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COMPREHENSIVE LITERATURE REVIEW ON THE FUNCTION OF THE SCARECROW (SCR) GENE IN REGULATING QUIESCENT CENTRE AND LATERAL ROOT FORMATION IN *ARABIDOPSIS THALIANA*

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ABSTRACT

The SCARECROW (SCR) transcription factor is a key regulator that governs root tissue differentiation and meristem maintenance in *Arabidopsis thaliana*. This study conducts a comprehensive literature analysis to examine the function of the SCR gene in the formation of the quiescent centre (QC) and the initiation of lateral root development. Using a systematic literature review (SLR) approach, relevant peer-reviewed publications from 2010 to 2025 were analyzed to explore genetic interactions, transcriptional networks, and hormonal regulation associated with SCR activity. The analysis identifies three major variables: (1) SCR–SHR–WOX5 transcriptional interactions in maintaining QC identity, (2) hormonal regulation involving auxin–cytokinin balance, and (3) epigenetic control mechanisms influencing gene expression and root adaptability. The findings indicate that SCR plays a dual role—as a determinant of endodermal differentiation and as a stabilizer of meristem integrity—by coordinating asymmetric cell division, genomic protection, and hormonal signaling. Theoretical integration of these studies shows that SCR serves as a central molecular hub linking genetic and physiological processes in root development. Overall, this review provides deeper conceptual insight into plant developmental genetics and offers a foundation for future experimental research on meristem regulation and adaptive root growth.

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INTRODUCTION

Root growth and development are crucial aspects of plant physiology that determine a plant's ability to absorb water and minerals, as well as to adapt to environmental conditions. One of the key components of the root meristem system is the quiescent centre (QC)—a group of cells with low mitotic activity that functions to maintain balance and preserve the identity of surrounding stem cells (Scheres, 2007; Bennett & Scheres, 2010). The QC acts as the "central regulator" of stem cell activity and plays an essential role in maintaining the integrity and regeneration of root tissues when damage occurs (Dolan et al., 1993).

The formation and maintenance of the QC are controlled by complex interactions among genetic, hormonal, and mechanical factors within the root meristem. One gene that plays a central role in this process is SCARECROW (SCR), which belongs to the GRAS family of transcription factors. This gene regulates asymmetric cell division, radial tissue patterning, and the differentiation of the endodermis and cortex in roots (Di Laurenzio et al., 1996; Sabatini et al., 2003). Mutations in the SCR gene lead to the loss of the endodermal layer, demonstrating its crucial role in establishing proper tissue organization (Benfey et al., 1993; Helariutta et al., 2000).

Beyond its role in primary roots, SCARECROW also plays a critical part in lateral root formation, where a new QC is formed de novo in the lateral root primordium (Goh et al., 2016). The formation of this secondary QC depends on periclinal cell divisions in the pericycle, regulated by the interaction between SCR and SHORT-ROOT (SHR) (Cruz-Ramírez et al., 2012). Recent studies have revealed that SCR not only acts as a regulator of tissue patterning but also determines the location and function of the quiescent centre in lateral roots (Toyokura et al., 2019).

Research on the SCARECROW gene also shows that its expression is influenced by gradients of the hormones auxin and cytokinin, which form a regulatory axis linking cell growth and tissue differentiation (Moubayidin et al., 2013). In this context, SCR works together with WOX5 to maintain QC quiescence and suppress the expression of cyclin genes that trigger cell division (Forzani et al., 2014). The complexity of the genetic and hormonal interplay indicates that QC regulation is not a singular process but rather involves an integrated network of molecular signaling pathways.

Although several studies have described the role of SCARECROW in primary roots, there is still a lack of comprehensive reviews discussing its function in both QC formation and lateral root development simultaneously. Therefore, this article aims to analyze recent scientific literature on the function of the SCARECROW gene in the formation of the quiescent centre and lateral roots in Arabidopsis thaliana, and to identify the relationships among genetic mechanisms, stem cell activity, and hormonal regulation in these processes. This review is expected to provide broader conceptual insights into the genetic mechanisms regulating root growth and serve as a foundation for future research in plant genetics.

