Vascular Cambium: The Source of Wood Formation

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Wood is the most abundant biomass produced by land plants and is mainly used for timber, pulping, and paper making. Wood (secondary xylem) is derived from vascular cambium, and its formation encompasses a series of developmental processes. Extensive studies in Arabidopsis and trees demonstrate that the initiation of vascular stem cells and the proliferation and differentiation of the cambial derivative cells require a coordination of multiple signals, including hormones and peptides. In this mini review, we described the recent discoveries on the regulation of the three developmental processes by several signals, such as auxin, cytokinins, brassinosteroids, gibberellins, ethylene, TDIF peptide, and their cross talk in Arabidopsis and Populus. There exists a similar but more complex regulatory network orchestrating vascular cambium development in Populus than that in Arabidopsis. We end up with a look at the future research prospects of vascular cambium in perennial woody plants, including interfascicular cambium development and vascular stem cell regulation.

Keywords: wood, vascular cambium, hormones and peptides, cross talk regulation, Arabidopsis and Populus

INTRODUCTION

Vascular plants, particularly tree species, undergo two distinct phases of growth and development. During primary growth, shoot apical meristems (SAMs) and root apical meristems (RAMs) are responsible for the aboveground and underground organ growth, respectively. At the peripheral region of SAM, procambium cells produce primary vascular bundles (Figure 1; also see Nieminen et al., 2015). After the primary vascular system is established, fascicular cambium located at the center of primary vascular bundles undergoes extension into the interfascicular region, forming a ring of vascular cambium (Figure 1; Nieminen et al., 2015). Vascular cambium is a cylindrical secondary meristem whose activity gives rise to the secondary growth. Like SAM and RAM, vascular cambium contains bifacial cambium stem cells in Arabidopsis (Shi et al., 2019; Smetana et al., 2019). However, stem cell activities of the three types of meristems are preferentially regulated by different members of the WUSCHEL-RELATED HOMEOBOX (WOX) and CLAVATA3/EMBRYO SURROUNDING REGION-RELATED (CLE) gene families: SAM is associated with WUSCHEL (WUS) and CLAVATA3 (CIV3; Mayer et al., 1998; Schoof et al., 2000), RAM with WOX5 and...
that the establishment and maintenance of vascular cambium involve the coordination of multiple regulators, including hormones, peptides, and transcription factors (Figure 2; also see the reviews by Miyashima et al., 2013; Mizrahi and Myburg, 2016; Chiang and Greb, 2019). However, our knowledge about the development and regulation of vascular cambium, compared to SAM and RAM, is limited. This mini review focuses on recent progresses in the regulatory networks responsible for the vascular cambium identity and activity in poplar.

**ESTABLISHMENT OF THE VASCULAR CAMBium**

Because vascular procambial cells are imbedded under layers of other tissues in stems, our current understanding of procambium initiation and regulation is derived from studies in Arabidopsis embryos, RAMs, and leaf venation systems. Functional characterization of a serial of Arabidopsis mutants shows that vascular cambium initiation requires the cross talk regulation of multiple hormones (Figure 2A). Auxin plays a central role in regulating the initiation and maintenance of procambial stem cells (Ibañes et al., 2009; Weijers and Wagner, 2016). In pre-procambial strands, MONOPTEROS (MP)/AUXIN RESPONSE FACTOR 5 (ARF5) is activated in response to auxin and positively regulates the number of vascular initial cells through induction of the expression of the auxin efflux carrier gene PIN-FORMED1 (PIN1; Wenzel et al., 2007). Periodic auxin maxima controlled by polar transport but not overall auxin levels is required to determine the radial pattern of vascular bundles in postembryonic growth (Ibañes et al., 2009). MP/ARF5 positively regulates TARGET OF MONOPTEROS 5 (TMOS), which forms a dimer complex with LONESOME HIGHWAY (LHW) to control the procambium cell divisions in roots (De Rybel et al., 2014; Ohashi-Ito et al., 2014). MP/ARF5 activates ATHB8-targeted PIN1 in response to auxin, forming a self-reinforcing mechanism of auxin flow during the formation of vein procambium (Donner et al., 2009). ATHB8, a HD-ZIP III transcription factor, is shown to restrict preprocambial cell specification to a narrow zone and stabilize preprocambial cell fate (Baima et al., 2001; Donner et al., 2009). REVOLUTA is another member of the Arabidopsis HD-ZIP III gene family, and its Populus ortholog, PopREVOLUTA, influences vascular cambium initiation in Populus stems (Robischon et al., 2011).

