

Systematic Review

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Molecular Mechanisms of Cambium Formation and Activity Maintenance: A Systematic Review of the Collaborative Regulation of Tree Stem Cells in Growth, Development, and Environmental Adaptation

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Abstract Seasonal changes and environmental conditions, especially temperature, significantly affect cambium activation and wood formation, affecting tree growth and adaptation. Advanced genetic and epigenome analyses have revealed the importance of DNA methylation and miRNA in regulating cambium activity. The synergistic regulation of cambium activity involves a multifaceted network of genetic, hormonal, and environmental interactions, and understanding these mechanisms provides valuable insights into tree growth and development, with important implications for forestry management and climate change adaptation. This study synthesizes findings from a variety of related studies highlighting the complex interplay of genetic, hormonal, and environmental factors in cambium regulation. Through the identification of specific genes and signaling pathways regulating auxin homeostasis such as MADS-box genes *VCM1* and *VCM2*, the molecular regulation of secondary growth was further clarified. The aim of this study was to elucidate the molecular mechanisms of cambium formation and activity maintenance in trees, focusing on the synergistic regulation of tree stem cells in growth, development and environmental adaptation.

Keywords Cambium; Secondary growth; Phytohormones; Gene regulation; Environmental adaptation

1 Introduction

The cambium is a critical meristematic tissue in trees responsible for secondary growth, which leads to the thickening of stems and roots. This tissue is composed of stem cells that divide to produce secondary xylem (wood) and secondary phloem (bast) (Fischer et al., 2019; Turley and Etchells, 2021). The cambium's activity is essential for the formation of wood, which constitutes a significant portion of the world's biomass (Turley and Etchells, 2021). The regulation of cambial growth involves complex interactions between genetic, hormonal, and environmental factors (Savidge, 2001; Groover and Robischon, 2006; Ursache et al., 2013). Understanding these mechanisms is crucial for comprehending how trees grow, develop, and adapt to their environments.

Studying cambium formation and activity maintenance is vital for several reasons. Firstly, it provides insights into the fundamental processes of plant growth and development, particularly in woody plants (Groover and Robischon, 2006; Turley and Etchells, 2021). Secondly, the cambium's role in wood production has significant ecological and economic implications, as wood is a major renewable resource (Etchells et al., 2015; Turley and Etchells, 2021). Additionally, understanding how environmental factors such as temperature and seasonal changes influence cambial activity can help predict and mitigate the impacts of climate change on forest ecosystems (Begum et al., 2013; Chen et al., 2021). Moreover, advances in genetic and molecular research on cambium regulation can lead to improved tree breeding and biotechnology applications, enhancing wood production and quality (Agustí et al., 2011; Etchells et al., 2015).

This study elucidates the molecular mechanisms underlying cambium formation and activity maintenance in trees, which includes exploring the genetic, hormonal, and environmental factors that regulate cambial stem cell dynamics and secondary growth. By synthesizing current knowledge and recent discoveries, this study aims to provide a comprehensive understanding of the collaborative regulation of tree stem cells in growth, development, and environmental adaptation and discusses potential areas for future research and applications in forestry and biotechnology.



2 Identification and Functional Analysis of Cambium-Specific Expression Genes

2.1 Methods for identifying cambium-specific genes

The identification of cambium-specific genes has been facilitated by various advanced techniques. One notable method involves the use of laser capture microdissection combined with transcriptome profiling, which allows for the precise isolation and analysis of cambium tissues. This approach was effectively utilized to identify genes induced during different phases of cambium formation in *Arabidopsis thaliana* (Agustí et al., 2011). Additionally, the use of in vitro systems to induce cambium formation in isolated stem fragments has proven valuable in characterizing transcriptome remodeling in a tissue- and stage-specific manner (Agustí et al., 2011). In coniferous trees, such as *Pinus sylvestris*, the expression profiles of cambium-specific genes were studied by collecting trunk tissue samples at different stages of ontogenesis and cambial growth. This method enabled the identification of spatial and temporal expression patterns of key regulatory genes (Galibina et al., 2023). Furthermore, comprehensive analyses of transcriptome profiles, DNA methylome, and miRNAs during the transition from dormancy to activation in *Populus tomentosa* have provided insights into the molecular mechanisms underlying cambium activity (Chen et al., 2021).

