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Multi-Scale Regulation Mechanisms of Tree Stem Cells: From Molecular Level to Ecosystems

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Abstract Tree stem cells are fundamental to the growth, development, and adaptation of trees, necessitating a comprehensive understanding of their multi-scale regulation. This study examines the intricate regulation of tree stem cells from molecular to ecosystem levels. At the molecular level, genetic control, transcription factors, and epigenetic modifications govern stem cell maintenance and differentiation. Cellular regulation involves signaling pathways, hormonal control, and cell-to-cell communication. Tissue and organ-level regulation is focused on stem cell niches, their role in tissue regeneration, and integration into organ development. The whole plant level considers the coordination of stem cell activity with overall plant growth and environmental responses. Ecosystem-level regulation explores the impact of biotic and abiotic factors on stem cells and their role in ecosystem resilience. This study underscores the potential applications in forestry and conservation, highlighting emerging technologies and future research directions. Understanding these regulatory mechanisms is crucial for advancing tree biology, improving forest management, and enhancing ecosystem resilience.
Keywords Tree stem cells; Multi-scale regulation; Genetic control; Hormonal interactions; Ecosystem resilience

1 Introduction

Tree stem cells are fundamental units of plant growth and regeneration, possessing the remarkable ability to differentiate into various cell types and contribute to the formation of new tissues and organs. These cells are located in specific regions known as meristems, which include the shoot apical meristem, root apical meristem, and vascular cambium (Aichinger et al., 2012; Heidstra and Sabatini, 2014). The maintenance and regulation of these stem cells are crucial for the continuous growth and longevity of trees, which can span several centuries (Aichinger et al., 2012). Recent advances in molecular biology have begun to unravel the complex regulatory networks that govern stem cell behavior, including the roles of transcriptional regulators, phytohormones, and cell wall components (Groover and Robischon, 2006; Hata and Kyozuka, 2021).

The regulation of tree stem cells occurs at multiple scales, from molecular and cellular levels to whole ecosystems. At the molecular level, various signaling pathways and genetic mechanisms ensure the balance between stem cell self-renewal and differentiation (Heidstra and Sabatini, 2014; Ikeuchi et al., 2016; Pérez-García and Moreno-Risueno, 2018; Hata and Kyozuka, 2021). Cellular interactions within the stem cell niches provide the necessary microenvironment for stem cell maintenance and function (Aichinger et al., 2012; Hoggatt and Scadden, 2012). Additionally, environmental factors and stress conditions can influence stem cell behavior, highlighting the importance of understanding these regulatory mechanisms in the context of changing ecosystems (Ikeuchi et al., 2016; Díaz-Sala et al., 2019). This multi-scale regulation is essential for the adaptation and resilience of trees, enabling them to respond to environmental challenges and maintain their regenerative capacity over long periods.

This study aims to provide a comprehensive overview of the multi-scale regulation mechanisms of tree stem cells, from the molecular level to ecosystems. We will explore the latest research findings on the molecular pathways involved in stem cell maintenance and differentiation, the role of stem cell niches, and the impact of environmental factors on stem cell behavior. By integrating knowledge from various scales, we hope to shed light on the complex regulatory networks that underpin tree growth and regeneration. This study will also discuss the implications of these findings for forest management and conservation, emphasizing the importance of preserving the regenerative potential of trees in the face of environmental changes.

2 Molecular Level Regulation

2.1 Genetic control of stem cell maintenance and differentiation

Genetic control of stem cell maintenance and differentiation is primarily governed by a network of transcription factors and signaling pathways. Key transcription factors such as NANOG, OCT4, and SOX2 play crucial roles in maintaining stem cell pluripotency and regulating differentiation. These factors form a mutual regulatory circuit with polycomb repressive complexes and microRNAs, ensuring a balance between self-renewal and differentiation (Kashyap et al., 2009). Additionally, the interplay between cell cycle regulators and transcription factors is essential for coordinating stem cell proliferation and differentiation, highlighting the evolutionary significance of these interactions (Engström, 2021).

2.2 Role of transcription factors in stem cell regulation

Transcription factors are pivotal in regulating stem cell behavior by modulating gene expression. NANOG, for instance, enhances embryonic stem cell self-renewal by promoting chromatin accessibility and maintaining repressive histone marks at developmental regulators (Heurtier et al., 2018). The integration of signaling pathways with transcriptional networks further influences stem cell fate, as seen in the dynamic regulation of chromatin-modifying enzymes and nucleosome occupancy (Figure 1) (Fagnocchi et al., 2015). This intricate network of transcription factors and signaling pathways ensures the precise control of stem cell pluripotency and differentiation.

