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Review

Tansley insight

Autocrine regulation of root hair size by the RALF-FERONIA-RSL4 signaling pathway

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Contents

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Summary

Root hair (RH) size has vital physiological implications, since it influences the surface area of the root and thus the ability of the plant to absorb water and nutrients from the soil. Arabidopsis ROOT HAIR DEFECTIVE 6-LIKE 4 (RSL4), a bHLH transcription factor, controls the expression of hundreds of RH genes, and *RSL4* expression itself can trigger ectopic RH growth. Recent studies reveal an autocrine mechanism governing plant RH cell growth in which the extracellular peptide RAPID ALKALINIZATION FACTOR 1 (RALF1) and receptor FERONIA (FER) act as a central hub between the cell surface and downstream signaling events. RALF1-FER promotes the phosphorylation of eIF4E1. Then, phosphorylated eIF4E1 further regulates the synthesis of RH proteins, including RSL4, to promote RH growth. High levels of RSL4 exert a negative feedback on *RALF1* expression via directly binding to the *RALF1* gene promoter, slowing RH growth and determining final RH cell size.

I. Introduction

Cell size is determined by a well-defined developmental process that integrates cell-intrinsic factors and external environmental cues. Autocrine signaling, in which signals are perceived by the same cells from which they arise, contributes to plant cell growth. Unicellular root hairs (RHs), which extend to several hundred times their original cell bulge size within hours of emerging, provide a unique model system in which to study cell size regulation. The hairs on the surface of vascular plant roots, which evolved from much simpler structures, are exposed to heterogeneous soil microenvironments, including highly variable nutrient and water conditions and beneficial and pathogenic microorganism interactions.

Root hair size has vital physiological implications, since it influences the surface area of the root and thus the plant's ability to absorb water and nutrients from the soil. The study of the Arabidopsis ROOT HAIR DEFECTIVE 6-LIKE 4 (RSL4), a

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bHLH transcription factor that regulates hair cell elongation by controlling the expression of genes, has revealed an exquisite network that responds to specific perceived cues, such as substrate concentration or environmental conditions (for example, phosphate and auxin concentrations) (Yi *et al.*, 2010; Vijaykumar *et al.*, 2016; Mangano *et al.*, 2017; Bhosale *et al.*, 2018). Recent studies have revealed that the duration of RH growth is determined by the regulation of RSL4 protein synthesis and degradation within RHs (Datta *et al.*, 2015). Here, we discuss our current understanding of the mechanisms that control the *RSL4* mRNA translation and related RH proteins in the determination of RH cell size.

II. The RALF1-FERONIA-eIF4E1 module promotes RSL4 protein synthesis

A novel autocrine mechanism, referred to as Receptor Associated with Protein Synthesis Machinery (RAPSM), in which the RAPID ALKALINIZATION FACTOR 1 (RALF1) peptide is secreted into the apoplast and binds to the *Catharanthus roseus* receptor-like kinase 1-like (*Cr*RLK1L) FERONIA (FER) on the membrane surface of the same cell, was shown to influence RH cell size in Arabidopsis (Du *et al.*, 2016; Zhu *et al.*, 2020). This interaction triggers the recruitment of RPM1-induced protein kinase (RIPK) and the phosphorylation of both FER and RIPK in a mutually dependent manner (Du *et al.*, 2016), followed by the recruitment and activation via phosphorylation of an early translation initiation factor (eIF4E1) (Zhu *et al.*, 2020). The RALF1-FER-mediated phosphorylation enhances the mRNA binding ability of eIF4E1 and increases the protein synthesis rate of specific RH proteins, including RSL4 (Zhu *et al.*, 2020) (Fig. 1). Thus, RSL4 levels are upregulated via the RALF1–FER pathway. Then, high levels of RSL4 suppress *RALF1* mRNA expression by directly binding to the *RALF1* promoter, thus negatively impacting the RALF1–FER signaling pathway (Zhu *et al.*, 2020).