Cytokinin (CK) is another major hormone that regulates procambium identity and activity in Arabidopsis (Figure 2A). Mutation of three CK receptor genes CYTOKININ RESPONSE 1 (CRE1), ARABIDOPSIS HISTIDINE KINASE 2 (AHK2), and AHK3 results in a severely reduced numbers of periclinal divisions in the procambium cells of the primary roots (Inoue et al., 2001). Accordingly, transgenic Arabidopsis plants overexpressing CYTOKININ OXIDASES/DEHYDROGENASES 2 (CKX2), a CK degrading enzyme gene, under the control of CRE1 promoter show the cre1ahk2ahk3 phenotype (Mähonen et al., 2006). Moreover, the establishment of
procambium cell identity requires a mutually inhibitory interaction between CK and auxin signaling (Figure 2A). Reduced CK signaling changes the subcellular polarity of PIN1, PIN3, and PIN7, while auxin is able to activate the expression of ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER 6 (AHP6), an inhibitor of CK signaling (Mährönen et al., 2006; Bishopp et al., 2011). Auxin-induced TMO5/LHW dimer directly activates LONELY GUY 4 (LOG4) that encodes for a rate-limiting enzyme in CK biosynthesis (De Rybel et al., 2014). CK-dependent procambium cell divisions are controlled by the DOF transcription factor DOF2.1 downstream of TMO5/LHW (Smet et al., 2019).

Brassinosteroids (BRs) serve as a key promoting signal for procambial division during primary growth (Figure 2A). In the stem of Arabidopsis, the number of vascular bundles (VB) is obviously increased in gain-of-function BR-signaling mutants, such as brassinosteroid insensitive 2 (bin2) and brassinazole-resistant 1-1D (bZR1-1D), while loss-of-function BR-signaling mutant brassinosteroid insensitive 1-116 (bri1-116) and BR synthesis mutant constitutive photomorphogenesis and dwarfism (cpd) have fewer VBs than wild-type plants (Ibañes et al., 2009).

**REGULATION OF VASCULAR CAMBIUM ACTIVITY**

Trees display prominent secondary growth in the stem and root, with similar vascular cell types to Arabidopsis (Mizrachi and Myburg, 2016). Studies in Arabidopsis stems and roots indicate an important regulatory function for hormones (auxin, CK, and ethylene) and TRACHEARY ELEMENT differentiation inhibitory factor (TDIF) peptide in the proliferation of vascular cambium (Ortega-Martinez et al., 2007; Matsumoto-Kitano et al., 2008; Suer et al., 2011; Fischer et al., 2019; Smetana et al., 2019). WOX4 is considered to be a central regulator of vascular cambium division (Figure 2A), because it activates a cambium-specific transcriptional network and integrates auxin, ethylene, and TDIF-PXY signaling for cambium division (Hirakawa et al., 2010; Ji et al., 2010; Suer et al., 2011; Etchells et al., 2012; Brackmann et al., 2018; Zhang et al., 2019). WOX4 is required for auxin-dependent stimulation of cambium activity (Suer et al., 2011). Auxin-induced MP/ARF5 directly attenuates the activity of the stem cell-promoting WOX4 gene, and cell-autonomously restricts the number of stem cells in stems (Brackmann et al., 2018). The TDIF peptides encoded by CLE41 and CLE44 are synthesized in the phloem and travel to the cambium where they bind and activate PXY, stimulating WOX4 transcription and promoting cambium proliferation in stems (Hirakawa et al., 2010). Ethylene and TDIF signaling converge at WOX4 to regulate cambium activity (Etchells et al., 2012; Yang et al., 2020b). BIN2-LIKE 1 (BIL1), a glycogen synthase kinase 3, functions as a mediator that links auxin-CK signaling with TDIF-PXY signaling for the maintenance of cambial activity (Han et al., 2018).
Phosphorylation of MP/ARF5 by BIL1 enhances its negative effect on the activity of vascular cambial, which upregulates ARABIDOPSIS RESPONSE REGULATOR 7 (ARR7) and ARR15, two negative regulators of CK signaling. BIL1 activity is inhibited by PXY, attenuating the effect of MP/ARF5 on ARR7 and ARR15 expressions and increasing vascular cambial activities.

