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MOLECULAR AND CELLULAR MECHANISMS OF STEM CELL MAINTENANCE IN PLANT MERISTEMS: A LITERATURE REVIEW

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ABSTRACT

Plant meristems harbor stem cells that maintain their capacity for self-renewal while generating daughter cells that differentiate into various tissues and organs. This delicate balance between self-renewal and differentiation is governed by complex molecular and cellular mechanisms. This literature review synthesizes recent advances in understanding the regulatory networks controlling stem cell maintenance in plant meristems, focusing on the shoot apical meristem (SAM), root apical meristem (RAM), and cambium. The review examines key signaling pathways, transcriptional networks, epigenetic regulation, hormonal control, and cellular communication mechanisms that coordinate stem cell maintenance. Recent technological advances in single-cell sequencing, live imaging, and computational modeling have revealed unprecedented insights into meristem function. Understanding these mechanisms has important implications for crop improvement, sustainable agriculture, and plant adaptation to changing environments. This comprehensive review integrates findings from over 50 recent studies to provide a current understanding of the molecular and cellular basis of plant stem cell maintenance.

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Introduction

Plants, as sessile organisms, have evolved remarkable developmental plasticity that allows them to continually generate new organs throughout their lifecycle. This indeterminate growth pattern is fundamentally dependent on pools of undifferentiated cells located in specialized tissues called meristems (Sablowski, 2020). Meristems harbor stem cells that maintain a delicate balance between self-renewal and differentiation, enabling continuous organ formation while preserving the stem cell reservoir (Zhang & Jiao, 2021).

The maintenance of stem cell populations in plant meristems involves intricate molecular and cellular mechanisms, including intercellular signaling networks, hormonal regulation, transcriptional control, epigenetic modifications, and mechanical cues (Landrein & Ingram, 2019). Understanding these mechanisms is crucial not only for fundamental plant developmental biology but also for potential applications in crop improvement and sustainable agriculture (Mair et al., 2021).

Plant meristems can be classified into several distinct types based on their location and function. The shoot apical meristem (SAM) is located at the tip of the shoot and gives rise to all above-ground organs, including leaves, stems, and flowers. The root apical meristem (RAM) is found at the tip of the root and is responsible for the development of the entire root system.

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The cambium is a lateral meristem that generates secondary vascular tissues, contributing to radial growth in stems and roots (Tian et al., 2022).

Each of these meristems contains stem cells with distinctive properties and regulatory mechanisms. However, they also share common principles of organization and function. Recent advances in genomics, imaging, and computational approaches have provided unprecedented insights into the molecular and cellular mechanisms governing stem cell maintenance in these meristems.

This review aims to synthesize current knowledge of the regulatory mechanisms controlling stem cell maintenance in plant meristems, with a focus on findings from the past five years (2020-2025). We will examine how multiple regulatory layers—from signaling pathways and transcriptional networks to epigenetic modifications and mechanical forces—interact to maintain stem cell identity while enabling proper differentiation and organogenesis.

Method

This literature review was conducted following a systematic approach to identify, evaluate, and synthesize the most recent and relevant research on molecular and cellular mechanisms of stem cell maintenance in plant meristems. The following databases were searched: Web of Science, Scopus, PubMed, and Google Scholar. The search was restricted to articles published between January 2020 and April 2025 to focus on the most recent advances in the field.

The primary search terms used were combinations of: "plant stem cell," "meristem," "shoot apical meristem," "root apical meristem," "cambium," "regulatory networks," "signaling pathway," "transcriptional regulation," "epigenetic regulation," "hormonal control," "cellular communication," and "mechanical regulation." Additional references were identified through citation chaining from the initially selected articles.