RALF-*Cr*RLK1L ligand-receptor complexes are central regulators of plant cell size that mediate the plant's response to environmental changes. In contrast to RIPK, FER works with either its chaperone and coreceptor LORELEI-like glycosylphosphatidylinositol-anchored protein (LLG1) and LORELEI (LRE, which is only expressed in the ovule), thus regulating similar functions in different biological contexts (Li *et al.*, 2015; Xiao *et al.*, 2019). In addition to FER, another *Cr*RLK1L present in RH tips, named ERULUS (ERU), is expressed and phosphorylated when auxin activates the expression of Auxin Response Factor (ARF)7 and ARF19 (Schoenaers *et al.*, 2018). ERU may phosphorylate FER, but it is unclear how ERU contributes to RALF1-FER-RIPK-eIF4E-mediated RH growth (Fig. 1).

III. Transcriptional regulatory networks driving *RSL4* expression

Previous work has described in detail how a developmental program controlled by ROOT HAIR DEFECTIVE 6 (RHD6), hormones, and environmental cues converge to regulate the expression of the transcription factor genes *RSL4* and *RSL2* (Bhosale *et al.*, 2018). RSL4 is able to self-activate at the transcriptional level, enhancing its own expression (Hwang *et al.*, 2017), and is regulated by auxin. The level of *RSL4* expression determines the final size of the RH cell (Datta *et al.*, 2015). Recently, it was shown that ectopic expression of *RSL4* driven by the GLABRA2 (GL2) promoter induces RH growth in atrichoblasts in Arabidopsis, which typically do not produce RHs (Hwang *et al.*, 2017). This suggests that *RSL4* expression itself can trigger ectopic RH growth (Hwang *et al.*, 2017). Furthermore, RSL4 controls the expression of hundreds of genes (Vijaykumar *et al.*, 2016), most of which contain an RH-specific *cis*-element (RHE) in their regulatory regions (Hwang *et al.*, 2017), thus representing the smallest subset of genes necessary and sufficient to trigger RH growth. Together, these properties make RSL4, and possibly also RSL2, master regulators of RH growth and thus final cell size (Fig. 1). Recently, more genetic components that regulate RH growth were reported, including ZINC FINGER PROTEIN1 (AtZP1), which negatively regulates *RHD6*, *RSL4*, and *RSL2* expression and thereby represses RH growth (Han *et al.*, 2020). In a similar manner, GT-2-LIKE1 (GTL1) and its homolog DF1 bind to the *RSL4* promoter and repress RH growth (Shibata *et al.*, 2018). Several regulatory layers may coordinately control the transcriptional activation of *RSL4* in RH growth.

Auxin is a key regulator of RH growth and triggers cell expansion *in situ*. The transcriptional auxin response involves several ARFs, which bind to *cis*-auxin response elements (AuxREs) in the promoter of *RSL4* and directly upregulate *RSL4* expression several fold, linking auxin stimulation to *RSL4* expression at the molecular level (Mangano *et al.*, 2017). In addition, RSL4 promotes the expression of the NADPH oxidases C and J (also known as RBOH, RESPIRATORY BURST OXIDASE HOMOLOG proteins) and several Class-III apoplastic Peroxidases (PRXs; e.g. PRX73), thus controlling reactive oxygen species (ROS) homeostasis (Mangano *et al.*, 2017). Auxin stimulation and the downstream transcriptional program of ROS production in RH cells involve both RSL4 and the related transcription factor RSL2; however, it remains unclear how this hormonal program is coordinated to control polar growth. These findings suggest a molecular connection between auxin-regulated *ARF* and *RSL4/RSL2* expression and ROS-mediated RH growth (Mangano *et al.*, 2017; Marzol *et al.*, 2017; Mangano *et al.*, 2018). Nonetheless, the molecular mechanism linking ROS homeostasis to polar RH growth merits further investigation.

