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(Review Article)

Mechanisms of secondary growth and regulation of stem cells in stems

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Abstract

Wood development and the accumulation of plant biomass are mostly caused by secondary (radial) growth, which is propelled by the vascular cambium. In this article, the cellular and molecular mechanisms governing cambial stem cell activity and lineage specialization into secondary xylem (wood) and phloem are compiled. Specifically, we focus on the hormone and peptide signaling networks, transcriptional regulators, and intercellular communication signals that govern stem cell identity, proliferation, and differentiation. In order to produce adaptable wood features, we also look into how environmental inputs alter these basic programmings.We highlight the unique experimental advantages of the cambial system and discuss how bridge a longstanding knowledge gap requires this basic insight. We conclude by outlining how modern biotechnology, underpinned by a more profound understanding of mechanisms, can leverage this knowledge to design trees with ideal growth and wood characteristics, offering a methodical approach to enhancing the sustainability and productivity of forest ecosystems amidst global transformation.

Keywords: Mechanisms; Secondary growth; growth; Regulation; Stem; Stems

1. Introduction

A feature that sets woody plants apart and contributes significantly to terrestrial biomass is secondary growth, or the radial thickening of stems and roots [1]. A bifacial lateral meristem called the vascular cambium regulates it. It produces secondary xylem (wood) inward and secondary phloem (inner bark) outward. Not only does this mechanism provide mechanical support and facilitate the long-distance transport of water, photosynthates, and signaling molecules, but it also acts as the largest biological carbon sink on Earth [2]. Therefore, understanding secondary growth control is closely related to both fundamental plant development difficulties and real-world challenges like climate change mitigation and producing sustainable forest products [3].

The focal point of this dynamic process is the cambial stem cells. Having intrinsic multipotency, these cells respond to a variety of complex endogenous and exogenous stimuli. Depending on their precise position within the expanding radial file, progenitor cells derived from the initial stem cells of the vascular cambium differentiate into either secondary xylem or secondary phloem [1,2]. Coordinating this cell fate specification requires intricate intercellular communication. An interconnected and flexible vascular system is created by the resulting differentiation programs, which produce the numerous, functionally specialized cell types (such as vessels, fibers, sieve elements, and companion cells) that define wood and phloem tissues [5].

It must continuously adjust the rates of tissue formation and the patterns of cell differentiation in response to seasonal cycles and environmental perturbations, making this system extremely accurate. This flexibility results in the formation of distinct wood anatomical features, such as the large-lumened vessels of earlywood and the dense, thick-walled fibers of latewood, which act as a physical record of the plant's environmental history and adaptive responses [6]. Therefore, understanding the molecular rationale that guides cambial stem cell selection and synchronizes these complex

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developmental outputs is a major component of plant biology coursework. Additionally, this understanding is more crucial than ever from an applied perspective.

Strategies to increase forest productivity on scarce land are essential as human activity reduces the amount of forested area worldwide and the demand for wood products rises. Although traditional tree breeding has been successful, faster methods are required due to trees' sluggish generation rates. Molecular-assisted breeding and genetic engineering are two examples of contemporary biotechnology that have enormous potential for customizing tree growth and wood characteristics. Nevertheless, a thorough and predictive understanding of the genes and pathways that control cambial activity is necessary for the efficient use of these techniques; this knowledge base is still lacking[7].

Our goal in this study is to summarize the current understanding of the mechanisms governing stem cell development and function within the vascular cambium. First, we will describe the cambium's cellular structure. The hormonal and signaling networks, transcriptional regulators, and intercellular communication systems that determine and preserve stem cell identity and direct xylem vs. phloem specification will then be covered. We will then examine how environmental cues alter these developmental programs to create adaptive wood characteristics. Lastly, We will discuss the experimental approaches that have enabled these findings. We will conclude by showing the translational potential of the underpinning science for the development of next-generation, climate-resilient forests, highlighting current knowledge gaps and possible future research directions [8].

2. Vascular Cambium Cellular Organization: A Niche for Stem Cells

One well-known illustration of a stratified stem cell niche in plants is the vascular cambium. It is arranged as a thin, cylindrical layer of cells between the phloem and secondary xylem([9].

2.1. Cell Lineages and Cambial Zone Structure

The two main cell types found in the cambial zone are the ray initials (isodiametric cells that give rise to the radial system: parenchymatous rays for radial transport) and the fusiform initials (highly elongated cells that give rise to the axial system: vascular elements, fibers, sieve tubes) [3]. These initials occur within a spectrum of developmental states rather than as a static population[10].