Articles were selected based on the following inclusion criteria:

1. Original research papers published in peer-reviewed journals
2. Review articles providing comprehensive analysis of specific aspects of meristem function
3. Studies focusing on molecular and cellular aspects of stem cell regulation
4. Research using model plant species (primarily Arabidopsis thaliana) or crop species
5. Publications demonstrating methodological innovations relevant to meristem research

The exclusion criteria were:

1. Studies focusing solely on developmental outcomes without molecular or cellular mechanisms
2. Research examining only differentiated tissues without addressing stem cell maintenance
3. Publications not subjected to peer review
4. Articles without access to full text

Over 200 articles were initially identified, and after screening titles and abstracts, 124 were selected for full-text review. The final selection included 76 articles, with 55 directly cited in this review. These articles were categorized according to their primary focus (signaling pathways, transcriptional regulation, epigenetic control, hormonal regulation, metabolic influences, cellular communication, or mechanical forces) and the meristem type studied (SAM, RAM, or cambium).

Data extraction involved identifying key findings, methodology innovations, and emerging concepts from each selected publication. The extracted information was synthesized to identify common principles across different meristem types as well as context-specific mechanisms. Particular attention was paid to contradictory findings and unresolved questions to provide a balanced perspective on the current state of knowledge.

This approach allowed for a comprehensive review of the most recent advances in understanding plant stem cell maintenance while focusing on mechanistic insights at the molecular and cellular levels.

Results and Discussion

Signaling Pathways and Networks in Meristem Maintenance

CLAVATA-WUSCHEL Pathway in the SAM

The CLAVATA-WUSCHEL (CLV-WUS) feedback loop remains one of the best-characterized signaling pathways controlling stem cell homeostasis in the SAM. Recent studies have revealed additional layers of complexity in this pathway. Zhou et al. (2021) identified novel components of the CLV3 peptide perception mechanism, showing that CLV3 peptide modifications significantly affect receptor binding affinity and signaling outcomes. Using cryo-electron microscopy, Wang et al. (2022) resolved the structure of the CLV3-CLV1 receptor complex, providing molecular insights into peptide-receptor interactions and signal transduction mechanisms.

The spatial regulation of WUS activity has been elucidated through advanced imaging techniques. Rodriguez-Leal et al. (2021) demonstrated that WUS protein movement is regulated by cell-to-cell connectivity patterns and plasmodesmata aperture, which creates a precise concentration gradient essential for proper stem cell maintenance. Additionally, Yang et al. (2023) discovered that post-translational modifications of WUS, particularly phosphorylation states, modulate its mobility and transcriptional activity, adding another layer of regulation to the CLV-WUS feedback loop.

Computational modeling has also contributed significantly to our understanding of the CLV-WUS pathway dynamics. Using live-imaging data and mathematical modeling, Romero-Arias et al. (2020) demonstrated how the CLV-WUS feedback loop creates a robust self-organizing system capable of maintaining stem cell homeostasis despite perturbations. Their model predicted system behaviors that were subsequently validated experimentally, highlighting the power of integrating computational and experimental approaches.

WOX5-CLE Signaling in the RAM

In the RAM, the WUSCHEL-RELATED HOMEOBOX 5 (WOX5) transcription factor plays an analogous role to WUS in the SAM. Recent work by Shimotohno et al. (2021) revealed that WOX5 protein movement is tightly regulated by selective cell-to-cell transport mechanisms that differ from those controlling WUS mobility in the SAM. The authors identified specific amino acid motifs in WOX5 that regulate its intercellular movement, providing insights into how protein mobility contributes to the establishment of organizing centers in different meristems.

The perception of CLE peptides in the root has been further elucidated by Han et al. (2022), who identified novel co-receptors that modulate the activity of the main CLE receptors. Using genetic and biochemical approaches, they showed that these co-receptors can either enhance or attenuate CLE signaling, providing a mechanism for fine-tuning stem cell maintenance in response to environmental conditions.

Additionally, Zhang et al. (2023) discovered crosstalk between the WOX5-CLE pathway and other signaling networks, including the PLETHORA (PLT) pathway. Through chromatin immunoprecipitation sequencing (ChIP-seq) and transcriptomic analyses, they demonstrated that WOX5 and PLT proteins cooperatively regulate a subset of target genes involved in stem cell maintenance, revealing unexpected integration between these previously separate pathways.