2.2 Functional roles of identified genes

The functional roles of identified cambium-specific genes are diverse and critical for the regulation of cambium activity and secondary growth. For instance, the receptor-like kinases REDUCED IN LATERAL GROWTH1 (RUL1) and MORE LATERAL GROWTH1 (MOL1) have been identified as opposing regulators of cambium activity in Arabidopsis, with RUL1 inhibiting and MOL1 promoting lateral growth (Agustí et al., 2011). In *Populus*, two MADS-box genes, *VCM1* and *VCM2*, were found to modulate auxin homeostasis, thereby regulating vascular cambium proliferation and secondary growth (Zheng et al., 2020; Haas et al., 2022). The WUSCHEL-RELATED HOMEOBOX (WOX) gene family, particularly WOX4, plays a crucial role in maintaining and proliferation in the cambial zone, indicating its importance in cambial activity (Galibina et al., 2023). Similarly, in *Populus, WOX4-like* genes were shown to control cell division activity in the vascular cambium, with their expression regulated by *CLE41*-related genes (Kucukoglu et al., 2017).

2.3 Comparative analysis of cambium-specific genes across different tree species

Comparative analysis of cambium-specific genes across different tree species reveals both conserved and species-specific regulatory mechanisms. For example, the CLE41/44-PXY-WOX signaling module, which regulates cambial growth in Scots pine, is also conserved in *Populus*, where it controls cell division activity in the vascular cambium (Kucukoglu et al., 2017; Galibina et al., 2023). This suggests an evolutionarily conserved program for the regulation of vascular cambium activity between angiosperm and gymnosperm tree species (Wang, 2020). In addition, the identification of stress-response transcription factors that control cambium activity in radish and their comparison with Arabidopsis data highlights the conservation of gene-regulatory networks that integrate environmental sensing and growth (Hoang et al., 2020; Furuya et al., 2021). The role of miRNAs and DNA methylation in regulating cambium activity in *Populus* further underscores the complexity and diversity of epigenomic regulation across different species (Chen et al., 2021). These studies provide valuable insights into the molecular mechanisms of cambium formation and activity maintenance, highlighting the collaborative regulation of tree stem cells in growth, development, and environmental adaptation.

3 Regulatory Mechanisms of Hormones in Cambium Formation and Activity Maintenance 3.1 Overview of hormone regulation in plant stem cells

Hormones play a crucial role in the regulation of plant stem cells, particularly in the cambium, which is responsible for secondary growth. The cambium's activity is influenced by a complex interplay of hormonal signals, including auxin, cytokinin, gibberellin, and strigolactones, among others. These hormones coordinate to regulate the balance between cell proliferation and differentiation, ensuring the proper formation and maintenance of the cambium (Groover and Robischon, 2006; Turley and Etchells, 2021; Ben-Targem et al., 2021; Hu et al., 2021).



3.2 Cytokinin regulation

3.2.1 Pathway components

Cytokinins are a class of plant hormones that promote cell division and differentiation. Key components of the cytokinin signaling pathway include cytokinin receptors (such as AHKs), histidine phosphotransfer proteins (AHPs), and response regulators (ARRs). These components work together to mediate the effects of cytokinins on cambial activity (Elo et al., 2009; Oles et al., 2017).

3.2.2 Role in cambium formation

Cytokinins are essential for the initiation of cambium formation. They promote the proliferation of cambial stem cells and the establishment of the cambial zone. Studies have shown that cytokinin signaling is crucial for the early stages of cambium development, facilitating the transition from primary to secondary growth (Groover and Robischon, 2006; Turley and Etchells, 2021).

3.2.3 Role in cambium activity maintenance

In addition to their role in cambium formation, cytokinins are also vital for maintaining cambial activity. They help sustain the division of cambial cells and the production of secondary xylem and phloem. The balance between cytokinin and auxin signaling is particularly important for the continuous activity of the cambium, as these hormones often have antagonistic effects (Oles et al., 2017; Ben-Targem et al., 2021).

3.3 Auxin regulation

3.3.1 Pathway components

Auxins are another critical group of plant hormones involved in cambium regulation. The auxin signaling pathway includes auxin receptors (such as TIR1/AFB), Aux/IAA proteins, and ARF transcription factors. These components interact to modulate gene expression in response to auxin levels, influencing cambial activity (Oles et al., 2017; Turley and Etchells, 2021; Hu et al., 2021).

