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Spotlight

Root Development and Endosymbioses: DELLAs Lead the Orchestra

Camille Fonouni-Farde,[1] Anouck Diet,[1] and Florian Frugier[1,*]

DELLA proteins, acting as integrators of gibberellin (GA) action, are emerging as key regulators of root system architecture. Recent studies have revealed how they dictate the dynamics of root growth and are required for the establishment of root endosymbioses with rhizobial bacteria and mycorrhizal fungi. Like conductors, DELLAs can thereby harmonize root development depending on soil environments.

The plasticity of the root system development is crucial for plant adaptation to changing soil environments. External cues control root growth and differentiation as well as beneficial plant–microorganism symbiotic associations. Arbuscular mycorrhizal (AM) and rhizobial endosymbioses are mutualistic interactions respectively formed between most Angiosperms and Glomeromycota soil fungi under nutrient (e.g., phosphorus) starvation, and between legume (Fabacae) plants and soil bacteria collectively referred to as Rhizobia when soil nitrogen availability is limiting. In both cases, microorganisms colonize host roots depending on related signaling pathways, and in the rhizobial symbiosis, the plant additionally forms nodule organs allowing nitrogen fixation.

DELLA proteins are GRAS transcriptional regulators whose accumulation highly depends on the GA hormonal pool [1]. Indeed, GAs promote a targeted degradation of DELLA proteins mediated by the SCF/26S proteasome. As a result of their capacity to interact with multiple transcription factors from diverse families [1,2], DELLA proteins are emerging as integrators of transcriptional networks associated with various signaling pathways, and notably controlling root growth and endosymbiotic associations.

Root Apical Meristem (RAM) Maintenance and Cell Elongation Require DELLA Proteins

Root growth is determined by the relative rates of cell proliferation and elongation in the RAM. Cells in the RAM first undergo repeated rounds of divisions before increasing their size in the elongation zone and finally differentiate (Figure 1). The ratio between cell division and differentiation mainly results from the antagonist effects of auxins and cytokinins, respectively promoting cell division and differentiation, and involves a crosstalk relying on the activation of *SHY2* (Short HYpocotyl 2) auxin-repressor gene by the cytokinin-signaling transcription factor *Arabidopsis* response regulator (ARR)1 (Figure 1). Upstream of this regulatory circuit, DELLA proteins promote both *ARR1* expression and transcriptional activity thanks to a physical interaction [2,3]. DELLA–ARR heterodimers thereby represent new regulatory modules ensuring RAM maintenance and growth.

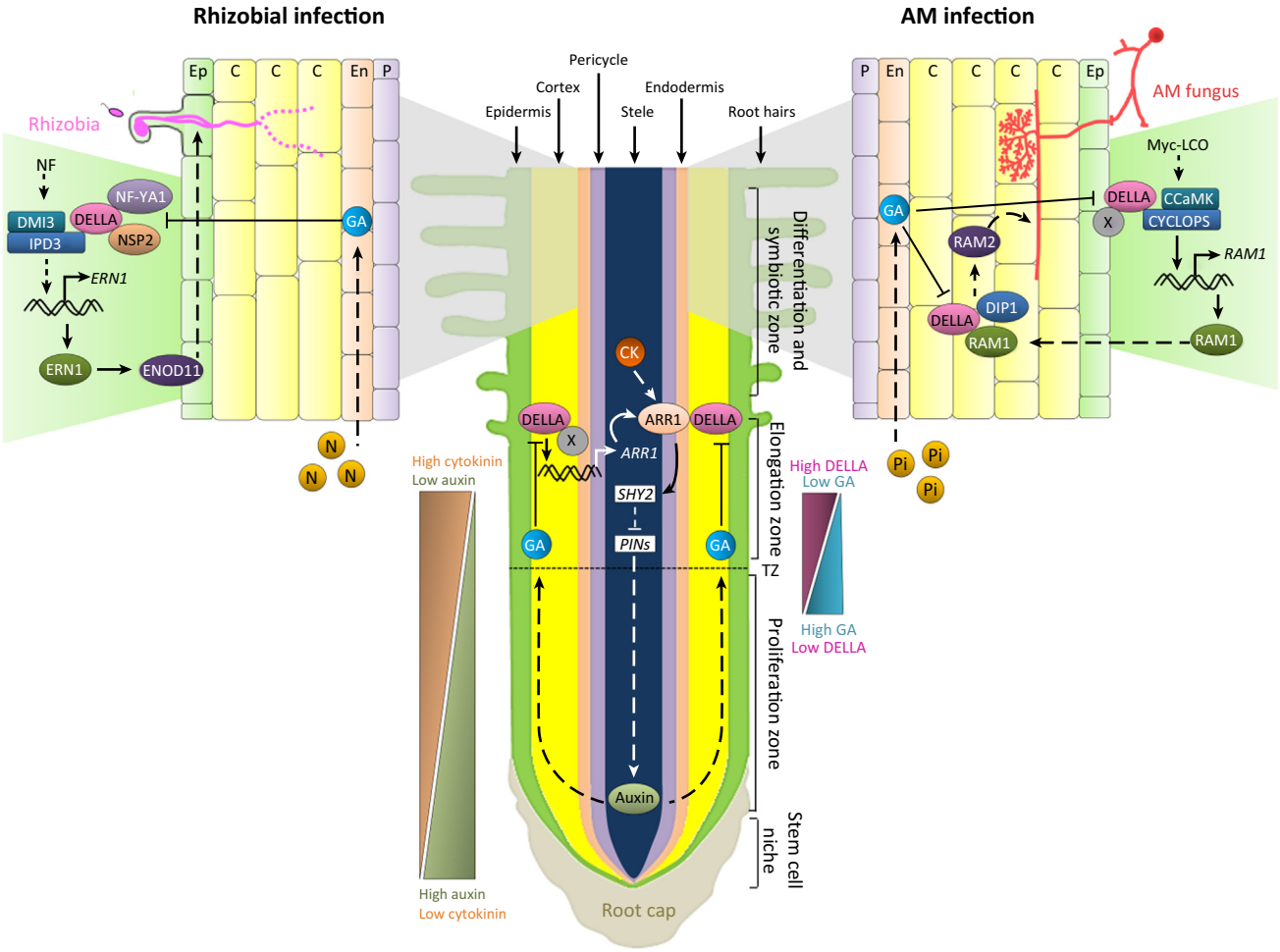
In addition to their role in cell division, DELLA proteins also negatively regulate cell elongation in the RAM. A multiscale mathematical model proposes that cell expansion affects the levels and distribution of GAs and consequently of DELLA proteins, resulting in a DELLA gradient with high levels at the proximal end of the RAM that ultimately regulates cell size [4] (Figure 1).

