

Editorial

An introduction to a Virtual Issue on Wood Biology

This Virtual Issue ‘The biology of wood’, highlights the central role of wood biology in basic plant science, as well as critical ecological, environmental, economic and societal issues. Wood, or secondary xylem, is produced by the vascular cambium and plays myriad interacting roles in plant development, physiology and biochemistry. Wood is not simply the terminal product of secondary cell wall development in specialized cells, but is the tissue which enables water conduction and provides structural support for the production of complex plant bodies including massive forest trees. Additionally, woody tissues participate in specialized biochemistry, and store and mobilize nutrients and carbohydrates, in addition to the water vital to survival. Recent research on wood biology has been driven, in part, by the economic value of wood for forest industries and, more recently, bioenergy applications. However, the increasing pressure on forests by anthropogenic climate change and its related episodic heat and drought is driving a need to understand how water transport in tree stems relates to water stress.

The papers in this collection are associated with a *New Phytologist* symposium ‘The biology of wood: from cell to trees’ that was held in Lake Tahoe, California, in July 2018 (42nd New Phytologist Symposium <https://www.newphytologist.org/symposia/42>). The symposium stressed a need for integrative research that addresses how development, cell differentiation, genetics, physiology, and evolution intersect and contribute to the requirements of a comprehensive understanding of wood biology (Mizrachi, 2019). A fascinating aspect of wood biology is the dynamic interplay among environmental cues, development, and physiology. For example, wood development is highly responsive to environmental conditions – as illustrated in angiosperm trees that modify wood development in response to water stress – to create newly formed wood that is more resistant to water stress-induced cavitation and mortality (Rodriguez-Zaccaro & Groover, 2019). Elucidating how environmental signals are perceived and translated into changes in development, and how these changes in development interplay with system-level tree physiology, are current examples of critical research areas that require cross-disciplinary approaches which have historically been underrepresented in this field.

As outlined below, the papers within this collection illustrate the growing integration of wood biology research across disciplines, and highlight opportunities for new research that will undoubtedly provide new insights and applications for practical issues including forest utilization and responses to climate change, as well as basic insights into the evolution, development, and physiology of forest trees.

Biochemistry and metabolism of wood

The coordination of carbon metabolism between the nuclear, plastid and mitochondrial genomes was examined using a gene co-expression approach (Pinard *et al.*, 2019). It seems as though the plastid and mitochondrial carbon metabolism pathway genes show a coordinated expression with their nuclear gene counterparts, and with specific stages of wood development. Unexpected findings in this study included evidence for a potential role of epigenetic modifications in regulating and coordinating carbon metabolism-associated genes.

Lignin has seen much research activity, both for the fundamental role that it plays in secondary cell walls, but also because lignin is a major determinant of the properties of wood and influences its use in pulp, lumber and biofuel applications. The genes encoding cinnamyl alcohol dehydrogenase (CAD) and cinnamoyl-CoA reductase (CCR) belong to large gene families in poplar, and are vital to monolignol production for secondary cell wall lignification. Yan *et al.* (2019) used a combination of genetic modifications, protein interaction assays and biochemical assays to provide evidence for direct physical interactions between poplar PtrCAD1 and PtrCCR2 as a protein complex during monolignol biosynthesis. The consequences of such a complex for the sequential processing of enzymes include their potential effects on the fundamental properties of kinetic behaviour and/or substrate specificity.

Structure and function of wood

Wood, as mentioned, is an amalgam of dead and living cells. It is well established that wood transports water and associated solutes long distances through tissues comprised largely of vessels or tracheids. However, what remains poorly understood is how solutes – including macromolecules such as proteins – can move from the apoplastic compartment of dead vessels into the symplastic compartment of neighbouring, living cells. Ślupianek *et al.* (2019) showed that endocytosis is an active process required for the transport of macromolecules from vessels into neighboring ‘vessel-associated cells’. Their results help to provide a comprehensive picture of transport within wood, including not only the movement of water, but also the long distance transport of macromolecules axially through the tree, followed by the uptake and radial transport of cargo within the living parenchyma of wood. This study opens interesting possibilities for new research into the movement of potential signalling molecules, as well as nutritive cargo throughout the tree.

