

MINI-REVIEW



Mechanisms for Abscisic Acid Inhibition of Primary Root Growth

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ABSTRACT

Abscisic acid (ABA) plays pivotal roles in plant growth and development and in responses to diverse stresses. It also modulates the growth of primary and lateral roots. Much evidence indicated that key cellular components auxin, ethylene, PLETHs, reactive oxygen species and Ca^{2+} are involved in the regulation of ABA suppression of root elongation. In this review, we summary the molecular mechanism for ABA inhibiting primary root growth, focusing on the roles of these components in Arabidopsis.

ARTICLE HISTORY

Received 20 June 2018
Accepted 1 July 2018

KEYWORDS

Abscisic acid; primary root growth; auxin; PLETHs; ethylene; reactive oxygen species; Ca^{2+}

Abscisic acid (ABA) is a key phytohormone that controls many cellular processes including stomatal movement, seed maturation and germination, leaf senescence and responses to multiple abiotic and biotic stresses.^{1–3} It also regulates primary root growth and lateral root branching in plants.^{3–5} To date, both positive and negative effects of ABA on primary root growth have been documented, depending on ABA concentrations, environmental conditions, developmental contexts, genotypes and plant species. Typically, low concentrations of ABA stimulate but high concentrations inhibit root formation.^{4–6}

The key mechanisms for low concentrations of ABA promoting primary root development are that ABA enhances the activity of stem cells through maintaining the activity of quiescent center (QC), and suppresses the differentiation of stem cells and their daughter cells in root meristem.^{7,8} Both the QC center and stem cells, which constitute stem cell niches, have been demonstrated to play a central role in determining root meristem activity.⁹ Low concentrations of ABA also stimulate root growth by positively modulating the transport and signaling of auxin.^{4,5,10}

In recent years, great progress has been made on the mechanisms of high concentrations of ABA inhibiting root growth. Many components such as auxin, ethylene, reactive oxygen species (ROS) and Ca^{2+} have been found to mediate the processes, and the functions of these components are being uncovered.^{5,11–19} In this review, we summarize the main mechanisms underlying ABA suppression of primary root growth in Arabidopsis.

ABA signaling components mediate the inhibitory effects of ABA on root growth

Much evidence has indicated that high concentrations of ABA not only inhibits cell division in the apical meristems but also repress cell expansion in the elongation zone in roots.^{8,11,18} Moreover, ABA exerts these effects largely through ABA

signaling. At present, many key components of ABA signaling have been identified in Arabidopsis. They include PYR/PYL/RCAR (Pyrabactin resistance1/PYR1-like/Regulatory components of ABA receptor) ABA receptors, type 2C protein phosphatases (PP2Cs) ABI1 (ABA-insensitive1), ABI2, HAB1 (Hypersensitive to ABA1) and PP2CA, sucrose nonfermenting (SNF) 1-related kinases (SnRK2s) SnRK2.2, SnRK2.3 and SnRK2.6, Ca^{2+} -dependent protein kinases (CPKs), G protein, ROS, Ca^{2+} , transcription factors, and so on.^{2,3} There exist 14 ABA receptors (AtPYR1 and AtPYL1–13) in Arabidopsis.^{20,21} Of these, AtPYR1, AtPYL1, AtPYL2, AtPYL4, AtPYL5 and AtPYL8 redundantly and positively regulate ABA inhibition of primary root formation.^{21–23} ABI1, ABI2, HAB1 and PP2CA redundantly block the effects of ABA on root growth.^{15,24,25} SnRK2.2, SnRK2.3 and SnRK2.6 act downstream of PP2Cs and promote the ABA inhibition of primary root development.^{26,27} Besides, CPK4, CPK11, proline-rich extensin-like receptor kinase 4 (PERK4), ROS, Ca^{2+} and transcription factor ABI5 (ABA insensitive5) increase while G protein subunits $G\alpha$ and $G\beta$, and G protein-coupled receptors decrease the inhibitory effects of ABA on root growth.^{11,14,15,18,28–30}

