

Rooting for order: How CIKs keep lateral growth in check

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Roots are essential for plant survival, anchoring them in the soil and absorbing water and nutrients they rely on to grow. The ability of a plant to thrive in different environments is influenced by the efficiency of its root system, which is shaped by the formation and arrangement of lateral roots branching from the main root (Gruber et al. 2013; Bao et al. 2014). Proper lateral root development maximizes soil exploration, optimizes resource acquisition, and helps plants adapt to various environmental conditions (Kenrick and Strullu-Derrien 2014; Shekhar et al. 2019).

RECEPTOR-LIKE KINASE 7 (RLK7) plays a key role in regulating lateral root patterning by detecting inhibitory signals from the TARGET OF LBD SIXTEEN 2 (TOLS2) peptide, which is secreted by neighboring cells. TOLS2 triggers the upregulation of the APETALA2-type transcription factor PUCHI, downstream of RLK7 (Hirota et al. 2007; Toyokura et al. 2019). This pathway limits lateral root initiation, ensuring even spacing of lateral roots and preventing resource competition in the soil. However, the molecular mechanisms by which RLK7 perceives and transduces the TOLS2 signal remain unsolved.

In this issue of *Plant Physiology*, Meng et al. (2024) identify a novel role for CLAVATA3 INSENSITIVE RECEPTOR KINASES (CIKs) in the RLK7-mediated signaling pathway. The authors propose that RLK7 works together with CIK proteins to transduce the TOLS2 signal during lateral root development (Fig. 1). Genotypic and phenotypic analyses revealed that CIKs are expressed similarly to RLK7 in lateral root founder cells and lateral root primordia (LRP). Moreover, the *cik1/2/4/5/6* mutants displayed a phenotype similar to that of *rlk7-3* (Toyokura et al. 2019), with increased LRP and lateral roots. These findings suggest that CIKs and RLK7 are likely in the same pathway to regulate LRP initiation and spacing.

Co-immunoprecipitation assays revealed interactions between RLK7 and the CIK proteins (CIK1, CIK2, CIK3, and CIK5), supporting the idea that CIKs are integral to the RLK7 signaling complex. The interaction between RLK7 and CIK4 was confirmed using yeast 2-hybrid and bimolecular fluorescence complementation assays. These results suggest that CIK proteins form part of a receptor complex with RLK7, which mediates the perception and transduction of the TOLS2 signal.

In wild-type plants, TOLS2 treatment reduced LRP number, consistent with the role of RLK7s in suppressing LRP initiation. However, TOLS2 treatment had no effect on *rlk7-3* or *cik1/2/4/5/6* mutants, highlighting the necessity of both RLK7 and CIKs in

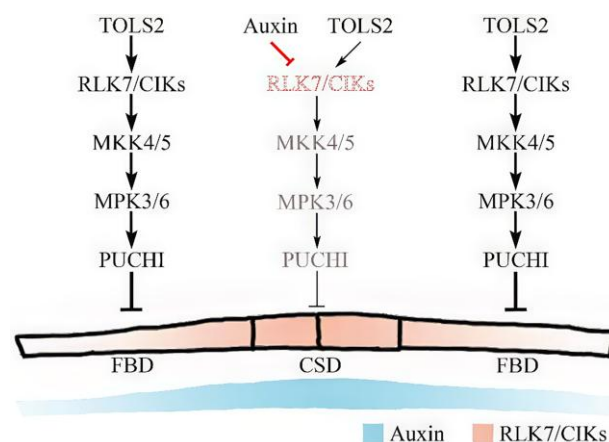


Figure 1. CIKs regulate the initiation and spacing of LRP via auxin and TOLS2 signaling. During lateral root initiation, high auxin levels in central smaller daughter (CSD) cells direct CIK proteins to the vacuole, disrupting TOLS2 signaling and promoting increased cell division. In contrast, flanking bigger daughter (FBD) cells, which have lower auxin concentrations, maintain active TOLS2 signaling, inhibiting further root initiation. Thin black arrows and brown text illustrate weakened signaling in auxin-enriched regions, while red lines and dotted text represent the promotion of vacuolar localization of RLK7/CIK complexes by auxin. Adapted from Meng et al. (2024).

TOLS2 signaling. Additionally, TOLS2 treatment enhanced CIK phosphorylation in wild-type plants but not in *rlk7-3* mutants, suggesting that CIK phosphorylation is also integral to the signaling pathway. Moreover, PUCHI expression was unresponsive to TOLS2 treatment in *cik1/2/4/5/6* mutants, confirming that CIKs are essential for transmitting the TOLS2 signal and activating downstream responses.

The study also establishes a connection between CIK proteins and the MKK4/5-MPK3/6 cascade, which, among other functions, is a well-known component of auxin signaling in RLK pathways (Jourquin et al. 2022). In wild-type plants, TOLS2 treatment enhances MPK3/6 phosphorylation, but this response is absent in both *cik1/2/4/5/6* and *rlk7-3* mutants, suggesting that CIKs act upstream of MPK3/6 in regulating lateral root initiation (Fig. 1). These results indicate potential cross-talk between the TOLS2-RLK7 pathway and auxin-mediated signaling, which could reveal new layers of regulation in lateral root development.

Received October 25, 2024. Accepted November 18, 2024.

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Meng et al. (2024) provide compelling evidence that CIK proteins, previously associated with shoot development, also play a critical role in shaping root system architecture by regulating lateral root spacing in *Arabidopsis*. By identifying CIKs as key regulators of lateral root development, this study opens new opportunities to improve crop performance through targeted manipulation of root architecture. Future research could explore how environmental factors, such as nutrient availability or drought, affect the CIK-RLK7 signaling pathway to better understand the adaptability of root systems to changing conditions.

Data availability

No data were generated or analysed in this study.

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