A specific example of a xylem transmission of signalling peptides is reported by Endo *et al.* (2019), who showed that CLE peptides are regulators of plant development and are present in xylem sap. The uptake and transport of fluorescent tracer dyes and fluorescently-labelled CLE peptides in *Arabidopsis* demonstrated that transport

appears to be a regulated and cargo-dependent process that is influenced by changes in xylem cell wall properties (Endo *et al.*, 2019). Taken together, these studies showcase a fascinating new area of research which examines the transport of long-distance signals in wood, that could have important ramifications for our study of the coordinating development, physiology, and responses to environmental cues in large woody plants, including trees.

Genetic and hormonal regulation of wood formation

Transcription is a key point of regulation for wood formation, including the regulation of cell differentiation. Two papers describing the functions of individual transcription factors during wood formation are included in this Virtual Issue. Class I KNOX transcription factors are evolutionarily ancient, and have been co-opted to regulate cell differentiation during secondary growth and wood formation. The functional characterization of a poplar Class I KNOX gene, *KNAT2/6b*, concluded that this gene is important for the regulation of cell differentiation, in part through its influence on the expression of NAC transcription factors (Zhao *et al.*, 2020, in this issue of *New Phytologist*, pp. 1531–1543). A poplar gene encoding a poplar AP2/ERF class transcription factor, ERF139, was shown to affect multiple aspects of wood formation, including the radial expansion and dimensions of water-conducting vessel elements, as well as positively influencing the deposition of the secondary cell wall chemical constituents of lignin and xylan (Wessels *et al.*, 2019).

Hormones have long been implicated in secondary growth and wood formation. The hormone abscisic acid (ABA) appears to be a primary signal for water stress during drought, and promotes complex changes in physiology and development, including changes to wood development where it promotes the formation of wood with anatomical features similar to that observed during water stress. Multiple transgenic poplar lines that displayed an altered ABA regulatory genes transcript abundance were created and assayed under drought conditions; they effected complex changes to leaf area, biomass production, and stomatal conductance (Yu *et al.*, 2019). The role of brassinosteroids on wood formation was previously uncertain, but initial results have indicated that these hormones are active during secondary growth and, overall, act to promote cell differentiation (Du *et al.*, 2020, in this issue of *New Phytologist*, pp. 1516–1530).

Integrative and systems views of wood biology

A fast-moving area of research seeks to use genomic and computational tools to provide integrated and comprehensive views of wood development, as well as a predictive atlas for refining breeding and selection operations. A genome-wide assessment of open chromatin associated with active gene transcription was assayed for Eucalyptus wood-forming tissues (Brown *et al.*, 2019). These observations were refined by the use of DAP-seq to identify the binding sites of specific MYB transcription factors associated with wood formation. Integration of these data showed an enrichment of specific epigenetic markers with genes expressed

during wood formation, and together represent an important advancement in our global understanding of gene regulation during wood formation.

Wood development is altered in response to environmental cues, including drought. Ployet and colleagues manipulated potassium and water availability in Eucalyptus plantations: potassium depletion and water stress both negatively impacted cell expansion during wood formation. Data were integrated in a gene co-expression framework from metabolome wood traits in order to understand the complex outcomes of these treatments on development (Ployet *et al.*, 2019). Interesting findings from this study included the identification of co-expressed genes associated with the trade-off between stress response and growth.

Again in Eucalyptus, a systems genetics analysis revealed a coordination of metabolic pathways associated with xylan modification in wood forming tissues (Wierzbicki *et al.*, 2019). Using expression quantitative trait locus (eQTL) mapping, the study identified potential regulatory polymorphisms affecting gene expression modules (14 putative genes) associated with xylan synthesis and modification. This work provides new avenues and/or strategies for targeted breeding or genetic engineering to alter secondary cell wall traits for improved industrial utility and processability.

Evolution of wood

How woody growth evolved is an historic and ever-evolving topic in itself. Our ever-expanding knowledge regarding the molecular and genetic basis of wood growth makes it clear that many developmental processes can be cast in terms of the recycling and repurposing of genes and mechanisms. Tomescu & Groover (2019) drew on information from living seed plants, living seed-free plants, and fossils to explore the idea of developmental modules being recruited and modified to produce the extensive variations in secondary growth seen during land plant evolution.

Summary

We hope that this Virtual Issue will stimulate further attention and support for integrative wood biology research. The relevance of wood biology to subjects of increasing importance, including climate change effects on forests, combined with the fascinating interconnections of development, physiology and evolution make this a rich subject for future endeavours.

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