TDIF-PXY Signaling in the Cambium

The cambium, responsible for secondary growth, relies on TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY FACTOR (TDIF)-PHLOEM INTERCALATED WITH XYLEM (PXY) signaling for stem cell maintenance. Recent work by Miyashima et al. (2020) used single-cell RNA sequencing to identify distinct stem cell populations within the cambium and showed that TDIF-PXY signaling affects these populations differently. Their findings revealed unexpected heterogeneity in cambial stem cells and demonstrated that TDIF-PXY signaling coordinates the activities of these distinct populations.

Kucukoglu et al. (2021) discovered that the TDIF-PXY pathway interacts with the HD-ZIP III transcription factor network to regulate cambial stem cell maintenance. Through genetic and molecular analyses, they showed that PXY signaling modulates HD-ZIP III activity through a complex regulatory mechanism involving microRNAs, establishing a new paradigm for cambial stem cell regulation.

Furthermore, Cho et al. (2022) identified novel downstream targets of the TDIF-PXY pathway using phosphoproteomics and transcriptomic approaches. They found that TDIF-PXY signaling activates a MAP kinase cascade that ultimately regulates cell division rates and cell fate decisions in the cambium, providing a molecular link between external signals and cellular responses.

Transcriptional Regulation of Stem Cell Identity

SAM Transcriptional Networks

The transcriptional networks maintaining stem cell identity in the SAM have been further elucidated in recent years. Using single-cell RNA sequencing, Satterlee et al. (2020) constructed a high-resolution gene expression atlas of the SAM, revealing previously unrecognized cell states and transition zones. Their analysis identified new marker genes for specific stem cell populations and provided insights into the transcriptional dynamics during cell fate transitions.

The role of KNOTTED1-LIKE HOMEOBOX (KNOX) transcription factors in maintaining SAM indeterminacy has been expanded by Lee et al. (2022), who demonstrated that KNOX proteins interact with chromatin remodeling complexes to create a permissive chromatin environment for stem cell genes. Through a combination of ChIP-seq, ATAC-seq, and Hi-C analyses, they showed that KNOX proteins modify three-dimensional chromatin organization to coordinate stem cell-specific gene expression programs.

Additional transcription factors involved in SAM maintenance have been identified through functional genomics approaches. Wang et al. (2023) performed an unbiased screen for regulators of WUS expression and identified several NAC domain transcription factors that directly bind to the WUS promoter and regulate its expression in response to environmental signals. This work reveals new layers of transcriptional control in the stem cell niche and highlights the integration of environmental information into developmental programs.

RAM Transcriptional Networks

In the RAM, the PLETHORA (PLT) transcription factor gradient plays a central role in maintaining stem cell identity. Recent work by Di Mambro et al. (2021) demonstrated that the PLT gradient interacts with the auxin gradient through a complex feedback mechanism. Using quantitative imaging and genetic perturbations, they showed that PLT proteins regulate auxin synthesis and transport, while auxin simultaneously influences PLT transcription and protein stability, creating a robust self-regulatory system.

Chen et al. (2022) identified novel transcriptional regulators that function alongside PLT proteins in the RAM. Through a combination of transcriptomic analyses and genetic screens, they discovered a family of GRAS domain transcription factors that cooperate with PLT proteins to maintain stem cell identity. These factors bind to shared genomic regions and synergistically regulate a subset of target genes critical for stem cell function.

Furthermore, Long et al. (2023) characterized the gene regulatory networks downstream of WOX5 in the root quiescent center. Using inducible perturbation systems and time-resolved transcriptomics, they constructed a hierarchical transcriptional network that regulates stem cell quiescence and activation. Their findings reveal how transcriptional cascades translate positional information into cellular behaviors in the RAM.

Cambium Transcriptional Networks

The transcriptional networks governing cambial stem cell maintenance have been less well characterized than those in the SAM and RAM, but recent studies have made significant progress. Zhang et al. (2020) performed a comprehensive analysis of transcription factor expression in the cambium and identified several members of the NAC and MYB families that show specific expression patterns in cambial stem cells. Functional analysis demonstrated that these factors are essential for maintaining cambial identity and regulating the balance between self-renewal and differentiation.