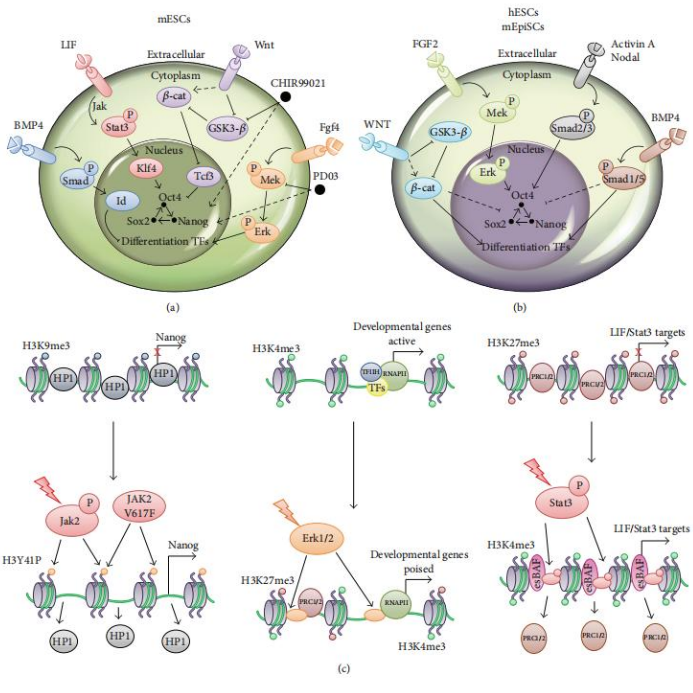

Figure 1 Signaling affecting stem cells identity and their interplay with chromatin (Adopted from Fagnocchi et al., 2015)

Image caption: Key signaling pathways and relative factors contributing to the maintenance of mESCs (a) or hESCs/EpiSCs (b) identity or to their differentiation (see details in the main text). Black circles in (a) indicate the two chemicals used in the 2i culturing medium (CHIR99021 and PD03). Solid black arrows and lines indicate positive or negative modulation, respectively. Dashed black lines indicate indirect effects. Colored circles with "P" indicate phosphorylation. (c) Key examples of signaling to chromatin in ESCs. The upper panels are relative to a more differentiated state in which the LIF/Stat3 and Nanog targets are repressed while developmental genes are active. Lower panels, instead, describe embryonic stem cells chromatin features. On the right, effect of Jak2, or its constitutive active form Jak2V617F, on H3Y41P and HP1 loading on chromatin. In the middle, interconnection between Erk1/2 and the loading of PRC2 and RNA polymerase II activity at developmental genes. On the left, interplay between the esBAF complex and Stat3 in regulating LIF/Stat3 signaling pathway targets (Adopted from Fagnocchi et al., 2015)

2.3 Epigenetic modifications influencing stem cell function

Epigenetic modifications, including DNA methylation, histone modifications, and non-coding RNA-mediated events, are critical for regulating stem cell function. These modifications establish heritable gene expression patterns that guide stem cell differentiation and maintain cellular memory (Wu and Sun, 2006). Histone acetylation and methylation, for example, play significant roles in promoting or repressing gene expression during cell differentiation (Ikeuchi et al., 2015). The dynamic nature of epigenetic regulation is further exemplified by the role of microRNAs in controlling stem cell fate by repressing the translation of specific mRNAs (Gangaraju and Lin, 2009). The interplay between epigenetic mechanisms and transcriptional networks is essential for maintaining stem cell identity and ensuring proper differentiation (Li and Zhao, 2008; Wutz, 2013).

3 Cellular Level Regulation

3.1 Signaling pathways involved in stem cell regulation

Stem cell regulation is critically dependent on various signaling pathways that control their self-renewal, differentiation, and response to environmental cues. Key pathways include the Wnt, Notch, and BMP signaling pathways, which are essential for maintaining stem cell properties and ensuring proper tissue development and regeneration (Zhang and Li, 2005; Guo et al., 2015; Sonnen and Janda, 2021). For instance, the Notch signaling pathway is known to regulate stem cell maintenance and proliferation, and its dysregulation can lead to diseases such as cancer (Figure 2) (Janghorban et al., 2018; Sonnen and Janda, 2021). Similarly, the BMP signaling pathway plays a crucial role in stem cell self-renewal and differentiation across different stem cell systems, including embryonic and hematopoietic stem cells (Zhang and Li, 2005). These pathways often interact with each other and with other cellular mechanisms to create a robust regulatory network that ensures the proper functioning of stem cells.