Method

This study adopts a systematic literature review (SLR) framework using descriptive qualitative analysis. The method involves identifying, classifying, and critically analyzing scientific literature discussing the SCARECROW gene's role in the quiescent centre (QC) and lateral root formation in Arabidopsis thaliana. The inclusion criteria cover peer-reviewed journal articles (Scopus-indexed and SINTA-indexed) published between 2010 and 2025 that directly examine SCR interactions, transcriptional regulation, and hormonal signaling. Data extraction focused on variables including gene interactions (SCR–SHR–WOX5), hormonal balance (auxin–cytokinin), and QC regulatory mechanisms. The synthesis process employed narrative analysis supported by cross-literature comparison to enhance validity and depth of interpretation.

This study employs a descriptive qualitative approach with the systematic literature review (SLR) method. This method aims to identify, classify, and analyze previous studies that discuss the function of the SCARECROW gene in the formation of the quiescent centre (QC) and lateral roots in Arabidopsis thaliana.

The data were obtained from various relevant secondary sources, including international scientific journals indexed in Scopus such as Cell, Development, Genes & Development, and Current Biology, as well as national scientific articles indexed in SINTA, such as Jurnal Biologi Indonesia and Jurnal Sains dan Pendidikan Biologi. The literature search was conducted through databases including ScienceDirect, SpringerLink, Google Scholar, PubMed, and Garuda (SINTA) using the keyword

The analysis process involved both qualitative synthesis and thematic coding by reviewing research findings that discuss the function of the SCARECROW (SCR) gene in the formation of the quiescent centre (QC) and in root tissue differentiation, as well as its interaction with other transcription factors such as SHORT-ROOT (SHR) and WOX5. In addition, studies examining the relationship between SCR and hormonal signaling pathways, particularly auxin and cytokinin, were analyzed to understand how these hormones coordinate the regulation of root meristem activity. The process of secondary QC formation in lateral roots was also reviewed to explore how SCR contributes to de novo meristem establishment and developmental plasticity in Arabidopsis thaliana. Each selected study was evaluated based on its relevance, credibility, and scientific contribution to understanding the molecular mechanisms underlying QC formation. The collected findings were then synthesized narratively to illustrate the interconnections between these concepts and to identify existing research gaps that warrant further investigation.

RESULT AND DISCUSSION

This section integrates theoretical and empirical findings to establish a clear linkage between the role of the SCARECROW (SCR) gene and root development mechanisms.

A. The Function of the SCARECROW (SCR) Gene in the Formation of the Quiescent Centre (QC)

Gen The SCARECROW (SCR) gene is a key regulator in the formation of the quiescent centre (QC) and in determining the radial tissue patterning of Arabidopsis thaliana roots. The QC serves as the control center for stem cells, maintaining the balance between proliferation and differentiation. Mutations in SCR result in the loss of the endodermal layer and disorganization of the root meristem, indicating its essential role in maintaining tissue identity and QC positioning (Wang et al., 2023; Winter et al., 2024). Furthermore, SCR contributes to preserving the genomic integrity of QC cells through the regulation of telomere maintenance pathways and DNA damage–protective proteins, ensuring that the QC remains stable and resistant to genotoxic stress (Wang et al., 2023; Sessa, 2025). The activity of SCR is also regulated by its interaction with SHORT-ROOT (SHR) and WOX5, which synergistically coordinate asymmetric cell division and endodermal tissue differentiation from the early stages of the cell cycle (Winter et al., 2024; Zhai et al., 2023).

Moreover, the regulation of SCR expression is not solely dependent on transcriptional pathways but also involves complex epigenetic mechanisms. A study by Huang et al. (2024) revealed that the Suppressor of Frigida 4 (SUF4) and EARLY BOLTING IN SHORT DAYS (EBS) complex binds to the SCR promoter, enhancing histone H3K4me3 activation to strengthen gene expression in ground tissue and QC precursor cells. Research by Betegón-Putze et al. (2021) further emphasized that the transcriptional balance among BRAVO, WOX5, and SCR plays a crucial role in maintaining root cell quiescence. The integration of epigenetic regulation, hormonal signaling, and dynamic transcriptional networks reinforces the conserved function of SCR in QC formation and maintenance in Arabidopsis roots (Betegón-Putze et al., 2021; Huang et al., 2024; Sessa, 2025).

