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BRIEF REPORT

RSL4, an integrator of environmental and hormonal signals, shapes root hair morphology

Lu-Shen Li*

College of Agriculture and Biology, Liaocheng University, Liaocheng 252000, China

***Corresponding author:** Lu-Shen Li, College of Agriculture and Biology, Liaocheng University, Liaocheng 252000, China, Email: lilushen521@sina.com

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Abstract

Root hairs significantly expand the surface area of roots in contact with the soil, thereby promoting water and nutrient uptake. Root Hair Defective 6 Like 4 (*RSL4*) is a key transcription factor regulating root hair development, yet the mechanisms underlying its post-translational regulation remain incompletely understood. Recently, we demonstrated that Calcium-dependent Protein Kinases (CPKs) integrate hormonal signals to phosphorylate *RSL4*, thereby enhancing its transcriptional activity. This Brief Report summarizes recent evidence on how *RSL4* integrates environmental and hormonal cues at multiple regulatory levels to promote root hair growth.

Keywords: Root hairs, Root Hair Defective6-Like4 (*RSL4*), Transcription, Phosphorylation, Phytohormone, Transcription factor

Introduction

Root hairs serve as morphological indicators of soil nutrient conditions and play vital roles in anchoring plants to the soil, absorbing water and mineral ions, and facilitating interactions between the root system and the external environment. Root hair morphology exhibits pronounced plasticity, as multiple phytohormones and environmental factors can modulate their density and length to enable adaptive responses to changing environments (Gifford, et al. 2020, Lopez, et al. 2024). Therefore, studies of root hairs can elucidate how cells integrate internal and external signals to coordinate developmental processes and may also provide a basis for genetic improvement of crops and enhanced environmental adaptability.

Root hair development

Root hair development comprises three major stages: Cell fate determination, initiation, and elongation (Gifford, et al. 2020, Li, et al. 2022). In *Arabidopsis*, the Werewolf (WER)-Glabra3 (GL3)/Enhancer of GLABRA3 (EGL3)-Transparent Testa Glabra (TTG) transcriptional complex activates GLABRA2 (GL2), a key determinant of non-root hair cell fate, while repressing Hair Defective 6 (RHD6) and Rhd6-Like1 (RSL1), thus steering cells toward the non-hair cell lineage. By contrast, in root hair cells, Caprice (CPC) competes with WER for association with GL3/EGL3-TTG1 complex, thereby suppresses *GL2* and allowing root hair differentiation to proceed. At the initiation stage, the root hair-specific transcription factor complex RHD6-RSL1 induces the expression of *RSL4* and *RSL2*.

RSL4 function

RSL4 is a key transcription factor that promotes root hair growth by activating a suite of genes involved in root hair elongation. The products of these genes participate in vesicle trafficking, ROS homeostasis, cell wall synthesis and remodeling, metabolism, and signal transduction (Gifford, et al. 2020, Li, et al. 2022, Lopez, et al. 2024). In the *rsl4* mutant, root hair cells exhibit either a hairless phenotype or a markedly shortened elongation phenotype (Yi, et al. 2010), whereas ectopic expression of *RSL4* induces non-root hair cells to differentiate into root hair cells (Hwang, et al. 2017). Moreover, the duration of *RSL4* protein persistence contributes to determining final root hair length (Datta, et al. 2015).

Environmental signals regulate root hair

Existing studies indicate that external nutrient signals are transduced into endogenous hormonal signals to remodel root hair morphology (Lopez, et al. 2024). Low-nitrogen conditions induce auxin biosynthesis, increasing auxin levels in the root tip, which is subsequently transported to the root hair zone, where it promotes root hair elongation *via* Auxin Response Factor 6/8 (ARF6/8) (Jia, et al. 2023). Low-phosphate conditions induce auxin biosynthesis and promote root hair elongation through ARF19 (Bhosale, et al. 2018). They also activate the ethylene pathway by increasing the protein of Ethylene-Insensitive 3 (EIN3), a key transcription factor in ethylene signaling, thereby promoting root hair development (Hake, et al. 2016).

Hormonal signals regulate root hair

Multiple plant hormones regulate root hair development, particularly auxin and ethylene, both of which promote root hair growth (Gifford, et al. 2020, Li, et al. 2022, Lopez, et al. 2024). Transcriptomic data indicate that approximately 90% of the root hair-regulated genes responsive to auxin and ethylene overlap, and that the two hormones mutually promote each other's biosynthesis, thereby coordinately regulating root hair growth (Bergmann, et al. 2012). Other hormones, such as strigolactones, jasmonic acid, brassinosteroids, and cytokinins, mediate signaling pathways that ultimately integrate with auxin- and/or ethylene-mediated pathways to coordinate root hair growth (Gifford, et al. 2020, Li, et al. 2022).