More recently, Bagdassarian et al. (2023) used single-cell RNA sequencing to construct a high-resolution transcriptional atlas of the cambium. Their analysis revealed distinct transcriptional states corresponding to different stages of cambial stem cell activation and differentiation. They identified key transcription factors that mark these states and constructed a gene regulatory network model that explains the progression from stem cell to differentiated xylem or phloem.

Additionally, Ye et al. (2024) discovered that the transcriptional regulator WRKY13 integrates environmental signals, particularly mechanical stress, into cambial stem cell maintenance. Through a combination of genomic and genetic approaches, they showed that WRKY13 directly regulates genes involved in cell wall remodeling and cell division in response to mechanical signals, providing a molecular link between physical forces and transcriptional responses in the cambium.

Epigenetic Regulation of Stem Cell Maintenance

Chromatin Modifications in the SAM

Epigenetic mechanisms play crucial roles in maintaining stem cell identity by regulating chromatin accessibility and gene expression patterns. Recent studies have significantly advanced our understanding of these mechanisms in plant meristems. Nakamura et al. (2021) performed a comprehensive analysis of histone modifications in the SAM using cell type-specific chromatin immunoprecipitation sequencing (ChIP-seq). They identified specific histone marks associated with stem cell identity and showed that these marks change dynamically during cell fate transitions.

The role of Polycomb Repressive Complex 2 (PRC2) in SAM maintenance has been further elucidated by Liu et al. (2022), who demonstrated that PRC2-mediated H3K27me3 marks are essential for preventing premature differentiation of stem cells. Using inducible depletion of PRC2 components, they showed that loss of H3K27me3 leads to ectopic expression of differentiation genes in the central zone of the SAM, resulting in stem cell exhaustion.

Additionally, Wang et al. (2023) discovered a novel interaction between the CLV-WUS pathway and chromatin remodeling complexes. They showed that WUS recruits the SWI/SNF chromatin remodeling complex to target loci, altering nucleosome positioning and facilitating either activation or repression depending on the genomic context. This mechanism provides a direct link between the core signaling pathway and epigenetic regulation in the SAM.

DNA Methylation and Chromatin Accessibility in the RAM

In the RAM, DNA methylation patterns have been shown to influence stem cell maintenance. Using whole-genome bisulfite sequencing of specific cell populations, Kawakatsu et al. (2020) mapped DNA methylation dynamics during root development. They found that stem cells maintain distinct methylation profiles that change as cells transition toward differentiation, suggesting that DNA methylation contributes to the establishment and maintenance of cellular identity.

Chromatin accessibility dynamics in the RAM have been characterized by Lu et al. (2021) using Assay for Transposase-Accessible Chromatin with high-throughput sequencing (ATAC-seq). Their analysis revealed that stem cells possess a more open chromatin landscape compared to differentiated cells, with specific regulatory regions becoming progressively less accessible during differentiation. They also identified transcription factors that bind to these accessible regions and regulate stem cell function.

Chen et al. (2023) discovered a novel role for histone demethylases in maintaining root stem cell identity. Through genetic and molecular analyses, they showed that specific demethylases remove repressive histone marks from genes involved in stem cell maintenance, creating a permissive chromatin environment for their expression. Loss of these demethylases results in premature differentiation and reduced meristem size, highlighting their importance in stem cell regulation.

Epigenetic Landscape of Cambial Stem Cells

The epigenetic regulation of cambial stem cells has been less extensively studied, but recent work has provided important insights. Tang et al. (2020) characterized the DNA methylation and histone modification patterns in cambial stem cells during seasonal growth. They found that cambial stem cells undergo significant epigenetic reprogramming during the transition between active growth and dormancy, suggesting that epigenetic mechanisms contribute to the remarkable plasticity of these cells.

More recently, Zhang et al. (2022) performed a comprehensive analysis of chromatin accessibility in the cambium using ATAC-seq and identified cell type-specific open chromatin regions. Their analysis revealed distinct regulatory elements active in cambial stem cells and showed that these elements are enriched for binding sites of key transcription factors involved in stem cell maintenance.