DELLA Proteins Are Required for the Legume Root Colonization by Endosymbiotic Nitrogen-Fixing Rhizobial Bacteria

The formation of nitrogen-fixing nodules on legume roots requires infection by Rhizobia at the root epidermis, and concomitantly the initiation of cortical cell divisions that lead to nodule organogenesis. At the molecular level, rhizobial infections rely on a signaling network triggered following the plant recognition of bacterial Nod factor (NF) signals. This pathway involves nuclear calcium spikes decoded by the calcium–calmodulin-dependent kinase/does not make infection 3 (CCaMK/DMI3), which associates with and phosphorylates CYCLOPS/interacting protein of DMI3 (IPD3) [5]. Downstream, several nuclear transcriptional regulators, such as nodulation signaling pathway (NSP)1 and NSP2, nuclear factor (NF)-YA1, ethylene response factor required for nodulation (ERN)1, coordinate the expression of symbiotic genes in the root epidermis, such as the *Early NODulin (ENOD)11* symbiotic infection marker [5,6]. Recently, DELLA proteins were identified as novel components of the NF signaling. In the model legume *Medicago truncatula*, they are necessary and sufficient to activate the expression of *ERN1* and *ENOD11* in the epidermis in the absence of NFs or symbiotic bacteria [7]. In addition, DELLA proteins physically interact with different transcription factors associated with early nodulation stages, namely NSP2, IPD3, and NF-YA1 [7,8]. A model is proposed in which, in response to NFs, DELLAs can bridge NSP2 and IPD3 transcriptional complexes, and potentially also NF-YA1, to transactivate *ERN1* expression (Figure 1). Thereby, DELLA proteins emerge as coactivators of early nodulation transcription factors and are essential for root colonization by Rhizobia.

DELLA Proteins Are Required for Root Colonization by Endosymbiotic *Glomeromycota* Fungi

