

Phytohormonal Control of Root Development and Architecture

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A B S T R A C T

Root System Architecture (RSA) is a critical determinant of plant water and nutrient acquisition, stress tolerance, and anchorage. Its development is orchestrated by a complex network of phytohormones that integrate genetic programs with environmental cues. Auxin acts as the central regulator for directing meristem differentiation, cell elongation, and lateral root initiation, xylem differentiation while hormones like cytokinins, gibberellins, ethylene, jasmonic acid, abscisic acid, strigolactones, and brassinosteroids modify the activity of Auxin or influence specific RSA traits independently. The crosstalk among the hormones decides the dynamic reprogramming of growth patterns of root under various stresses such as drought, salinity, and nutrient limitations. Understanding these regulatory interactions provides valuable opportunities for crop breeding with optimised root traits for improved resource-use efficiency and tolerance against changing climate.

Keywords: root system architecture, phytohormones, cross talk, climate change, use-efficiency

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1. INTRODUCTION

RSA is the three-dimensional arrangement and structural organisation of a plant root system under the soil matrix. It comprises diverse components such as the primary root, lateral/secondary roots, adventitious roots, root hairs, root surface area, root volume, root length, the angles, and branching patterns. Together, they describe how efficiently a plant can access nutrients and water, withstand physical stress, and adapt to changing climate. In both natural and agricultural systems, the Root System Architecture (RSA) plays a pivotal role in ensuring plant growth and survival (Smith & De Smet, 2012). A well-developed root system enhances nutrient use efficiency by enabling plants to explore larger soil volumes and optimise the uptake of

essential minerals, including trace elements. It also contributes significantly to water uptake and drought tolerance, as plants can adjust root depth and distribution in response to moisture availability, thereby sustaining themselves under water-deficient conditions. Additionally, RSA provides anchorage and structural support, with the spread and depth of roots stabilising plants against wind and soil erosion. Beyond these functions, RSA is central to stress responses and adaptability, dynamically reshaping itself under abiotic stresses such as salinity, temperature extremes, and drought, as well as biotic stresses like pathogen attacks, thereby optimising survival and resilience. The development and plasticity of RSA are not controlled solely by genetic programming. Phytohormones, act as biochemical messengers that regulate the growth, patterning, and

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branching of roots intricately. These hormones not only affect cell division and elongation but also mediate signal transduction pathways that integrate internal developmental cues with external environmental signals.

2. AUXIN

Auxin, largely in the form of indole-3-acetic acid (IAA), is integral to root development, composing processes such as meristem maintenance, lateral root formation, root hair development, and geotropic responses via a dynamic concentration gradient mediated by active transporters like PIN-FORMED (PIN) efflux carriers. Such gradients regulate the key genes expressions involved in cell elongation, division and differentiation. Higher auxin

levels at the root tip maintains meristem activity, while the same in pericycle cells induce lateral root formation. Additionally, auxin promotes unicellular root hair elongation and thus surface area expansion for nutrient uptake. Environmental stimuli, like edaphic factors including phosphate deficiency as well as mechanical resistance, induce localised auxin redistribution, thereby controlling RSA. Live-imaging studies by Grieneisen et al. (2007) confirmed that PIN proteins dynamically re-localise in response to environmental cues, reshaping auxin distribution and, consequently, root architecture. Notably, shifts in PIN polarity fine-tune root branching angles and density under stress conditions such as salinity or soil compaction, highlighting the plasticity of RSA mediated by auxin transportation mechanisms (Satbhai et al., 2015).