Regulation of vascular cambium activity by auxin, CK, ethylene, and TDIF-PXY signaling is relatively conserved between trees and Arabidopsis (Figure 2). Auxin shows the highest level at the cambium zone, and its level declines near the mature xylem cells during wood formation in trees (Nilsson et al., 2008; Immanen et al., 2016). Overexpression of the stabilized form of INDOLE ACETIC ACID 3 (IAA3) that perturbs auxin signaling in hybrid aspen represses periclinal division of vascular cambia but enlarges cell file harboring anticlinal cell division (Nilsson et al., 2008). Auxin-responsive PaC3H17-PaMYB199 module promotes cambium division by a dual regulatory mechanism in Populus stems (Tang et al., 2020). Auxin promotes direct repression of PaMYB199 expression by PaC3H17 and also enhances the PaC3H17-PaMYB199 interaction, attenuating PaMYB199 inhibition of cambial cell division. Consistent with this, dominant repressors of PaC3H17 or overexpression of PaMYB199 result in a reduction in the number of cambial cell layers, while transgenic poplars overexpressing PaC3H17 or repressing PaMYB199 have the opposite phenotype. In addition, the regulation of vascular cambium activity is associated with feedback mediation of auxin homeostasis in trees. Downregulation of the Populus HD-ZIP III gene PttHB4 enhances PttPIN1 expression and causes drastic defects in interfascicular cambium, indicating that PttHB4 induces interfascicular cambium formation during the development of the secondary vascular system (Zhu et al., 2018). VASCULAR CAMBIUM-RELATED MADS 1 (VCM1) and VCM2 inhibit vascular cambium proliferation activity and secondary growth through direct upregulation of PttPIN5 expression in Populus stems (Zheng et al., 2021). These findings indicate more fine regulation of cambial activity by auxin signaling in trees than in Arabidopsis.

CK is another important regulator of cambial activity during wood formation (Figure 2B). Inhibition of cambial CK signaling by overexpression of Arabidopsis AtCKX2 under the promoter of a birch CREI gene leads to a reduced number of cambial cells in poplar stems, while increased vascular division is observed in transgenic poplars expressing the Arabidopsis CK biosynthetic gene ISOPORENYL TRANSFERASE 7 (IPT7) under the control of the cambium-specific PttLMX5 promoter (Nieminen et al., 2008; Immanen et al., 2016). Elevated CK levels cause an increase of auxin level at the cambium zone, highlighting the interconnected nature of auxin and CK gradients (Immanen et al., 2016). A recent study uncovers the mechanism of CK signaling associated with its spatial enrichment to regulate vascular development in Populus (Fu et al., 2021). The local CK signaling in the developing secondary phloem regulates the activity of vascular cambium in a non-cell-autonomous manner.

In addition to auxin and CK, gibberellin (GA), ethylene, and TDIF-PXY signaling promote cambial cell division and radial growth in trees (Figure 2B). Transgenic poplar lines overexpressing GA 20-OXIDASE, encoding a GA biosynthesis enzyme, promote over-production of GA and cambium proliferation (Eriksson et al., 2000). Ethylene-overproducing and ethylene-insensitive poplars show increased and reduced cambium division, respectively (Love et al., 2009). Overexpression of PtcCLE41, a TDIF-like peptide, together with its receptor PttPXYa affects the rate of cambial cell division and woody tissue organization in both hybrid aspen and poplar (Etchells et al., 2015; Kucukoglu et al., 2017). PttWOX4 stimulates the cambium proliferation downstream of TDIF-PXY signaling, as is similar to the manner of the Arabidopsis TDIF-PXY-WOX module. One difference is that in Populus, PttWOX4a/b expression is not responsive to auxin treatments, but upstream genes, such as PttPXYa and PtcCLE41a/d, are responsive (Kucukoglu et al., 2017). The cross talk of hormones in regulation of cambium activity was also found in trees. For instance, GA coordinates with auxin for inducing cambium division through upregulating 83% of auxin-responsive genes, including PttPIN1, while auxin treatment upregulates GA biosynthesis genes and downregulates GA degradation genes in wood-forming tissues (Björklund et al., 2007).

