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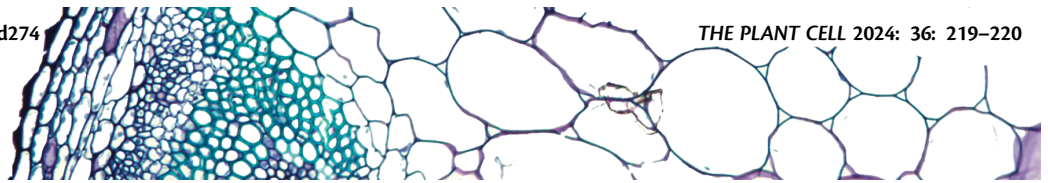
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# Filling the gaps: Monitoring Casparian strip integrity in rice

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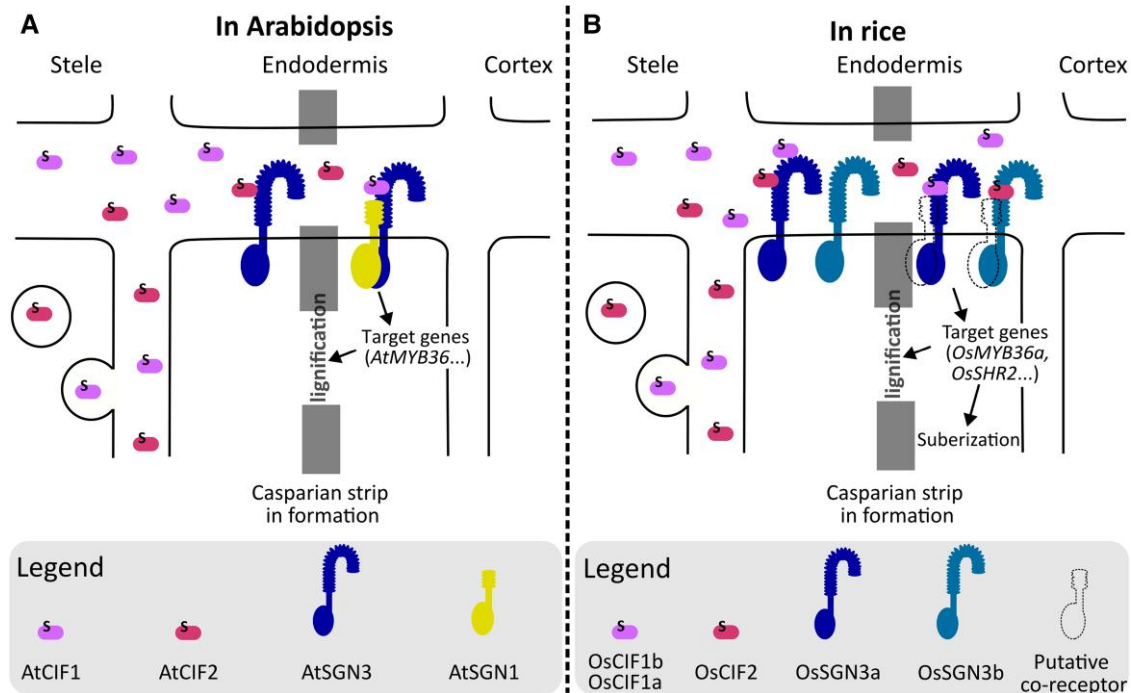
Selective uptake of mineral ions from the soil is crucial for plants to control electrolyte levels. In vascular plant roots, the diffusion of water and mineral nutrients through the apoplast is impeded by the Casparian strip, a band of polymerized lignin that seals the apoplastic space around the endodermis. A continuous Casparian strip is critical for the plant to control the passage of water and ions from the cortex into the stele and what is subsequently transported through the vasculature toward the shoot (Geldner 2013).

In Arabidopsis, a specific signaling pathway monitors the integrity of the Casparian strip. Small sulfated peptides, which are encoded by the *CASPARIAN STRIP INTEGRITY FACTOR 1* and *2* (*AtCIF1/2*) genes, are specifically secreted from the root stele (Fig. 1A). If the Casparian strip is discontinuous, these peptides diffuse toward the endodermis, where they can bind to the leucine-rich repeat receptor-like kinase *SCHENGEN3* (*AtSNG3*). This interaction allows the recruitment of the co-receptor *SCHENGEN1* (*AtSGN1*), specifically located at the cortical side of the endodermis. The downstream signaling cascade activates the production of lignin and clogging of the gaps (Fig. 1A). When the Casparian strip is continuous, the *AtSGN3/AtSGN1* receptors become physically separated from the *AtCIF* peptides, and the signaling stops (Doblas et al. 2017; Nakayama et al. 2017).