3.2 Hormonal control and interaction with stem cells

Hormones such as auxin and cytokinin are pivotal in regulating stem cell niches, particularly in plant systems. These phytohormones exhibit complex interactions that are crucial for the maintenance and function of stem cells in both shoot and root meristems (Zhao et al., 2010; Schuster et al., 2014; García-Gómez et al., 2017). For example, in the shoot apical meristem (SAM) of *Arabidopsis thaliana*, cytokinin promotes stem cell proliferation, while auxin has a more nuanced role, sometimes inhibiting cytokinin signaling to fine-tune stem cell activity (Zhao et al., 2010). The interplay between these hormones is mediated by specific transcription factors and response regulators, which integrate hormonal signals to modulate stem cell behavior (Schuster et al., 2014; García-Gómez et al., 2017). This hormonal control is essential for the dynamic regulation of stem cell niches, allowing plants to adapt to environmental changes and developmental cues.

3.3 Cell-to-cell communication and its impact on stem cell behavior

Cell-to-cell communication is a fundamental aspect of stem cell regulation, enabling the coordination of stem cell activities within their niches and with surrounding differentiated cells. This communication is mediated through various signaling pathways and direct cell contacts, which collectively influence stem cell fate decisions (Burgess et al., 2014; Guo et al., 2015; Sonnen and Janda, 2021). For instance, signaling pathways such as Wnt and Notch not only regulate stem cell properties but also facilitate interactions between stem cells and their niche, ensuring a balanced environment for stem cell maintenance and differentiation (Guo et al., 2015; Sonnen and Janda, 2021). Additionally, metabolic signals and feedback mechanisms play a significant role in this communication, linking cellular metabolism with stem cell function and ensuring that stem cells can respond appropriately to changes in their microenvironment (Burgess et al., 2014). Understanding these intricate communication networks is crucial for unraveling the complex regulation of stem cells and their roles in development and tissue homeostasis.

4 Tissue and Organ Level Regulation

4.1 Stem cell niches in trees: structure and function

Stem cell niches are specialized microenvironments that regulate the behavior of stem cells, ensuring their self-renewal and differentiation. In trees, these niches are crucial for maintaining the balance between stem cell proliferation and differentiation, which is essential for growth and regeneration. The structure of stem cell niches in trees is similar to those found in other organisms, comprising various cellular and extracellular components that provide biochemical and mechanical signals to the stem cells (Singh, 2012; Ema and Suda, 2012; Chacón-Martínez et al., 2018). These niches are located in specific regions such as the shoot, root, and vascular meristems, which are responsible for the formation of new organs and tissues throughout the tree's life (Aichinger et al., 2012).

