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Target of Rapamycin is involved in root hair development in *Phaseolus vulgaris*

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ABSTRACT

Root hairs are essential for nutrient acquisition and rhizosphere interactions in vascular plants. While the Target of Rapamycin (TOR) kinase is a well established regulator of growth and metabolism, its role in root hair development in *Phaseolus vulgaris* remains underexplored. In this study, we investigated the role of TOR in root hair morphogenesis using RNA interference (RNAi)-mediated downregulation of *PvTOR* and transcriptomic profiling. Microscopic examination of *PvTOR*-RNAi roots confirmed significant reductions in root hair length and density. Transcriptomic analysis revealed differential expression of 148 *P. vulgaris* homologs of *Arabidopsis thaliana* root hair-related genes, with 63 genes downregulated and 85 upregulated. Gene Ontology enrichment analysis indicated that these differentially expressed genes (DEGs) were primarily involved in cellular development, cell differentiation, and redox regulation. Upregulation of phosphoinositide metabolism genes, ROS generators, and cell wall-related extensins suggests compensatory tip growth responses under TOR suppression. On the otherhand, repression of key auxin signaling genes and cell wall-loosening proteins such as *EXPA1* and *ENDOGLUCANASE5* indicates a shift away from elongation processes. Protein – protein interaction network analysis highlighted phosphoinositide and ROP GTPase signaling hubs as major pathways affected by TOR inhibition, suggesting that TOR indirectly modulates cell polarity and membrane dynamics essential for root hair development. These findings provide further evidence of TOR as a central integrator of hormonal, metabolic, and structural cues during root hair formation.

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Introduction

Root hairs are extensions of root epidermal cells, a characteristic of vascular plants. They increase the contact area of the root to the rhizosphere, increase the absorption area for nutrient and water uptake and are the gateways to most of the rhizobia interactions.[1] The Target of Rapamycin (TOR) kinase is a highly conserved serine/threonine protein kinase that functions as a master integrator of nutrient, energy, and hormone signaling pathways.[2–5] TOR coordinates cellular metabolism with developmental programs by regulating protein synthesis, autophagy, and cell cycle progression.[6] In plants, TOR is activated by favorable energy conditions and is repressed under stress, thereby fine-tuning growth responses to environmental changes.[7]

Although the role of TOR in shoot and root meristem activity has been extensively studied, its function in the differentiation of specialized cell types such as root hairs is only beginning to be understood. Emerging evidence suggests that TOR is intricately involved in the regulation of root epidermal patterning and polar growth processes that define root hair morphogenesis. TOR signaling has been shown to interact with auxin, a central hormonal regulator of root hair development, affecting auxin transport and sensitivity in root tissues.[8] Furthermore, TOR modulates the expression of genes involved in cell wall remodeling, cytoskeletal dynamics, and vesicle trafficking all essential components of tip growth in root hairs.[9]

Recent phosphoproteomic analyses have highlighted TOR-dependent phosphorylation events that correlate with changes in root hair length and density, particularly under fluctuating nutrient availability.[10] Moreover, TOR has been implicated in ROS-mediated signaling pathways that drive tip-focused cell expansion, suggesting it may coordinate both metabolic and structural components of root hair growth.[11] Notably, under conditions of phosphate starvation, a well-known inducer of root hair proliferation TOR activity appears to act as a molecular switch, modulating the extent of root hair elongation in accordance with energy and resource availability.[12]

In previous work, we demonstrated the involvement of TOR in regulating root hair length and density under TOR-downregulated conditions in *Phaseolus vulgaris*.[13] This article seeks to consolidate existing knowledge on TOR signaling within the context of root hair formation, examining the molecular mechanisms underlying the observed phenotypes signaling networks in which TOR operates.

Materials and method

Plant material and transcriptomics analysis

Phaseolus vulgaris cv. Negro jamapa was used in the current study. The plasmid construction of pTdT-RNAi-PvTOR and generation of composite plants were as described in our earlier

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publication.[13] The transgenic hairy roots expressing pTdT-RNAi-*PvTOR* (*PvTOR*-RNAi here after) or pTdT-RNAi empty vector controls were selected based on reporter gene expression and transcript downregulation of *PvTOR* was validated by qRT-PCR analysis. High-quality total RNA was isolated from frozen root tissues of *PvTOR*-RNAi and controls from two biological replicates using the RNeasy Plant Mini Kit according to the manufacturer's instructions (Qiagen, Hilden, Germany). Further, analysis such as mRNA enrichment, library preparation and sequencing to obtain RNA-Seq data were carried out as outlined by Nanjareddy and coworkers.[14]