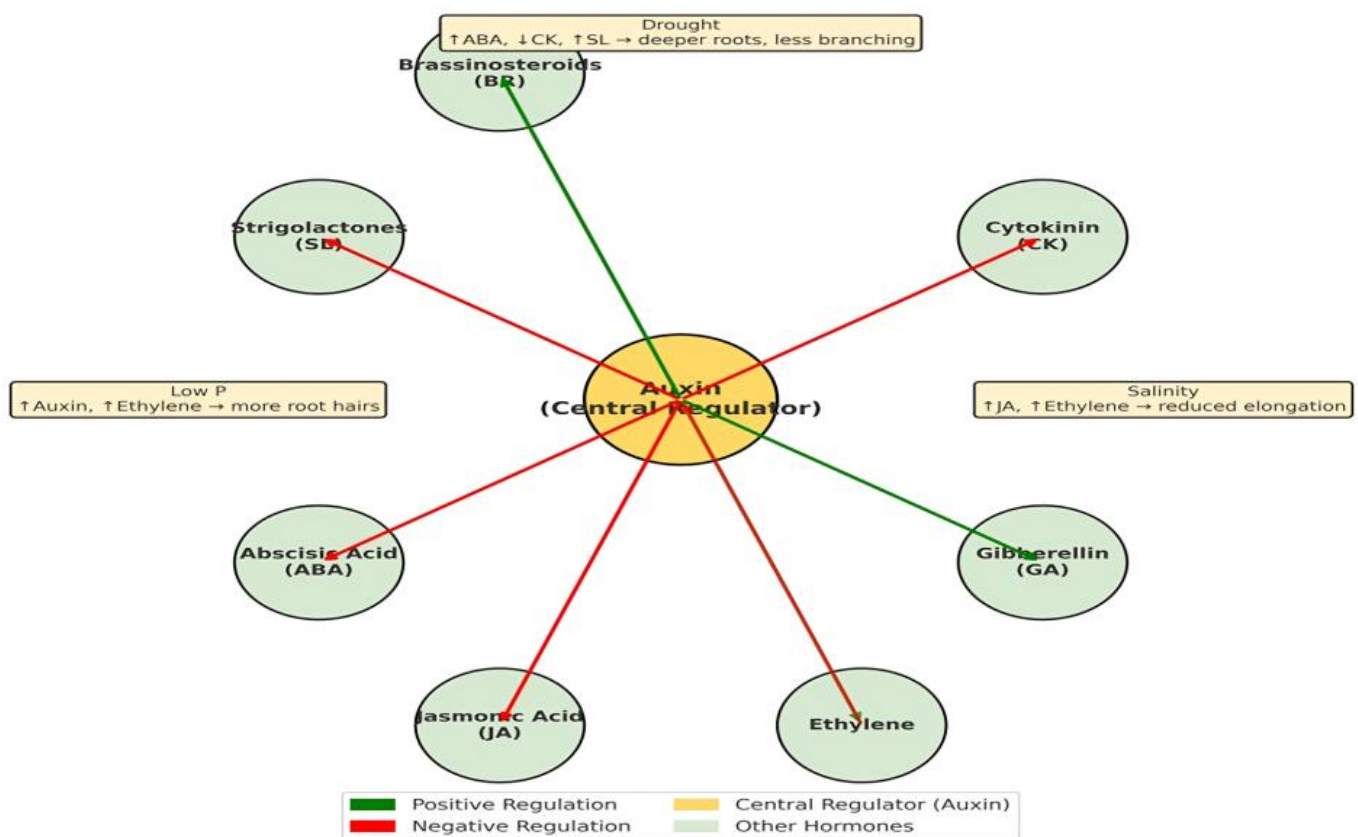


Figure 1. Phytohormonal Crosstalk Regulating Root System Architecture with Auxin as the Central Regulator

3. CYTOKININ

Cytokinin is one of the vital classes of phytohormone which regulates root architecture by often acting antagonistically to auxin; in the root apical meristem. They control horizontal growth by promoting cell division and differentiation, thereby reducing meristem size and overall root growth. It

interferes with auxin-mediated lateral root formation by modulating PIN protein expression, decreasing PIN distribution and altering its polarity, which dulls local auxin concentration. Additionally, it plays a pivotal role in nutrient-dependent RSA plasticity, balancing growth in diverse soil conditions to prevent excessive branching and promote efficient nutrient acquisition. The study by Laplaze et al. (2007)

illustrates this hormonal crosstalk, showing that external application represses lateral root formation by downregulating LBD genes, direct auxin targets and destabilising auxin gradients necessary for primordia development (Coudert et al., 2010). This antagonistic interaction allows exogenous cytokinin to supersede auxin signals, effectively banning lateral branching under nutrient-rich conditions, thus ensuring a structured and resource-efficient root system.

4. GIBBERELLIN

Gibberellin (GA), a diterpenoid phytohormone renowned for promoting cell elongation, particularly in the root elongation zone, play a crucial role in faster seedling growth by establishing vigorous root systems for efficient water and nutrient uptake. It regulates root apical meristem activity primarily via suppression of cytokinin mediated transcription factors such as ARR1, a negative regulator of cell elongation. Downregulating the same enables sustained cell division and elongation. They also act synergistically with auxin, reinforcing elongation processes and promoting deeper, more penetrative roots under favourable conditions. Beyond these effects, GA modifies cell wall architecture, and modulate downstream hormonal interactions, thereby fine-tuning root system architecture (RSA). The study by Ubeda-Tomás et al. (2009) using GA-deficient mutants (e.g., *ga1-3* and *gai*) demonstrated that lack of GA signaling results in petite primary roots, undersized meristems, and shorter elongation zones due to elevated ARR1 levels inhibiting cell expansion. Exogenous application restored root length and suppressed ARR1 expression, highlighting its essential role in overcoming the genetic constraints on root growth and maintaining robust RSA.

5. ETHYLENE

Ethylene, a gaseous phytohormone, shows intricate roles in RSA, acting as both an inhibitor and a promoter depending on environmental conditions and hormonal interaction. It generally suppresses root elongation and lateral root formation by destabilising auxin gradients through upregulation of SHY2/IAA3, a repressor of auxin signalling (Goh et al., 2012). This leads to reduced auxin-responsive gene expression. Conversely, ethylene promotes root hair growth, especially under stress conditions like phosphate deficiency or waterlogging, by activating ethylene-responsive transcription factors (ERFs) that induce genes responsible for root hair elongation and tissue

restructuring. Thus, it increases nutrient and air distribution. This hormonal cross-talk is vital during abiotic stresses, where ethylene modulates RSA to adapt and survive. For example, flooding in rice triggers ethylene accumulation, which induces adventitious roots and enhances root hair growth, facilitating oxygen uptake in hypoxic soils. Steffens et al. (2011) demonstrated that ERF-mediated activation of genes responsible for these modifications, illustrating how ethylene remakes RSA into a stress-resilient configuration for plant survival in adverse environment.

