Regulation and Expression of Phytohormones for Root Architectural Trait Development in Rice: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Review Article

ABSTRACT

The root system architecture (RSA) in monocotyledonous plants like rice is consists of primary roots, lateral roots, seminal/crown roots, and root hairs. The soil nutrients also influence many physiological processes *via* various root parameters like root length, root diameter and root angle for growth and development. The variation in root system architecture in rice is influenced by the

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intrinsic factors (phytohormones, transcription factors) and extrinsic factors (light, temperature and moisture) and their collective effect. The phytohormones such as; auxin, cytokinin, abscisic acid and ethylene, and their mutual effects play vital role for root architectural trait development. Many genes/QTLs were identified in rice which are strong role player for root development. But the biochemical signaling pathways are not completely understood. The modern molecular tools like genome editing, sequencing and multi-omics (transcriptomics and proteomics) approaches and multi-disciplinary system biology studies can provide a better solution for this issue. To improve the sustainable food grain production under extreme environment, it is important to understand the physiological and biochemical mechanism of root development. Moreover, it is imperative to establish a resilient root system in rice cultivation in order to mitigate the overuse of chemical fertilizers, enhance nutrient efficiency, and improve climate resilience of the plant.

Keywords: Rice; hormonal signaling; root system architecture; QTLs; transcription factors.

1. INTRODUCTION

Roots are critical for plant growth and development because they anchor the plant to its growing substrate, facilitate absorption of nutrients and water from the soil. Roots also play role in sensing and responding to environmental stimuli such as biotic and abiotic stresses [1,2]. Root growth is frequently influenced by macronutrient levels in the soil, which activate regional and systemic signaling pathways and plants regulate their growth in response to the supply of nutrients. These demands are fulfilled after communication between the root and the shooting part of the plant. Besides, the notable systemically signaling systems regulated by cytokinin, auxin and carbohydrates, additional pathways have been discovered in plants. Recently found are novel systemic and local pathways that regulate versatile root improvement concerning phosphorus and nitrogen deficiency. Furthermore, the potential of the *NITRATE TRANSPORTER 1.1* to carry auxin has established a useful connection between auxin, root development, and nitrate supplies in soil for the very first time [3]. Learning about how plants adjust their development because of the environmental signals can be gained by interpreting and integrating various signaling routes with the whole-plant level. To stimulate the plant organogenesis process and regrowth in *in-vitro* micropropagation, the equilibrium among two hormones such as; cytokinin and auxin, must be fine-tuned [4]. Sugar aids in the instruction of root development, nitrate and phosphate intake, as well as the plant's overall carbon status [5].

Environmental stresses, such as water and nutrient availability, force developing plants to adjust their root architecture. To maximize mineral nutrient uptake, these responses usually result in increased localized branching and root system development in rich soil areas. This is a root system's adaptive developmental responsiveness to nutrition accessibility in the soil [6]. The commencement and establishment of lateral roots are stimulated by a local rise in concentrations of nitrates, allowing the plant to inhabit and utilize nitrate-rich soil locations [7]. A MADS-box transcription factor (*ARABIDOPSIS NITRATE REGULATED 1* (*ANR1*)), was first discovered to enhance lateral root formation regarding nitrate was reported by Zhang and Forde [8]. In plants with antisense suppression of *ANR1* expression, the lateral root formation is slowed in reaction to nitrate, and root hair density is enhanced [9,10]. Adventitious roots are recognized from primary and lateral roots by this broad concept. In rice, ethylene is the essential chemical that progresses adventitious root improvement [11]. Auxin signaling is needed for ethylene-intervened adventitious root development in rice [12,13]. Inhibitor tests with N-1-naphthylphthalamic acid in flooded rice showed that polar auxin transport through the *PIN-FORMED (PIN)* class of auxin efflux transporters is fundamental for adventitious root for both grown-up and young plants [14]. Therefore, interplay of different hormone circuits is required for root induction. Auxin encourages adventitious and lateral root commencement, while roots restrain elongation through strigolactones and cytokinin hormones. In rice, *OsAUX1* regulates auxin-mediated lateral root advancement by managing polar auxin transportation [15], whereas auxin-cytokinin intermodulation additionally assumes a practical role in the regulation of rice root development and growth. An auxin-induced gene (*CRL5*) enhances crown root development by suppressing cytokinin signing [16]. Furthermore, OsMPK3/6 and OsMKK4/5 are employed with the regulation of root design through calibrating the auxin-cytokinin association [17].