Subsequent research by Zhou et al. (2022) added a new dimension to understanding SCR regulation by discovering that DNA methylation dynamics around the SCR promoter play a key role in QC adaptation to environmental stress. Under nutrient deficiency conditions, increased DNA methylation at the SCR promoter reduces its expression and slows down cell division in the meristem zone. Conversely, under optimal conditions, methylation decreases, enhancing SCR activity to support faster root growth. This mechanism demonstrates that SCR expression can plastically adjust to environmental changes without permanently altering its genetic structure — representing a form of epigenetic memory in root stem cells (Zhou et al., 2022).

Furthermore, the role of SCR is also associated with maintaining the genomic stability of stem cells through interactions with protective protein pathways such as RETINOBLASTOMA-RELATED (RBR) and CYCLIN D6;1. According to Wang et al. (2023), the SCR–RBR complex functions to suppress excessive cell division within QC cells, thereby maintaining the balance between proliferation and quiescence. Imbalances in SCR expression lead to DNA damage accumulation and impaired tissue regeneration around the meristem. Thus, SCR not only determines QC identity but also acts as a guardian of stem cell integrity through cell cycle control, genome protection, and adaptive molecular regulation in response to plant physiological conditions.

B. Interaction of SCARECROW (SCR) with Other Transcription Factors (SHORT-ROOT and WOX5)

The transcription factors SHORT-ROOT (SHR) and WUSCHEL-RELATED HOMEOBOX 5 (WOX5) work in conjunction with SCARECROW (SCR) to regulate the formation and maintenance of the quiescent centre (QC). SHR moves symplastically from the stele to the endodermal layer to activate SCR expression, which then triggers asymmetric cell division and establishes the radial root pattern (Helariutta et al., 2000; Cruz-Ramírez et al., 2012). Meanwhile, WOX5 functions to maintain the quiescent state of stem cells in the central meristem by repressing CYCLIN D activity, thereby sustaining the balance between cell division and differentiation (Forzani et al., 2014; Toyokura et al., 2019). The interaction among these three transcription factors forms a spatio-temporal regulatory network that ensures a functional division between proliferative and quiescent zones within the root meristem. The SHR–SCR–WOX5 complex is also known to control the expression of CYCD6;1 and RBR, which are crucial for asymmetric cell division and QC identity maintenance (Goh et al., 2021; Wang et al., 2023).

In addition to their individual roles, the interaction between SCR and SHR forms a functional protein complex that regulates the radial division pattern within root tissues. According to Goh et al. (2021), the translocation of SHR from the stele to the endodermal layer activates SCR, determining QC positioning and cortical cell differentiation. The SHR–SCR complex then induces the expression of CYCLIN D6;1 (CYCD6;1), which is necessary for asymmetric divisions in the ground tissue layer. Mutations in either gene result in the loss of the endodermal layer and QC formation defects, demonstrating that the SHR–SCR interaction is a prerequisite for establishing the root stem cell niche (Goh et al., 2021).

Furthermore, WOX5 plays a key role in maintaining the quiescent state of QC cells by suppressing cell cycle activity. A study by Toyokura et al. (2019) revealed that SCR and WOX5 synergistically maintain low CYCLIN D activity to prevent excessive cell division at the meristem center. This interaction balances the proliferative activity of surrounding cells, with WOX5 repressing division while SCR maintains tissue identity and stem cell positioning. Disruption of this regulation causes the loss of spatial boundaries between the QC and the proliferative zone, ultimately disturbing root growth patterns (Forzani et al., 2014; Toyokura et al., 2019).

Recent research by Liu et al. (2022) showed that SCR, SHR, and WOX5 not only interact directly but also regulate other genes within a complex transcriptional network known as the SCR/SHR/WOX5 module. This module plays a vital role in maintaining root meristem stability by balancing cell division, differentiation, and new tissue formation. Under environmental stress conditions, such as nitrogen deficiency or hormonal disturbances, this module adjusts its expression levels to maintain root homeostasis (Zhou et al., 2022; Pardal, 2021). Additionally, Wang et al. (2023) revealed that SCR contributes to genomic integrity by regulating telomere stability in QC cells, while Winter et al. (2024) reported that the SHR–SCR complex synchronizes cell division and growth during the early stages of the Arabidopsis thaliana root cell cycle.