3.3.2 Role in cambium formation

Auxins play a pivotal role in the formation of the cambium by promoting the differentiation of procambial cells into cambial stem cells. High auxin concentrations are typically found in regions where cambium formation is actively occurring, indicating its importance in initiating secondary growth (Groover and Robischon, 2006; Elo et al., 2009; Turley and Etchells, 2021).

3.3.3 Role in cambium activity maintenance

Auxins are also crucial for the maintenance of cambial activity. They regulate the balance between cell division and differentiation within the cambium, ensuring a steady supply of new cells for secondary xylem and phloem production. Auxin gradients within the plant tissue help direct the pattern of cambial growth and activity (Oles et al., 2017; Ben-Targem et al., 2021; Hu et al., 2021).

In summary, the regulation of cambium formation and activity by hormones such as cytokinins and auxins is a complex and finely tuned process. These hormones interact with each other and with other signaling pathways to ensure the proper development and maintenance of the cambium, which is essential for the secondary growth of plants. Understanding these regulatory mechanisms provides valuable insights into plant development and has potential applications in forestry and agriculture (Groover and Robischon, 2006; Elo et al., 2009; Oles et al., 2017; Turley and Etchells, 2021; Ben-Targem et al., 2021; Hu et al., 2021).

4 Adaptive Response Mechanisms of Cambium Stem Cells Under Environmental Stress Conditions

4.1 Types of environmental stress affecting cambium

Cambium stem cells in trees are subjected to various environmental stressors that can significantly impact their activity and function. These stressors include abiotic factors such as temperature fluctuations, drought, and nutrient availability, as well as biotic factors like pathogen attacks and herbivory. Temperature, in particular, plays a crucial role in the timing of cambial reactivation and xylem differentiation. Elevated temperatures from late



winter to early spring can lead to earlier initiation of cambial activity, extending the growth period but also increasing the risk of frost damage due to decreased cold tolerance post-reactivation (Begum et al., 2013). Additionally, the immediate environment of cambial cells, including weather and nutritional factors, continuously varies, influencing wood formation and the variability in wood properties (Downes et al., 2009).

4.2 Molecular response mechanisms to abiotic stress

Cambium stem cells employ various molecular mechanisms to respond to abiotic stress. For instance, temperature-induced changes in the stability of microtubules are crucial for the reactivation of cambial cells and subsequent xylem differentiation (Begum et al., 2013). Hormones, peptides, and mechanical cues are also believed to orchestrate the response of cambial activity to environmental factors, although the exact mechanisms remain to be fully uncovered (Fischer et al., 2019). In *Populus*, the peptide PtrCLE20 has been identified as a repressor of vascular cambium activity, suggesting a role in modulating growth in response to environmental cues (Zhu et al., 2019). Furthermore, conserved gene-regulatory networks involving stress-response transcription factors, such as ERF-1, integrate environmental sensing with cambium-driven growth, highlighting the complex interplay between environmental signals and cambial activity (Chiatante et al., 2018; Hoang et al., 2020).

4.3 Molecular response mechanisms to biotic stress

In response to biotic stress, such as pathogen attacks, cambium stem cells activate specific molecular pathways to mitigate damage and maintain growth. The identification of receptor-like kinases, such as REDUCED IN LATERAL GROWTH1 (RUL1) and MORE LATERAL GROWTH1 (MOL1), which act as opposing regulators of cambium activity, underscores the importance of cell-to-cell communication in the cambium's response to biotic stress (Agustí et al., 2011). These signaling components help coordinate the cambium's activity, ensuring the production of secondary phloem and xylem even under stress conditions. Additionally, the dynamic nature of cambial stem cell activity, influenced by mobile signals and intercellular communication, plays a critical role in the plant's ability to adapt to biotic stress (Bhalerao and Fischer, 2017; Fischer et al., 2019).

4.4 Integration of stress signals in cambium regulation

The integration of stress signals in cambium regulation involves a complex network of molecular interactions. Phytohormones, transcription factors, and peptide-receptor modules are key players in this process. Recent studies have highlighted the roles of mobile transcription factors and intercellular signaling in the regulation of cambium activity, emphasizing the crosstalk between different regulatory pathways (Turley and Etchells, 2021). The environment of cambial cells, including fluxes in phytohormones, carbohydrates, and physical factors, influences gene expression and enzyme kinetics, thereby modulating cambial activity in response to stress (Savidge, 2001). Understanding these integrative mechanisms is crucial for developing strategies to enhance tree growth and resilience under changing environmental conditions.