Identification of root hair formation genes in Phaseolus vulgaris

A comprehensive search for root hair formation genes in *Arabidopsis thaliana* was carriedout in literature from 2000 to present at PubMed (https://pubmed.ncbi.nlm.nih.gov/, accessed on 1 January 2024) website. *Arabidopsis thaliana* nucleotide sequences of root hair formation genes were retrieved from TAIR (https://www.arabidopsis.org/, accessed on 25 January 2024) database. BLASTP and BLASTN searches were carriedout to retrieve *P. vulgaris* homologs of root hair formation genes from Phytozome v13 (https://phytozome.jgi.doe.gov/., accessed on 8 February 2024) using *Arabidopsis* sequences. Log fold change values were extracted from the RNA-seq dataset to construct the final gene expression profiles.

Gene ontology analysis

Gene Ontology (GO) enrichment analysis was performed on the diferentially expressed genes using the GO enrichment online tool of PlantRegMap (http://plantregmap.gao-lab.org/., accessed on 20 March 2024) with a p value threshold ≤ 0.01. The bubble plots were generated with the *R* package ggplot2 with the retrieved GO terms considering only the top 10 GO terms of each category with p-value ≤ 0.0004.The pie chart was generated with all the retrieved GO terms using ChartGo (https://www.chartgo.com/, accesed on 28 March 2024).

Differential expression and PPI analysis

The volcano plot was generated with the package EnhancedVolcano in *R* studio (version 4.2.2) using the diferentially expressed genes and a Log10 (p-value) < 1e-1/5 and a Log2 (Fold Change) ≥1 was used as a cutoff for showing the most significant upregulated and downregulated genes. The heatmap was generated with the function heatmap.2 of the gplot package in *R* studio (version 4.2.2) using the diferentially expressed root hair specific genes identified from the transcriptomics data and a Log2(Fold Change) ≥1 was used as a cutoff for showing the most upregulated and downregulated genes. The pie chart was generated with all the retrieved diferentially expressed genes using SRPLOT (https://www.bioinformatics.com.cn/, accessed on 10 April 2024) online tool. Protein interaction network was obtained using STRING (https://string-db.org/, accessed on 1 May 2024) online tool (version 11.5) and disconnected nodes in the protein network were removed. The new genes identified with PPI analysis were underlined with yellow color.

Results and discussion

Identification of root hair growth and development related genes

A list of 211 root hair specific genes were chosen based on a Google and PubMed search for the published articles of *Arabidopsis thaliana*. The gene IDs of *Arabidopsis* genes were retrieved and BLASTN and BLASTP searches were carried out in NCBI and Phytozome to identify the homologs in *P. vulgaris* genome. A total of 148 homologs from the *Phaseolus* genome were identified as the remaining 63 genes were overlapping.

TOR downregulation alters root hair development

TOR was transcriptionally downregulated by expressing pTdT-*TOR*-RNAi construct in *P. vulgaris* hairy roots generated by *Agrobacterium rhizogenes*. The *TOR* transcript downregulation was verified by RT-qPCR where a reduction of 86% of expression was noted (Figure 1a). Microscopic observation of these roots confirmed the previously reported root hair phenotype[13] where *TOR*-RNAi root hairs either grew short or were absent in the root elongation zone (Figure 1b) compared to control (Figure 1c).

Transcriptomics analysis revealed differential regulation of root hair genes

In order to investigate transcriptional regulation of root hair development related genes, during *TOR* transcript downregulation, we subjected the RNA extracted from *TOR*-RNAi and control (pTdT-RNAi) expressing hairyroots to RNA-sequencing. The DEGs presented herein are for 148 genes identified as regulators of root hair development (Figure 2a; Table S1). Among these genes, 63 were downregulated and 85 were upregulated (Log_2 FC ≥ 2.0; P-value >0.05; Figure 2b). The volcano plot (Figure 2c) illustrates the distribution of these differentially expressed genes based on their fold change and statistical significance. To verify the accuracy of the transcriptome results, we selected root hair formation and development genes *viz*., *Peroxidase 64*, *Cysteine-rich secretory protein*, *Syntaxin*, and *Extensin* (Figure 2d) for RT-qPCR using RNA from transgenic roots. The results showed that the trends for the relative expression of genes were consistent between the RNA-seq and the RT-qPCR.

