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Strigolactone signaling in root development and phosphate starvation

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Strigolactones (SLs), have recently been recognized as phytohormone involve in orchestrating shoot and root architecture. In, roots SLs positively regulate root hair length and density, suppress lateral root formation and promote primary root meristem cell number. The biosynthesis and exudation of SLs increases under low phosphate level to regulate root responses. This hormonal response suggests an adaptation strategy of plant to optimize growth and development under nutrient limitations. However, little is known on signal-transduction pathways associated with SL activities. In this review, we outline the current knowledge on SL biology by describing their role in the regulation of root development. Also, we discuss the recent findings on the non-cell autonomous signaling of SLs, that involve PIN polarization, vesicle trafficking, changes in actin architecture and dynamic in response to phosphate starvation.

Strigolactones (SLs) are carotenoid derived plant metabolites, produced by diverse plant species, [1-3] and has attracted a great scientific interest since their recognition as a new group of phytohormone during the last few years. The first report on SL existence in 1996 from cotton root exudates postulated their potential role as a stimulant for the germination of parasitic plant seeds such as *Orobanche* and *Striga*.[4] However, later SLs have also been identified as stimulants of hyphal branching and root colonization of arbuscular mycorrhiza fungi (AMF).[5] It is only recently demonstrated that SLs are involved in orchestrating the shoot architecture by acting as shoot branching suppressor[6-8] and root architecture, by regulating lateral and adventitious root formation, and root hair development.[9-13]

SLs are synthesized mainly in root and other plant parts such as epicotyl and internode tissue; however the identified SLs to date are most abundant in roots.[3] Natural SLs share a common tricyclic lactone structure consisting of 3 rings (ABC), connected to a D-ring butenolide group via an enol-ether bridge.[1-2] In fact, the D-ring and enol-ether bridge are the characteristic feature for all active SLs.[14] The biosynthesis of SLs involve carotenoid isomerase (DWARF27, encoded by *AtD27/PsD27/D27*), catrotenoid cleavage dioxygenase-7 (CCD7, encoded by *MAX3/RMS5/D17orHTD1/DAD3*) and 8 (CCD8, encoded by *MAX4/RMS1/D10/DAD1*) which have been well characterized in Arabidopsis, pea, rice and petunia respectively.[15-18] It is suggested that D27 (an iron-binding protein) convert all *trans* β-carotene into 9′-*cis* β-carotene, which later oxidatively tailored, cleaved and cyclized by double bond specific CCD7 and CCD8 resulting in the bioactive SL precursor named carlactone (CL).[17] Downstream to these proteins, MORE AXILLARY GROWTH1 protein (MAX1, encoded by *MAX1/2PsMAX1/5OsMAX1/ PhMAX* in Arabidopsis, pea, rice and petunia respectively) which is a class III cytochrome P450 monooxygenase catalyze the oxidation and hydroxylation of CL resulting in to SL.[19]

Today, the knowledge on SLs biosynthesis pathway is well established,[1-3] however, the understanding on their perception, active transport and long distance travel for root development is still in its incipient stage but emerging in recent years.[20-23] Two proteins namely MORE AXILLARY GROWTH 2 (MAX2, encoded by *MAX2/RMS4/D3/PhMAX2A-B* in Arabidopsis, pea, rice and petunia) and DWARF14 (D14, encoded by *AtD14/D14/DAD2* in Arabidopsis, rice and petunia) are likely players involved in SL signaling.[15,20,22] For SL transport, a protein PLEIOTROPIC DRUG RESISTANCE 1 (PDR1) belonging to ATP-binding cassette (ABC) transporters has been identified involving in long distance transport of SLs from root to shoot and also in root tissues.[24] It is involve in efficient AMF colonization and inhibition of lateral bud outgrowth and is co-expressed with *CCD8* in root hypodermal cells with limited expression in shoot vascular and nodal tissues.[25] Here, we summarize the recent updates on SL biology by describing their role in the regulation of root development. Also, we discuss the recent findings on the non-cell autonomous signaling of SLs, that involve PIN polarization, vesicle trafficking and actin bundling in response to phosphate starvation.