ABA regulate DNA replication and the expression of cell cycle-related genes

Root growth involves cell division of apical meristem and elongation of the divided cells. Cell division requires DNA replication. Yin et al reported that an Arabidopsis ABA-overly sensitive mutant *abo4-1*, in which DNA polymerase ϵ catalytic subunit gene *POL2a/TILTED1 (TIL1)* is disrupted, exhibits clearly ABA supersensitive phenotypes in terms of root growth inhibition.¹² Moreover, the expression of the G2/M specific cyclin *CycB1;1* gene becomes constitutive in root meristems from *abo4-1* mutant. Likewise, Yao et al described that mutations in the DNA replication factor *C1* gene confer Arabidopsis sensitivity to ABA suppressed root growth.¹⁶ Moreover, deletions of genes encoding other DNA replication

related proteins such as DNA replication protein A2 and chromatin remodeling factor 1 also cause the susceptibility of the Arabidopsis mutants to ABA-arrested root development.¹² These results indicate that ABA inhibits root formation by regulating DNA replication.

ABA has been shown to increase the expression of *KRP1/ICK1*, a gene encoding the cell cycle-dependent protein kinase (CDK) inhibitor, resulting in the suppression of G1/S transition in the cell cycle.³¹ Xu et al provided evidence that ABA inhibition of primary root growth is mediated at least in part by ABA down-regulation of the expression of cell cycle B-type cyclin gene *CYCB1* at the G2/M checkpoint.³² Other researchers also found that ABA inhibits the expression of the *CYCB1;1* gene.^{18,33} These findings imply that ABA suppresses primary root growth through modulation of the transcriptional abundances of cell cycle genes.

ABA inhibits root growth by affecting auxin accumulation, transport and signaling

Auxin plays pivotal roles in controlling root formation. Its accumulation, distribution, transport and signal transduction events significantly affect primary root development.^{9,34} At the root tip, an auxin gradient is generated with a maximum in the stem cell niche, which controls the arrangement and fate of apical meristem cells, further determining root architecture.^{9,35} The formation of the auxin gradient is regulated by the auxin inward transport carrier *AUX1/LAX* (Auxin resistant1/Like *AUX1*) and the outward transport carrier PINs (PIN-FORMEDs). PIN family contains 8 members (PIN1-8) in Arabidopsis, of which PIN1, PIN2, PIN3, PIN4, and PIN7 play a crucial role in root growth.³⁶ Auxin also negatively affects the expression of *WOX5* (*WUSCHEL RELATED HOMEBOX5*), a key regulator of root development in plants.^{9,35,37}

ABA has been addressed to reduce the auxin level in roots, resulting in root growth arrest in Arabidopsis. Moreover, the inhibitory effects of ABA rely on ABA-induced ROS production.¹⁴ High concentrations of ABA also decrease the expression of *AUX1*, *PIN1*, *PIN3*, *PIN4* and *PIN7* genes in roots.^{18,19} Consistently, Arabidopsis mutant *aux1*, *axr4* (*auxin resistant4*) and *pin2* show markedly decreased sensitivity to ABA inhibition of primary root growth compared with WT.^{5,6,25} Moreover, *ABI4* and *ABI5*, two key factors of ABA signaling, also suppress *PIN1* expression; and the *abi4* mutant exhibits enhanced root auxin transport.^{38,39} These results suggest that ABA inhibits root development through impacting auxin transport.

ABA negatively regulate some essential components of auxin signaling like transport inhibitor response 1 (*TIR1*), *IBR5* (*IBA response5*), *AXR1* (*Auxin resistant1*), *AXR4*, and *Aux/IAA16* (*Aux/Indole-3-acetic acid*) in Arabidopsis. Compared with WT, the mutants of these protein-encoding genes are clearly less sensitive to ABA inhibition of root growth.^{5,6,25} Wang et al found that *ARF2* (*Auxin response factor2*), an important transcription factor of auxin signaling, negatively modulates ABA-inhibited root elongation by repressing its homeobox protein, *HB33* (*Homeobox protein33*) in Arabidopsis.³³ *ARF2* increases the expression of *PIN1*, *PIN3* and *PIN7*, but lowers the

abundances of *PIN4* transcripts in the presence of ABA.¹⁹ Besides, researchers have demonstrated that high concentrations of ABA prominently attenuate the response of roots to auxin using Arabidopsis transgenic plants overexpressing *proDR5::GUS* and *ProIAA2::GUS*.^{18,19,33} Collectively, these results indicate that ABA regulates auxin signaling and root response to auxin, thus suppressing primary root development.