In growing RHs, ROS homeostasis is essential for balancing cell wall stiffening, via the crosslinking of extensin (EXT) networks (Marzol *et al.*, 2018) and loosening processes (Marzol *et al.*, 2018), and also for ROS-mediated Ca^{2+} channel stimulation in the plasma membrane. In several plants, RH growth is enhanced in low-Pi conditions, which increases Pi uptake. A recent study showed that exposure to Pi-deficient conditions immediately triggers auxin biosynthesis by upregulating the expression of *TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1* (*TAA1*) in the root apex, auxin transport mediated by AUX1 in the root epidermis cells, and activation of *RSL2* and *RSL4* expression, which promote RH growth (Bhosale *et al.*, 2018). This proposed global response in roots appears to be conserved in dicots and monocots, although the mechanistic connections among these molecular components remain to be established.

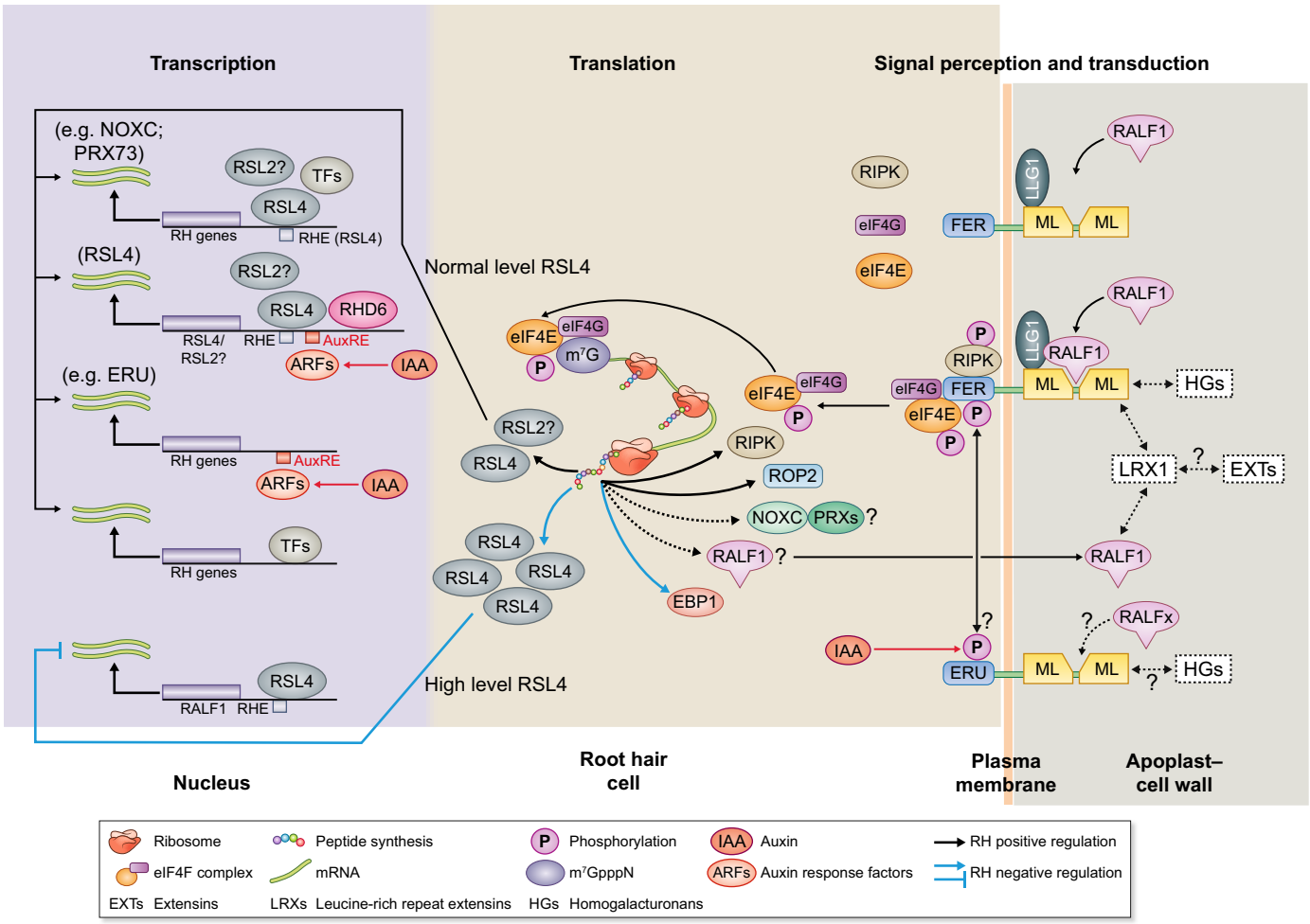

Fig. 1 The RALF1-FER-eIF4E1-RSL4 signalling module controls root hair (RH) cell size. RAPID ALKALINIZATION FACTOR 1 (RALF1) peptide binds to the extracellular domain of FERONIA (FER) and triggers the mutual phosphorylation of FER/RIPK kinase complexes. Polar-localized FER interacts with eIF4E1 (an early translation factor) and forms a complex with the translation machinery at the tips of growing RHs. Phosphorylated eIF4E1 regulates the translation of mRNAs, increasing the synthesis of several RH proteins such as NOXC, PRX73, ROP2, RIPK and RSL4 in a spatiotemporal manner. Both RAC/ROPs and reactive oxygen species (ROS) generated by NOXC regulate myriad biological processes, and are thus ideal for mediating the diverse functional roles of FER. In addition to FER, ERU also acts on growing RHs. The accumulation of RSL4 triggers the transcription of RH genes. However, high levels of RSL4 exert negative feedback on *RALF1* expression by directly binding to the *RALF1* promoter. In addition, RSL4 is developmentally regulated by RHD6 (and RSL1), and controls the expression of several other proteins. Auxin is a key hormone that causes multiple auxin response factors (ARFs) to bind to AuxRE sites on the *RSL4* promoter and upregulate *RSL4* expression. In addition, ARFs trigger the expression of genes independently of RSL4. Environmental