5 Collaborative Regulation Networks of Cambium, Xylem, and Phloem Development 5.1 Gene networks involved in cambium development

The development and activity of the vascular cambium are regulated by complex gene networks. Key transcription factors such as WUSCHEL-RELATED HOMEOBOX 4 (WOX4) and KNOTTED-like from *Arabidopsis thaliana* 1 (KNAT1) play crucial roles in cambium development. Mutations in these genes can lead to significant changes in cambial activity, highlighting their importance in the regulatory network (Zhang et al., 2019). Additionally, MADS-box genes like *VCM1* and *VCM2* have been identified to modulate auxin homeostasis, which is essential for cambium proliferation and secondary growth in *Populus* (Zheng et al., 2020). The interaction between these genes and hormonal pathways, such as auxin and gibberellin signaling, further underscores the complexity of the gene networks involved in cambium development (Ben-Targem et al., 2021).

5.2 Interactions between cambium, xylem, and phloem gene networks

The gene networks regulating cambium activity are intricately linked with those controlling xylem and phloem development. For instance, the transcription factors WOX4 and SHORT VEGETATIVE PHASE (SVP) have dual roles in cambial cell proliferation and xylem differentiation (Zhang et al., 2019). Hormonal signaling pathways, including auxin and gibberellin, also play a pivotal role in coordinating the development of these tissues. Auxin



gradients across the cambium area are crucial for regulating the differentiation of cambial derivatives into xylem and phloem (Zheng et al., 2020). Moreover, the interaction between auxin and gibberellin signaling pathways has been shown to promote xylem expansion and maintain cambium homeostasis (Ben-Targem et al., 2021). The dual regulation of xylem formation by the *Pa*C3H17-*Pa*MYB199 module in *Populus* further exemplifies the collaborative regulation of these gene networks (Tang et al., 2019).

5.3 Case studies of collaborative regulation in specific tree species

In *Populus*, the MADS-box genes *VCM1* and *VCM2* have been shown to regulate cambium activity and secondary growth by modulating auxin homeostasis (Figure 1). Knock-down of these genes enhances cambium proliferation and xylem differentiation, while their overexpression suppresses these processes (Zheng et al., 2020). Another study in *Populus* identified the *Pa*C3H17-*Pa*MYB199 module, which regulates xylem formation through an auxin-mediated pathway. This module controls cambial cell proliferation and secondary cell wall thickening, highlighting the complex regulatory networks involved in wood formation (Figure 2) (Tang et al., 2019).



Figure 1 *VCM1* and *VCM2* expression and phenotypes of their transgenic lines (Adopted from Zheng et al., 2020) Image caption: (A and B) qRT-PCR analysis of *VCM1* (A) and *VCM2* (B) expression in different tissues. Values are means \pm SD (n = 3 biological replicates). SMT, shoot meristem tissue; YL, young leaf; IN, internode; YT, young roots. (C and D) GUS activity in transgenic *Populus* driven by the *VCM1* promoter (C) and the *VCM2* promoter (D). Ca, cambium; Xy, xylem; Ph, phloem. Scale bar corresponds to 100 µm. (E) Phenotypes of the wild-type (WT), *VCM1* and *VCM2* knock-down lines, (*DR4* and *DR15*) and *VCM1* overexpression lines (*UR13* and *UR25*). Scale bar corresponds to 10 cm. (F) qRT-PCR analysis of *VCM1* and *VCM2* expression in transgenics. Values are means \pm SD (n = 3 biological replicates). (G–I) Cross-section of the 13th internode stained with toluidine blue (above) and enlarged rectangle area (below). (G) WT; (H) *VCM1* and *VCM2* knock-down lines; (I), *VCM1* overexpression lines. Xy, xylem; Ph, phloem; Ca, cambium. Scale bars correspond to 200 µm (50 µm in enlargements). (J) Number of cambium cell layers (n > 50). (K) Number of xylem cell layers (n > 50). Plants used for analysis were grown in a phytotron for 3 months. Values are means \pm SD. (Adopted from Zheng et al., 2020)





Figure 2 PaMYB199 interacts with PaC3H17 (Adopted from Tang et al., 2019)