SLs regulate root development in a MAX2 dependent fashion

The role of SLs in roots development was first evident from the studies of Kapulnik et al.[9] and Ruyter-Spira et al[26] wherein Arabidosis mutants for SL response (*max2*) and biosynthesis (*max3* and *max4*) exhibited more lateral roots than the wild type (WT). However, supplementation of GR24 (a synthetic and biologically active strigolactone)[6,7] repressed the lateral root formation in both WT and SL-synthesis mutants (*max3* and *max4*) but not in strigolactone-response mutant (*max2*). These results

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suggested that SLs negatively regulate lateral root formation in MAX2 dependent fashion.[9,26] Further, SLs have also been suggested to regulate primary root length, root hair length and meristem cell number in a MAX2 dependent manner.[27] Furthermore, the exogenous supplementation of diverse synthetic SLs analogs induced root hair elongation in Arabidopsis in WT and SL-synthesis mutants (*max3* and *max4*) but not in the strigolactone-response mutant *max2*, suggesting that the effect of SLs on root hair elongation is mediated by MAX2.[9,28]

SL reception

In SL signaling, MAX2 (a leucine-rich F-box protein) is considered to be a part of SKIP-Cullin-F-box (SCF) ubiquitin ligase that mediates protein degradation.[29,30] However, D14 belongs to α/β-hydrolase superfamily and play a crucial role in perception of SL, binding and conversion of SLs into bioactive form.[31] It has recently been suggested that the interaction of D14, MAX2 and D53 (a class I Clp ATPase)[21] is crucial for SL signaling. When SL bind with D14, it promotes the interaction between D14 and D53 leading to formation of D14-SL-D53 complex that enhances the interaction of D53 with F-box component of the $SCF^{D3/MAX2}$ complex. This interaction eventually leads to polyubiquitination of D53 protein and subsequent degradation *via* 26S proteasome pathway. It is further suggested that D53 negatively regulate SL signaling downstream to D14 and D3/MAX2 by allowing transcriptional activity of FC1 transcriptional factor which inhibits shoot branching in rice.[21,22,32] Moreover, it is also suggested that SL, in a MAX2-dependent way, induces the proteasome mediated degradation of D14. Hence, SL may limit their own signaling as a result of a regulatory negative feedback circuit on their own perception.[33]

SLs signaling act in non-cell-autonomous manner in root development

It has recently been demonstrated that epidermis play a crucial role in SL mediated regulation of root architecture. The expression of *MAX2* under SCARECROW (*SCR*) promoter, which is expressed mainly in root epidermis and quiescence center [34] is sufficient for GR24 sensitivity in roots for lateral root formation, meristem size and root-hair elongation.[27] Being regulation of root hair elongation takes place in epidermis, thus the sufficiency of endodermal expression of SL signaling to regulate root hair elongation supports the view that SLs also act in non-cell-autonomous manner. Further, restoration of SL sensitivity in *max2-1* mutants by expressing *MAX2* under xylem-specific promoter *NST3* for the development of adventitious root from pericycle cells in Arabidopsis suggests SL signaling acted in short-range, non-cell-autonomous manner.[35] However, *MAX2* expression under different tissue-specific promoters (such as *WOX4, SCR* and *APL* promoters specific for pro-cambium, starch sheath and phloem tissue respectively) in *max2-1* mutants suggests that SL act in a cell-autonomous manner in the regulation of shoot secondary growth.[35]

SL-associated root development involve changes in auxin efflux, PINs polarization, vesicle trafficking and actin bundling