The mother cells, also known as immediate derivatives, are located right next to the actual initials and go through multiple rounds of division before to terminal differentiation [4]. The radial file layout creates a spatiotemporal gradient from the stem cells (cambial initials) to fully developed xylem or phloem cells via expanding and committed progenitors [11].

2.2. The Concept of the Stem Cell Niche

Stem cell identity preservation and the balance between self-renewal and differentiation are regulated by signals from the surrounding niche. Key components of this niche include:

Phloem-side (Bark) Influence: Phloem cells that are mature and differentiating, particularly the phloem parenchyma and companion cells, are a source of vital signals that promote proliferation, such as specific peptides and cytokinins [12].

The Xylem-side (Wood) Influence: The xylem parenchyma and developing xylem cells contribute indications, including auxin efflux and possibly feedback inhibitors, that help define the boundary of the meristematic zone [6].

The Ray Cell Network The ray parenchyma cells from phloem to xylem constitute a live continuity that is vital for intertissue communication, nutrient distribution, and radial hormone trafficking [7].

The condition and requirements of the mature vascular tissues are constantly taken into consideration while making stem cell decisions thanks to this organized niche[13].

3. The Molecular Toolbox: Transcriptional Regulation, Peptides, and Hormones

A core collection of plant hormones together with downstream transcriptional networks and peptide signaling pathways control the behavior of cambial stem cells[14].

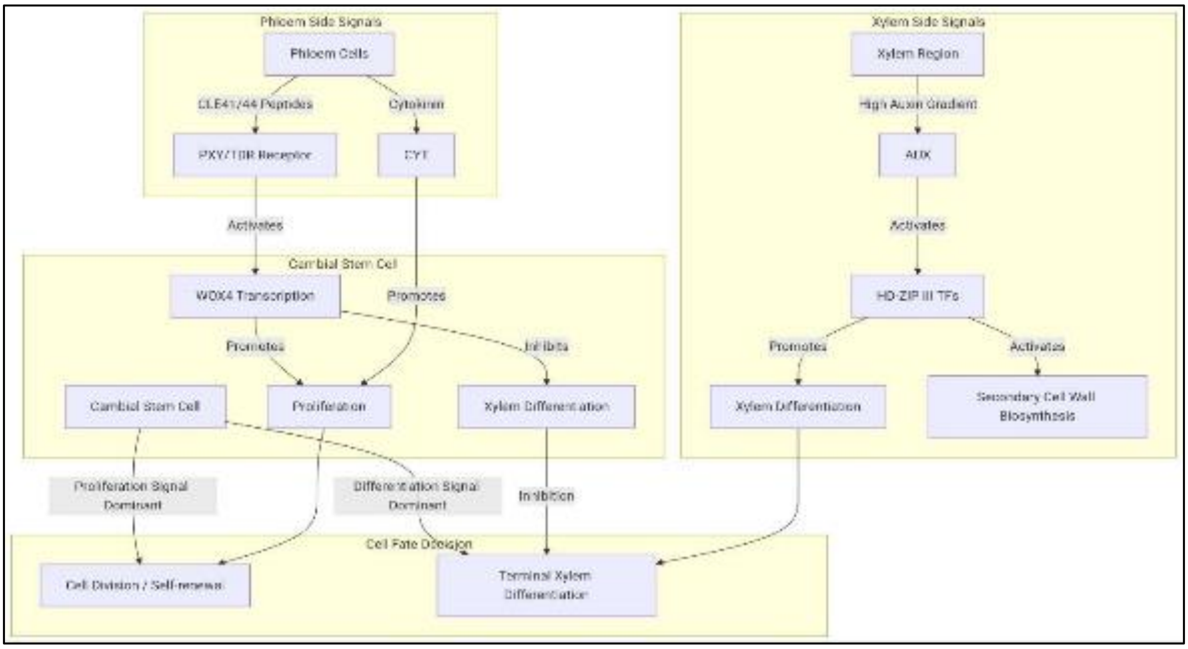

Figure 1 Regulatory network governing cambial stem cell fate decisions.

3.1. Hormonal Control: Antagonistic Directors of Auxin and Cytokinin

Auxin and cytokinin combine to form a core antagonistic module that controls xylem-phloem patterning and cambial activity.