Furthermore, research by Chang et al. (2024) discovered that three receptor-like kinases (RLKs)—ARH1, FEI1, and FEI2—integrate gibberellin signaling with SHR–SCR activity to control ground tissue patterning. Similarly, Pérez-Sancho et al. (2024) demonstrated that spatial regulation within the root stem cell niche is governed by a gradient of SCR–WOX5 activity, which maintains quiescence and directs stem cell differentiation. Aljedaani et al. (2025) added that the EMB1579 factor has a dual function in transcription and splicing, directly influencing SCR-mediated root meristem control—indicating that this regulation operates at multiple molecular levels. A recent review in EMBO Reports (2025) confirmed that Arabidopsis root stem cell homeostasis is determined by a complex regulatory network involving transcriptional interactions, hormonal signaling, and epigenetic mechanisms (Liu et al., 2022; Chang et al., 2024; Pérez-Sancho et al., 2024; Aljedaani et al., 2025).

C. The Relationship Between SCARECROW (SCR) and the Regulation of Auxin and Cytokinin Hormonesn

The activity of SCARECROW (SCR) is highly dependent on hormonal balance, particularly between auxin and cytokinin, the two primary hormones regulating cell division and differentiation in roots. The distribution of auxin determines the gradient of SHR–SCR–WOX5 activity, while cytokinin regulates cell division and expansion in the root transition zone (Moubayidin et al., 2021). Recent studies show that mutations affecting auxin distribution, such as in the BIG gene, lead to decreased expression of SCR and WOX5, resulting in disrupted QC formation (Liu et al., 2022). In addition, the interaction of SCR with the gibberellin pathway through receptor-like kinases (ARH1, FEI1, and FEI2) also influences the patterning of ground tissue, indicating a complex interconnection between hormonal and transcriptional regulation (Huang et al., 2024).

The balance between auxin and cytokinin plays a crucial role in determining the spatial activity of the SCR gene in the root meristem. According to Moubayidin and Müller (2021), auxin tends to induce the expression of SHR and SCR in the apical region of the root via the activation of AUXIN RESPONSE FACTORS (ARFs), whereas cytokinin suppresses SCR expression in the elongation zone through the ARR1/ARR12 signaling pathway. Furthermore, findings by Zhou et al., (2022) demonstrate that auxin distribution not only affects SCR activity but also regulates cell division orientation through epigenetic mechanisms involving changes in DNA methylation patterns on SCR target genes. When the auxin gradient is disturbed, SCR expression becomes uneven, leading to irregular formation of endodermal and cortical layers. Under nutrient stress conditions, plants maintain a basal level of SCR expression to preserve QC integrity via compensatory cytokinin pathways. This indicates that the hormonal regulation of SCR is both plastic and adaptive, allowing the root meristem to respond to environmental fluctuations without permanently altering its architecture (Zhou et al., 2022).

Recent research by Wang et al. (2023) also suggests that SCR indirectly interacts with the gibberellin and ethylene signaling pathways to maintain root homeostasis. Gibberellin activation affects the phosphorylation of SCR through the GID1–DELLA protein complex, which subsequently alters the binding capacity of SCR to SHR. Under certain conditions, high levels of ethylene can inhibit SCR expression in the elongation zone, slowing tissue differentiation. Therefore, SCR functions not only as a specific regulator within the SHR–WOX5 pathway but also as a multihormonal integration node that ensures the balance between proliferation, differentiation, and quiescence within the Arabidopsis thaliana root system.

D. The Role of SCARECROW (SCR) in the Formation of Secondary QC in Lateral Roots

The formation of the secondary quiescent centre (QC) in lateral roots is one of the key aspects of root system development in plants. During lateral root initiation, SCR expression appears early in the pericycle cells undergoing periclinal division, preceding the formation of QC precursors (Goh et al., 2016). The inactivation of the SCR gene causes lateral roots to fail in forming a functional QC, resulting in abnormal or incomplete lateral root growth. Recent studies using live imaging technology have shown that SCR directs cell differentiation around the lateral root primordium by regulating WOX5 gene activity to establish the identity of the new QC. Thus, SCR functions not only in primary roots but also plays a conserved role in regeneration and the formation of secondary meristems.