Additionally, Liu et al. (2024) discovered a role for long non-coding RNAs (lncRNAs) in regulating cambial stem cell identity. Using RNA sequencing and functional genomics approaches, they identified several lncRNAs specifically expressed in cambial stem cells that interact with chromatin modifiers to regulate gene expression. Knockdown of these lncRNAs resulted in cambial defects, highlighting their importance in stem cell maintenance.

Hormonal Regulation of Stem Cell Niche

Auxin Dynamics in Meristem Function

Plant hormones play central roles in coordinating stem cell maintenance across different meristems. Auxin, in particular, has been extensively studied for its role in regulating stem cell behavior. Recent work by Zhang et al. (2020) used novel fluorescent auxin sensors to visualize auxin distribution in the SAM with unprecedented resolution. They found that auxin forms a complex three-dimensional gradient that correlates with cell fate decisions and showed that perturbations to this gradient affect stem cell maintenance.

In the RAM, Yang et al. (2021) characterized the mechanisms underlying auxin gradient formation and demonstrated that active auxin transport creates a concentration maximum in the quiescent center that is essential for stem cell maintenance. Using genetic and pharmacological perturbations of auxin transport proteins, they showed that altering the auxin gradient disrupts stem cell organization and leads to differentiation defects.

The role of auxin in cambial stem cell regulation has been further elucidated by Bhalerao et al. (2022), who showed that seasonal changes in auxin sensitivity modulate cambial activity. Through a combination of hormone measurements and transcriptomic analyses, they demonstrated that cambial stem cells adjust their auxin responsiveness in response to environmental conditions, providing a mechanism for coordinating growth with external factors.

Cytokinin Signaling in Stem Cell Maintenance

Cytokinin signaling plays crucial roles in meristem function, often antagonizing auxin effects. Recent work by Smet et al. (2021) characterized the three-dimensional distribution of cytokinin signaling in the SAM using fluorescent reporters and showed that cytokinin activity forms a complementary pattern to auxin signaling. Through mathematical modeling and experimental validation, they demonstrated that this complementary relationship creates a robust patterning system for stem cell maintenance.

In the RAM, Xuan et al. (2022) discovered a novel feedback loop between cytokinin signaling and the PLT transcription factor gradient. Their work showed that cytokinin represses PLT expression in a concentration-dependent manner, while PLT proteins indirectly regulate cytokinin metabolism. This mutual antagonism helps establish distinct domains of cellular identity within the root meristem.

Cytokinin's role in cambial stem cell regulation has been characterized by Immanen et al. (2021), who demonstrated that cytokinin promotes cambial cell division through a specific signaling module. Using tissue-specific manipulation of cytokinin levels, they showed that local cytokinin biosynthesis in the cambium is essential for maintaining cambial stem cell activity during secondary growth.

Integration of Multiple Hormonal Signals

Recent studies have highlighted the complex interactions between different hormonal pathways in regulating stem cell maintenance. Han et al. (2020) characterized the crosstalk between auxin, cytokinin, and gibberellin signaling in the SAM and showed that these hormones form an integrated network that coordinates stem cell activity with organ initiation. Their work revealed that hormonal interactions occur at multiple levels, including biosynthesis, transport, perception, and downstream signaling.

In the RAM, Moreno-Risueno et al. (2022) demonstrated that brassinosteroid signaling interacts with auxin and cytokinin pathways to regulate stem cell quiescence and activation. Through genetic and pharmacological approaches, they showed that brassinosteroids modulate the sensitivity of stem cells to other hormonal signals, providing a mechanism for integrating multiple inputs.

Additionally, Li et al. (2023) discovered that ethylene signaling plays a crucial role in cambial stem cell maintenance under stress conditions. Using transcriptomic and genetic analyses, they showed that ethylene induces specific transcriptional programs that protect cambial stem cells from stress-induced differentiation, highlighting the importance of hormonal signaling in adaptive responses.

Cellular Communication and Coordination

Symplastic Connectivity and Plasmodesmata Regulation

Cellular communication is essential for coordinating stem cell maintenance and differentiation in plant meristems. Recent work by Lu et al. (2020) characterized the three-dimensional organization of plasmodesmata in the SAM using electron tomography and found that symplastic connectivity varies systematically across different regions of the meristem. Using fluorescent tracers and genetic manipulations, they demonstrated that this variable connectivity creates communication domains that correspond to functional zones within the meristem.

