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Phytohormone-Mediated Homeostasis of Root System Architecture

Dongyang Xu and Masaaki K. Watahiki

Abstract

Unlike animals, most of the plants are sessile. This may be a reason why they developed the powerful ability of organ generation throughout their lifetime, which is distinct from the animals, whose generation potential is restricted in a certain period during development. Half part of the plant body, the root system, is hidden under the ground, where there is a competition of resources, for example, water and nutrients or biotic stresses and abiotic stresses surrounding the root system. With its strong regeneration ability, the architecture of the root system is shaped by all of these environmental cues together with the internal developmental signals. In this process, phytohormones work as the regulatory molecules mediating the internal and external developmental signals, thus controlling the morphology and function of the root system architecture. This chapter introduces the development of root system regulated by various phytohormones, like auxin, cytokinin, etc.

Keywords: root architecture, auxin, cytokinin, postembryonic organogenesis

1. Anatomy and development of root

1.1 Root system architecture

In different plant species, root system architecture (RSA) has diverse morphologies. There are basically two types of RSA, the taproot system (or allorhizic system) in gymnosperms and dicotyledons, like *Arabidopsis thaliana* (*Arabidopsis*), tomato (*Solanum lycopersicum* L.), carrot (*Daucus carota*), and poplar (*Populus* spp.) and the fibrous root system (or homorhizic system) in monocotyledons such as maize (*Zea mays* L.), rice (*Oryza sativa* L.), onion (*Allium cepa*), garlic (*Allium sativum*), and tulip (*Tulipa* spp.) [1]. The taproot system consists of a single thick central primary root (PR) with thin or no lateral roots (LRs); the fibrous root system has small and short-lived primary and adventitious roots (ARs) derived from shoots, stems, or leaves [1].

1.2 Intrinsic developmental signals and environmental conditions modify root system architecture

Arabidopsis as a eudicot has a taproot system, which consists of an embryonic radicle-derived PR and postembryonic-developed LR and ARs. Root regeneration

exists throughout the plants' lifetime; it is a distinctive feature of plants and contributes to their robustness in adverse conditions.

In *Arabidopsis*, LR initiation starts from pairs of pericycle cells that possess developmental potential as plant stem cells. These pericycle cells are selected and directed to become LR founder cells and form LR primordia by both intrinsic and environmental signals [2–5]. The primary LR is initiated from the basal meristem of the PR, where root cap-derived auxin influences the amplitude of oscillatory gene expression in the basal meristem and the elongation zone of the root, which leads to the pre-patterning of LR initiation sites [6, 7]. The pre-patterning process is marked by the expression of a series of genes, like *GATA23*, *MEMBRANE-ASSOCIATED KINASE REGULATOR 4 (MAKR4)*, and *IAA19* [7]. In the basal meristem and elongation zone, *DR5::Luciferase* expression was observed to rhythmically pulse with a period of ~6 h, which matched with the period of LR pre-branch site production [6]. It is recently reported that the source of auxin is provided by the cyclic programmed cell death of root cap cells [8, 9].

It is noteworthy that not all of the pre-branch sites emerge to be LR primordia [6]. The dormant pre-branch sites may present a selective mechanism for LR formation under certain growth conditions, such as water availability, nutrient levels, physical obstacles, or damage [5, 10–13]. It is interesting that many of the external signals converge on phytohormones to regulate root development. Among these phytohormones, auxin functions as a central mediator.

Mechanical forces are important regulators for plant morphogenesis. LR primordia always emerge from the convex side of PR bending, resulting in a left-right alternation of LR primordia. Bending caused by gravitropic curvature led to the initiation of LR primordia, where a subcellular relocalization of PIN1 was observed [11]. Release the pericycle cells from the restraints of adjacent endodermis by targeted single cell ablation of endodermal cells triggered the pericycle to reenter the cell cycle and induced auxin-dependent LR initiation [14]. Excision of the *Arabidopsis* PR leads to the promotion of LR formation, which is mediated by activated auxin biosynthesis and auxin transport [15].

2. Roles of phytohormones on root formation

2.1 Auxin

The phytohormone auxin which plays fundamental roles in many aspects of plant growth and development is also a well-documented key regulator of LR development [16, 17]. The natural auxin, indole-3-acetic acid (IAA), is mainly synthesized in a two-step pathway from tryptophan. First, tryptophan is converted to indole-3-pyruvate (IPA) by the TAA1/SAV3 family of aminotransferases; IPA is then converted to IAA by the YUCCA (YUC) family of flavin monooxygenases [18–23]. Auxin biosynthesis has been shown to play an essential role on both programmed and wound-induced LR and AR developments [15, 24, 25].

Polar auxin transport (PAT), mediated by auxin influx (AUX1 and LAXs) and efflux carriers (PINs and MDR/PGPs) [26–29], generates auxin gradients and maintains an auxin maximum to regulate LR formation and positioning [17, 30–33].