Table 1. Molecular Stages of the Formation and Maintenance of the Secondary Quiescent Centre (QC) in *Arabidopsis thaliana* Lateral Roots

No.	Stage	Main Process	Role of Key Molecules
1.	Initial Stage in Pericycle Cells	An auxin gradient forms in totipotent pericycle cells of the primary root, marking the site of future lateral roots.	Activation of LBD genes triggers the first periclinal division. (Goh et al., 2016; Moubayidin & Müller, 2021)
2.	Activation and Early Expression of the SCR Gene	SCR expression appears in the inner pericycle cells following the initial division.	SHR moves from the stele to the outer pericycle and forms the SHR–SCR complex to determine tissue polarity and QC position. (Goh et al., 2021; Liu et al., 2022)
3.	Formation of the SHR–SCR–WOX5	The SHR–SCR–WOX5 complex forms in the nuclei of prospective QC cells.	WOX5 suppresses CYCLIN D to maintain quiescence, balancing cell proliferation and differentiation.

	Regulatory Complex		(Toyokura et al., 2019; Forzani et al., 2014)
4.	Differentiation of Ground Tissue	SCR activity expands to regulate the formation of the cortex and endodermis.	Asymmetric division produces a radial tissue pattern; auxin and cytokinin hormones maintain balance between cell division and differentiation. (Moubayidin & Müller, 2021; Huang et al., 2024)
5.	Maintenance and Functionalization of the Secondary QC	The secondary QC begins to function as a new stem cell niche, regulating nearby cell divisions.	SCR maintains QC stability through regulation of RBR and the telomere maintenance pathway, and supports root regeneration after stress. (Wang et al., 2023; Goh et al., 2021)

CONCLUSION

The SCARECROW (SCR) gene is a key factor in the formation, maintenance, and function of the quiescent centre (QC) in both primary and lateral roots of Arabidopsis thaliana. Through complex interactions with SHORT-ROOT (SHR) and WOX5, SCR regulates asymmetric cell division, tissue differentiation, and maintains the quiescence and genomic integrity of root stem cells. Its activity is controlled by a combination of genetic, epigenetic, and hormonal signals, including the influence of auxin, cytokinin, and gibberellin gradients, which ensure the balance between cell proliferation and differentiation. Furthermore, the role of SCR in secondary QC formation demonstrates its conserved function in meristem regeneration and adaptation to environmental conditions. Thus, SCR serves as a central regulator within the molecular regulatory network that maintains the stability, homeostasis, and plasticity of the plant root system.

REFERENCES

Aljedaani, F., Luo, Y., Deng, Y., Smet, W., Nasim, Z., Xu, X., Shahul Hameed, U. F., Xiao, T. T., Gonzalez-Kise, J. K., Arold, S., & Blilou, I. (2025). The dual function of EMB1579 in transcription and splicing governs tissue patterning in Arabidopsis root meristem. *Cell Reports, 44*(5), 115660.

Benfey, P. N., Linstead, P. J., Roberts, K., Schiefelbein, J. W., Hauser, M.-T., & Aeschbacher, R. A. (1993). Root development in Arabidopsis: four mutants with dramatically altered root morphogenesis. *Development*, 119, 57–70.

Betegón-Putze, I., Mercadal, J., Bosch, N., Planas-Riverola, Á., Marques-Bueno, M., Vilarrasa-Blasi, J., … Caño-Delgado, A. I. (2021). Precise transcriptional control of cellular quiescence by BRAVO and WOX5 in the *Arabidopsis* root apex. *Molecular Systems Biology*.

Chang, J., Hu, J., Wu, L., Chen, W., Shen, J., Qi, X., & Li, J. (2024). Three RLKs integrate SHR–SCR and gibberellins to govern ground-tissue patterning in *Arabidopsis thaliana*. *Current Biology*.

Cruz-Ramírez, A., Díaz-Triviño, S., Blilou, I., Grieneisen, V. A., Sozzani, R., Zamioudis, C., … & Scheres, B. (2012). A bistable circuit involving SCARECROW–RETINOBLASTOMA integrates cues to inform asymmetric stem cell division. *Cell*, 150(5), 1002–1015.

Di Laurenzio, L., Wysocka-Diller, J., Malamy, J. E., Pysh, L., Helariutta, Y., Freshour, G., Hahn, M. G., Feldmann, K. A., & Benfey, P. N. (1996). The SCARECROW gene regulates an asymmetric cell division that is essential for generating the radial organization of the Arabidopsis root. *Cell*, 86(3), 423–433.