Analysis of differentially expressed genes in TOR-RNAi roots

We annotated 148 DEGs using GO database to investigate their functions. According to GO enrichment, 83% DEGs were enriched in biological process (BP), 11% in molecular function and 6% under cellular components (Figure 3a, Table S2). The DEGs were enriched to 22 GO terms, including 10, 7, and 5 terms in biological process (BP), cellular component (CC), and molecular function (MF), respectively

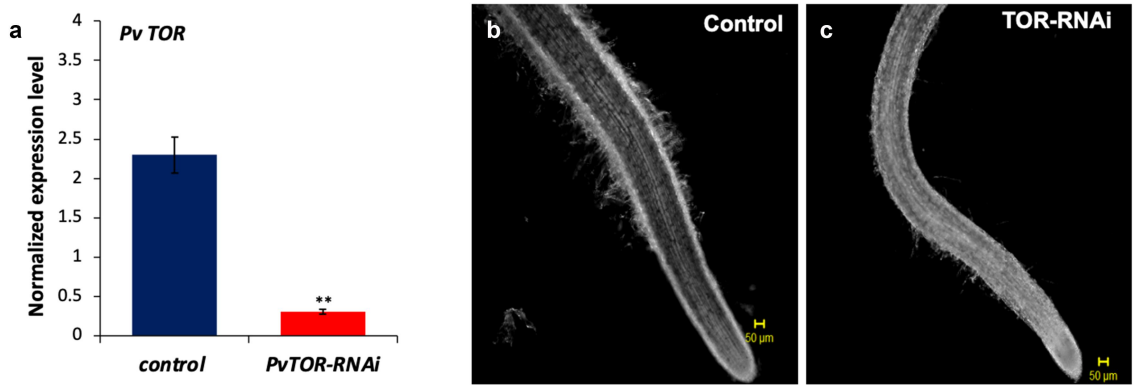

Figure 1. *TOR* expression and root phenotypic analysis. a) quantitative RT-PCR results of TOR down-regulation in uninoculated TOR-RNAi transgenic roots relative to transgenic control (empty vector) roots at 10 dpe. Transcript accumulation was normalized based on the expression of *Ef1a* and *IDE*, which were used as reference genes. Statistical significance was determined using an unpaired two-tailed Student's *t* test (**$p < 0.01$), and the data are presented as means ± SD. Representative images showing root hair density on the primary roots of transgenic roots b) control (empty vector) and c) *TOR-RNAi* root at 10 dpe. dpe -days post emergence. Scale bar (B-C) 50*µ*.