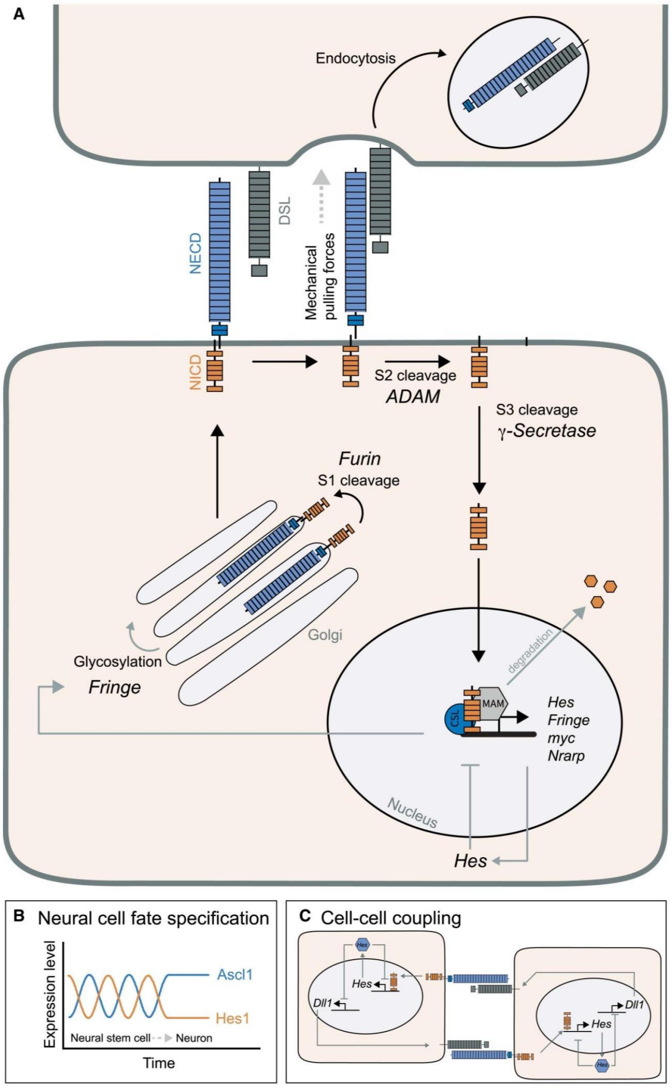

Figure 2 Dynamics of Notch signalling (Adopted from Sonnen and Janda, 2021)

Image caption: (A) Notch is generated in the endoplasmic reticulum and travels to the plasma membrane via the Golgi apparatus. In the Golgi, the first proteolytic cleavage is mediated by Furin, which leads to the formation of a Notch heterodimer. There, Notch binding affinities can be modulated by post-translational modifications, e.g. glycosylation by Fringe. When the ligand from a neighbouring cell interacts with Notch, a mechanical pulling force results in a conformational change in Notch. This allows the proteolytic cleavage of Notch by ADAM and then γ-Secretase, which finally releases NICD (Notch intracellular domain) into the cytoplasm. In the nucleus, NICD interacts with the transcription factor CSL and the co-activator Mam to induce the expression of Notch target genes. Among these are Hes genes, which initiate a delayed negative feedback loop, as well as Fringe and Nrarp, which both feed back onto Notch signalling. Finally, NICD is phosphorylated and degraded by the proteasome. (B) Due to the negative feedback loop of Hes proteins, Hes expression oscillates in many systems. In neural stem cells of the developing brain Hes1 oscillates alternatingly with pro-neural genes. When Hes1 oscillations cease and pro-neural proteins get stabilized, cells differentiate. (C) Neighbouring cells can couple via Notch signalling and synchronize their intracellular oscillations, for instance during periodic segmentation of vertebrate embryos. This is thought to be achieved by reciprocal activation of Notch signalling in neighbouring cells and induction of the ligand Dll1 (Adopted from Sonnen and Janda, 2021)

4.2 Role of stem cells in tissue regeneration and repair

Stem cells play a pivotal role in tissue regeneration and repair by replacing damaged or lost cells. In trees, stem cells located in the meristems are activated in response to injury or environmental stress, leading to the regeneration of tissues and organs. The dynamic regulation of stem cell fate by niche-derived cues ensures that stem cells can adapt to changing conditions and meet the needs of the tissue (Ema and Suda, 2012; Hoggatt and Scadden, 2012; Chacón-Martínez et al., 2018; Mannino et al., 2021). For instance, the redox and metabolic states of the niche can influence stem cell behavior, promoting differentiation and migration in response to oxidative stress, which is crucial for efficient healing and revascularization (Ushio-Fukai and Rehman, 2014).

4.3 Integration of stem cells in organ development

The integration of stem cells into organ development is a complex process that involves coordination between multiple stem cell-niche units distributed across the tissue. In trees, this process is regulated by both local and systemic signals that ensure the proper spatial and temporal control of stem cell activity (Moore and Lemischka, 2006; Ema and Suda, 2012; O'Brien and Bilder, 2013). The specialized niches in the shoot, root, and vascular meristems provide the necessary signals to maintain stem cell pluripotency and guide their differentiation into specific cell types required for organ formation (Aichinger et al., 2012). Additionally, the interplay between intrinsic and extrinsic factors within the niche ensures that stem cells can respond to developmental cues and environmental changes, facilitating the continuous growth and adaptation of the tree (Lutolf and Blau, 2009; Singh, 2012). By understanding the multi-scale regulation mechanisms of tree stem cells, from the molecular level to ecosystems, we can gain insights into the fundamental processes that drive plant growth, regeneration, and adaptation. This knowledge can inform strategies for improving tree health and resilience in the face of environmental challenges.

