

MINI REVIEW
REGULATION OF ROOT SYSTEM BEHAVIOR BY ABIOTIC STRESS.

ISAAC ZEPEDA JAZO*
UNIVERSIDAD DE LA CIÉNEGA DEL ESTADO DE MICHOACÁN DE OCAMPO

RECEIVED DATE: 23-02-2016; ACCEPTED DATE: 23-03-2016; PUBLISHED DATE: 28-03-2016

CORRESPONDENCE AUTHOR: ISAAC ZEPEDA JAZO
E-MAIL: z_isaac@hotmail.com

CONFLICTS OF INTEREST
THERE ARE NO CONFLICTS OF INTEREST FOR ANY OF THE AUTHORS.

ABSTRACT:

Soils abiotic stress is the biggest individual stress that limits the productivity of crops and distribution of plant species worldwide. Salt and drought soils affects the development of the radical system and thereby the entire plants organisms. Many aspects on how roots grow, develop and respond to changes in soil conditions are poorly understood. To achieve adaptation to soil environment of root growth, plants can adjust their root growth rate and direction determining the architecture of the radical system and the exploration of the medium. Almost all of this growth happens in the first millimeters of the root apex. What happens in this relatively small mass of cells can impact the performance of the crops under not optimal conditions like the hydric and salt stress. Many of the phenomena implicated in root cells response to external stimulus are regulated by membrane transport activity and their regulation factors. This review focuses in what we have learnt about the adaptation of plants to drought and salinity: how the roots sense and continues his growth in soils under abiotic stress.

INTRODUCTION

In plants the radicular system development is stimulated by cell divisions in meristem zone of all root apices. Some of behavior of roots are controlled by tropism responses in epidermal cell of different radical zones, allowing plant to reach water, nutrients and oxygen. Nevertheless, the formation and emergence of secondary roots is influenced also by the environment and determines the root system architecture in soil. Malamy (10) named the essential factors for the organogenesis and root growth as "intrinsic", and the ones that determine how plants respond to external signals to modulate the intrinsic factors as "response factors". How roots respond to these factors is one of the most intriguing cues for scientists today.

Effects of abiotic stress

The radical system is the first to perceive the stress signals for drought and salinity, therefore its development is deeply affected by the availability of water in soil. The soil solution salinity reduces its hydric potential, due to a decrease of its osmotic component.

There is no total agreement on which of two effects has more importance on the decrease of plant growth, which is probably because it depends of environmental conditions and the specie under consideration. The first effect whereby the plant's growth decline when the soil's hydric potential is reduced is not well established. By subjecting the plants to salt conditions, Termaat et al., (6) found that in a first phase predominate a similar osmotic effect to those produced by a water stress. Munns and Termaat (7) named the water stress induced by salinity: "short term effect of salinity", due to its immediate effect on plants. In a more critical revision (8), it's mentioned that the lack of turgor pressure is not the cause of the decrease of plant growth for it is not essential for its production. These authors suggest the existence of a chemical compound produced in the roots by detecting salinity conditions, which triggers the physiological response in plants in stress conditions revealing a high level of plasticity in the root system development. However, many of the implied mechanisms in

this roots plasticity are still unknown, for example: How they have the unique potential of incorporate information from the environment for making decisions that will determine its development? (9). There are different parameters to study and identify how the changes in water availability and distribution and salt stress affect the development of the root; these same factors of response are of big importance because often they can modulate indirectly the architecture of the root producing unfavorable changes in nutritional composition of soil, the distribution of nutrients, the density and compaction of soil and the type of soil particles and the production of secondary metabolites in plants (10). Their interactions however complicate the dissection of specific transduction pathways involved in root growth and development (11). In many cultivated species, the growth of roots and stem is inhibited during the lack of water, but the roots continue growing under water potentials that are completely inhibitors for the growth of the aerial part (12). This difference in sensitivity may confer a growth advantage for the plants under limited water condition encouraging a major exploration of soil while limiting water loss through the tissues of the aerial part. Understanding how the growth is regulated by the water deficit and the salt stress is necessary to find ways to improve the productivity of crops.