REGULATION OF CAMBIUM DERIVATIVE CELLS DIFFERENTIATION

The regulatory roles of auxin, BR, and GA in cell differentiation in the vascular cambium are studied in Arabidopsis or/and trees (Figure 2). Since 20 years ago, the IAA12/BODENLOS (BDL)-ARF5/MP module in auxin signaling has been identified to control provascular specification and patterning during embryo-genesis in Arabidopsis (Hardtke and Berleth, 1998). Recently, the PtoIAA9-PtoARF5 module from Populus has been validated to mediate auxin-triggered cell differentiation of early developing xylem (Xu et al., 2019). With auxin treatment, PtoIAA9 protein is degraded, inducing PtoARF5-activated gene expression, and the activated PtoIAA9 switches-off auxin signaling in a self-controlled manner during wood formation. BRs play a regulatory role in differentiation of vascular tissues, in addition to inducing cambium initiation during primary growth. Mutation of both BRI-LIKE 1 (BRL1) and BRL3, two Arabidopsis vascular-specific BR receptors, causes expanded phloem development at the expense of xylem in stems (Cano-Delgado et al., 2004). br1-ethylmethylsulfone-suppressor 1-D (bes1-D), a gain-of-function BR-signaling mutants, exhibits an increase of xylem differentiation (Kondo et al., 2014). Similarly, inhibition of BR synthesis results in decreased secondary vascular differentiation and cell wall biosynthesis, while elevated BR levels cause increases in secondary growth in Populus (Du et al., 2020). A recent study indicates that BR signaling is tightly connected with local intracellular auxin homeostasis during cell differentiation in the vascular cambium of tomato stems (Lee et al., 2021). BZR1/BES1-activated WASHINGTONIANS ARE THIN1 (WAT1), an auxin efflux carrier, facilitates cell differentiation in the vascular cambium by enhancing local auxin signaling. In addition, GA is shown to induce vascular cell differentiation and lignification downstream of WOX14 gene in the stem of Arabidopsis (Mauriat and Moritz, 2009; Denis et al., 2017).
TDIF-PXY signaling is a mediator that induces cell differentiation in the vascular cambium in Arabidopsis (Figure 2A). Transgenic plants overexpressing CLE41 or CLE44 display abnormal vascular patterning with a xylem intermixed with phloem phenotype during both primary and secondary growths (Fisher and Turner, 2007; Etchells and Turner, 2010). TDIF signaling regulation of xylem differentiation is fine-tuned by the NAC transcription factor XYLEM DIFFERENTIATION AND ALTERED VASCULAR PATTERNING (XVP; Yang et al., 2020a). XVP negatively regulates the TDIF-PXY module, and it also forms a complex with TDIF co-receptors PXY-BAK1 (BR11-associated receptor kinase 1). XVP expression is suppressed by TDIF by a feedback mechanism. Overexpression of PttCLE41 or PtPXY (the orthologs to Arabidopsis CLE41 and PXY, respectively) in hybrid aspen or poplar causes defects in the patterning of the vascular tissues and shows inhibited plant growth (Etchells et al., 2015; Kucukoglu et al., 2017), suggesting a similar regulation of xylem differentiation by the TDIF-PXY module in plants. The cross talk between TDIF-PXY signaling module and BR or auxin occurs in controlling vascular cell differentiation in Arabidopsis (Figure 2A). PXY physically interacts with BIN2 at the plasma membrane, and the treatments by TDIF peptide enhance the activity of BIN2 in a PXY-dependent manner (Kondo et al., 2014). Transcriptional regulatory network mediated by PXY comprises 690 transcription factor-promoter interactions, of which a feed-forward loop containing WOX14, TM06 and their downstream gene LATERAL ORGAN BOUNDARIES DOMAIN4 (LBD4) determines the arrangement of vascular tissue (Smit et al., 2020).