5 Whole Plant Level Regulation

5.1 Coordination of stem cell activity with overall plant growth

The coordination of stem cell activity with overall plant growth is a complex process that involves the integration of various signaling pathways and environmental cues. Stem cells in the shoot apical meristem (SAM) and root apical meristem (RAM) are regulated by a network of transcription factors and phytohormones. For instance, the homeodomain transcription factor WUSCHEL (WUS) and the bHLH transcription factor HECATE1 (HEC1) play crucial roles in maintaining stem cell proliferation in the SAM by controlling genes involved in metabolism and hormone signaling (Schuster et al., 2014). Additionally, the vascular cambium, a stem cell-like tissue responsible for secondary growth, is regulated by long-distance signaling molecules such as auxin and strigolactones, which coordinate cambium activity with other growth processes (Agustí et al., 2011). This intricate regulatory network ensures that stem cell activity is synchronized with the overall growth and development of the plant.

5.2 Response of stem cells to environmental cues

Stem cells in plants are highly responsive to environmental cues, which allows them to adapt their growth and development to changing conditions. Environmental factors such as light, temperature, and nutrient availability influence stem cell activity through various signaling pathways. For example, cell elongation in the *Arabidopsis hypocotyl* is regulated by a central circuit of interacting transcription factors, including ARF6, PIF4, and BZR1, which integrate hormonal and environmental signals to modulate growth (Oh et al., 2014). Additionally, the activity of meristems is influenced by environmental conditions such as nitrate availability and drought, which affect the balance between self-renewal and differentiation of stem cells (Shimotohno and Scheres, 2019). This responsiveness to environmental cues enables plants to optimize their growth and development in diverse environments.

5.3 Long-distance signaling and its effects on stem cell regulation

Long-distance signaling plays a critical role in the regulation of stem cell activity in plants. The vascular system, comprising xylem and phloem, serves as the main conduit for the transmission of long-distance signals, including RNAs, proteins, and phytohormones (Figure 3) (Kondhare et al., 2021). These mobile signals regulate various physiological processes such as flowering, leaf and root development, and stress responses. For instance, auxin and strigolactones are key hormones involved in long-distance signaling that regulate cambium activity and secondary growth (Agustí et al., 2011). Additionally, reactive oxygen species (ROS) and other signaling molecules are integrated with pathways involving Ca^{2+} signaling, protein kinases, and hormones to modulate defense mechanisms and stress responses (Suzuki and Katano, 2018). The integration of long-distance signals with local regulatory networks ensures coherent growth and development across the entire plant.