So far, it has been suggested that under optimal conditions SL regulates the roots architecture by repressing lateral root formation, suppressing adventitious root formation and promoting root hair elongation.[9,26,35] Elongation of the root hair tip is affected by auxin transport in the epidermal cell layer containing the hair cells and flanking non-hair cells, including in the root elongation zone.[36] Recently, Pandya Kumar et al.[12] provide better insights on the mechanism of SL's mediated root hair elongation and associated auxin transport in epidermal cells of primary root elongation zone. In this study, SLs (G24) treatment resulted in greater root hair elongation, PIN2-GFP signal, PIN2 polarity without affecting AUX1 polarity in apical PM of the epidermal cells of primary root elongation zone together with the higher *PIN2* gene expression in WT but not in *max2-1*. These results suggest that SL affect the auxin flux and trafficking pathway *via* PIN2 polar localization only and is not associated with AUX1 polar localization in promoting root hair elongation. Further, SL possibly may use SHY2 as a molecular switch in reducing PINs level in PM that affect auxin homeostasis, in determining meristem size and promoting lateral root development.[27,37]

Apparently, polar position of PINs in the PM is vital in determining the direction of auxin flux.[38] PINs proteins undergo constitutive cycling between the PM and the endosomes. This dynamic vesicle trafficking that largely determines the PIN's PM polarization[39] is highly sensitive to Brefeldin A (BFA). Pandya Kumar et al.[12] demonstrated a high number of PIN2-containing BFA bodies per cell and endosomal movement velocity in epidermal cells of primary root elongation zone with GR24 treatment in WT but not in *max2-1* signifying that SLs induces PIN2 endocytosis in a MAX2-dependent manner in enhancing root hair elongation. Further, this study signifies that SLs alter actin architecture by reducing actin filament bundling but increasing F-actin dynamics that results in higher PIN2 localization in PM of epidermal cells in a MAX2-dependent manner thus promote root hair elongation. These findings were further supported by examining the effect of SL and auxin (IAA, Indole acetic acid) in mutants of ACTIN2 (*der1*), PIN2 (*eir1*) and PIN-trafficking-associated protein TRANSPORT INHIBITOR RESISTANT 3(*tir3*). Higher sensitivity of all the tested mutants to IAA but *eir1* mutants to GR24 treatments for root hair elongation compared to WT confirmed that GR24, unlike auxin utilize at least in part *via* vesicle trafficking associated with actin filament bundling for root hair elongation. F-actin has been shown to play a key role in vesicle trafficking in the cells, including vesicles that are involved in PIN recycling in PM of epidermal and cortical cells in roots.[39,40]

Therefore, it could be that although strigolactones are perceived in only certain cells (e.g., root endodermis), the progression of their signal to distinct cells and tissues (e.g., epidermis or pericycle cells in the root) mainly occurs through auxin. As a result, in the root, the initial signal from strigolactone to change auxin transport may lead to a regulatory circuit between polar auxin transport and actin organization and auxin-positive regulation of its own transport.[41]

Strigolactone signaling in phosphate starvation

The plasticity of root development in response to nutrient deficiency is vital. Phosphorus (Pi) is a building block for many essential molecules, involves in diverse metabolic process in plants and is the most limiting nutrient for plant growth. In coping with low Pi availability, plants increases the roots absorptive surface area by altering their root system architecture by increasing root-to-shoot ratio, lateral root (LR) formation, root hair length and density and decreasing primary root length, as an acclimation strategy (see reviews [42-44] and references therein). There are accumulating evidences confirming auxin as a major determinant in establishing LR primordium and the emergence of LR in the response of root system architecture to Pi deprivation (see reviews [45-47]).

An elevated level of SL in root and root exudates under low Pi conditions has been suggested as an adaptive response contributing to increased mycorrhizal colonization and nodulation.[2] Also, SLs were shown to be involved in shoot architecture under Pi deficiency.[7,44] Moreover, Mayzlish-Gati et al.[48] suggested that Strigolactones (SLs) regulate root hair elongation and lateral root formation under low Pi condition (48 h post germination) in Arabidopsis in a MAX2 dependent manner and by promoting transcriptional induction of auxin receptor TIR1 and several phosphate-starvation induced genes [*PSI* such as *ACP5* (alkaline phosphatase), *IPS1* (induced by phosphate starvation1), *PHO2* (phosphate 2) and phosphate-transporter (PHT1)]. These results relating to TIR1 expression are in agreement to those of Perez-Torres et al.[49] that demonstrated that TIR1induction under Pi starvation accelerate the degradation of transcriptional repressors called AUX/IAA proteins through the action of ubiquitin protein ligase SCF^{TIR1}, and thereby allow auxin response transcription (ARFs) to regulate genes involved in LR formation and emergence.