ABA downregulates PLETHs (PLTs) expression

PLTs belong to the transcription factor family with AP2 (APETALA 2) domain. They display a graded distribution with a maximum near the root tip, very similar to auxin. High concentrations of PLTs are present near the QC, and responsible for regulation and maintenance of the stem cell activity. Medium concentrations of PLTs promote cell division whereas low concentrations of PLTs stimulate cell differentiation.^{35,37} The Arabidopsis PLTs family has six members (PLT1-6). PLT1-4 play an important role in root development, and the functions of PLT1 and PLT2 are extremely crucial. The expression of *PLT1* and *PLT2* is regulated by auxin, and their transcriptional gradients highly correlate with the auxin gradients in root meristem.^{35,37}

It has been addressed that high concentrations of ABA significantly reduce the expression of *PLT1* and *PLT2* at protein levels in roots.^{18,19} ABA can also dampen the promoting effect of *PLT2* on cell differentiation.^{18,19} Moreover, *ARF2* stimulates the protein expression of *PLT1*, but decreases the expression of *PLT2* in ABA signaling. These data indicate that ABA inhibits cell division in the root tip by regulating the level of PLTs in roots.

ABA negatively affects root elongation via modulation of ethylene signaling and synthesis

Ethylene plays a key role in root development. It controls root elongation through regulating the biosynthesis, transport, distribution and signaling of auxin.⁴⁰⁻⁴² Evidence suggests that ABA positively impacts ethylene signaling, and suppresses root growth. Moreover, *ETR1* (*Ethylene receptor1*), *EIN2* (*Ethylene insensitive2*) and *ETO1* (*Ethylene overproducer1*), key regulators of ethylene signaling pathway, have been demonstrated to be required for ABA inhibition of primary root growth.^{25,43,44} In addition, Luo et al. found that ABA inhibits root elongation by blocking the biosynthesis of ethylene. ABA activates *CPK4* and *CPK11*, which phosphorylate and stabilize *ACS6* (*1-Aminocyclopropane -1-carboxylic acid synthase6*), one of key rate-limiting enzymes for ethylene synthesis, and promote the generation of ethylene.¹⁷ Recently, Ludwików et al reported that *ABI1* negatively modulate ethylene production by counteracting the phosphorylation of *ACS2/ACS6* mediated by *MPK6*.⁴⁵ Together, these results hint that ABA blocks root development by activating ethylene signaling and increasing its biosynthesis.

ABA inhibits root formation by induction of ROS production

ROS are second messengers and play an important role in ABA signaling.⁴⁶ ROS regulates the cell division of apical meristems, the transition from proliferation to differentiation

and cell elongation through reducing the expression of cell cycle-related genes, altering cellular redox balance, disrupting DNA replication, and damaging cell wall structure.⁴⁶ ROS also decrease the level of auxin, negatively affecting auxin signaling in roots.¹⁴ ABA has been addressed to activate NADPH oxidases AtrbohD and AtrbohF in roots, leading to ROS synthesis and further inhibiting primary root elongation.^{15,47} ABA can also induce ROS production in mitochondria, thereby suppressing primary root growth.^{14,18}

ABA elevates the level of cytoplasmic Ca²⁺ and suppresses root development

Ca²⁺ is a vital secondary messenger in ABA signaling pathway in plants. It required for ABA-regulated primary root growth. Bai et al reported that PERK4 activates plasmamembrane Ca²⁺-permeable channels, and stimulates the increase of cytosolic Ca²⁺, mediating ABA-inhibited root elongation.¹¹ Likewise, Jiao et al found that ABA triggers the generation of ROS in roots, which activate Ca²⁺-permeable channels and promote the enhancement of Ca²⁺ levels in roots, hence inhibiting primary root growth.¹⁵ Ca²⁺ may function in ABA signalling in roots through activating CPK4 and CPK11, or via modulating ROS levels.^{30,48} The detailed mechanisms need to be further investigated.