RSL4 transcriptional regulation

RSL4 responds to hormonal signals at the transcriptional level to regulate root hair morphology (Fig. 1). Overexpression of auxin-responsive *ARF5/7/8/19* induces root hair elongation, and ARF5 directly bind to the *RSL4* promoter to activate its transcription (Mangano, et al. 2017). Ethylene-responsive EIN3 forms a complex with RHD6 to synergistically promote *RSL4* expression (Feng, et al. 2017). In the cytokinin pathway, the B-type response regulators *Arabidopsis* Response Regulator 1 and 12 (*ARR1* and *ARR12*) directly bind to the *RSL4* promoter and induce its expression, thereby promoting root hair elongation (Takatsuka, et al. 2023). Collectively, these studies demonstrate that transcription factors from multiple hormone signaling pathways can directly regulate *RSL4* gene expression.

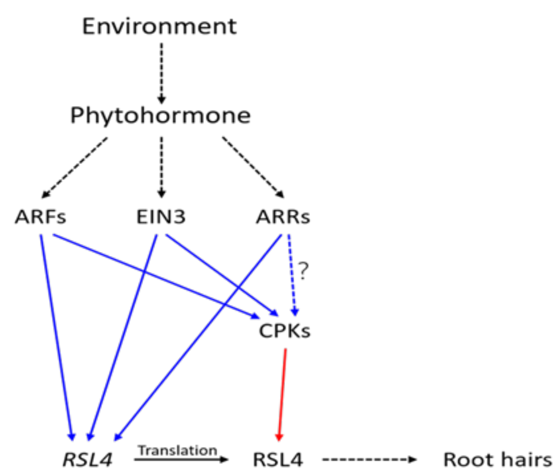

Figure 1: Model illustrating *RSL4* as a central integrator of environmental-hormonal signals at both transcriptional and post-translational levels in the regulation of root hair morphology. Note: ARFs: Auxin Response Factors; EIN3: Ethylene-insensitive 3; ARRs: Arabidopsis Response Regulators; *RSL4*: Root Hair Defective 6 like 4; CPKs: Calcium-Dependent Protein Kinases. The blue arrow represents transcriptional regulation; The red arrow represents post-translational regulation.

RSL4 post-translational regulation

RSL4 responds to hormonal signals at the protein level to regulate root hair morphology (Fig. 1). A recent study demonstrated that *RSL4* undergoes phosphorylation (Li, et al. 2026). Multiple CPKs that are highly expressed in root hairs interact with and phosphorylate *RSL4*, thereby modulating its transcriptional activity and the expression of root hair-associated genes. The auxin-responsive ARFs and the ethylene-responsive EIN3 directly regulate *CPK4/11* expression, suggesting that CPKs integrate hormonal signals at the transcriptional level and subsequently phosphorylate *RSL4* to modulate its activity and root hair morphology. Interestingly, *RSL4* also regulates *CPK4/11* expression at the transcriptional level, thereby forming a positive feedback loop (Li, et al. 2026).

Discussion

Collectively, *RSL4* acts as a central hub that integrates environmental and hormonal signals at both the transcriptional and protein levels to remodel root hair morphology (Fig. 1), thereby contributing to the optimization of nutrient uptake. On the one hand, environmental and hormonal signals directly induce RSL4 transcript *via* hormone-responsive transcription factors, including ARFs, EIN3, and ARRs. On the other hand, these signals upregulate *CPKs* expression through the same transcription factors, and the resulting CPK4/11 phosphorylate *RSL4* to enhance its transcriptional activity. Consequently, environmental and hormonal signals promote root hair growth through a dual mechanism: by increasing *RSL4* transcript abundance and by potentiating its transcriptional activity on downstream target genes.

Nevertheless, several aspects of *RSL4*-mediated signal integration remain unclear. For instance, it remains unknown whether and how other abiotic cues, including temperature and pH, and biotic factors, such as symbiotic microbial communities, influence *RSL4* function. Moreover, given that *RSL4* translation and protein turnover are tightly regulation (Datta, et al. 2015, Li, et al. 2026), it remains to be determined whether these processes are also regulated by environmental and hormonal signals. Addressing these outstanding questions will provide further insights into the regulatory networks underlying root hair morphogenesis and may ultimately inform strategies for improving crop performance under changing environmental conditions.

Conclusion

Hormones act through two convergent mechanisms: Firstly, they directly upregulate *RSL4* transcription *via* hormone-responsive transcription factors, including ARFs, EIN3, and ARRs; secondly, they induce *CPK* expression, and the resulting CPK4/11 proteins phosphorylate *RSL4*, thereby fine-tuning its transcriptional activity and promoting the expression of root hair-associated genes.

Author contributions

Lu-Shen Li: Writing-original draft; Writing-review and editing.

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