developmental. Our understanding of the molecular basis of these changes is still sketchy. However, it is clear that genes of the lignin biosynthesis (phenylpropanoid) pathway and the NAC genes (key developmental regulators) underlie some of these building blocks of xylogenesis in land plants. Increased knowledge of the function of these genes in mosses, liverworts, hornworts, and lycophytes will be especially important in understanding how these building blocks have been put together. Another important question is how changes in regulation of these building blocks allowed the evolution of massively woody plants (trees). The existence of whole-genome resources for several trees (the first being *Populus*) is accelerating our understanding of this by enabling comparisons with herbaceous models such as *Arabidopsis*.

Trees evolved independently in lycophytes, and an important question is whether the mechanisms used are the same or different at the molecular level. Although all tree lycophytes are extinct, analysis of the molecular basis of secondary growth of their closest relative, the herbaceous *Isoetes*, would be instructive. In this context a whole genome of *Isoetes* would be a particularly valuable resource, although unfortunately some

This content downloaded from 170.144.6.61 on Thu, 26 Sep 2013 19:12:57 PM
All use subject to JSTOR Terms and Conditions

species of *Isoetes* have a dauntingly large genome size (Hanson and Leitch 2002).

In many flowering plant lineages, the woody habit appears to have been lost with the evolution of herbaceousness, a derived condition. An interesting question is which genes have been lost or downregulated to reduce the amount of woody tissue produced in herbaceous groups and the relationship of perenniality to woodiness. Large groups such as the legumes, in which herbaceousness has evolved repeatedly, potentially provide excellent study systems for this question. Related to this are questions concerning the origin of secondary woodiness. Is this a de novo reinvention or a reactivation of preexisting pathways? The ease at which woodiness seems to be reacquired (e.g., on islands) points to a simple reactivation of retained functions. However, this begs the question of why these genes should be retained in herbaceous lineages and what pleiotropic functions might assure their retention.

Finally, there is a huge diversity of patterns of wood anatomy that has been well documented. Understanding the function and interactions among each of the thousands of genes expressed during secondary growth would provide insights into the production of wood in individual species, e.g., through use of network biology approaches. Knowledge of regulatory networks could also be used to make comparisons among regulation of woody growth across taxa with divergent wood anatomical features, and it is an intriguing thought that one day (hopefully soon) we will understand the changes in gene content, sequence, and regulation that underlie such diversity. The wood anatomy that fascinated Nehemiah Grew can then be taken fully into the genomic age.

The Special Issue

A surprising feature of angiosperm evolution is the extreme plasticity of woody growth during speciation. In this issue, Sherwin Carlquist (2013) presents a fascinating treatise that draws from a long career of wood research and his famous ability to synthesize observations from anatomy, evolution, phylogenetics, physiology, and the effects of environmental cues on wood development. Indeed, the evolution of wood goes hand in glove with that of the angiosperms, playing an important role in both the origins and diversification of the overwhelming numbers of species. Practically all angiosperms, with the exception of monocots, can undergo at least some modest amount of secondary growth that may be restricted to vascular bundles. Carlquist posits that early angiosperms were defined by limited woody growth, with increased woodiness and growth forms such as trees produced in various clades. Woodiness has been greatly reduced or lost in some species derived from woody ancestral species. Perhaps more surprising is the frequency with which the woody habit is regained in lineages derived from largely herbaceous species, a feature famously noted by Darwin as being common to oceanic islands. The subject of so-called insular woodiness is also taken up by Lens et al. (2013), who focus on flora of the Canary Islands. These islands contain at least 220 insular woody species from 34 genera. While the evolutionary forces behind insular woodiness remain uncertain, Lens et al. propose that drought resistance could be a factor.

Many other examples of the extreme plasticity of woody growth can be cited, including the dramatic anatomical features found in the tropical species of the Bignoniaceae. This family contains trees, shrubs, and lianas and is incredibly diverse anatomically. Strikingly, so-called cambial variants in lianas of this family display dramatic xylem furrowed with phloem wedges as a result of disproportionate contributions of cambial daughter cell to secondary phloem versus xylem. Pace and Angyalossy (2013) used the diversity of woody growth and anatomy in this family to ask questions about how wood anatomy reflects ecophysiology and growth habit. Molecular phylogenies for the family were overlaid with information about wood anatomy, growth habit, and ecological features to define trends in anatomical changes. In another example, succulent growth forms include woody species that can form extensive ray or axial parenchyma derived from the vascular cambium, such as in baobab trees. Hearn and colleagues (2013) used sophisticated phylogenetic analyses to determine that above- and belowground succulent growth are evolutionarily correlated and that evolutionary origins of succulence do not necessarily lead to increases in species diversity.