In summary, ABA interacts with key cellular components auxin, ethylene, ROS and Ca²⁺, and regulates the expression of *PLTs* and some cell cycle-related genes, thus affecting DNA replication, cell division and cell elongation in roots and inhibiting primary root growth. Further work need to elucidate the interactional mechanisms of these components in response to high concentrations of ABA in plant roots.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Funding

This work was supported by the National Natural Science Foundation of China [31070239]; National Natural Science Foundation of China [30970235]; Program for young backbone teachers in universities of Henan Province [2016GG]S-024].

References

- Finkelstein RR, Gampala SS, Rock CD. Abscisic acid signaling in seeds and seedlings. *Plant Cell*. 2002;14:S15–S45.
- Cutler SR, Rodriguez PL, Finkelstein RR, Abrams SR. Abscisic acid: emergence of a core signaling network. *Annu Rev Plant Biol*. 2010;61:651–679.
- Sah SK, Reddy KR, Li J. Abscisic acid and abiotic stress tolerance in crop plants. *Front Plant Sci*. 2016;7:571.
- Harris J. Abscisic acid: hidden architect of root system structure. *Plants*. 2015;4:548–572.
- Li X, Chen L, Forde BG, Davies WJ. The biphasic root growth response to abscisic acid in *Arabidopsis* involves interaction with ethylene and auxin signalling pathways. *Front Plant Sci*. 2017;8:1493.
- Rowe JH, Topping JF, Liu J, Lindsey K. Abscisic acid regulates root growth under osmotic stress conditions via an interacting hormonal network with cytokinin, ethylene and auxin. *New Phytol*. 2016;211(1):225–239.
- Zhang H, Han W, De Smet I, Talboys P, Loya R, Hassan A, Rong H, Jurgens G, Paul Knox J, Wang MH. ABA promotes quiescence of the quiescent centre and suppresses stem cell differentiation in the *Arabidopsis* primary root meristem. *Plant J*. 2010;64:764–774.
- Takatsuka H, Umeda M. Hormonal control of cell division and elongation along differentiation trajectories in roots. *J Exp Bot*. 2014;65:2633–2643.
- Petricka JJ, Winter CM, Benfey PN. Control of *Arabidopsis* root development. *Annu Rev Plant Biol*. 2012;63:563–590.
- Xu W, Jia L, Shi W, Liang J, Zhou F, Li Q, Zhang J. Abscisic acid accumulation modulates auxin transport in the root tip to enhance proton secretion for maintaining root growth under moderate water stress. *New Phytol*. 2013;197:139–150.
- Bai L, Zhang GZ, Zhou Y, Zhang ZP, Wang W, Du YY, Wu ZY, Song CP. Plasma membrane-associated proline-rich extensin-like receptor kinase 4, a novel regulator of Ca²⁺ signalling, is required for abscisic acid responses in *Arabidopsis thaliana*. *Plant J*. 2009;60:314–327.
- Yin H, Zhang X, Liu J, Wang Y, He J, Yang T, Hong X, Yang Q, Gong Z. Epigenetic regulation, somatic homologous recombination, and abscisic acid signaling are influenced by DNA polymerase epsilon mutation in *Arabidopsis*. *Plant Cell*. 2009;21:386–402.