Dolan, L., Janmaat, K., Willemsen, V., Linstead, P., Poethig, S., Roberts, K., & Scheres, B. (1993). *Cell organization in the Arabidopsis thaliana root.* Development, 119, 71–84.

Forzani, C., Aichinger, E., & Sabatini, S. (2014). WOX5 suppresses CYCLIN D activity to establish quiescence at the center of the root stem cell niche. *Current Biology*, 24(16), 1939–1944.

Goh, T., Toyokura, K., Wells, D. M., Fukaki, H., & Guyomarc'h, S. (2021). SCR-dependent initiation of the quiescent centre in lateral root primordia of *Arabidopsis*. *Development, 148*(5), dev195859.

Goh, T., Toyokura, K., Wells, D. M., Swarup, K., Yamamoto, M., Mimura, T., Weijers, D., Fukaki, H., Laplaze, L., Bennett, M. J., & Guyomarc'h, S. (2016). Quiescent centre initiation in the Arabidopsis lateral root primordia is dependent on the SCARECROW transcription factor. *Development*, 143(18), 3363–3371.

Helariutta, Y., Fukaki, H., Wysocka-Diller, J., Nakajima, K., Jung, J., Sena, G., Hauser, M.-T., & Benfey, P. N. (2000). The SHORT-ROOT gene controls radial patterning of the *Arabidopsis* root through movement of a transcription factor. *Cell, 101*(5), 555–567.

Huang, C., Wang, D., Yang, Y., Zhang, H., Li, Y., & Yuan, W. (2024). Suppressor of Frigida 4 cooperates with the histone methylation reader EBS to positively regulate root development. *Plant Physiology, 196*(1), 225–239.

Liu, Z., Zhang, R., Duan, W., Xue, B., Pan, X., Li, Y., & Sun, P. (2022). *BIG Modulates Stem Cell Niche and Meristem Development via SCR/SHR Pathway in Arabidopsis Roots.* International Journal of Molecular Sciences, 23(12), 6784.

Moubayidin, L., & Müller, B. (2021). Auxin–cytokinin crosstalk in the *Arabidopsis* root meristem. *Plant Cell Reports, 40*(8), 1513–1525.

Moubayidin, L., Di Mambro, R., & Sabatini, S. (2013). Coordination of plant stem cell activities: auxin and cytokinin cross talk. *Current Opinion in Plant Biology*, 16(1), 39–44.

Pardal, R. (2021). Root stem cell niche networks: It's complexed! Insights from *Arabidopsis*. *Journal of Experimental Botany, 72*(19), 6727–6738.

Pérez-Sancho, J., et al. (2024). Insights into multilevel spatial regulation within the root stem cell niche of *Arabidopsis thaliana*. *Planta*.

Review: Root stem cell homeostasis in *Arabidopsis thaliana* involves a complex regulatory network crucial for growth and developmental plasticity. (2025). *EMBO Reports*.

Sabatini, S., Heidstra, R., Wildwater, M., & Scheres, B. (2003). SCARECROW is involved in positioning the stem cell niche in the Arabidopsis root meristem. *Genes & Development,* 17(3), 354–358.

Sessa, G. (2025). Out of the niche: A bird's-eye view of the molecular mechanism of the plant stem cell niche. *Journal of Experimental Botany*.

Toyokura, K., Goh, T., Shinohara, H., Shinoda, A., & Fukaki, H. (2019). WOX5 and SCARECROW are required for the maintenance of quiescent centre in lateral roots. *Plant and Cell Physiology, 60*(5), 1073–1083.

Wang, B., Shi, X., Gao, J., Liao, R., Fu, J., Bai, J., & Cui, H. (2023). SCARECROW maintains the stem cell niche in *Arabidopsis* roots by ensuring telomere integrity. *Plant Physiology, 192*(2), 1115–1131.

Winter, C. M., et al. (2024). SHR and SCR coordinate root patterning and growth early in the cell cycle. *Nature*.

Zhai, N., et al. (2023). Developmental trajectory of pluripotent stem cell gene network involving SCR, SHR, and WOX5 in *Arabidopsis* callus formation. *Development, 150*(5), dev200879.

Zhou, J., Li, H., Wang, Y., & Li, Y. (2022). DNA methylation dynamics modulate root meristem adaptation under nutrient stress in *Arabidopsis thaliana*. *Frontiers in Plant Science, 13*, 845971.