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Review

The *Arabidopsis* wood model—the case for the inflorescence stem

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ABSTRACT

Arabidopsis thaliana has successfully served as a model to discover genes and proteins that have roles in a wide range of plant traits, including wood-related traits, such as lignin, cellulose and hemicellulose biosynthesis, secondary growth regulation, and secondary cell wall synthesis. Both the radially thickened hypocotyl and the inflorescence stem (flower stalk) have been studied. In this review, we address lingering doubts regarding the utility of *Arabidopsis* as a model for wood development by highlighting studies that provide new biochemical and biophysical evidence that extend support for the *Arabidopsis* inflorescence stem as a model for wood development beyond what is currently thought.

We describe different aspects of *Arabidopsis* that make it a highly versatile tool for the study of wood development. One would likely utilise the radially thickened hypocotyl because of its more fully developed vascular cambium for traits related specifically to secondary (i.e. cambial) growth. It is more productive to utilise the inflorescence stem for wood-like biophysical traits. Accession variation has been underexploited as a powerful method to discover genes governing wood-like traits. We discuss recent findings that survey the accession variation in *Arabidopsis* for biochemical and biophysical properties of various wood traits, such as microfibril angle, tensile strength and cellulose/hemicellulose content. Furthermore we discuss how larger-scale studies of this nature using plants grown in long days (as opposed to the current short-day paradigm) could accelerate gene discovery and our understanding of cell wall and wood development. We highlight some relatively unexplored areas of research relating to the secondary cell wall composition, architecture and biophysical properties of the inflorescence stem, and how these traits are relevant to wood formation. The *Arabidopsis* inflorescence stem has other characteristics, expressed genes and traits held in common with woody species that have not been widely characterised or discussed to date. We discuss how this conservation may indicate the more general potential for "true" woodiness in herbaceous species, in the context of so-called secondary woodiness.

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1. Does the concept of the *Arabidopsis* "wood model" have merit?

In our admittedly anecdotal experience, the use of *Arabidopsis thaliana* as a model for wood development has been questioned, at times quite strongly over the years, despite its extensive use for this purpose by laboratories all over the world. *Arabidopsis* is a small rosette plant, perhaps as far from a tree in stature and architecture as an angiosperm plant can be. Nonetheless, it is clear that wild-type accessions (ecotypes) of this species are capable of making some form of wood [1,2, see photo therein].

Arabidopsis gained favour as a model for wood development with the demonstration of a classical vascular cambium in radially thickening hypocotyls/rosette compressed stems grown in short-day environmental conditions [3]. The *Arabidopsis* in vitro tracheary element system has proven to be an excellent tool for elucidating the molecular mechanisms involved in secondary cell wall synthesis and the role(s) of microtubules in vascular patterning [4]. The *Arabidopsis* root has also played a pivotal role in our understanding of vascular development, particularly with regard to the role of cytokinin in this process [5,6]. Such contributions of the root model continue, with the finding that the CLAVATA3/ENDOSPERM SURROUNDING REGION-45 (CLE45) peptide [7] appears to be the ligand for the BARELY ANY MERISTEM-3 (BAM3) receptor, with a role in primary protophloem differentiation [8]. Comparative genomic data suggest that the *Arabidopsis*, *Eucalyptus* and *Populus* xylem-related gene sets appear to be about equally similar to one another [9], with significant similarity to pine [9,10], suggesting that xylem transcriptional networks are conserved across these species. Furthermore, it is clear that genes that regulate wood and wood-like characteristics appear to be functionally conserved, at least between woody angiosperm species and *Arabidopsis* [11–14], with concomitant microsynteny in at least one case [13]. There are also expected developmental differences in *Arabidopsis* relative to woody species, such as asynchronous cell division among adjacent files in the vascular cambium, atypical of woody species [15]. However, the discovery of wood formation in the *Arabidopsis soc1/ful* double mutant [16] revealed the innate potential for wood formation in this species via allelic variation. Additionally, lignin, which makes up about 30% of typical secondary cell walls of wood, is present in *Arabidopsis* and its synthesis and deposition has been comprehensively studied using *Arabidopsis* as a model with excellent inroads made into identifying key genes and transporters. These insights bear close relevance to lignin in trees [17–19]. Thus, we think that the answer to the question: "Does the concept of the *Arabidopsis* wood model have merit?" is "yes".

The purpose of this review is to examine strengths and weaknesses of the more recent (and more or less ad hoc) extension of the radially thickened hypocotyl model to the use of the inflorescence stem (flower stalk). We discuss findings that provide a stronger biochemical/biophysical justification for its use as well as the potential for more rapid progress via the power of short rotation growth in studies of accession variation.

2. The *Arabidopsis* radially thickened hypocotyl and inflorescence stem have different utilities for the study of wood-like traits

2.1. The radially thickened hypocotyl model and its use for analysing secondary growth

Arabidopsis has served successfully as a model to discover genes and proteins that have roles in a wide range of plant traits. These include wood-related traits, such as cellulose and hemicellulose biosynthesis, secondary growth regulation and secondary cell wall synthesis. The hypocotyl is perhaps the *Arabidopsis* organ of choice as a secondary growth/wood trait model due to its established capacity for secondary growth that initiates shortly after germination under the right growth conditions, particularly in short-day (i.e., 8 h light) photoperiods [3,20]. Many genes, particularly transcription factors, have been identified as having roles in secondary growth and the development of other aspects of wood-like characteristics using this model (see [4,20,21] for reviews).

2.2. The secondary growth and cell wall thickening of the inflorescence stem

A critical biophysical shortcoming of the radially thickened hypocotyl as a wood model system is the fact that, unlike the inflorescence stem, the hypocotyl is by and large not load-bearing. In contrast, like a tree trunk, the inflorescence stem is a load-bearing organ. Regardless, a perceived limitation of the *Arabidopsis* inflorescence stem as a 'true' model for wood formation is that it undergoes only limited secondary growth in the classical sense of a tree-like vascular cambium (Fig. 1). This perception has spurred several lines of research to create more "wood-like" phenotypes/models in *Arabidopsis* (discussed in [22]). Ironically, non-woody *Arabidopsis* lines may have been inadvertently bred through an unconscious selection over the decades away from wild-type secondary growth [23]. Nevertheless, several microarray studies have used the *Arabidopsis* inflorescence stem to identify genes and networks that are involved in activation of secondary cell wall development and cellulose synthesis [24–26]. Despite the lack of a well-defined vascular cambium in the inflorescence stem, parallels continue to arise between the inflorescence stem vascular cambium and those of woody plants. These are evinced by similar expression patterns of and cross-complementation by the *SHORT ROOT* (*SHR*) transcription factor gene in *Arabidopsis* and poplar [27].