Olson et al. (2013) seek to understand broadscale patterns in xylem structure. Specifically, these authors focused on the observation that plant size tends to be positively correlated with the diameter of vessel elements. Vessel diameter has also long been assumed to be reflective of adaptation to specific environments; e.g., vessel diameters tend to be narrower in plants adapted to dry climates. Additionally, one might suspect that phylogenetic relatedness would be a factor in predicting vessel diameter. These researchers assembled an extensive data set including stem dimensions and wood anatomical features from five clades of angiosperms distributed across Africa, Asia, Madagascar, and the Americas. A major conclusion from their analysis is that neither climate nor phylogeny provides significant predictive power to the relationship between vessel element diameter and stem diameter. These results suggest caution in interpretation of vessel diameter as reflecting adaptation to specific environments.

As well as great variation in patterns of wood anatomy, there is considerable variation in patterns of woodiness in angiosperms. The Asteraceae is a family in which trees are rare, most members being herbs or shrubs with limited, if any, secondary growth. However, this family has repeatedly undergone evolutionary transitions to increased woodiness, especially on islands. Examples are *Dendrosonchus* of the Canary Islands (see Lens et al. 2013) and the Hawaiian silversword group. With the increasing practicability of genomics approaches, such systems are increasingly attractive for such approaches. Moyers and Rieseberg (2013) describe a transcriptomic approach to understanding differences in gene regulation between the herbaceous common sunflower and a woody derivative, clearly demonstrating how new genomic tools can be brought to unanswered but fundamental questions of plant biology dating to Darwin.

An increasingly tractable challenge is to comprehensively model the regulation of wood formation at the molecular genetic level. Ultimately, models of regulatory networks could provide test beds for hypothesis generation and testing that could focus research efforts and maximize outcomes. Network models present a more realistic view of the interactions among hundreds or even thousands of genes that underlie complex

This content downloaded from 170.144.6.61 on Thu, 26 Sep 2013 19:12:57 PM
All use subject to JSTOR Terms and Conditions

wood trait phenotypes than any other current approach. Ultimately, network models could also be used as tools in other areas of genomics, e.g., providing a framework for describing the relationships among genes underlying quantitative trait loci for complex traits including wood anatomy and wood chemistry. The evolution of regulatory networks could ultimately be used to precisely define the changes associated with evolution of species with diverse wood traits. El-Showk and colleagues (2013) describe the status of modeling gene regulatory networks regulating vascular development during primary growth in roots. While the root network models draw heavily on results from classical developmental genetics in *Arabidopsis*, there is a dramatic shift in the data types used for modeling networks toward genomic data types that can be captured for wood-forming tissues from virtually any species (e.g., mRNA-seq). As this trend accelerates with more powerful and creative sequencing technologies, it seems likely that there will be a shift of focus from examining the function of one or a few genes across species to comprehensive surveys of all genes expressed in woody tissues and/or analysis of network models across phylogenetic frameworks.

The Future

As nucleic acid sequencing becomes cheaper and more powerful, it seems likely that there will be a paradigm shift from one-species-at-a-time to comparative approaches. Such comparative approaches could serve as an organizing center to draw information, interest, and expertise from the many disciplines associated with the study of wood and woody growth. A critical mass of sequence data is quickly accumulating that will also allow researchers to develop and test initial hypotheses at the computer, before testing them experimentally. Excitingly, genomic sequence is quickly extending to many woody plant species and taxa; e.g., the sequencing of conifer genomes is under way, and significant expressed gene sequence is already available for many conifers. Such resources make questions such as homology relationships between cambia in angiosperms and gymnosperms tractable at the molecular genetic level. As evo-devo and comparative genomics approaches bring together historically disparate fields in collaboration, we may hope to soon see publications that synthesize the inputs of fields such as paleobotany, wood anatomy, genomics, and systems biology into unified views of the evolution and development of woody plants.

Forests occupy more than 4 billion hectares, or about 30% the earth's total land area. Forest trees and other woody plants underpin ecosystems, provide ecosystem services such as clean water, are the basis of forest industry, provide fuelwood for developing countries and biofuels, and play a fundamental role in carbon cycling and sequestration. In addition to the fascinating questions of basic plant biology presented by woody plants, these practical contributions of woody plants to economies and ecosystems in themselves provide compelling justification for woody plant research. We hope that in the near future a next generation of genomics-assisted woody plant evolution and development research will provide both insights into basic questions of plant biology and new solutions to problems of environmental and economic importance.