The *CIF/SGN3* signaling pathway thus acts as surveillance machinery for Casparian strip integrity in Arabidopsis. The extent to which this machinery is conserved in other plant species has remained unknown. In this article, Baolei Zhang and colleagues (Zhang et al. 2023) investigated the conservation of the *CIF/SGN3* pathway in rice. They identified 2 orthologous genes of *AtSGN3*, *OsSGN3a* and *OsSGN3b*, both expressed in the endodermis, and 3 orthologs of the *AtCIFs*, expressed in the stele.

*OsCIF1a* and *OsCIF1b* are 2 identical genes expressed in tandem, the third being *OsCIF2*. Loss of function of the 3 *CIF* peptides in *Oscif1ab,2* triple mutants or the 2 *SGN3* receptors in *Ossgn3ab* double mutants resulted in a notably thinner and discontinuous Casparian strip, rendering it more permeable to small apoplastic molecules. Isothermal titration calorimetry experiments showed that both *OsCIF1* and *OsCIF2* peptides have a strong affinity for the ectodomain of *OsSNG3a* with dissociation constants of 1600 nM and 439 nM, respectively. Furthermore, RNA-seq analyses conducted in *Oscif1ab,2* and in a line misexpressing *OsCIF1* in the cortex revealed that many orthologs of Arabidopsis genes involved in the Casparian strip formation are expressed downstream of the *CIF/SGN3* pathway in rice, such as *OsMYB36a*. Altogether these results indicate that the *CIF/SGN3* machinery monitoring Casparian strip integrity is extensively conserved in rice (Fig. 1B).

Interestingly, the authors identified some differences between Arabidopsis and rice. Firstly, in a normal context, the Arabidopsis *CIF/SGN3* pathway does not affect the endodermal suberization that follows Casparian strip lignification. In contrast, both *Oscif1ab,2* and *Ossgn3ab* mutants exhibit a clear reduction in endodermal suberization. Secondly, in rice, the misexpression of *OsCIFs* in the cortex induces ectopic lignification and suberization, whereas in Arabidopsis, this only occurs when the transcription factor *SHORT ROOT* (*AtSHR*) is misexpressed in the cortex as well. This difference may come from the expression of a second *SHR* (*OsSHR2*) gene in the rice cortex or from *OsCIF*-induced expression of *OsSHR1* or *OsSHR2*. Thirdly, the *CIFs-SHR1* combination can induce the formation of Casparian strip-like structures in more cortical layers in rice than in Arabidopsis, indicating a distinct ability of the *CIFs* to induce ectopic Casparian strip formation in these two species.



**Figure 1.** Casparian strip integrity surveillance machinery in Arabidopsis (A) and rice (B). Sulfated CIF peptides are secreted by the stele, diffuse through discontinuous Casparian strip, and bind the SGN3 receptor(s) in the endodermis. Co-receptor recruitment at the cortical side leads to a signaling cascade that activates target genes involved in Casparian strip lignification and clogging, as well as endodermis suberization specifically in rice. CIF/SGN signaling stops when a continuous Casparian strip blocks the diffusion of the CIF peptides. Figure made by NM Doll with Inkscape.

In conclusion, the SGN/CIF pathway plays a crucial role in the formation of a functional Casparian strip in rice and any defects in this pathway have a significant impact on the plant, affecting agronomically important traits such as tiller number, plant height, and grain set. Notably, the shoots of Casparian strip-defective plants display significant alterations in the concentration of various ions, indicating impaired ion homeostasis. This is likely a result of the defective control of ion movement toward the vasculature by a nonfunctional Casparian strip. Interestingly, the aerial parts of the *cif1ab,2* mutant plants are less affected than those of *sgn3ab*, which exhibits male sterility. This indicates additional functions of the OsSGN3 receptors in other contexts, in line with the pleiotropic roles of AtSGN3, such as monitoring embryonic cuticle and pollen coat integrity (Truskina et al. 2022). Further analyses of these functions would provide valuable insights into the conservation of the CIF/SGN3 pathway for the formation of apoplastic barriers between other tissues in rice.

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