Recently, Kumar et al.[13] reported that SL signaling under low Pi condition (at least during early developmental stage, 48 hpg) transmits in a MAX2 dependent manner,[48] also involve regulation of PIN2 polar localization in PM and actin bundling and dynamics in Arabidopsis. In Kumar et al.[13] studies, Arabidopsis seedlings under low Pi condition showed reduced PIN2 trafficking and polarization in the PM (similar to the results presented for PIN2 and 7 in Gonzalez-Mendoza et al.[50]), decreased ARA7-labeled endosome trafficking, and increased actin filament bundling in root cells of WT. The *max4-1*, but not *max2-1*, with supplementation of synthetic SL (GR24) exhibited depletion of PIN2 from the PM under low-Pi conditions. Only minor changes in PIN2 expression were detected under low- compared with high-Pi conditions in both WT and max2-1. This suggests that the reduction in PIN2 PM polarity is not a result of changes in PIN2 gene expression under low Pi conditions but rather mainly due to changes in PIN2 trafficking under these conditions. Together, these results suggest that SLs are necessary for depletion of PIN2 proteins from the PM of epidermal root cells, and that this depletion is associated with the response to low-Pi conditions in terms of increased root-hair density. Similarly, Sun et al.[51] reported that SLs regulate the development of rice roots in a MAX2 dependent manner by down regulating most of PIN family genes such as *PIN1, PIN5, PIN9* and *PIN10* under N- and Pi- deficient conditions.

Being, PINs polar localization in PM is primarily determined by the constitutive trafficking of PIN vesicles between the PM and endosomes which requires F-actin bundling.[40] Kumar et al.[13] studied this and observed a significant reduction in the accumulation of BFA bodies, reduced movement of ARA7-labeled endosomes and increased actin bundling under low Pi condition in WT but not in *max2-1*. In addition, mutants for MAX2, MAX4, PIN2 and TIR3 (required for polar auxin transport) and one ACTIN2 mutant line had a reduced response (in term of root hair density) to low Pi compared with WT. This reduced response was restored by auxin (for all mutants) and GR24 (for all mutants except *max2-1*). Together, these findings implicate that increased F-actin bundling, and reduced PIN2 levels in the PM are part of an active plant response to low-Pi conditions wherein SLs regulate these cellular responses *via* MAX2 signaling at the early stages of development leading to disturbances in auxin flux. Gonzalez-Mendoza et al.[50] also suggested that reduced expression of *APSR1* (Altered Phosphate Starvation Response 1 transcription factor) negatively regulate PIN7 proteins resulting in long root hairs and reduced primary root length under Pi depleted condition in Arabidopsis.

Concluding remarks

The accumulating evidences suggest that in roots SLs execute their regulation on plant development through a close cross-talk with auxin. At least in the case of root response to conditions of Pi deficiency by increasing root hair density, SLs probably act in more than one way to manipulate auxin. By depletion of PIN2 from the plasma membrane they dampen auxin transport,[13] and at the same time they induce expression of *TIR1* and thus auxin perception.[48] As a consequence, alterations in root development probably occur such as reduced root elongation, and increased root hair density, both are distinctive root responses to low Pi conditions. However, SL signaling is probably integrated in roots with those of additional hormones than auxin (e.g., cytokinin, ethylene), which are involved in determination of root development and responses. Together these hormones probably create a carefully coordinated network for regulation of plant growth and its response to adverse growth conditions.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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