6. JASMONIC ACID

Jasmonic acid (JA), is a lipid-derived phytohormone, primarily functions as a growth suppressor in RSA during stress conditions such as pathogen attack, salinity, or mechanical impedance. It represses key regulators like PLETHORA (PLT1/2) via MYC2, which integrates stress signals to inhibit primary root growth. It also modulates auxin transport and sensitivity, affecting lateral root formation and root hair development. It downregulates PIN proteins, redirecting auxin flow to support surface structures over root elongation. In response to mechanical hinderances, its accumulation promotes root hair growth, enhancing nutrient absorption at the surface, a process driven by its influence on epidermal cell and auxin responses. This strategic reallocation of growth resources exemplifies how JA shifts RSA towards surface expansion, prioritising survival and nutrient uptake over deep soil penetration during adverse conditions.

7. ABSCISIC ACID

Abscisic acid (ABA) plays a crucial role in adapting RSA under low moisture stress by inhibiting lateral root emergence through mechanisms involving MYB96 and GH3 gene regulation. This results in conjugation making active auxin to inactive forms, affecting lateral root zones. At the same time, it promotes primary root elongation, enabling deeper root penetration and enhances aquaporin expression to improve water uptake, as observed in rice where ABA-mediated modulation of auxin gradients minimises lateral branching while boosting hydraulic conductivity. This dual strategy allows roots to conserve energy, prioritise water acquisition, and survive in arid environments, exemplifying how ABA orchestrates hormonal and molecular responses such as hormone pathway regulation and water channel protein expression to optimize root function under drought conditions.

8. STRIGOLACTONE

Strigolactone (SL), derived from carotenoids, serve as key regulators of RSA, especially under nutrient-poor and drought conditions, by suppressing lateral root formation via pathways involving MAX2 and SHY2, which modulate auxin transport through PIN protein localisation. This hormonal control reduces metabolic costs and encourages deeper root growth for water acquisition. In crops like rice, SL accumulation under drought conditions promotes a more vertical RSA with fewer lateral roots, enhancing drought resistance and water uptake efficiency. SL enables association with mycorrhiza, improving nutrient acquisition in phosphate-deficient soils, thereby integrating structural adaptation with nutrient strategy. SL composes a shift in root development, enabling plants to optimise water access and conserve resources during stress, exemplifying their role as pivotal modulators of adaptive root architecture.

9. BRASSINOSTEROID

Brassinosteroid (BR) are steroid that promote root hair formation and elongation by stimulating epidermal cell differentiation and expansion, thereby increasing the surface area, while also regulating non-hair cell growth to maintain root integrity. This plays a pivotal role in root elongation through cell wall loosening and interact synergistically with ethylene to enhance density of root hair and root length. In Arabidopsis exogenous BR application strengthens effects of ethylene, and BR mutants show reduced hair development that can be rescued by both hormones. It also influences gravitropism by modulating auxin distribution, especially under stress conditions. This hormonal interplay maximises nutrient and water uptake by fine-tuning epidermal cell fate and growth dynamics, underscoring their importance in adaptive root development.

Table 1. Phytohormonal Regulation of Root System Architecture under Different Stress Conditions (Koevoets et al., 2016)

Stress Condition	Key Hormonal Players	Root Response
Drought	Auxin, Abscisic Acid (ABA), Cytokinin (CK), Strigolactones (SL)	Suppressed lateral branching; deeper root penetration
Salinity	Auxin, Jasmonic Acid (JA), Ethylene	Reduced root meristem size; inhibited elongation
Low Phosphorus	Auxin, Ethylene, Jasmonic Acid (JA)	Increased root hair formation; denser lateral roots
Low Nitrate	Auxin, Cytokinin, Abscisic Acid (ABA)	Enhanced lateral root elongation
Elevated CO ₂	High Auxin, Low Cytokinin (under low N)	Increased lateral root density

10. CONCLUSION

RSA is a result of finely tuned process governed by multiple phytohormones acting individually and synergistically to balance growth and adaptability. Auxin serves as the central architect, while cytokinin, gibberellin, ethylene, jasmonic acid, abscisic acid, strigolactones, and brassinosteroids modulate its effects to optimize RSA under diverse environmental conditions. This crosstalk governs traits such as primary root elongation, lateral branching, root hair formation, and gravitropic responses, preparing plants to adjust to stresses like low moisture, salinity, and nutrient deficiency or toxicity. Insights into these mechanisms not only advance our understanding of plant developmental biology but also hold practical value for breeding programs aimed at improving water and nutrient use efficiency. Leveraging phytohormonal regulation offers a promising pathway toward developing

climate-resilient crop varieties with optimised RSA for sustainable agriculture.

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