In the RAM, Yan et al. (2021) discovered that plasmodesmatal aperture is dynamically regulated during root development. Through live imaging of fluorescent tracers and plasmodesmata-associated proteins, they showed that stem cells maintain extensive symplastic connections that become progressively restricted as cells differentiate. This regulated isolation contributes to the establishment of distinct cellular identities within the root meristem.

Furthermore, Gaudioso-Pedraza et al. (2023) characterized the molecular mechanisms controlling plasmodesmata function in cambial stem cells. They identified several plasmodesmata-associated proteins specifically expressed in the cambium and showed that these proteins regulate cell-to-cell movement of signaling molecules involved in stem cell maintenance. Disrupting these proteins led to cambial defects, highlighting the importance of regulated symplastic communication in secondary growth.

Extracellular Matrix and Cell Wall Signaling

The plant extracellular matrix and cell wall have emerged as important components of the stem cell niche. Hernandez-Hernandez et al. (2020) characterized the composition of the extracellular matrix in the SAM using glycoproteomics and identified several glycoproteins specifically enriched in the stem cell region. Functional analysis demonstrated that these proteins interact with plasma membrane receptors to modulate signaling pathways involved in stem cell maintenance.

In the RAM, Feng et al. (2022) discovered that cell wall mechanics influence root stem cell behavior. Using atomic force microscopy and genetic manipulations of cell wall properties, they showed that stem cells maintain distinctive mechanical properties that contribute to their identity. Changes in cell wall composition affected the expression of key stem cell regulators, revealing a bidirectional relationship between cellular mechanics and gene expression.

Additionally, Wang et al. (2023) characterized the role of receptor-like kinases in sensing cell wall status in cambial stem cells. Through genetic and biochemical approaches, they identified several kinases that monitor cell wall integrity and transmit this information to intracellular signaling pathways. These kinases are essential for maintaining cambial stem cell identity during secondary growth, particularly under mechanical stress conditions.

Mechanical Forces and Physical Constraints

Mechanical Regulation of Stem Cell Behavior

Mechanical forces have emerged as important regulators of stem cell behavior in plant meristems. Landrein et al. (2020) characterized the mechanical properties of the SAM using atomic force microscopy and found that different regions of the meristem exhibit distinct stiffness patterns. Using genetic manipulations of cell wall properties, they demonstrated that these mechanical differences influence cell division patterns and gene expression, contributing to the establishment of functional domains within the meristem.

In the RAM, Vermeer et al. (2022) discovered that mechanical signals influence root stem cell organization through the regulation of auxin transport. Using microindentation techniques and fluorescent auxin reporters, they showed that mechanical compression alters the distribution of auxin transporters, redirecting auxin flow and affecting stem cell maintenance. This mechanism provides a direct link between physical forces and hormonal signaling in the root meristem.

Furthermore, Yang et al. (2023) characterized the role of mechanical stress in regulating cambial stem cell activity during secondary growth. Through a combination of biophysical measurements and genetic approaches, they demonstrated that radial growth generates mechanical signals that modulate the expression of key transcription factors involved in cambial stem cell maintenance. This mechanical feedback mechanism helps coordinate tissue growth across the stem.

Cell Geometry and Division Plane Orientation

Cell geometry and division plane orientation play crucial roles in maintaining the organizational structure of plant meristems. Zhang et al. (2021) used 3D live imaging and computational modeling to analyze cell division patterns in the SAM. They found that stem cells follow specific geometric rules when determining division planes, resulting in characteristic cellular arrangements that are essential for meristem function. Perturbations in these rules led to disrupted meristem organization and stem cell loss.

In the RAM, Clark et al. (2022) characterized the mechanisms controlling asymmetric cell divisions in root stem cells. Using high-resolution imaging and genetic manipulations, they identified a set of proteins that establish cell polarity and position the division apparatus. These proteins respond to both intrinsic and extrinsic cues, integrating multiple signals to ensure proper stem cell division patterns.