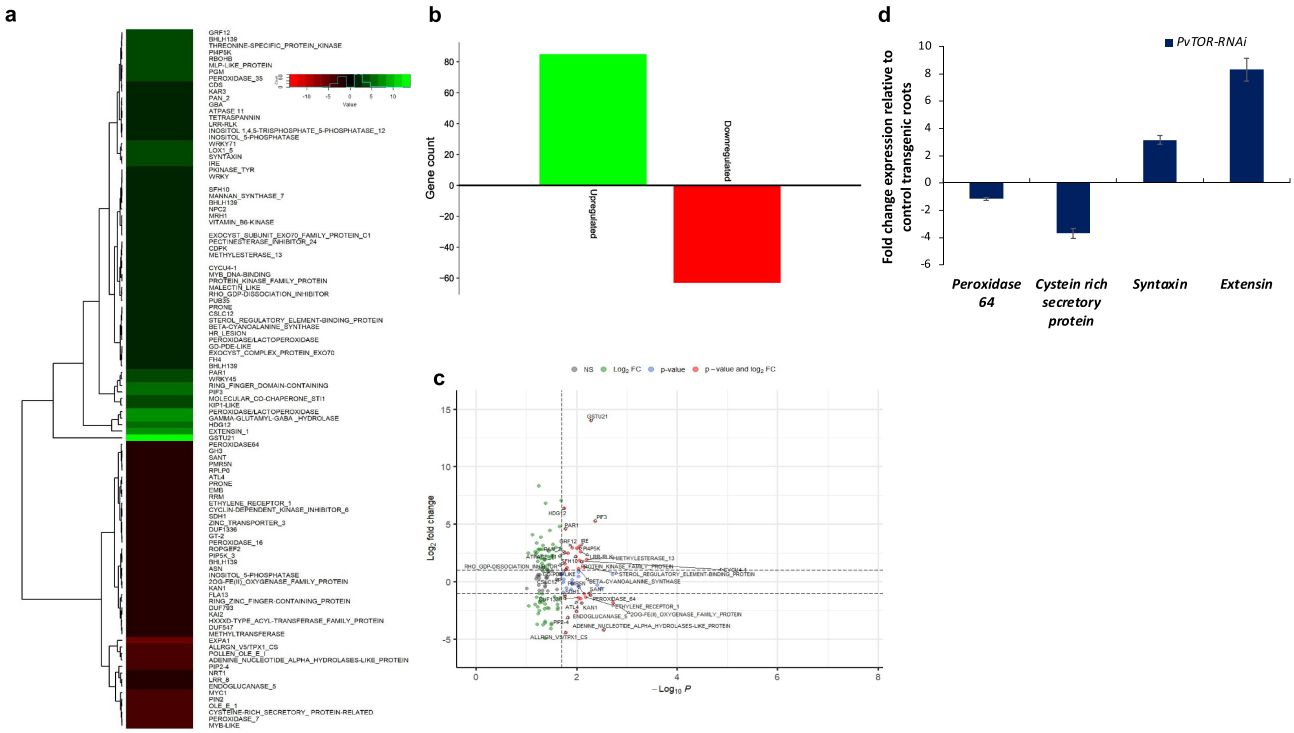

Figure 2. Differential expression analysis of 148 *Phaseolus vulgaris* genes. (a) heatmap showing the $\log_2$ Fold change values of differentially expressed genes (DEGs). Upregulated genes are shown in green and positioned toward the top, while downregulated genes are shown in red. The color key indicates the scale of $\log_2$ Fold change and gene count. (b) Bar graph representing the number of upregulated (85) and downregulated (63) genes. (c) Volcano plot of DEGs. Each point represents a gene, with $\log_2$ Fold change values on the y-axis and $-\log_{10}$(p-value) on the x-axis, indicating the level of differential expression and statistical significance, respectively. RT-qPCR analysis of root hair development genes. (d) Transcript abundance of *peroxidase 64*, *cysteine-rich secretory protein*, *Syntaxin*, and *Extensin* in TOR-RNAi transgenic roots relative to transgenic control roots. Expression levels are presented as Fold changes relative to the control and represent the means ± standard error (SE) from three biological replicates ($n > 9$). *DEGs: differentially expressed genes. See table S1 for the complete list of DEGs.*

(Figure 3b-d). Among the biological processes, 24 genes were involved in cellular developmental processes, 21 in cell differentiation, 18 in cell, and epidermis development and remaining genes are involved in epidermal cell differentiation. Under the category of cellular components maximum number (11) of genes were found to be involved in extracellular region and the remaining genes enriched in this category were involved in plasma membrane, cell projection and cortex and molecular function category involved peroxidase activity, oxidoreductase activity and antioxidant activity. The expression of cell wall encoding Extensins required for RH growth was found to be directly or indirectly controlled by other transcription factors.

Several phosphoinositide metabolism-related genes, including *PI4P5K*, *inositol-1,4,5-trisphosphate 5-phosphatase*, and *inositol-5-phosphatase*, were significantly upregulated. These genes regulate phosphatidylinositol signaling, a pathway crucial for root hair initiation and tip growth via vesicle trafficking