Acknowledgments

We would like to thank the authors who contributed to this special issue; the many excellent reviewers; and James Ellis, Pat Herendeen, and the editorial staff of *IJPS*. This special issue was inspired by the National Evolutionary Synthesis Center–funded meeting, "Evolutionary Origins and Development of Woody Plants," October 2011. Funding for research in the laboratory of A. Groover is provided by USDA AFRI, US Department of Energy Office of Science (BER), and the US Forest Service. Funding for research in Q. Cronk's laboratory is provided by the National Science and Engineering Research Council, Canada (NSERC), and Genome Canada.

Literature Cited

Baas P 1982 Antoni van Leeuwenhoek and his observation on the structure of the woody cell wall. IAWA Bull, NS, 3:3–5.

——— 2005 Leeuwenhoek's observations on the anatomy of bark. Holzforschung 55:123–127.

Carlquist S 2007 Successive cambia revisited: ontogeny, histology, diversity, and functional significance. J Torrey Bot Soc 134:301–332.

——— 2012 Monocot xylem revisited: new information, new paradigms. Bot Rev 78:87–153.

——— 2013 More woodiness/less woodiness: evolutionary avenues, ontogenetic mechanisms. Int J Plant Sci 174:964–991.

Carlquist S, DA Gowans 1995 Secondary growth and wood histology of *Welwitschia*. Bot J Linn Soc 118:107–121.

Darwin C 1859 On the origin of species. 1st ed. J Murray, London.

El-Showk S, M Taylor-Teeples, Y Helariutta, SM Brady 2013 Gene regulatory networks during *Arabidopsis* root vascular development. Int J Plant Sci 174:1090-1097.

Gerrienne P, PG Gensel, C Strullu-Derrien, H Lardeux, P Steemans, C Prestianni 2011 A simple type of wood in two Early Devonian plants. Science 333:837.

Green WA 2010 The function of the aerenchyma in arborescent lycopsids: evidence of an unfamiliar metabolic strategy. Proc R Soc B 277:2257–2267.

Grew N 1672 The anatomy of vegetables begun. Royal Society, London.

——— 1682 The anatomy of plants. Royal Society, London.

Hanson L, IJ Leitch 2002 DNA amounts for five pteridophyte species fill phylogenetic gaps in C-value data. Bot J Linn Soc 140:169–173.

Hearn DJ, T Poulsen, R Spicer 2013 The evolution of growth forms with expanded root and shoot parenchymatous storage is correlated across the eudicots. Int J Plant Sci 174:1049–1061.

Hooke R 1665 Micrographia. Royal Society, London.

Larson PR 1994 The vascular cambium. Springer, Berlin.

Lens F, N Davin, E Smets, M del Arco 2013 Insular woodiness on the Canary Islands: a remarkable case of convergent evolution. Int J Plant Sci 174:992–1013.

Malpighi M 1675 Anatomia plantarum. Vol 1. Royal Society, London.

——— 1679 Anatomia plantarum. Vol 2. Royal Society, London.

Meyer-Berthaud B, SE Scheckler, J Wendt 1999 *Archaeopteris* is the earliest known modern tree. Nature 398:700–701.

Moyers BT, LH Rieseberg 2013 Divergence in gene expression is uncoupled from divergence in coding sequence in a secondarily woody sunflower. Int J Plant Sci 174:1079–1089.

Olson ME, JA Rosell, C León, S Zamora, A Weeks, LO Alvarado-

This content downloaded from 170.144.6.61 on Thu, 26 Sep 2013 19:12:57 PM
All use subject to JSTOR Terms and Conditions

Cárdenas, NI Cacho, J Grant 2013 Convergent vessel diameter–stem diameter scaling across five clades of New and Old World eudicots from desert to rain forest. Int J Plant Sci 174:1062–1078.
Pace MR, V Angyalossy 2013 Wood anatomy and evolution: a case study in the Bignoniaceae. Int J Plant Sci 174:1014–1048.
Spicer R, A Groover 2010 The evolution of development of the vascular cambium and secondary growth. New Phytol 186:577–592.
Wetmore RH, ES Barghoorn, WL Stern 1974 The Harvard University Wood Collection in the rejuvenation of systematic wood anatomy. Taxon 23:739–745.

This content downloaded from 170.144.6.61 on Thu, 26 Sep 2013 19:12:57 PM
All use subject to JSTOR Terms and Conditions