Auxin signaling is known to be an integrator of endogenous and exogenous signals for root branching [17, 30, 34, 35]. It begins with the degradation of a class of AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA) through TRANSPORT INHIBITOR RESPONSE 1 (TIR1) auxin receptor [36, 37], resulting in the activation of the AUXIN RESPONSE FACTOR (ARF) [38, 39]. ARF7 and ARF19 transcription factors further induce the expression of downstream target genes like *LATERAL*

ORGAN BOUNDARIES DOMAIN/ASYMMETRIC LEAVES2-LIKE (LBD/ASL) family genes *LBD16/ASL18* and *LBD29/ASL16*, promoting LR initiation at the protoxylem-pole pericycle cells [40–43].

2.2 Cytokinin

Cytokinin is also a main player in root development. In higher plants, isopentenyladenine (iP), trans-zeatin (tZ), and dihydrozeatin (dZ) are the predominant cytokinins [44]. Cytokinin level and patterning in plant are controlled by a fine equilibrium between cytokinin synthesis and catabolism [44, 45]. Cytokinin biosynthesis is dependent on the activity of *ATP/ADP-isopentenyltransferase* (*IPT*) and *LONELY GUY* (*LOG*) gene family [46–48], and the metabolism is mainly through the *CYTOKININ OXIDASE/DEHYDROGENASE* (*CKX*) genes [44, 45]. Cytokinin can also be inactivated through conjugation to glucose [49]. The spatial and temporal distribution of cytokinin is in part due to the specific expression of cytokinin synthesis and catabolism genes [45, 47, 48, 50–52].

In *Arabidopsis*, cytokinin signaling starts with the perception by the transmembrane cytokinin receptors ARABIDOPSIS HISTIDINE KINASE (*AHK*), *AHK2*, *AHK3*, and *AHK4/WOL1/CRE1* [53–55], which target the histidine phosphotransfer protein AHPs to activate the type-A and type-B ARABIDOPSIS RESPONSE REGULATORS (*ARRs*) that negatively and positively regulate cytokinin signaling, respectively [55–61]. Two type-A *ARRs*, *ARR7*, and *ARR15* were induced by both cytokine and auxin and are essential for embryonic root development [62].

Although some evidences showed that cytokinins act as both local and long-distance signals [51, 63–65], and some transporter proteins have been shown to be involved in cytokine transport [66–70], the molecular mechanisms of cytokinin transport are still not well characterized.

Postembryonic root development is regulated by the root apical meristem (*RAM*), where cytokinin is known to act antagonistically with auxin to control the balance of cell division in the division zone and cell differentiation in the transition zone, which is essential for the maintenance of the *RAM* and affects the growth and patterning of the root [64, 71]. Application of cytokinin reduces the number of meristem cells and the size of *RAM* and promotes cell differentiation in the transition zone; cytokinin biosynthesis and signaling mutants as well as *CKX* overexpression mutants have a larger *RAM* with more meristem cells [45, 64, 72]. Conversely, auxin treatment increases meristem size and promotes cell division in the proximal meristem, and auxin transporter *PIN* mutants display a smaller *RAM* [64, 73]. The cross-talk of cytokine and auxin in regulating *RAM* activity was shown to converge on the auxin-inducible *AUX/IAA* family gene *SHORT HYPOCOTYL 2/INDOLE-3-ACETIC ACID 3* (*SHY2/IAA3*) in the transition zone, where cytokinin activates *SHY2* via the *AHK3/ARR1* two-component signaling pathway to suppress *PIN3* and *PIN7* expression and promote cell differentiation, while auxin suppressed *SHY2* protein, leading to the activation of *PINs* and promotion of cell division [71]. Furthermore, Moubayidin et al. [74] revealed that in transition zone, *SCR*, a member of the *GRAS* family of transcription factors, directly represses the expression of *ARR1*, which controls auxin production via the *ASB1* gene and sustains stem cell activity, to simultaneously control stem cell division and differentiation and ensure coherent root growth. Cytokinin affects the expression of multiple *PINs* differentially in a tissue-specific manner to regulate auxin distribution [75, 76]. Auxin-cytokinin interactions lead the generation of distinct hormonal response zones, thus controlling the development of root vascular tissue.

On contrary to auxin, which is a positive regulator of LR development, cytokinin acts as a negative regulator of LR formation. Cytokinin suppresses LR initiation

through downregulating *PIN* expression and preventing the establishment of auxin gradient in LR founder cells [77]. Mutants with reduced cytokinin level or deficient cytokinin signaling increased the number of LRs [45, 58, 60, 78], while cytokinin treatment suppresses LR initiation and development [77, 79, 80]. Li et al. [80] reported that cytokinins inhibit LR initiation by blocking the cell cycle of pericycle founder cell at G₂ to M transition phase while promoting LR elongation by stimulation of the G₁ to S transition.