signals such as low phosphate (Pi) also influence RH cell size by activating *RSL4* expression. Still, unknown TFs may act in an auxin-RSL4 independent manner to control gene expression in RHs. A, apoplast; AuxRE, Auxin Responsive Element; *Cr*RLK1Ls, *Catharanthus roseus* receptor-like kinase 1-like; CW, cell wall; ERU, ERULUS (another CrRLKL1 closely related to FER); LLG1, Lorelei-Like GPI-AP1 (co-chaperone and co-receptor of FER); LRX, Leucine-Rich Repeat Extensin; PM, plasma membrane; PRX, Type-III Peroxidase; NOX, NADPH oxidase (or RBOH, Respiratory Burst Oxidase Homolog protein); RHE, Root Hair-specific Element; RIPK, RPM1-induced protein kinase. Positive regulatory actions are indicated by black arrows, negative regulatory actions are indicated by blue lines, and possible physical interactions are indicated by dotted lines. Question marks denote interactions that remain to be demonstrated.

IV. FER as a central hub orchestrating complex intracellular and extracellular signals

FER has recently emerged as a potential target for crop improvement and protection because of its versatile, fundamental and tissue-specific roles in plant growth (Liao *et al.*, 2017; Li *et al.*, 2018), yield control (Yu *et al.*, 2014; Li *et al.*, 2016), stress responses (Yu *et al.*, 2012; Chen *et al.*, 2016; Yang *et al.*, 2020) and energy and RNA metabolism (Xu *et al.*, 2019; Zhu *et al.*, 2020). Leucine-Rich Repeat LRR4, a truncated version of Leucine-Rich Repeat Extensin 4 (LRX4) that contains the LRR domain but lacks the C-terminal extensin (EXT) domain, was recently shown to physically interact with the FER malectin domain and with RALF1 on the surface of epidermis cells (Dünser *et al.*, 2017). In addition, the LRR domain of several LRXs, including LRX1, was shown to interact with the malectin domain of FER and also with RALF1 peptide (Herger *et al.*, 2019). Furthermore, the higher-order mutant *lrx1,2,3,4,5* phenocopies the *fer-4* extremely short RH phenotype (Herger *et al.*, 2019) in a similar manner to the *lrx8,9,10,11* and *anx1,2* mutants in pollen tube growth (Wang *et al.*, 2017; Ndinyanka *et al.*, 2017; Mecchia *et al.*, 2017; Sede *et al.*, 2018; Fabrice *et al.*,

2018), suggesting that LRXs and FER/ANXs are components of the cell wall integrity pathway in polar growing cells.