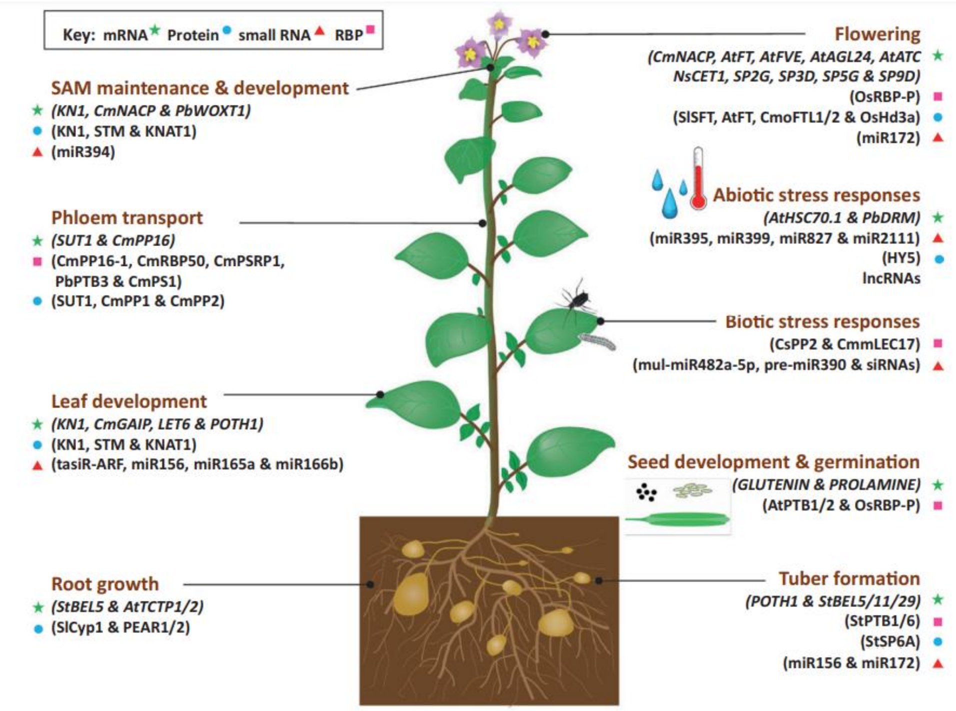

Figure 3 Schematic representation of phloem-mobile signals in plants (mRNAs, RBPs, sRNAs, and proteins) (Adopted from Kondhare et al., 2021)

Image caption: Grouped by their functions in growth, development, and biotic/abiotic stress responses (Adopted from Kondhare et al., 2021)

6 Ecosystem Level Regulation

6.1 Impact of biotic factors on stem cells

Biotic factors, including symbiotic relationships, play a crucial role in the regulation of tree stem cells. Symbiotic fungi, for instance, form mutualistic associations with tree roots, enhancing nutrient uptake and promoting stem cell activity and growth. These interactions are essential for maintaining the health and functionality of forest ecosystems. The complexity of trophic networks and biotic associations significantly influences ecosystem multifunctionality, as demonstrated in subalpine forests where species richness across multiple trophic levels enhances ecosystem functions (Luo et al., 2022). Additionally, plant growth regulators (PGRs) are involved in plant-plant communications and defense mechanisms against biotic stress, further influencing stem cell behavior and tree resilience (Johnson, 1987).

6.2 Influence of abiotic factors on stem cell function

Abiotic factors such as climate, soil properties, and environmental stressors have profound effects on the function and regulation of tree stem cells. For instance, temperature, water availability, and soil nutrients directly impact the physiological processes of trees, including stem cell activity. Long non-coding RNAs (lncRNAs) and MYB transcription factors are key molecular players that help plants adapt to abiotic stresses like drought, salinity, and temperature extremes by regulating stress-responsive genes (Jha et al., 2020; Wang et al., 2021). Furthermore, the synthesis of cellulose, a critical component of plant cell walls, is influenced by abiotic factors such as osmotic conditions, ionic stress, light, and temperature, which in turn affects overall plant growth and stem cell function (Wang et al., 2016). The interplay between plant functional traits and abiotic site conditions also mediates ecosystem functions, with traits like specific leaf area and wood density responding to environmental changes and affecting aboveground carbon stocks (Bu et al., 2019).

6.3 Role of stem cells in ecosystem resilience and adaptation

Tree stem cells are pivotal in ensuring ecosystem resilience and adaptation to changing environmental conditions. The ability of stem cells to self-renew and differentiate is crucial for the regeneration and maintenance of tree populations, which in turn supports ecosystem stability. Mitochondrial dynamics within stem cells regulate their identity and fate decisions, influencing self-renewal and differentiation processes that are essential for adapting to environmental stresses (Khacho et al., 2016). Additionally, the regulatory mechanisms involving PGRs help trees minimize the impact of stress and enhance resistance to subsequent stressors, contributing to cross-adaptation and resilience (Johnson, 1987). The integration of biotic and abiotic signals by stem cells allows for a dynamic response to environmental cues, ensuring the long-term sustainability and functionality of forest ecosystems. By understanding the multi-scale regulation mechanisms of tree stem cells, from molecular to ecosystem levels, we can better appreciate the intricate balance that sustains forest ecosystems and their ability to adapt to a rapidly changing world.

7 Applications and Future Directions

7.1 Potential applications in forestry and conservation

The regulation of tree stem cells at multiple scales offers significant potential for applications in forestry and conservation. Advances in somatic embryogenesis (SE) and organogenesis have paved the way for improved clonal propagation programs, particularly for species with low regeneration capacity such as conifers. These biotechnologies can enhance forest tree improvement and support multi-varietal forestry, which is crucial for maintaining genetic diversity and resilience in forest ecosystems (Díaz-Sala, 2019). Additionally, the integration of genomics and epigenetics into forest management practices can help in adapting forests to environmental changes and preserving genetic resources (Plomion et al., 2016; Amaral et al., 2020). The ability to manipulate genetic and epigenetic factors can lead to the development of trees with enhanced growth, survival, and resistance to pests and pathogens, thereby supporting sustainable forestry and conservation efforts (Grossman et al., 2018).