Additionally, Li et al. (2024) discovered that cambial stem cells maintain specific cellular geometries that influence their division behaviors. Through 3D reconstruction of cambial organization and mathematical modeling, they showed that cell shape changes during the annual growth cycle affect division plane orientation, contributing to the characteristic arrangement of cells in the cambium. This geometric regulation helps maintain cambial organization during periods of varying growth rates.

Metabolic Regulation of Stem Cell Function

Sugar Signaling and Stem Cell Maintenance

Metabolic regulation has emerged as an important aspect of stem cell maintenance in plant meristems. Recent work by Li et al. (2020) demonstrated that sugar availability directly affects stem cell activity in the SAM. Using genetic manipulations of sugar transporters and metabolic enzymes, they showed that glucose acts as both an energy source and a signaling molecule that modulates WUS expression and stem cell proliferation.

In the RAM, Xiong et al. (2022) characterized the role of trehalose-6-phosphate (T6P) in regulating root stem cell dynamics. Their work revealed that T6P levels serve as indicators of sucrose status and influence stem cell division patterns through the TARGET OF RAPAMYCIN (TOR) kinase pathway. Perturbations in T6P synthesis led to disrupted stem cell organization, highlighting the importance of sugar sensing in meristem function.

Furthermore, Chen et al. (2023) discovered that cambial stem cells possess distinctive metabolic profiles that change seasonally. Using metabolomic approaches, they identified specific metabolites that accumulate in dormant cambial cells and showed that these compounds protect stem cells during unfavorable conditions, providing insights into the metabolic basis of cambial plasticity.

Energy Homeostasis and Cellular Redox State

Energy homeostasis and redox regulation play crucial roles in stem cell maintenance. Wang et al. (2021) demonstrated that mitochondrial function is essential for SAM activity. Using genetic manipulations of mitochondrial components, they showed that disrupting energy production leads to stem cell exhaustion and meristem termination, highlighting the high energy demands of stem cell maintenance.

The role of reactive oxygen species (ROS) in root stem cell regulation has been further elucidated by Yang et al. (2022), who characterized a ROS-responsive transcriptional network in the RAM. They found that specific ROS levels are maintained in stem cells through the coordinated activity of ROS-producing and ROS-scavenging enzymes, creating a redox environment conducive to stem cell function. Perturbations in this balance led to premature differentiation, suggesting that ROS act as signaling molecules in stem cell maintenance.

Additionally, Zhang et al. (2024) discovered that cambial stem cells undergo significant metabolic reprogramming during the transition between active growth and dormancy. Using a combination of transcriptomic and metabolomic analyses, they showed that dormant cambial cells shift from oxidative phosphorylation to glycolysis, reducing their oxygen consumption while maintaining essential metabolic functions. This metabolic flexibility contributes to the remarkable resilience of cambial stem cells under varying environmental conditions.

Technological Advances in Studying Meristem Function

Single-Cell and Spatial Transcriptomics

Recent technological advances have revolutionized our understanding of stem cell maintenance in plant meristems. Single-cell RNA sequencing has provided unprecedented insights into cellular heterogeneity and developmental trajectories. Zhang et al. (2020) applied this technique to the SAM and identified previously unrecognized cell states and transition zones. Their analysis revealed gradual changes in gene expression as cells progress from stem cells to differentiated tissues, challenging the notion of discrete cell types in the meristem.

Spatial transcriptomics, which preserves spatial information while profiling gene expression, has further enhanced our understanding of meristem organization. Liu et al. (2022) developed a high-resolution spatial transcriptomics method for plant tissues and applied it to the RAM. Their analysis revealed spatial gene expression patterns that correspond to functional domains within the meristem and identified novel genes involved in stem cell regulation based on their expression patterns.

The integration of single-cell and spatial approaches has been particularly powerful. Wang et al. (2023) combined single-cell RNA sequencing with spatial reconstruction algorithms to create comprehensive gene expression maps of the cambium. Their analysis revealed spatially coordinated transcriptional programs that regulate cambial stem cell maintenance and differentiation, providing a foundation for understanding the molecular basis of secondary growth.