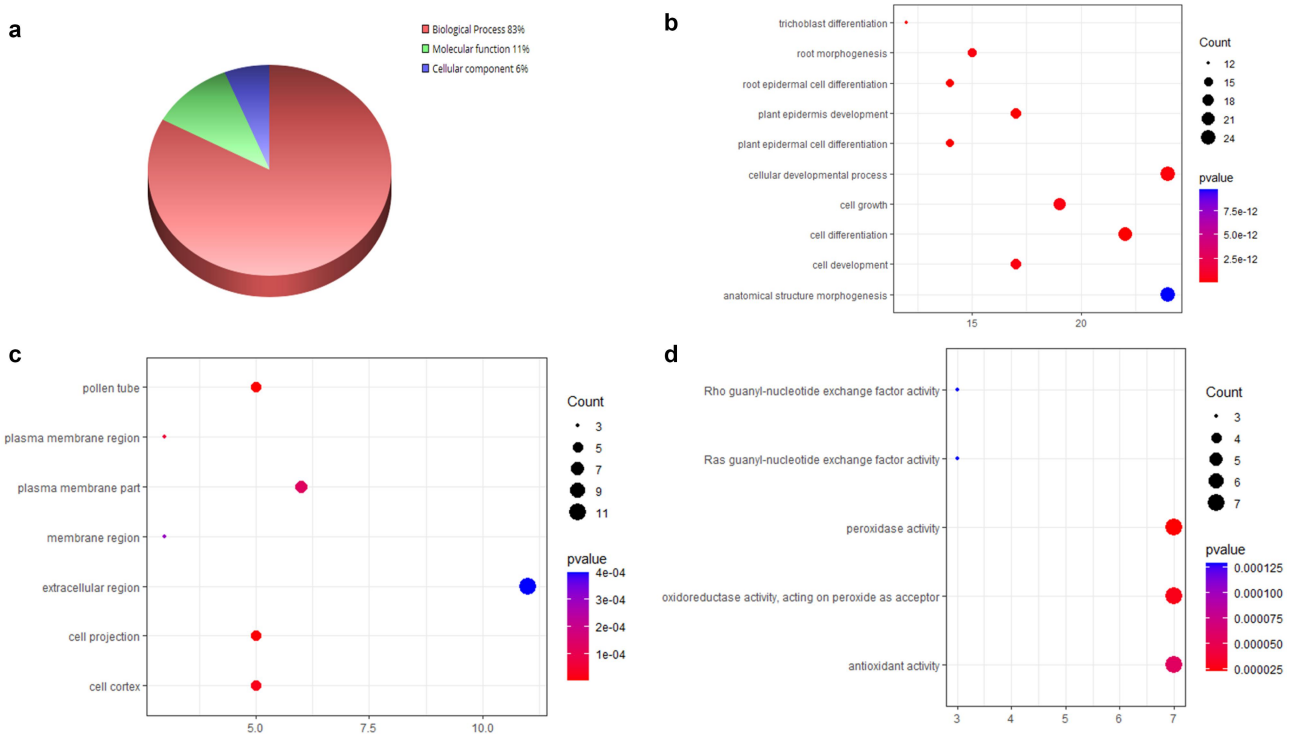

Figure 3. Gene ontology (GO) term enrichment analysis of 148 *Phaseolus vulgaris* genes. (a) pie chart showing the percentage of genes assigned to each GO category. (b–d) bubble plots representing the most significantly enriched GO terms in each category: (b) biological processes, (c) cellular components, and (d) molecular functions. GO enrichment analysis was performed using PlantRegMap (http://plantregmap.Gao-lab.Org/) with a significance threshold of $p \leq 0.01$. In the bubble plots, color indicates the level of significance (*red* = higher significance; *blue* = lower significance), and bubble size represents the number of genes associated with each term. The top significantly enriched GO terms ($p \leq 0.0004$) are highlighted in the plots. A full list of enriched terms is provided in table S2.

and actin cytoskeleton remodeling.[15,16] Concurrent upregulation of RBOHB, a NADPH oxidase involved in reactive oxygen species (ROS) generation at the root hair tip, supports the notion that TOR silencing maintains some components of tip growth machinery.[17,18] Transcriptional regulators such as *GRF12*, *WRKY71*, and *BHLH139* were also upregulated.

Interestingly, *MLP-like protein*, *CDS* (cytidine diphosphate diacylglycerol synthase), and *ATPase 11* were also induced. These genes participate in membrane biosynthesis and ion homeostasis, possibly reflecting increased metabolic demands or stress responses under TOR inhibition.[7] Enhanced expression of peroxidase 35, a member of the class III peroxidases, suggests remodeling of the cell wall and oxidative stress regulation.[19]

Extensins are cell wall glycoproteins belonging to the hydroxyproline-rich glycoprotein (HRGP) family, such as arabinogalactan proteins (AGPs) and proline/hydroxyproline-rich proteins (PRP). Proline hydroxylation, an early posttranslational modification of HRGPs that is catalyzed by *Prolyl 4-Hydroxylases* (*P4Hs*), defines the subsequent O-glycosylation sites in EXTs (which are mainly arabinosylated) and AGPs (which are mainly arabinogalactosylated). Biochemical inhibition or genetic disruption resulted in the blockage of polarized growth in root hairs and reduced arabinosylation of EXTs. Our results demonstrate that correct O-glycosylation of EXTs is essential for cell-wall self-assembly and, hence, root hair elongation in *A. thaliana*.[20–22]