Auxin: The main factor driving cell division and crucial for xylem differentiation is a high auxin concentration gradient that peaks in the cambial zone. This gradient is established by auxin transport, mainly via PIN-FORMED (PIN) efflux carriers [8]. Severe abnormalities in cambial organization and wood production result from mutations that interfere with polar auxin transport[15].

Cytokinin: Mainly derived from the phloem and root apex, cytokinins are thought to boost phloem differentiation and encourage the growth of cambial cells. The xylem-to-phloem ratio is influenced by the equilibrium between auxin and cytokinin signaling, possibly via the ARABIDOPSIS Histidine phosphotransfer proteins (AHPs) and response regulators (RRs) [9].

3.2. Peptide Signaling: Using the PXY/TDR-CLE41/44 Module to Organize Space

The discovery of a receptor-ligand pair essential for cambial organization was a significant advancement.

The phloem and surrounding tissues produce the ligands, CLE41 and CLE44 peptides[16].

The Receptor Cambial stem cells and xylem progenitor cells express the transmembrane receptor kinase PHLOEM INTERCALATED WITH XYLEM (PXY) or TDIF RECEPTOR (TDR).

The function of the CLE41/44-PXY/TDR signal is to sustain the stem cell population and define the phloem side of the niche by acting as a short-range, phloem-derived cue that stimulates stem cell proliferation and suppresses xylem differentiation [10, 11]. When this route is disturbed, the result is bloated, disordered stems with irregular vascular patterning.

3.3. Transcriptional Networks: Creating and Preserving Identity

Certain transcription factors (TFs) that carry out cellular programs are the targets of the convergence of hormonal and peptide signals[17].

WOX4 and WOX14: The PXY/TDR pathway primarily targets WUSCHEL-RELATED HOMEOBOX 4 (WOX4), which is crucial for stimulating cambial cell proliferation [12]. WOX14, a cousin of it, might have a more focused function in encouraging xylem differentiation.

HD-ZIP III Transcription Factors: Xylem cell fate specification depends on auxin-regulated genes such as REVOLUTA (REV), ATHB8, and CORONA (CNA). In tracheary elements, they encourage characteristics such as programmed cell death and secondary cell wall biosynthesis [13]. Class III KNOX and BELL TFs: It has been demonstrated that members such as BREVIPEDICELLUS (BP/KNAT1) in poplar control the ratio of primary to secondary growth and affect the characteristics of wood [18].

4. Seasonal and Stress-Related Environmental Modulation of Cambial Activity

Because of the environment's careful tuning of the intrinsic developmental program, trees are able to optimize their structure for survival[16].

4.1. Reaction Wood Formation and Seasonal Control

The two main indicators for the initiation and termination of cambial dormancy are photoperiod and temperature. They affect cell cycle regulator expression and hormone metabolism (e.g., gibberellin levels in spring) [19].

Reaction Wood: Trees produce specialized wood in response to mechanical stress or gravity.

Gymnosperms, which have lignified, thick-walled tracheids, develop compression wood on the lower side of leaning stems, whereas angiosperms, which have gelatinous, cellulose-rich fibers, develop tension wood on the top side. Significant changes in cell wall biosynthesis gene expression and hormone signaling (ethylene, auxin) are involved in these processes [20].

4.2. Abiotic Stress Reactions: Temperature Extremes and Drought

In order to avoid the risk of cavitation, drought stress usually results in the creation of narrower vessel elements with thicker walls and a smaller lumen area. This includes the modification of aquaporin and dehydrin expression as well as the activation of genes involved in the manufacture of lignin and suberin [21]. In modulating this reaction, ABA is crucial.

Temperature Stress: The effects of heat and cold on cambial activity, membrane fluidity, and enzyme kinetics. While cold adaptation includes changes in cell wall composition (increased hemicellulose acetylation) and the activation of antifreeze proteins, heat stress can lead to the formation of traumatic resin ducts or gum canals [22].

5. Model Systems and Experimental Methods

The study of secondary growth has been motivated by the development of significant model trees and specific methodological benefits.

Radial Gradient Analysis The inherent spatiotemporal gradient allows for high-resolution sampling and enables transcriptomics (microarrays, RNA-seq), proteomics, and metabolomics studies throughout developmental stages from a single tissue segment [18, 23].

Tools Specific to Cambium: Techniques such as cambial peel and laser capture microdissection (LCM) can be used to extract specific cell types from the niche for additional analysis.