Recently, a detailed study showed how the pollen-specific dimeric LRX8 physically interacts with RALF4 (Moussu *et al.*, 2020). This suggests that LRXs are directly connected to the EXT network through the EXT domain (Marzol *et al.*, 2018) on the external side of the cell wall and to the cell surface CrRLK1L sensors and RALF peptides close to the plasma membrane through the LRR domain on the inner side of the proteins (Fig. 1). Root hair and pollen tube LRXs are essential for proper polar growth and were recently proposed to maintain cell wall integrity in these rapidly expanding cells. For example, LRX8/LRX9 are highly produced in pollen tubes and bind to RALF4/19 peptides that have been secreted into the media, and RALF4/19 bind to both *Cr*RLK1Ls ANX1,2 (for ANXUR1 and 2) and BUDS1,2 (for BUDDHA'S PAPER SEAL1 and 2) (Ge *et al.*, 2017; Mecchia *et al.*, 2017; Feng *et al.*, 2019). Collectively, LRXs, CrRLK1Ls, and RALF4/19 act as an autocrine mechanism that monitors cell wall integrity during pollen tube growth (Ge *et al.*, 2017; Mecchia *et al.*, 2017; Feng *et al.*, 2019) in a similar manner to RALF1-FER described here for RH cells. RALF binding to FER and to other CrRLK1Ls requires the co-receptors LRE/LLG. Recent detailed studies have shown that, in the case of RALFs (RALF4 and RALF23), the N-terminus of RALFs binds to CrRLK1L (ANXs and FER, respectively), while its C-terminus binds to LLGs (Ge *et al.*, 2019; Feng *et al.*, 2019; Xiao *et al.*, 2019), providing insight into RALF's binding specificity. LLG2/3 interacts with ANX/BUPS in a RALF4-concentration-dependent manner, indicating that ANX/BUPS-LLG2/3 might act as a receptor–coreceptor complex (Ge *et al.*, 2019; Feng *et al.*, 2019). To further complicate these interlinked interactions at the cell surface, the malectin domain of FER was shown by *in vitro* assays to associate with non-esterified pectins (homogalacturonan-type, HG) (Feng *et al.*, 2018).

To date, only a few studies have provided evidence of a defined biological context in which these multiple interactions take place. In the case of salt stress, it was shown that, in the default state, RALFs are bound to LRX3, 4, and 5 proteins at the cell surface of root cells, which inhibits their interaction with FER. Then, in a high Na^+ environment (high NaCl), RALF22 and 23 are released from LRX proteins and bind to FER (possibly with the LRE/LLG complex), triggering an internalization of the complex (Zhao *et al.*, 2018). FER interacts with molecules both on the apoplastic side of the plasma membrane, including HG pectins, RALFs, LRE/LLG, LRX, and glycosylphosphatidylinositol-anchored proteins, and on the inside of the cell, including phosphatases, RLKs and small ROP-GTPases. This complexity suggests that FER represents a central hub that orchestrates signals and mediates polar growth responses at the cell wall and plasma membrane interface.

V. Concluding remarks

The recent advances highlighted here represent a substantial step toward understanding the RALF1-FER-RSL4 pathway that regulates RH cell size through interactions with auxin and low-Pi transcriptional activation. Future research prospects include determining how *RALF1* expression is mediated under conflicting growth signals or when plants are exposed to additive or synergistic cues. Detailed studies of how individual factors and combined signals affect *RALF1* expression linked to RSL4 levels are needed to unravel how cell size is optimized in a changing environment. In addition, putative FER-LRX1 and LRX1-RALF1 interactions are yet to be described in clearer biological contexts within our current model of cell size regulation.

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Author contributions

SZ and JMP wrote specific parts of text of the article and provided technical assistance. FY and JME conceived the project and wrote the article with contributions from all authors. SZ and JMP contributed equally to this work.

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