A number of QTLs have been linked to a variety of root properties were identified in rice and many other crops including the model crop Arabidopsis. A QTL (*qRT9*) affecting root length & thickness was discovered an *OsbHLH120* transcription factor with a basic helix-loop-helix (*bHLH*) structure. The drought-response hormone abscisic acid (ABA), polyethylene glycol, and salt, all are significantly increased *OsbHLH120* expression, implying a link to the drought adaptation mechanism in rice [18]. Not only auxin and cytokinin, but also ethylene appears to play a role in rice root growth. Rice root development is aided by *OsEIL1*, a transcription factor engaged in the ethylene flagging pathway [19]. Production of gibberellic acid, as well as root meristem tissue extension and propagation, are all affected by another gene, *SHB*, which codes an AP2/ERF transcription factor [20]. Rice isoforms of the Arabidopsis auxin receptors *TRANSPORT INHIBITOR RESPONSE 1 (TIR1)* and *AUXIN SIGNALING F-Box 2 (AFB2)*, that interrelate thru *OsIAA1*, an *AUXIN/INDOLE ACETIC ACID (AUX/ IAA)* guiding protein, was discovered to impact signing auxin to facilitate primary and adventitious root development by guiding their target genes (*OsTIR1* and *OsAFB2*) [21]. Genetic instructions, hormonal signaling components and environmental stimuli all have a strong influence on the development of root architecture in rice. All phytohormones regulate root development and growth, either cooperatively or combatively. Therefore, in this review, we focused on the role of different phytohormones for root architectural traits such root apical meristem, radicle, crown and lateral root growth to fulfill the plant nutritional and water requirement under environmental stresses.

2. HORMONAL SIGNALING AND THEIR ROLE IN ROOT TRAITS DEVELOPMENT IN RICE

The growth and development of roots in plants are promoted by endogenous and exogenous factors [9]. Auxin which predominantly produced in shoots and actively transported to roots [22]; whereas cytokinin takes part in root-to-shoot signaling and move acropetally in the plant to stimulate shoot development [23]. A hypothetical illustration has been shown in Fig. 1 to elucidate the cooperative connection between auxin, cytokinin, sucrose, transcription factors and their influence for root trait development and nutrient availability to the plant through vascular connection. ABA and auxin promote the formation of lateral roots, however, cytokinin suppresses the formation of ethylene has interacted with auxin and may play a role in lateral root formation via cortical cell breakdown. Under flooded rice, gibberellic acid collaborates with ethylene to promote adventitious root development. The systemic mechanisms that regulate adaptive root progress in response to nitrogen and phosphorus deficiency were also currently revealed.