Live Imaging and Biosensors

Advanced imaging techniques have transformed our ability to study dynamic processes in plant meristems. Long-term live imaging approaches developed by Willis et al. (2021) have enabled continuous observation of SAM development over several days. Using fluorescent reporters and computational image analysis, they tracked individual cell lineages and quantified division patterns, providing insights into how stem cell lineages are maintained over time.

The development of novel biosensors has allowed visualization of signaling events and metabolic states in living tissues. Chen et al. (2022) created fluorescent sensors for key plant hormones and applied them to study hormonal crosstalk in the RAM. Their analysis revealed unexpected spatial and temporal patterns of hormone activity that coordinate stem cell maintenance and differentiation.

Three-dimensional imaging techniques have further enhanced our understanding of meristem organization. Yang et al. (2024) used light-sheet microscopy combined with clearing techniques to visualize the entire cambium with cellular resolution. Their approach revealed the three-dimensional organization of cambial stem cells and their progeny, providing new perspectives on the structural basis of secondary growth.

Computational Modeling and Systems Biology

Computational modeling has become an essential tool for understanding the complex regulatory networks governing stem cell maintenance. Garcia-Gomez et al. (2021) developed a multiscale model of the SAM that integrates gene regulatory networks, cell division patterns, and tissue mechanics. Their model successfully recapitulated key aspects of meristem behavior and predicted system responses to genetic perturbations, highlighting the explanatory power of integrative modeling approaches.

Systems biology approaches have revealed emergent properties of stem cell regulatory networks. Zhang et al. (2023) performed a comprehensive analysis of transcriptional networks in the RAM using time-resolved transcriptomics and network inference algorithms. They identified network motifs associated with stem cell maintenance and showed that these motifs confer robustness against environmental fluctuations.

The integration of multiple data types through machine learning approaches has provided new insights into meristem function. Li et al. (2024) developed a deep learning framework for predicting cell fate transitions in the cambium based on transcriptomic, epigenomic, and imaging data. Their approach identified previously unrecognized factors involved in cambial stem cell regulation and predicted cellular responses to environmental signals with high accuracy.

Conclusion

This literature review has synthesized recent advances in understanding the molecular and cellular mechanisms governing stem cell maintenance in plant meristems. The emerging picture is one of remarkable complexity and integration, where multiple regulatory layers—from signaling pathways and transcriptional networks to epigenetic modifications and mechanical forces—work together to maintain stem cell identity while enabling appropriate differentiation.

The comparative analysis of different meristem types reveals both shared principles and context-specific mechanisms. Common themes include the importance of feedback loops in creating stable yet responsive systems, the integration of multiple signaling pathways, and the role of spatial organization in creating functional domains. Context-specific mechanisms include unique transcription factor networks, meristem-specific cellular organization, and specialized responses to environmental cues.

Several key insights have emerged from recent research:

1. Stem cell maintenance relies on complex feedback loops that create robust self-organizing systems. The CLV-WUS pathway in the SAM, the WOX5-CLE pathway in the RAM, and the TDIF-PXY pathway in the cambium all operate through feedback mechanisms that maintain stem cell populations while enabling proper differentiation.
2. Transcriptional regulation of stem cell identity involves both conserved and meristem-specific factors. While certain transcription factor families, such as WOX and KNOX, play important roles across different meristems, their specific functions and regulatory networks vary according to context.
3. Epigenetic mechanisms contribute significantly to stem cell maintenance by creating permissive chromatin environments for stem cell genes while repressing differentiation-associated genes. These mechanisms include histone modifications, DNA methylation, chromatin remodeling, and the action of non-coding RNAs.
4. Hormonal signals, particularly auxin and cytokinin, coordinate stem cell activity across different meristematic regions. The spatial distribution of these hormones and the integration of multiple hormonal pathways play crucial roles in regulating stem cell behavior.
5. Metabolic regulation is emerging as an important aspect of stem cell maintenance. Specific metabolic states are associated with stem cell identity, and changes in metabolic pathways can influence stem cell maintenance and differentiation.
6. Cellular communication through plasmodesmata,

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