Arabidopsis is a model woody plant that offers genetic tools for basic research despite having little secondary growth.

Because of its sequenced genome and transformation efficiency, poplar (Populus spp.), eucalyptus (Eucalyptus spp.), and pine (Pinus spp.) are the most important true woody models [24].

Advanced Imaging: X-ray microtomography, live-cell imaging with fluorescent reporters, and confocal microscopy are transforming our capacity to see cambial dynamics and wood microstructure in three dimensions and across time[25].

6. Translational Potential, Future Directions, and Knowledge Gaps

There are still important frontiers despite tremendous advancements. By addressing them, transformational applications will become possible[26].

6.1. Important Information Gaps

Systems-Level Integration: In a single cell, how are auxin, cytokinin, CLE-PXY, and other signals (brassinosteroids, gibberellins) quantitatively integrated to generate an accurate output?

The Function of Epigenetics: How do chromatin changes and short RNAs support perennial trees' long-term environmental adaptation, seasonal programming, and stem cell memory?

Single-Cell Dynamics: The cambial "zone" exhibits heterogeneity. To define the entire spectrum of cell states, find new regulators, and locate uncommon cell populations, single-cell RNA-sequencing (scRNA-seq) of the cambium is required[27].

Long-Distance Communication: How does the cambium accurately receive and interpret systemic signals from roots (such as drought cues) or leaves (such as photosynthetic status)?

6.2. Prospects for Further Research

creating a high-resolution atlas of the cambial stem cell niche using single-cell and spatial multi-omics.

creating tissue-specific, inducible gene editing systems (like CRISPR/Cas9) in trees to carry out functional genetics without having to wait a long time for phenotypic expression.

constructing predictive computer models that, depending on genetic and environmental inputs, may mimic cambial growth and wood property outcomes[28].

extending comparative research across various tree species (tropical vs. temperate, angiosperms vs. gymnosperms) in order to find species-specific innovations and conserved core mechanisms[29].

6.3. Forestry and Climate Resilience's Translational Potential

This overview of mechanistic understanding offers a clear path forward for biotechnology:

Molecular Breeding Markers: Important genes controlling fiber length, drought-responsive vessel characteristics, or lignin composition (such as CCoAOMT and CAD) can be employed as markers for expedited selection.

Precision Genetic Engineering: Goals consist of:

- altering the CLE-PXY pathway to change biomass production and stem cell proliferation rates.
- modifying transcription factors (such MYB and NAC) to modify the density and composition of wood for particular applications (like bioenergy and high-strength lumber).
- improving drought and cold resistance without sacrificing development by increasing the expression of osmoprotectant genes or stress-responsive TFs.

Synthetic Biology Approaches: "smart" forests that are climate-adaptable could be created by creating genetic circuits that enable trees to change their wood property programs in response to predetermined environmental stimuli[30].

6.4. Combining Primary and Secondary Growth Programs in a Synergistic Way

Although the focus of this analysis is secondary growth, the dynamics of primary growth are inextricably linked to the beginning and rate of secondary growth. The vascular cambium and shoot apical meristem (SAM) create a continuous developmental continuum rather than functioning independently.

Establishment of Procambium and Canalization of Auxin: According to the auxin canalization hypothesis, auxin flow is directed into distinct strands during primary growth, creating the pattern of primary vascular bundles (procambium). Later, these procambial strands unite to form the fascicular cambium, which combines with the interfascicular cambium (produced from parenchyma cells between bundles) to form the entire vascular cambium cylinder. Understanding this ontogenetic continuity is critical because variations in primary vascular architecture affect secondary growth potential over the long run [20].

Allocating Carbohydrates and Sink-Source Relationships: The cambium is an important sink tissue that competes for photosynthates with other sinks including developing leaves, fruits, and roots. Consequently, the pace of cambial activity is directly influenced by the strength of the canopy's supply and the signaling pathways that disperse carbon.

A signaling substance that can influence the expression of genes related to cell division and secondary cell wall formation, sucrose also functions as a fuel. Trehalose-6-phosphate, or T6P, is a key sugar signaling molecule that has demonstrated strong cambial activity regulation and may operate as a mediator of growth rate and metabolic state [31].

6.5. Plant-Microbiome Interaction in the Cambium: Protection and Growth

It is a new and emerging topic to understand how the internal microbiome, particularly endophytic bacteria and fungus, interacts with the vascular system and may influence cambial activity.