2.1 Role of Auxin in Root Apical Meristem Development

All root cells in plants are generated from the root apical meristem (RAM). The root tip's coordinated balance of cell division and differentiation is divided into three zones: proximal division zone, transition zone, and distal elongation zone [24]. The root tip of rice is formed by various types of cells arranged in concentric layers. The endodermis, cortex, sclerenchyma, exodermis, and epidermis surround the metaxylem, phloem, fibers, and pericycle. Following the first anticlinal division, eight successive asymmetrical periclinal cell divisions generate these five cell layers in rice from single epidermis-endodermis structural initial cells [25]. The quiescent center (QC) is located in the central position of the RAM and contains the cells which mitotically inactive. Auxin has vital role player for maintenance of QC. This region was reported in rice by using a marker gene *CYCLIN-DEPENDENT KINASE* (*CDK*) [26]. A *WUSCHEL* (*WUS*)-type homeobox gene named as *QUIESCENT-CENTER-SPECIFIC HOMEOBOX* (*QHB*) was spotted and expressed in central cells of QC. Similar expression result also noticed on an ortholog gene *WUS-RELATED HOMEOBOX 5* (*WOX5*) in Arabidopsis thaliana. Both the genes, *WOX5* and QHB performed parallel role in rice for maintenance of QC [27]. A mutation in a member of the *AUXIN (Aux)/INDOLE-3-ACETIC ACID* (*IAA*) gene family, *OsIAA23*, causes deformity in postembryonic QC maintenance due to the termination of root growth and breakdown of root cap in rice. The gene *OsSCR1* expressed in the endodermis part, whereas the gene *OsSHR1* is expressed in the stele region. These two genes regulate the epidermis and endodermis cell initiation in rice and the expression pattern in rice are similar with the expression reported in *Arabidopsis thaliana* [28]. More investigation is required in this direction to understand the role mechanism of hormonal regulation.
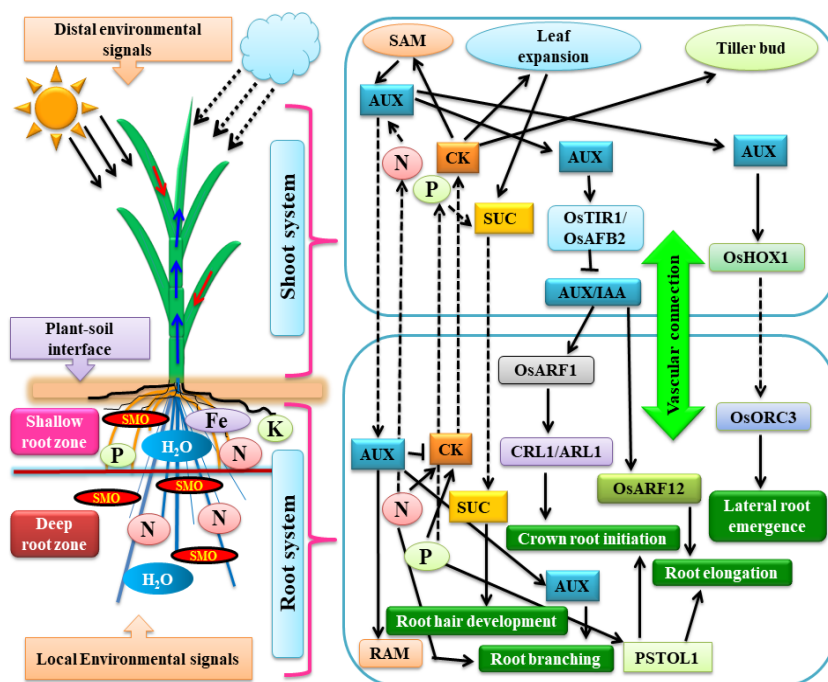
Fig. 1. A schematic representation of molecular (Hormonal) signaling pathways between root and shoot system for root traits development in rice, their effect on nutrient (N, P) uptake and possible hypothetical interactions

Two types of environmental signals are shown on the figure- (1) Distal environmental signals (solar radiation, rainfall); (2) Local environmental signals (soil-water, mineral nutrients (N, P, K, Fe), soil microorganisms). Under non-stress condition N, P, K and Fe are available on the shallow root zone and under stress condition Water and N available in deep root zone. Crown roots (black) and shallow adventitious roots (yellow) helps to uptake N, P, K, Fe and water from shallow root zone whereas, deep adventitious roots (blue) helps to uptake water and N from deep root zone.

Solid arrow- Positive regulatory action, Dashed arrow- Translocation of one molecule from one part to other part, T-shaped line- Negative regulatory action.

Blue arrow on the plant indicates upward movement of signals, Red arrow on the plant indicates downward movement of signals. Double head arrow indicates the vascular connection between root and shoot system.

Abbreviations: *AUX-Auxin, CK-Cytokinin, N-Nitrogen, P-phosphorous, K-Potassium, C-Carbon, Fe-Iron, H_2O-Water, SMO-Soil microorganisms, SAM-Shoot apical meristem, RAM-Root apical meristem, OsTIR1 and OsAFB2 - rice orthologs of the Arabidopsis auxin receptors TRANSPORT INHIBITOR RESPONSE 1 (TIR1) and AUXIN SIGNALING F-Box 2 (AFB2), OsORC3- A pivotal factor in DNA replication, ORIGIN RECOGNITION COMPLEX SUBUNIT 3, PSTOL1- QTL for low Phosphorous tolerance, OsARF12- OsAUXIN RESPONSE FACTOR 12 had shorter primary roots, ARL1/CRL1- first crown root development gene ADVENTITIOUS ROOTLESS 1/CROWN ROOTLESS 1*

2.2 Role of Auxin in Radicle Development

An embryo is developed by the cell division of zygote and no morphological differentiations were observed up to 3 days of planting. The radicle primordium is noticed at 4 days after planting along with the shoot apical meristem [29]. The genetic mechanism of radicle development in rice is presumed based on the available findings on *Arabidopsis thaliana*. Three *radicleless* (*ral*) mutant lines were identified by Hong et al. [30] and one of them is viable (*ral1*).

This gene is responsible for number of lateral and crown roots, but the growth is minimal and the plants with *ral1* gene have narrow leaves due to poor response of auxin [31].