Image caption: (a) Yeast two hybrid assays were performed using *Pa*MYB199 fused to the DNA binding domain (BD) and *Pa*C3H17 fused to the activation domain (AD). AH109 cells containing different plasmid combinations were grown on selective medium SD-LTHA (L, leucine; T, tryptophan; H, histidine; A, adenine) with 0 or 20 mM 3-amino-1,2,4-triazole, and stained for α -galactosidase activity. (b) *In vitro* pull-down assays. GST-*Pa*C3H17 and MBP-*Pa*MYB199 proteins were immunoprecipitated with an anti-GST antibody and then immunoblotted using an anti-MBP antibody. (c) Bimolecular fluorescence complementation assay showing that *Pa*C3H17-YFP^{NE} and *Pa*MYB199-YFP^{CE} interact to form a functional yellow fluorescent protein (YFP) in the nucleus of Arabidopsis leaf protoplasts. The DNA fluorochrome 4',6-diamidino-2-phenylindole (DAPI) was used to stain the cell nucleus (blue). Bars, 10 µm. (d) Co-immunoprecipitation assay. *35S:FLAG-PaC3H17* (*GFP-FLAG* as the control) and *35S:PaMYB199-HA* were co-transformed into Arabidopsis leaf protoplasts. Total proteins were immunoprecipitated using an anti-HA antibody and the immunoblots were probed with an anti-FLAG antibody (Adopted from Tang et al., 2019)

In Arabidopsis, the transcription factors WOX4 and KNAT1 are central to cambium development. Their interaction with other regulatory pathways, such as those involving phytohormones like auxin and cytokinin, underscores the collaborative nature of these gene networks (Zhang et al., 2019). Additionally, the role of DELLA proteins in mediating gibberellin signaling and their interaction with AUXIN RESPONSE FACTORS (ARF6 and ARF8) further illustrates the intricate regulation of cambium and xylem development (Figure 3) (Ben-Targem et al., 2021).

In *Betula pendula*, trunk girdling experiments have shown that changes in photoassimilate levels can significantly impact cambium activity and the differentiation of xylem and phloem. Increased photoassimilates lead to enhanced phloem formation and changes in the anatomical structure of the conducting tissues, demonstrating the environmental regulation of cambium activity (Serkova et al., 2022).

6 Applications and Prospects of Gene Editing Technology in Cambium Regulation

6.1 Overview of gene editing technologies

Gene editing technologies, such as CRISPR-Cas9, have revolutionized the field of plant biology by enabling precise modifications of specific genes. These technologies allow for targeted alterations in the genome,



facilitating the study and manipulation of gene functions in various biological processes, including cambium regulation. CRISPR-Cas9, in particular, has been widely adopted due to its simplicity, efficiency, and versatility in editing genes across different species (Shen et al., 2021).



Figure 3 ARF6 and ARF8 expression pattern overlaps with RGA and GAI during hypocotyl secondary growth (Adopted from Ben-Targem et al., 2021)

Image caption: (A–D) Hypocotyl vibratome cross-sections at 0, 8 and 20 d after flowering (daf). Left and middle panels: confocal images of sections cleared with ClearSee and stained with Calcofluor White showing GFP signal in the nuclei (red arrows). Right panels: GUS assay on vibratome sections stained with phloroglucinol (red arrows indicates the phloem). (A) *RGA:NLS-GFP-GUS* (left and middle panels) and *RGA:GUS* (right panel). (B) *GAI:NLS-GFP-GUS* (left and middle panels) and *GAI:GUS* (right panel). (C) *ARF6:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left and middle panels) and *ARF6:GUS* (right panel). (D) *ARF8:NLS-3xGFP* (left panel). (D) *ARF8:NLS-3xGFP* (left panel). (D) *ARF8:NLS-3xGFP* (left panel). (D) *ARF8:NLS-3xGFP* (left panel) (D) *ARF8*

6.2 Applications in modifying cambium-specific genes

Gene editing has been successfully applied to modify cambium-specific genes to understand their roles in secondary growth and wood formation. For instance, the CRISPR-Cas9 system was used to edit the *PdBR11* genes in *Populus*, which are involved in brassinosteroid signaling. The edited lines exhibited significant changes in cambial activity and wood development, highlighting the importance of these genes in regulating cambium function (Wang et al., 2022a). Similarly, the expression of the co-transcriptional regulator PanNOOT1 in *Parasponia andersonii* was manipulated using CRISPR-Cas9, demonstrating its essential role in controlling secondary growth (Shen et al., 2021).