7.2 Emerging technologies for studying stem cell regulation

Recent technological advancements have significantly enhanced our understanding of stem cell regulation in trees. Genomics and bioinformatics tools have been instrumental in uncovering the complexities of tree genomes, including gene regulation, genome evolution, and responses to biotic and abiotic stresses (Plomion et al., 2016). Epigenetic studies have also emerged as a promising field, providing insights into tree phenotypic plasticity and adaptive responses (Amaral et al., 2020). Furthermore, new genetic technologies, such as CRISPR and other gene-editing tools, are being applied to forest trees to study and manipulate developmental processes, including secondary growth and the maintenance of meristematic stem cells (Groover and Robischon, 2006). These technologies, combined with advanced cell and tissue culture techniques, offer new prospects for the mass production of improved forest tree stock and the preservation of genetic resources.

7.3 Future research directions and unanswered questions

Despite the progress made, several research directions and unanswered questions remain in the study of tree stem cell regulation. One key area is the need to better understand the molecular pathways involved in SE and organogenesis, particularly the interaction between auxin, stress conditions, and cell identity regulators (Díaz-Sala, 2019). Additionally, there is a need to explore the potential of epigenetic modifications in enhancing tree adaptability to climate change and other environmental stressors (Amaral et al., 2020). Future research should also focus on the long-term impacts of tree diversity on ecosystem functioning, as current experiments have mostly run for less than ten years (Grossman et al., 2018). Understanding the mechanistic bases of biodiversity-ecosystem functioning relationships in tree-dominated systems will be crucial for developing effective conservation strategies. Finally, integrating aboveground and belowground approaches, as well as utilizing remote sensing and spectral technologies, can provide a more comprehensive understanding of tree physiology and its implications for ecosystem health (Grossman et al., 2018). By addressing these research gaps and leveraging emerging technologies, we can develop innovative strategies for forest management and conservation, ensuring the sustainability and resilience of forest ecosystems in the face of global environmental challenges.

8 Concluding Remarks

The regulation of tree stem cells operates across multiple scales, from molecular mechanisms to ecosystem-level interactions. At the molecular level, single-cell RNA sequencing has revealed the complex regulatory networks that govern stem cell differentiation, highlighting the importance of transcriptional and epigenetic controls. In plants, stem cells exhibit remarkable developmental plasticity, enabling regeneration and the formation of new organs, with key regulatory mechanisms involving hormonal, genetic, and epigenetic factors. Specific transcription factors, such as BRAVO and WOX5 in Arabidopsis roots, play crucial roles in maintaining stem cell quiescence and regulating root architecture.

Additionally, the microenvironment, including biophysical and material cues, significantly influences stem cell behavior and fate. At the organismal level, secondary growth in woody plants involves the coordination of tissue patterning and cell differentiation, regulated by transcriptional regulators and phytohormones. The regenerative capacity of forest tree species, particularly conifers, is influenced by developmental factors such as genotype and tissue age, with molecular pathways involving auxin and stress conditions playing critical roles. Furthermore, redox regulation, involving reactive oxygen species (ROS), has been identified as a key mechanism in maintaining the balance between stem cell maintenance and differentiation.

Understanding the multi-scale regulation mechanisms of tree stem cells has profound implications for tree biology and ecology. At the molecular level, insights into the transcriptional and epigenetic regulation of stem cells can inform strategies for enhancing tree regeneration and growth, which is crucial for forest management and conservation. The identification of key regulatory factors and pathways provides potential targets for genetic engineering to improve tree resilience and adaptability to environmental stresses.

At the ecosystem level, the ability of trees to regenerate and maintain their growth through stem cell regulation is vital for ecosystem stability and biodiversity. Trees play a critical role in carbon sequestration, water regulation, and habitat provision, and their health directly impacts the broader ecological balance. Understanding the influence of microenvironmental factors on stem cell behavior can lead to better management practices that support tree health and forest sustainability.

Moreover, the knowledge of redox regulation in stem cell maintenance and differentiation offers new perspectives on how trees respond to oxidative stress and environmental changes, which is essential for predicting and mitigating the impacts of climate change on forest ecosystems. Overall, the multi-scale study of tree stem cell regulation enhances our ability to conserve and sustainably manage forest resources, ensuring their continued ecological and economic benefits.

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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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