Lipoxygenases (*LOXs*), naturally occurring enzymes, are widely distributed in plants and animals. *LOXs* can be non-sulfur iron, non-heme iron, or manganese-containing dioxygenase redox enzymes. *LOX1* is found to be involved in defense responses of leaf pathogens in *A. thaliana* [23] while, *LOX5* and *LOX6* are found to be involved in lateral root development and root specific expression.[24]

Transcription factor *Phytochrome-Interacting Factor 3* (*PIF3*) is a key basic helix-loop-helix transcription factor of *A. thaliana* that negatively regulates light responses, repressing chlorophyll biosynthesis, photosynthesis, and photomorphogenesis in the dark.[25] Recently, *PIF3* is identified to be a soil emergence-related transcription factor which is regulated by receptor kinase *Feronia* (FER) in *A. thaliana*. *Feronia* mutants showed defects in root hair development. Peroxidases *PRX62* and *PRX669* have been shown to regulate root hair elongation at low temperatures through modulation of ROS-homeostasis and cell wall EXT in solubilization.[26]

Conversely, several key genes associated with cell wall loosening and root hair elongation were strongly downregulated. *Expansin A1* (*EXPA1*),[27] *Endogucanase 5*, and *Cysteine-Rich Secretory Protein-related* genes critical for turgor-driven cell wall expansion were repressed, aligning with previous findings that TOR activity supports anisotropic cell expansion.[8]

Hormone signaling genes, including *PIN2* (auxin efflux), *GH3* (auxin conjugation), and ethylene receptor 1, were significantly repressed. TOR has been shown to modulate auxin

and ethylene signaling pathways,[28] and their downregulation likely contributes to reduced root hair elongation. The repression of *MYC1*, *MYB-like*, and a second isoform of *BHLH139* further highlights transcriptional rewiring associated with TOR inactivation.

Protein–protein interactions of root hair specific genes

The interactions between TOR and other 148 proteins selected to be highly overexpressing and downregulated in *TOR*-RNAi conditions were studied using STRING online website. The prediction revealed no specific interactions among the choosen proteins including TOR (Figure 4). TOR was only interacting with Feronia, as previously reported[29,30] Central to the network were Inositol Polyphosphate 5-Phosphatases, Phosphoinositide Phosphatases, and Phosphatidylglycerophosphate synthases, which formed densely interconnected clusters. Via these proteins, the interaction network was linking 60 other proteins. These proteins did not have any direct interactions with TOR and most of these interacting proteins were the genes that were upregulated in *TOR*-RNAi condition.