2.3 Role of Auxin in Crown Root Development

Auxin has a positive influence on crown root development in cereals, as evidenced by several cereal mutants impaired in auxin sensitivity and response, three of which have been cloned in

rice as *CROWN ROOT LESS* genes (*CRL1, CRL4, CRL5*) [16,32,33]. The *crl1* mutant is disrupt in a gene that code for a LATERAL ORGAN BOUNDARY DOMAIN (LBD) protein, which is controlled by rice AUXIN RESPONSE FACTOR 16 (OsARF16), an ortholog (*ARF7/ARF19*) of *Arabidopsis thaliana* [32]. *CRL4* encodes a protein factor that regulates polar moment of auxin and is homologous to Arabidopsis thaliana gene, GNOM (GN) [34]. Kitomi et al. [16] discovered that *CRL5* encodes an auxin-responsive AP2/ERF transcription factor that controls crown root formation by inducing the rice repressor of cytokinin signaling, type A RESPONSE REGULATOR 1 (OsRR1). The initiation of crown root in rice is damaged by the mutant gene in *crown rootless4* (*crl4*)/*osgnom1* [34,35]. Numbers of crown roots were decreases in rice by the gene *WUSCHEL-RELATED HOMEBOX GENE 11* (*WOX11*) which is due to the antagonistic effect of auxin on cytokinin. Thus, the genes WOX11 maintain balance between auxin and cytokinin in rice for proper development of crown root [22]. The key enzymes for biosynthesis of auxin in rice were *YUCCA 1* (*OsYUC1*) and *CONSTITUTIVELY WILTED 1* (*OsCOW1*) reported by Woo et al. [36] and Yamamoto et al. [37]. The crown root development in rice is increased by the Overexpression of *OsYUC1* gene, however the gene *OsYUC1* show retardation of root growth dramatically [37]. Likewise; many genes (*PIN-FORMED* (*PIN*)) that encode auxin efflux carriers play crucial role in crown root growth and these are mediated by the polar moment of auxin. The overexpression of the gene *OsPINOID*, *OsPIN2* [38,39] results irregular and reduced crown root development by controlling the distribution of auxin, whereas; the downregulation of genes such as *OsPIN1b* and *OsPIN3t* enhances crown root development [40].

2.4 Role of Auxin and cytokinin in Lateral Root Development

As proved auxin modulation is critical for lateral root development [41,42] and the rhizomere structure that allows the individual capacities of several specialized cell types to collaborate to direct auxin to the tender branch site at the xylem-pole pericycle and resulted either a left or right lateral root [43]. Laskowski et al. [44] showed that *AUX1* facilitate in auxin importation and up-regulated by auxin. This activates plant organ development. A transcription factor (*AUXIN RESPONSE FACTOR* proteins (*ARFs*)) in rice also regulates root enlargement [45]. Few more factors also responsible for lateral and

adventitious root development in rice were identified like; *CROWN ROOTLESS1 (CRL1)/ADVENTITIOUS ROOTLESS1* (*ARL1*), encoding a plant-specific *LATERAL ORGAN BOUNDARIES* protein [16,32]. The phenotypic expression of lateral root formation in some mutant lines indicate the significance of auxin signaling reconciled by *Aux/IAA* and *ARF*. The drastically lessening of lateral root number was attributed by the mutant genes *osiaa11* and *osiaa13*, and stabilizes mutations in the part of domain II of *Aux/IAA* protein [46,47]. Auxin dependent lateral formation was reported by a mutation on *HEME OXYGENASE* (*OsHO1*) gene in rice. The same mutation also affects the signals related to stress responses [48]. Some mutant genes (*lateral rootless 1* (*lrt1*), *lrt2*, *auxin-resistant mutant 1* (*arm1*), and *arm2*) have abnormal function and develop deformed lateral roots, that is facilitated by auxin [49,50]. All the developmental processes are regulated by the cell cycle and abnormal cell cycle mediated gene expression of *ORIGIN RECOGNITION COMPLEX SUBUNIT 3* (*OsORC3*) in rice blocked the appearance of primordia of lateral roots. This deformity is depends on temperature regulation in rice [51]. Many candidate genes (like; *WUSCHEL-related homeobox 3A* (*OsWOX3A*), and *OsARF16*) were identified for lateral growth and they were worked in response to Auxin response [52].

2.5 Role of Cytokinin in Root Development

Cytokinin prevents lateral root formation in plants. When the nitrogen status of soil is low this act as an indication of stress by dropping cytokinin content [53]. Auxin to cytokinin ratio is vital for the development and regulation of lateral root formation. The procedure of an antisense transgenic revealed that cytokinins play a positive role in rice root development [54]. It is well-known that root establishment is inhibited by cytokinin but encouraged by auxin. Thus, cytokinin functions antagonistically to auxin and guide the process of root morphogenesis. The antagonistic regulation of auxin to cytokinin balance in *Arabidopsis* controls the size of root meristem [55].