The HD-ZIP III and NAC transcription factors are important regulators of vasculature organization. In Arabidopsis vascular tissues, mutation of one or several members of HD-ZIP III family results in an amphicribal vascular bundle pattern (phloem surrounding xylem), whereas gain-of-function mutants display amphivasal bundles (McConnell et al., 2001; Emery et al., 2003; Ramachandran et al., 2017). PtrHB5 and PtrHB7 are the orthologs of Arabidopsis POPCORONA and AtHB8 in Populus, respectively. Both genes correspondingly induce cambium activity and xylem differentiation in stems during secondary growth (Du et al., 2011; Zhu et al., 2013). Interestingly, PtrHB7 was identified as a direct target of the PtraAA9-PtraARF5 module during xylem cell differentiation (Xu et al., 2019). This places PtrHB7 in the regulatory network of auxin-induced xylem differentiation in woody stems. The Arabidopsis NAC genes VASCULAR-RELATED NAC DOMAINS (VNDs) act as master regulators of xylem differentiation capable of switching on the developmental program (Kubo et al., 2005; Zhou et al., 2014), while other members of this family, NAC SECONDARY WALL THICKENING PROMOTING FACTOR 1, 3 (NST1, 3), can promote fiber differentiation in stems (Zhong et al., 2006; Mitsuda et al., 2007). Four Populus orthologs of NST1/3 redundantly control SCW formation in xylem fibers, phloem fibers, and xylem ray parenchyma cells (Takata et al., 2019), indicating a conserved role of these NACs in wood formation. Some NAC genes impede xylem differentiation and secondary wall deposition involving PagKNAT2/6b and PtoTCP20 in Populus (Hou et al., 2020; Zhao et al., 2020). PagKNAT2/6b directly activates PagXND1a expression but represses PagNST3s and PagVND6 expression in wood-forming tissues (Zhao et al., 2020).

PtoTCP20 interacts with PtoWOX4a to control vascular cambium proliferation and also activates PtoWND6 expression to promote secondary xylem differentiation (Hou et al., 2020).

**FUTURE OUTLOOK**

Wood formation of tree species involves a complex regulatory network underlying cambial initiation, tissue patterning, and cell differentiation. Understanding the vascular cambium development is a basis for genetic modification of wood biomass and properties in trees. Extensive studies in the model tree *Populus* indicate the cross talk regulation of vascular cambium development by multiple signals, including auxin, CK, BR, and TDIF-PXY, similar to regulatory programs of Arabidopsis vascular development (Figure 2). However, based on genome sequences, it is predicted that 1.4–1.6 *Populus* homologs correspond to each *Arabidopsis* gene (Tuskan et al., 2006). These *Populus* duplicated genes may undergo divergent fates, such as nonfunctionalization (loss of original functions), neofunctionalization (acquisition of novel functions), or subfunctionalization (partition of original functions). This may explain the emerging more complex mechanisms underlying vascular cambium maintenance and differentiation in trees than in Arabidopsis.

In recent years, the studies on the vascular cambium formation and regulation in trees have been greatly facilitated by new technologies, such as the genome-editing, integrated-omics, and more advanced microscopy. Therefore, the following key questions are anticipated to be addressed in the near future.

1. How do the interfascicular cambial cells function in woody stems?

   With the onset of the secondary growth, fascicular cambia are interconnected with interfascicular cambia located between the vascular bundles, forming a complete vascular cambium in woody stems (Figure 1). The interfascicular cambia are known to originate from the parenchymatic cells in the interfascicular region. Currently, our understanding regarding how the parenchymatic cells differentiate and develop into new procambium strands in the interfascicular region is limited, compared with extensive studies on fascicular cambia. To our knowledge, the HD-ZIP III gene *PtrHB4* is the only gene that is shown to induce interfascicular cambium division in *Populus* stems (Zhu et al., 2018). Analysis of time-spatial features of parenchymatic cells action and mining the related genes in trees are essential in the future. The application of single-cell RNA sequencing, computational modeling, or biosensor may be helpful for addressing this question.

2. How is the vascular cambium activity maintained in trees?

   Vascular cambium of trees is able to ensure both increased stem girth and annual renewal of vascular tissues over its lifespan. Even in 667-year-old *Ginkgo biloba* trees, the vascular cambium still maintains activity (Wang et al., 2020). A key question for wood biology is how vascular cambium activity maintained? In *Populus*, multiple signals mediate the coordinated regulation of vascular cambium activity, as is more complex than that in *Arabidopsis* (Figure 2). It is therefore critical to investigate what signals and how these signals drive the activity of cambial stem cells under certain circumstances? Identification of reliable cell-specific makers thus to analyze gene expression
in each layer of cambial cells is essential for understanding the gene regulation of vascular stem cells in trees.

**AUTHOR CONTRIBUTIONS**

DW and GC drafted the manuscript. GZ, YC, WI, QL, and ML edited the manuscript. All authors approved the final version.

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