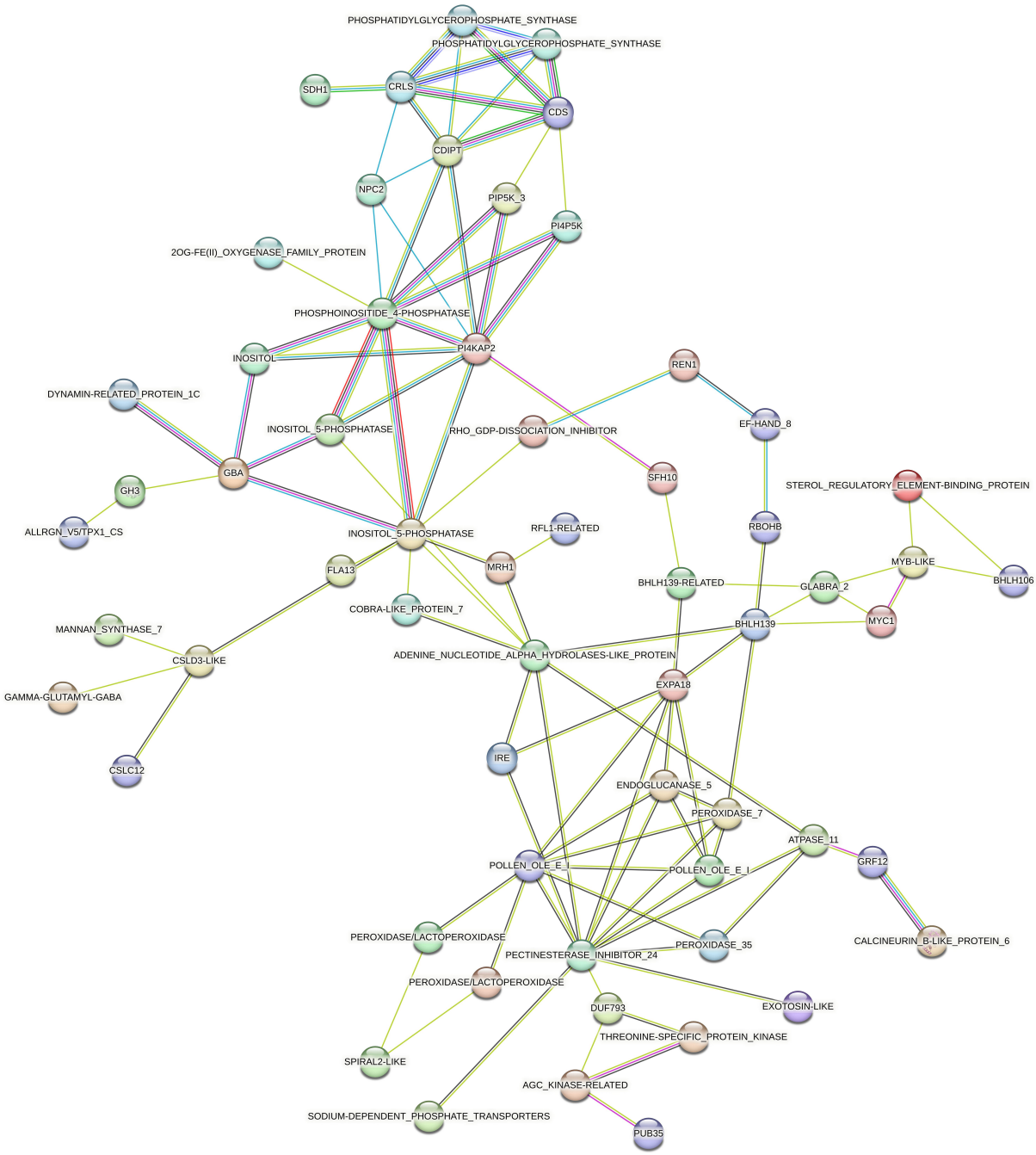

Figure 4. Protein – protein interaction (PPI) analysis of 148 *Phaseolus vulgaris* proteins. The interaction network comprises 60 nodes and 105 edges. Nodes represent proteins, and edges represent predicted protein – protein associations. The colored lines denote different types of supporting evidence: red = gene fusions, green = gene neighborhood, blue = gene co-occurrence, purple = experimentally determined, yellow = text mining, light blue = curated databases, black = co-expression, and gray = protein homology. Node color indicates interaction context: colored nodes represent query proteins and their first shell of interactors; white nodes indicate the second shell of interactors. Filled nodes represent proteins with known or predicted 3D structures, while empty nodes represent proteins with unknown 3D structures. Nodes underlined in yellow indicate newly identified genes through PPI analysis that interact with 60 *P. vulgaris* proteins. PPI analysis was conducted using STRING (https://string-db.org/). PPI = Protein – protein interaction.