- Liu Y, He J, Chen Z, Ren X, Hong X, Gong Z. ABA overly sensitive 5 (ABO5), encoding a pentatricopeptide repeat protein required for cis-splicing of mitochondrial nad2 intron 3, is involved in the abscisic acid response in *Arabidopsis*. *Plant J*. 2010;63:749–765.
- He J, Duan Y, Hua D, Fan G, Wang L, Liu Y, Chen Z, Han L, Qu LJ, Gong Z. DEXH box RNA helicase-mediated mitochondrial reactive oxygen species production in *Arabidopsis* mediates crosstalk between abscisic acid and auxin signaling. *Plant Cell*. 2012;24:1815–1833.
- Jiao Y, Sun L, Song Y, Wang L, Liu L, Zhang L, Liu B, Li N, Miao C, Hao F. AtrbohD and atrbohF positively regulate abscisic acid-inhibited primary root growth by affecting Ca²⁺ signalling and auxin response of roots in *Arabidopsis*. *J Exp Bot*. 2013;64:4183–4192.
- Yao T, Jin D, Liu Q, Gong Z. Abscisic acid suppresses the highly occurred somatic homologous recombination in *Arabidopsis rfc1* mutant. *J Genet Genomics*. 2013;40:465–471.
- Luo X, Chen Z, Gao J, Gong Z. Abscisic acid inhibits root growth in *Arabidopsis* through ethylene biosynthesis. *Plant J*. 2014;79:44–55.
- Yang L, Zhang J, He J, Qin Y, Hua D, Duan Y, Chen Z, Gong Z. ABA-mediated ROS in mitochondria regulate root meristem activity by controlling PLETHORA expression in *Arabidopsis*. *PLoS Genet*. 2014;10:e1004791.
- Promchuea S, Zhu Y, Chen Z, Zhang J, Gong Z. ARF2 coordinates with PLETHORAS and PINs to orchestrate ABA-mediated root meristem activity in *Arabidopsis*. *JIPB*. 2017;59(1):30–43.
- Ma Y, Szostkiewicz I, Korte A, Moes D, Yang Y, Christmann A, Grill E. Regulators of PP2C phosphatase activity function as abscisic acid sensors. *Science*. 2009;324:1064–1068.
- Park SY, Fung P, Nishimura N, Jensen DR, Fujii H, Zhao Y, Lumba S, Santiago J, Rodrigues A, Chow TF, et al. Abscisic acid inhibits PP2Cs via the PYR/PYL family of ABA-binding START proteins. *Science*. 2009;324:1068–1071.
- Gonzalez-Guzman M, Pizzio GA, Antoni R, Vera-Sirera F, Merilo E, Bassel GW, Fernandez MA, Holdsworth MJ, Perez-Amador MA, Kollist H, et al. *Arabidopsis* PYR/PYL/RCAR receptors play a major role in quantitative regulation of stomatal aperture and transcriptional response to abscisic acid. *Plant Cell*. 2012;24:2483–2496.
- Antoni R, Gonzalez-Guzman M, Rodriguez L, Peirats-Llobet M, Pizzio GA, Fernandez MA, De Winne N, De Jaeger G, Dietrich D, Bennett MJ, et al. PYRABACTIN RESISTANCE1-LIKE8 plays an important role in the regulation of abscisic acid signalling in root. *Plant Physiol*. 2013;161:931–941.
- Rubio S, Rodrigues A, Saez A, Dizon MB, Galle A, Kim TH, Santiago J, Flexas J, Schroeder JI, Rodriguez PL. Triple loss of function of protein phosphatases type 2C leads to partial constitutive response to endogenous abscisic acid. *Plant Physiol*. 2009;150:1345–1355.
- Thole JM, Beisner ER, Liu J, Venkova SV, Strader LC. Abscisic acid regulates root elongation through the activities of auxin and ethylene in *Arabidopsis thaliana*. G3 (Bethesda). 2014;4:1259–1274.