6.3 Potential for improving tree stress resistance

Gene editing technologies hold great potential for enhancing tree stress resistance by targeting genes involved in stress response pathways. For example, the manipulation of cytokinin signaling pathways through the expression of a constitutively active cytokinin receptor variant in poplar increased cambial activity and stem growth, which could potentially improve the tree's resilience to environmental stresses (Riefler et al., 2022). Additionally, the regulation of brassinosteroid biosynthesis via the overexpression of *PagDET2* in poplar promoted cambium cell division and xylem differentiation, suggesting a role in stress adaptation (Wang et al., 2022b).



6.4 Prospects for optimizing breeding strategies

The integration of gene editing technologies into tree breeding programs offers promising prospects for optimizing breeding strategies. By precisely modifying genes associated with desirable traits, such as increased biomass production or enhanced stress tolerance, gene editing can accelerate the development of superior tree varieties. For instance, the use of CRISPR-Cas9 to edit genes involved in cambium regulation, such as those in the CLE41/44-PXY-WOX signaling module, can provide insights into the genetic basis of wood formation and facilitate the breeding of trees with improved growth characteristics (Galibina et al., 2023). Furthermore, the ability to manipulate hormonal pathways, such as brassinosteroid and cytokinin signaling, through gene editing can lead to the development of trees with optimized growth and development (Wang et al., 2022a; Riefler et al., 2022). Gene editing technologies offer powerful tools for studying and manipulating cambium-specific genes, improving tree stress resistance, and optimizing breeding strategies. The continued advancement and application of these technologies hold great promise for enhancing researchers' understanding of cambium regulation and improving the productivity and resilience of forest trees.

7 Concluding Remarks

The review of the molecular mechanisms underlying cambium formation and activity maintenance has revealed several critical insights into the collaborative regulation of tree stem cells in growth, development, and environmental adaptation. The identification of receptor-like kinases, such as REDUCED IN LATERAL GROWTH1 (RUL1) and MORE LATERAL GROWTH1 (MOL1), as opposing regulators of cambium activity, highlights the complexity of signaling pathways involved in secondary growth. Temperature significantly influences cambial reactivation and xylem differentiation, with elevated temperatures leading to earlier cambial reactivation but increasing the risk of frost damage. Hormones such as auxin, cytokinin, gibberellin, and brassinosteroids play cooperative roles in promoting cambium activity, with hormonal pathways acting redundantly to sustain cambium proliferation. Transcription factors, including WOX4 and HD-ZIP III, are crucial in regulating cambium activity and wood formation, with their expression being modulated by environmental and developmental cues. Seasonal changes in cambium activity are accompanied by significant transcriptomic and epigenomic remodeling, affecting gene expression and methylation patterns. The PXY-CLE signaling pathway has been shown to regulate cambial cell division and wood formation, with precise manipulation of this pathway resulting in increased tree growth and productivity.

Future research should focus more on the following aspects. Further investigation into the molecular mechanisms of receptor-like kinases and their interaction with other signaling pathways will enhance researchers' understanding of cambium regulation. Research on the impact of climate change on cambium activity and wood formation will be crucial for developing strategies to mitigate environmental stress in trees. Detailed studies on the interplay between different hormonal pathways and their collective impact on cambium activity will provide insights into optimizing tree growth. Exploring the role of epigenetic modifications in cambium activity and wood formation will help in understanding the long-term adaptation of trees to environmental changes. The identification of key regulatory genes and pathways opens up possibilities for genetic engineering to enhance wood production and stress resilience in trees.

The insights summarized in this study have important implications for forestry and tree breeding. By manipulating key regulatory pathways, such as the PXY-CLE signaling pathway, it is possible to increase wood yield and improve tree growth, which is beneficial for timber production and carbon sequestration. Understanding the environmental regulation of cambium activity can aid in breeding trees that are more resilient to climate change, thereby ensuring sustainable forestry practices. The application of genetic engineering techniques to modify the expression of critical genes involved in cambium activity and wood formation can lead to the development of superior tree varieties with desired traits. Insights into the molecular mechanisms of cambium regulation can inform sustainable forestry management practices, optimizing tree growth and wood quality while maintaining ecological balance. By integrating these findings into practical applications, the forestry industry can achieve significant advancements in tree breeding, wood production, and environmental sustainability.



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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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