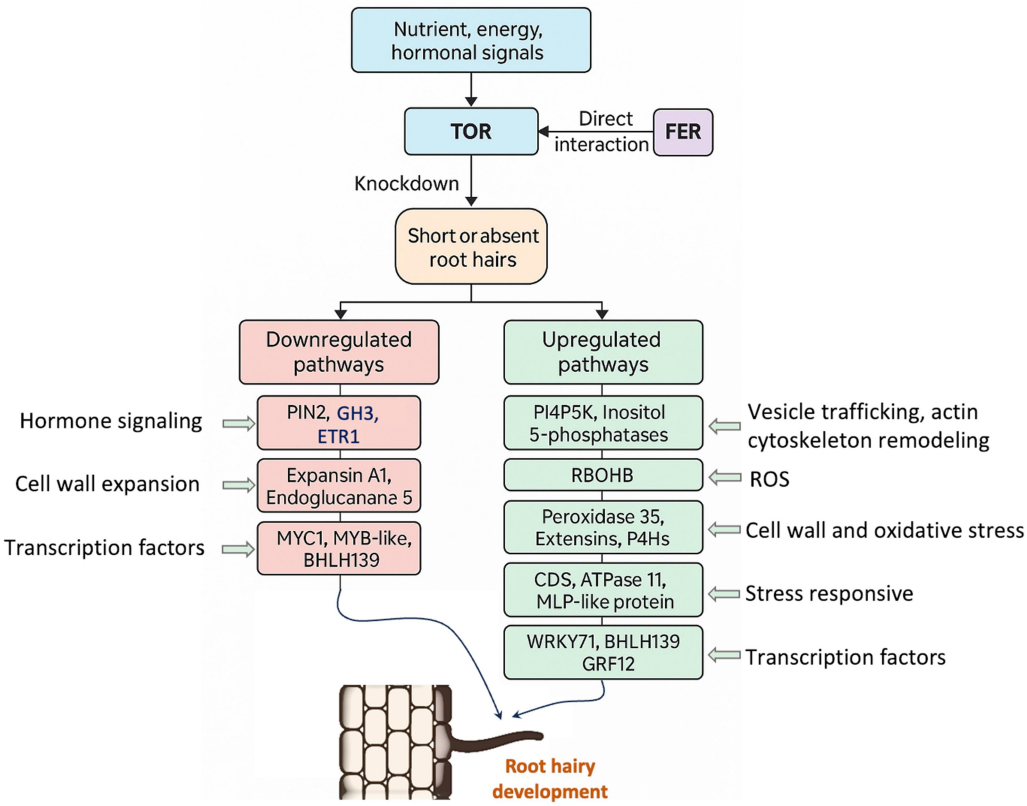

Figure 5. Proposed model of *TOR* signaling in root hair development in *Phaseolus vulgaris* under *TOR* silencing conditions. The model illustrates how *TOR* integrates nutrient, energy, and hormonal signals to regulate root hair formation. *TOR* silencing leads to short or absent root hairs, associated with downregulation of pathways related to hormone signaling, cell wall modification, and transcriptional regulation, and upregulation of pathways involved in stress response, signaling, and protein activity.

Suggesting, phosphoinositide signaling is a major regulatory axis affected by TOR inhibition, consistent with prior evidence linking PI metabolism to cytoskeletal dynamics and membrane trafficking during tip growth.[31] Notably, RHO GDP-dissociation inhibitor and CBL-interacting proteins were associated with these hubs, indicating modulation of Rho-of-plants (ROP) GTPase signaling, known to influence root hair polarity and elongation (Figure 5).

Several transcription factors, including MYC1, MYB-like, bHLH106, and bHLH139, were embedded within the network, suggesting TOR signaling modulates gene expression programs that regulate cell fate and morphogenesis. Their interactions with GABARA2 and RICHH1, known regulators of hormonal and calcium responses, point to a broader transcriptional reprogramming during root hair development under TOR suppression.[32] Proteins directly related to cell wall biosynthesis and expansion, such as COBRA-like protein 7, CSLD3-like, FLA13, and EXPA15, were also prominent. These proteins are well-documented components of the machinery required for anisotropic cell expansion and tip growth in root hairs.[33,34] Furthermore, peroxidases and pectin-modifying enzymes, such as Peroxidase 35 and Pectinesterase Inhibitor 24, were implicated, indicating changes in cell wall remodeling enzymes that may facilitate or restrict hair elongation (Figure 5).

Together, these findings highlight a complex interplay between phosphoinositide signaling, cytoskeleton regulation, transcriptional control, and cell wall remodeling in root hair development under TOR-inhibited conditions.

Conclusion

This study provides compelling evidence that Target of Rapamycin signaling plays a pivotal role in regulating root hair development in *Phaseolus vulgaris*. Through transcriptomic analysis of *TOR*-silenced roots, we demonstrate that TOR modulates the expression of a wide array of genes involved in root epidermal differentiation, tip growth, and cell wall remodeling. Notably, TOR suppression disrupted auxin and ethylene signaling pathways, repressed key genes required for cell wall loosening, and simultaneously upregulated genes related to phosphoinositide metabolism and ROS signaling indicating a complex reprogramming of cellular processes that govern root hair morphogenesis. Protein–protein interaction analysis further revealed that TOR, although interacting directly with few proteins like FER, exerts a broad influence through downstream networks involved in membrane dynamics, cytoskeletal organization, and transcriptional regulation. Collectively, our findings underscore the integrative role of TOR in coordinating nutrient, hormonal, and structural signals essential for root hair initiation and elongation. These insights not only deepen our understanding of TOR's function in root epidermal patterning but also offer potential molecular targets for enhancing root traits in legumes under nutrient-limited conditions.

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Disclosure statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authorship contribution

Kalpana Nanjareddy: Conceptualization, Project administration; Resources. Kalpana Nanjareddy and Manoj-Kumar Arthikala: Writing – review & editing, Writing – original draft, Formal analysis, Supervision and Funding acquisition. Hugo Alberto: Investigation, Methodology, Formal analysis. Miguel Lara: Data curation, Formal analysis, and original draft.

Data availability statement

Data will be made available on request.

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