The plant/Glomeromycota fungus AM endosymbiosis leads to the formation of



Trends in Plant Science

Figure 1. Role of Gibberellin (GA)/DELLA Regulatory Module in the Root Apical Meristem (RAM) and in Rhizobial and Arbuscular Mycorrhizal (AM) Endosymbioses. The RAM is divided into the stem cell niche, located around the quiescent center, the proximal meristem where cells divide, the elongation zone where cells elongate, and the differentiation zone where root hairs are notably formed and which also corresponds to the main rhizobial bacteria and AM fungi responsive region. RAM growth depends on the ratio between cell division and differentiation, which mainly results from the antagonistic effects of the cytokinin hormone, promoting cell differentiation, and of the auxin hormone, promoting cell division. To ensure an auxin/cytokinin crosstalk at the transition zone (TZ) between cell proliferation and differentiation, a model proposes that the cytokinin-signaling transcription factor ARR1 (authentic type B response regulator 1) negatively regulates PIN auxin-efflux carriers essential for polar auxin transport (black dotted arrows) through a direct activation of the *SHY2* (Short HYpocotyl 2) auxin-signaling gene, ultimately leading to a repression of auxin responses at the TZ. Upstream of this regulatory circuit, DELLA proteins activate or not ARR1 depending on GA levels: high GA levels induce the degradation of DELLA proteins and the repression of the expression of the *ARR1* gene, therefore promoting cell division. In contrast, decreased GA levels stabilize DELLA proteins and promote *ARR1* expression. A DELLA/ARR1 physical interaction additionally enhances the ARR1 transcriptional activity, ultimately promoting cell differentiation. Modeling approaches suggest that in the elongation zone, cell expansion provokes a dilution of the GA pool, resulting in the formation of a GA gradient and subsequently of a DELLA protein gradient regulating cell elongation dynamics. In the differentiation zone, signals produced by Rhizobia bacteria (Nod factors, NF) or AM fungi (mycorrhizal lipo-chito-oligossacharides, Myc-LCO) initiate symbiotic infections in the root epidermis. In the *Medicago truncatula* legume rhizobial symbiosis, DELLA proteins positively regulate NF–signaling transcriptional complexes by interacting with NSP2 (Nod factor signaling protein 2), IPD3 (interactor protein of does not make infection 3, DMI3), and NF-YA1 (nuclear factor-YA1) transcription factors to induce the expression of *ERN1* (*ERF Required for Nodulation 1*) and *ENOD11 (Early NODulin 11)* symbiotic genes, ultimately promoting symbiotic infections. This positive function of DELLA proteins is antagonized by GAs whose accumulation may by triggered by soil nitrogen (N). In the AM symbiosis, DELLA proteins interact with CYCLOPS (functionally equivalent to DMI3 in *Lotus japonicus*) as well as still unknown transcription factors ('X'), and in rice a RAM1 (Reduced AM1)/DELLA/DIP1 (DELLA interacting protein 1) complex may upregulate the expression of the *RAM2* AM symbiotic gene, both mechanisms ultimately promoting root hyphal colonization. This positive function of DELLA proteins in the AM symbiosis is antagonized by GAs and promoted by inorganic phosphorus (Pi). C, cortex; E, endodermis; Ep, epidermis; P, pericycle.

arbuscules in the root cortex, allowing nutrient exchanges between symbionts. Both plant–microbe interactions share a common symbiotic signaling pathway associated to symbiont recognition and to root infection, which was initially identified in legumes [5]. In response to mycorrhizal signals, additional components required for early stages of the AM interaction were identified such as the reduced arbuscular mycorrhization (RAM)1 transcription factor activating the *RAM2* mycorrhizal marker [5]. In the model legume *Lotus japonicus*, DELLA proteins interact with CCaMK–CYCLOPS to activate *RAM1* expression [9] (Figure 1). In addition, the unique rice DELLA protein slender rice (SLR)1 physically interacts with another GRAS protein, DELLA interacting protein 1 (DIP1), which is a positive regulator of the AM symbiosis because of its ability to interact with RAM1, to activate *RAM2* expression [10] (Figure 1). A RAM1/DIP1/SLR1 complex may then positively regulate the AM fungi root colonization by upregulating the expression of mycorrhizal genes such as *RAM2*. Overall, these data reveal that DELLA proteins are also positive elements in AM endosymbiosis early signaling pathways that can regulate the action of different sets of transcription factors.

Concluding Remarks: DELLA Proteins as Coordinators of Root Development and Endosymbioses?

The recent data highlighted here provide evidences that DELLA proteins play a pivotal role in regulating root development by controlling the dynamics of auxin/cytokinin-dependent root growth and the establishment of both rhizobial and AM endosymbioses, which themselves rely on auxin and cytokinin hormones [11]. DELLA proteins, whose activity is dictated by GA levels, modulate the action of core transcriptional regulators, providing an integrated regulatory mechanism to regulate simultaneously root development and symbioses. As rhizobial and AM symbioses are tightly regulated by the plant depending on nutrient availability, and as a negative correlation between DELLA levels and phosphate (Pi) availability was identified in the AM symbiosis [12] (Figure 1), DELLA proteins additionally likely integrate signal inputs from the environment to balance root growth with endosymbiotic interactions depending on soil nutrient availability. Capturing the dynamics and spatial specificities of the various transcriptional complexes involving DELLA proteins that can exist in the different root tissues and developmental zones is now essential to further understand their function in integrating environmental cues to modulate root growth and endosymbioses, and to ultimately decode molecular mechanisms driving root system plasticity.

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Spotlight

Strigolactones as Part of the Plant Defence System

Marek Marzec[1,2,*]

Strigolactones (SLs) are plant hormones, described as regulators of plant growth and development. Recently, it was proposed that these hormones might also be involved in the biotic stress response. However, SLs do not have a universal role in plant protection, instead only playing a part in resistance to specific pathogens.

SLs are a recently described group of phytohormones that are involved in many developmental processes [1]. In plant adaptation to nutrient-stress conditions, SLs play a crucial role in nitrogen- and phosphorus-deficiency reactions via modification of root and/or shoot architecture and promoting symbiosis with N-fixing rhizobial bacteria and arbuscular mycorrhizal fungi (AMF). The function of SLs in plant responses to other abiotic stresses such as salt or drought was also shown.

The first evidence for a possible role of SLs in the biotic stress response [2] came when promoter regions of genes involved in SL biosynthesis were found to contain motifs that are recognised by transcription factors (TFs) related to the response to pathogen (i.e., bacteria, fungi, viruses) resistance. It was subsequently observed that the expression of SL-biosynthesis genes in *Arabidopsis thaliana* and *Oryza*