26. Fujii H, Verslues PE, Zhu JK. Identification of two protein kinases required for abscisic acid regulation of seed germination, root growth, and gene expression in *Arabidopsis*. *Plant Cell*. 2007;19:485–494.
27. Zheng ZF, Xu XP, Crosley RA, Greenwalt SA, Sun YJ, Blakeslee B, Wang LZ, Ni WT, Sopko MS, Yao CL, et al. The protein kinase SnRK2.6 mediates the regulation of sucrose metabolism and plant growth in *Arabidopsis*. *Plant Physiol*. 2010;153:99–113.
28. Lopez-Molina L, Mongrand S, Chua NH. A postgermination developmental arrest checkpoint is mediated by abscisic acid and requires the ABI5 transcription factor in *Arabidopsis*. *PNAS*. 2001;98:4782–4787.
29. Pandey S, Chen JG, Jones AM, Assmann SM. G-protein complex mutants are hypersensitive to abscisic acid regulation of germination and postgermination development. *Plant Physiol*. 2006;14:243–256.
30. Zhu SY, Yu XC, Wang XJ, Zhao R, Li Y, Fan RC, Shang Y, Du SY, Wang XF, Wu FQ, et al. Two calcium-dependent protein kinases, CPK4 and CPK11, regulate abscisic acid signal transduction in *Arabidopsis*. *Plant Cell*. 2007;19:3019–3036.
31. Wang H, Qi Q, Schorr P, Cutler AJ, Crosby W, Fowke LC. *ICK1*, a cyclin-dependent protein kinase inhibitor from *Arabidopsis thaliana* interacts with both *Cdc2a* and *CycD3*, and its expression is induced by abscisic acid. *Plant J*. 1998;15:501–510.
32. Xu J, Gao GL, Du JJ, Guo Y, Yang CW. Cell cycle modulation in response to the primary root of *Arabidopsis* to ABA. *Pak J Bot*. 2010;42:2703–2710.
33. Wang L, Hua D, He J, Duan Y, Chen Z, Hong X, Gong Z. Auxin response factor2 (*ARF2*) and its regulated homeodomain gene *HB33* mediate abscisic acid response in *Arabidopsis*. *PLoS Genet*. 2011;7:e1002172.
34. Overvoorde P, Fukaki H, Beeckman T. Auxin control of root development. *Cold Spring Harbor Persp Biol*. 2010;2(6):a001537.
35. Mähönen AP, Ten Tusscher K, Siligato R, Smetana O, Díaz-Triviño S, Salojärvi J, Wachsman G, Prasad K, Heidstra R, Scheres B. *PLETHORA* gradient formation mechanism separates auxin responses. *Nature*. 2014;515:125–129.
36. Petrasek J, Friml J. Auxin transport routes in plant development. *Development*. 2009;136:2675–2688.
37. Galinha C, Hofhuis H, Luijten M, Willemsen V, Blilou I, Heidstra R, Scheres B. *PLETHORA* proteins as dose-dependent master regulators of *Arabidopsis* root development. *Nature*. 2007;449:1053–1057.
38. Shkolnik-Inbar D, Bar-Zvi D. Expression of *ABSCISIC ACID INSENSITIVE 4 (ABI4)* in developing *Arabidopsis* seedlings. *Plant Signal Behav*. 2011;6:694–696.
39. Yuan TT, Xu HH, Zhang KX, Guo TT, Lu YT. Glucose inhibits root meristem growth via *ABA INSENSITIVE 5*, which represses *PIN1* accumulation and auxin activity in *Arabidopsis*. *Plant Cell Environm*. 2014;37:1338–1350.
40. Růžicka K, Ljung K, Vanneste S, Podhorská R, Beeckman T, Friml J, Benková E. Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution. *Plant Cell*. 2007;19:2197–2212.
41. Stepanova AN, Alonso JM. Ethylene signaling and response: where different regulatory modules meet. *Curr Opin Plant Biol*. 2009;12:548–555.
42. Mao JL, Miao ZQ, Wang Z, Yu LH, Cai XT, Xiang CB. *Arabidopsis ERF1* mediates cross-talk between ethylene and auxin biosynthesis during primary root elongation by regulating *ASA1* expression. *PLoS Genet*. 2016;12:e1005760.
43. Beaudoin N, Serizet C, Gosti F, Giraudat J. Interactions between abscisic acid and ethylene signaling cascades. *Plant Cell*. 2000;12:1103–1115.
44. Ghassemian M, Nambara E, Cutler S, Kawaide H, Kamiya Y, McCourt P. Regulation of abscisic acid signaling by the ethylene response pathway in *Arabidopsis*. *Plant Cell*. 2000;12:1117–1126.
45. Ludwików A, Cieśla A, Kaspruwicz-Maluśki A, Mituła F, Tajdel M, Gałgański Ł, Ziółkowski PA, Kubiak P, Małecka A, Piechalak A, et al. *Arabidopsis* protein phosphatase 2C *ABI1* interacts with type I *ACC* synthases and is involved in the regulation of ozone-induced ethylene biosynthesis. *Mol Plant*. 2014;7(6):960–976.
46. Tsukagoshi H. Control of root growth and development by reactive oxygen species. *Curr Opin Plant Biol*. 2016;29:57–63.
47. Kwak JM, Mori IC, Pei ZM, Leonhardt N, Torres MA, Dangl JL, Bloom RE, Bodde S, Jones JD, Schroeder JI. *NADPH oxidase AtrbohD* and *AtrbohF* genes function in ROS-dependent ABA signaling in *Arabidopsis*. *EMBO J*. 2003;22:2623–2633.
48. Wilkins KA, Matthus E, Swarbreck SM, Davies JM. Calcium-mediated abiotic stress signaling in roots. *Front Plant Sci*. 2016;7:1296.