2.6 Role of Ethylene in Root Development

Ethylene is commonly known as fruit ripening hormone, but besides this it also works for stress tolerance mechanism in plants by improving the root characteristics. Though, this hormone can increases or limits the root growth as per the

available concentration in the plant. Phytohormones have a significant influence on root branching, but the complex interaction effect remains a key concern in plant physiology. When roots come into contact with dry soil, they can become a source of inhibitors of shoot growth and stomatal opening, limiting the plant's water loss [53]. Ethylene is also shown its effects on rice root growth mediated adventitious root growth and aerenchyma formation in flooded rice [56]. But, the radial oxygen loss is not affected by this hormone under submerged condition [57].

2.7 Role of Abscisic Acid (ABA) in Root Development

Abscisic acid is a role player in lateral root development, root tip swelling, formation of the root hairs, and water permeability. This is observed in roots of a historic rice cultivar Taichung native 1 [58]. An experiment with a mutant gene (*OsIAA3*) by Nakamura et al. [59] imply the significant role of auxin for growth of nodal, seminal, and lateral roots and gravitropism. Under water limited situation, growth of root is likely subjected by the interaction effect of phyto-hormones, such as gibberellin, ethylene and ABA for the development of adventitious roots under deepwater rice ecology [60]. Abscisic acid and cytokinin derived from root, function to stimulate the water signal from root to shoot via transpiration pull. Many physiological processes and the work of a number of genes were also controlled by the activity of the ABA hormone. This hormone also keep plant cells turgid without losing too much water, supports in root growth, to increase root to shoot ratio to extract more water from the deeper soil zone. The plants are able to decrease the dehydration loss of water when the upper layer of soil profile is dry [53]. Thus, ABA has a great role to escape plants from water stress by closing the stomata.

3. CONCLUSION AND FUTURE OUTLOOK

The plants can self-adjustment with the changing climate as per the environmental stimuli. In broad sense plants have two distinct parts such as root system and shoot system. The key functions in plants like nutrition, photosynthesis, metabolism, and reproduction were coordinated between the root and shoot part *via*., mutual signaling of phytohormones. This is a cross-talk between the roots and shoots part of the plants for how to

respond to the environment. The general functions of the phytohormones are commonly known to all, but the biochemical signaling pathway for root and shoot development under biotic and abiotic stress conditions is not much discussed. Systematic signaling processes mediated *via* auxin, cytokinin, gibberellin, ethylene, abscisic acid and sugar molecular are studied for root development. Deciphering these biochemical pathways at the whole-plant level will give a new direction of understanding regarding the role of root growth and development to cope with environmental cues. Auxin mainly synthesized in the shoot part and transported actively to the roots part to promote root development, whereas; cytokinin moves acropetally to regulate shoot development. The mutual balance between these two hormones regulates the cell regeneration capacity and organogenesis of plant. Other than these two hormones; abscisic acid, ethylene and gibberellic acid are also crucial role player for root growth under different stresses to maximize the nutrient and water absorption from soil. The root architectural trait development in rice is varies among the cultivars according to the genetic makeup, growth pattern, biosynthesis pathways and the existing environment. The genotypes with stable variation for root trait expression are crucial for future breeding programme to improve the root trait for higher yield. The root system architecture is well characterized in the model plant *Arabidopsis thaliana*, but in rice still it is unclear and poorly understood. Therefore, this is required to identify the donor species in rice with well-developed root characteristics to combat with climate change. The identified major QTLs or gene families can be incorporated into the high yielding popular genotypes to increase the yield by designing an ideal root model. Crop wild relatives of rice have unique root traits. If their genetic mechanism can be characterized, then they will be act as wonderful donor parent for many novel genes/QTLs. Transcriptome and proteome analysis are vital to uncover the hormonal signaling pathway, nutrient transport mechanism and to understand the physiological responses for biotic and abiotic stress tolerance in rice. The variations in root characteristics are very important to cope with the environmental cues such are salinity stress, water stress, nitrogen/phosphate transport and hormonal signaling. Even though, few links were identified among the signaling pathways for transfer of message from one part of the plant to the other parts, but the information are fragmented. Thus, to address these issues in future, systemic multi-

disciplinary research is required to bridge the gap.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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