Through mutant analysis Chang et al. [81] showed that cytokinin biosynthesis genes *IPT3* and *IPT5* and all three cytokinin receptor genes *AHK2*, *AHK3*, and *CRE1/AHK4* act redundantly during LR initiation, and early stages of lateral root primordia (LRP) formation are particularly cytokinin sensitive. They suggest that cytokinin may serve as a positional signal for new LRP formation. In rice, ERF3 interacts with WOX11 to promote crown root initiation and elongation by regulating the cytokinin-responsive gene *RR2* [82]. Cytokinin has also been shown to modulate LR formation by mediating environmental cues. Jeon et al. [83] showed that CYTOKININ RESPONSE FACTOR 2 (CRF2) and CRF3 encoding APETALA2 transcription factors regulate *Arabidopsis* LR initiation under cold stress.

2.3 Other phytohormones

Other phytohormones, like abscisic acid (ABA), gibberellic acid (GA), brassinosteroid (BR), jasmonic acid (JA), ethylene, and strigolactone (SL), also participate in root growth and development.

Signora et al. [84] showed that ABA plays an important role in mediating the effects of nitrate on LR formation in *Arabidopsis*. Brady et al. [85] reported that *ABSCISIC ACID INSENSITIVE 3 (ABI3)* is involved in auxin signaling and LR development. De Smet et al. [86] reported that ABA application leads to the inhibition of LR development immediately after the emergence of the LRP from the parent root and prior to the activation of the LR meristem in an auxin-independent manner. Shkolnik-Inbar and Bar-Zvi [87] showed that *ABI4*, which encodes an ABA-regulated AP2 domain transcription factor, mediates ABA and cytokinin inhibition of LR formation through the reduction of PAT. Ding et al. [88] reported that ABA signaling and auxin homeostasis regulate WRKY46 to modulate the development of LR in osmotic/salt stress condition.

Hansen [89] reported on the GA-mediated light dependent promotion and inhibition of AR formation. Through mutant analysis, Yaxley et al. [90] showed that GA is important for normal root elongation in pea. Fu and Harberd [91] showed that auxin regulates root growth through GA-mediated DELLA protein destabilization. Steffens et al. [92] showed that GA is ineffective on its own but acts synergistically with ethylene to promote the number of penetrating roots and the growth rate of emerged roots in deepwater rice.

BR is a positive regulator of root development [93]. Bao et al. [94] showed that BRs interact with auxin to promote LR development.

JA, a crucial plant defense hormone, also participated in the regulation of root development. Raya-González et al. [95] observed that low concentrations of JA inhibited PR growth through an auxin-independent manner and promoted LR formation auxin-dependently, and JA receptor COI1 is involved in JA-induced LR formation and LR positioning. Cross-talk between JA and auxin has been frequently reported. JA has been reported to be implicated in YUC9-mediated auxin biosynthesis in wounded leaves in *Arabidopsis* [96]. Cai et al. [97] also reported a cross-talk between JA and auxin biosynthesis during LR formation mediated by ERF109. Gutierrez et al. [98] showed that auxin controls *Arabidopsis* AR initiation through the regulation of JA homeostasis.

Ethylene is also a well-known phytohormone that participates in the plant defense signaling pathways. Strader et al. [99] reported that ethylene interact with auxin to control root cell expansion. Ivanchenko et al. [100] observed application of low level of ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) promotes LRP initiation, while higher doses of ACC strongly inhibits LRP initiation but promotes LRP emergence; this regulation of LR initiation and emergence by ethylene is through interactions with auxin. Lewis et al. [101] reported that ethylene suppresses LR formation through promotion of PIN3 and PIN7-mediated auxin efflux to prevent local auxin accumulation.

Jiang et al. [102] showed that SL analog GR24 negatively influenced LR priming and emergence, which is dependent on the intimate connection with auxins and cytokinins, with the PAT capacity as a central player.

3. Conclusions

The root system of higher plants is modified by intrinsic developmental signals and diverse environmental cues. Both the internal and the external signals converged on phytohormones to regulate the formation of a highly plastic and adaptive RSA, which sustains the growth of plants even in adverse conditions. Several lines of evidences suggest that cross-talks among different phytohormones are essential for the regulation of root development, and auxin plays a central role in these processes. Although auxin and cytokinin as the key regulators of root development have been extensively studied, the roles of other phytohormones still need to be further characterized to give us a full view of plant root development.

Conflict of interest

The authors declare no conflict of interest.

Acronyms and abbreviations

RSA	root system architecture
PR	primary root
LR	lateral root
AR	adventitious root
IAA	indole-3-acetic acid
PAT	polar auxin transport
iP	isopentenyladenine
tZ	trans-zeatin
dZ	dihydrozeatin
RAM	root apical meristem
LRPs	lateral root primordia
ABA	abscisic acid
GA	gibberellic acid
BR	brassinosteroid
JA	jasmonic acid
SL	strigolactone
ACC	1-aminocyclopropane-1-carboxylic acid

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