Through xylem colonization or coexistence with parenchyma cells, endophytes can stimulate a tree's defense mechanisms and induce systemic resistance (ISR). They can produce metabolites or initiate signaling that boosts the tree's own production of antimicrobial compounds (like phenolics and terpenoids) or fortify cell walls, altering the development of xylem cells to produce more resilient wood—a form of "developmental defense" [32].

Direct Control of Plant Hormones: Many endophytes have the ability to manufacture phytohormones, including auxin, cytokinin, gibberellin, and their precursors.

The stem's localized production of these hormones may have a subtle effect on the cambial niche's hormonal milieu, which could affect rates of differentiation or division in ways that benefit the microbe and the host (e.g., by improving food flow). The function of the wood microbiome in normal development versus stress conditions is still mostly unknown, which represents a significant gap in our thorough understanding of tree growth [33].

6.6. Evolutionary Developmental Biology of Secondary Growth (Evo-Devo)

The developments in the cambium that led to the diversity of woody forms and the emergence of woody plants can be found through an evolutionary examination.

Origin of the Bifacial Cambium: The transformation of a unifacial (generating cells on one side) meristem into a bifacial vascular cambium was a crucial evolutionary step.

The minimal genetic toolkit needed for this innovation can be determined by comparing investigations in non-woody angiosperms and basal vascular plants (such as lycophytes). It was probably crucial to recruit and co-opt existing genes for vascular patterning and lateral organ development (e.g., HD-ZIP III, KANADI, Class III KNOX) [23].

Diversity of Woody Growth Habits: Little is known about the molecular underpinnings of the astounding diversity in wood anatomy (e.g., vessel element size and grouping, fiber type, parenchyma distribution) and growth patterns (continuous vs. seasonal, monopodial vs. sympodial). Genetic alterations linked to particular woody characteristics can be identified by comparative genomics and transcriptomics across phylogenetically distinct trees. For example, are variations in the seasonal expression of auxin transporters or cell cycle genes responsible for the differences between diffuse-porous (maple) and ring-porous (oak) wood?

The Genetic Basis of Arborescence: What genetic alterations enable a herbaceous plant such as Arabidopsis to have a small cambium while its close relative, the genus Populus or the tree Arabidopsis lyrata, develops a large amount of woody tissue? These genetic switches for arborescence may be used to identify master regulators of wood making ability [24].

6.7. Socioeconomic, Ethical, and Regulatory Aspects of Biotechnology Implementation

Turning laboratory results into planted trees involves navigating a difficult environment that extends beyond the realm of pure science. Any evaluation with a strong applied focus must take these important factors into consideration.

Pollen-mediated gene transfer to wild relatives is a significant problem with genetically modified trees. Current research is examining methods like as male sterility, gene deletor technology, or chloroplast transformation (for maternal inheritance) to ensure biocontainment and address public and regulatory concerns [34].

Public Perception and Regulatory Pathways: Transgenic or gene-edited forest trees must pass a rigorous regulatory approval process in every country. Long-term field studies assessing environmental impact are essential, despite their cost and time commitment. Public involvement and candid communication regarding the goals (such climate adaptation and less stress on natural trees) and safeguards are essential for social licensing.

Access and Equity: Technology development and use must promote equity. This involves ensuring that smallholder foresters and communities in the Global South, which often face the greatest pressures from deforestation, benefit from the situation. An essential component of the field's ethical evolution is the establishment of open-source genetic resources for non-corporate tree species and frameworks for technology sharing [35].

7. Conclusion

The vascular cambium is a plant stem cell system of unparalleled ecological and economic importance. Research has advanced over the past 20 years from descriptive anatomy to a thorough understanding of molecules, however this information is still inadequate. Important transcriptional regulators, fundamental hormonal axis, and crucial peptide-receptor signaling modules that govern the fate of stem cells have all been identified. Rather than being a static factory, we view this system as a dynamic, adaptive processor of environmental input. The remaining challenges are formidable, but they are surmountable with modern tools.

Beyond merely being an academic activity, filling in these knowledge gaps is crucial to developing a new forestry paradigm. We might envision a future where trees are genetically optimized for rapid carbon sequestration, enhanced stress resilience, and customized material attributes. This would ensure that forests continue to provide vital ecological and economic benefits for future generations by moving away from traditional, phenotype-based selection and toward mechanism-informed design.

Compliance with ethical standards

Disclosure of conflict of interest

No conflict of interest to be disclosed.

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