Abiotic stress and root architecture

Notably, while the primary root growth is not appreciably affected by water deficit, the number of lateral roots and its growth are significantly reduced (9). It has been suggested that the reduction of the lateral roots formation may be caused by the suppression of the activation of the lateral root's meristem, not because of the reduction of the initiation in the lateral root per se (9, 10). Mutants with alterations in the development of lateral roots respond differently to drought stress (9, 13). Suppression of the development of lateral roots by drought has been widely accepted as an adaptive response to ensure the plant's survival under unfavorable growing conditions (13). Nevertheless new lateral root formation and/or lateral root growth as well as the differentiation/elongation of root hairs lead to a considerable increase of the overall absorption surface (11). Another factor that plays an important role in growing and development of plants to tolerate the drought stress is the hydrotropism (14, 15). In turn, the increase of the root's length mediated by the hydrotropism is one of the most important factors for the tolerance of crops to salinity and has been used to produce drought tolerant crops (16). A gradient of moisture

generated by water stress causes an immediate degradation of amyloplasts in columella cells of plant root, producing a minor response to gravity and an increase of hydrotropism (17). However, it is unknown how the gravity signals interact with other environmental signals to modulate the direction of the root's growth; less known are the adaptations in root's morphology and its relevance to salinity tolerance. Many halophytes have developed morphological adaptations, like the formation of specialized organs to expel salt out of their leaves, which allows them to keep the water and take out the salt in an active manner. Glycophytes have not developed permanent changes on its morphology to deal with salt, but they can adjust the root growth and its architecture in response to salinity, like in the case of *Arabidopsis* (figure 1 in (18)). Also it has been observed that *Arabidopsis* roots exhibit a reduced gravitropism under salt stress, growing against the gravity vector (16). These same authors speculate that the reduced gravitropism of root's growth could be an important mechanism of adaptation through the plants regulates the root system architecture to reduce the damage caused by salinity. *Arabidopsis*' roots exposed to a simultaneous salinity and gravity stimuli responded to salinity with a change in growing direction in a way that apparently represents an adaptive arrangement between gravitropic and saline simulation. Control of the relation between gravitropism and hydrotropism allows plants to redirect the root's growing for a better water uptake, giving an advantage during development of the radical system under stress conditions. It is known that the salt stress inhibits the growth of the primary roots in *Arabidopsis* seedlings, although it has been reported that salt stress also modulates root gravitropism of primary roots in young seedlings. In vertical position, five day seedlings germinate normally in MS medium (Murashige and Skoog) containing different concentrations of NaCl, however the direction of root growth changes according to the increase of NaCl concentrations, and the root curves in stressed plants with 150 mMNaCl in the medium (16). These results suggest that the salt stress and the induction of signal's translations by stress, not respect gravity and modulate the direction of the roots. Some reports suggest that the gravitropic signal and the answer in root's apex are controlled, at least partially by SOS signaling pathway (Salt Overly Sensitive). Therefore, this pathway might interact with the gravity sensor system in the cells of the columella to direct root growth in a coordinated way (16). A slight drought stress increases the expression of enzymes associated with root morphology (Xyloglucanendotransglucosylase) while other

structural proteins (actin and tubulin) are down regulated, these proteins are strongly correlated with root growth since its function is the vesicular carrying in cells with polarized growth (e.g. root hairs) allowing its growth and hence an augmentation in the surface of water uptake. However, when there is a greater stress, these structural proteins increase their expression. It is believed that alterations in the expression of these proteins are positively correlated with the modification of root architecture that partially has an indirect effect on whole plant photosynthetic process (57). While the decrease of lateral root development is a well-known response to water stress, none of the mutants that are resistant to drought stress have a reduced number of lateral roots (58). Only a few transcription factors have shown to regulate the formation of roots under drought conditions, among them stands the MYB96 transcription factor since it plays an important role in lateral root growth under drought stress conditions (58), these same authors found that overexpression of MYB96 promotes resistance to drought and reduced lateral root density.

Growth root regulators on abiotic stress

The radical system is the production place of various growth regulators of plants. Many growth hormones, particularly the abscisic acid (ABA) and the auxins, participate in a complex signal's system that plays a very important role in the development of root's architecture under drought conditions. These hormonal effects (levels) even though are considered as intrinsic (10) can change in response to environmental cues. Cytokinins, gibberellins and abscisic acid are produced in roots to be transported to other tissues, where they play their roles in development and growth. Although auxins are the major determinants of root growth (19), cytokinin and especially abscisic acid (ABA) (20-22); have been proposed as potential products that act as chemical signals in response to water stress to modulate root system architecture. The decrease in water potential of roots, not leaves, caused by salinity is the factor that triggers the production of ABA in different species (23). A condition of mild osmotic stress also inhibits the lateral root's formation in a dependent way of ABA (9, 10, 13, 24). For the case of *Arabidopsis*, the reduced water availability dramatically inhibits the formation of lateral roots of the lateral primordium, while the initiation of lateral roots is not affected. This inhibition does not occur in a lateral root mutant 2 (*lrd2*) nor in two ABA deficient (9, 10). Abscisic acid and a recently identified gen *LRD2*, are linked to repression of lateral root's formation in response to osmotic stress. It is very interesting to note that these regulators are

also related to the establishment of root architecture without apparent effect of osmotic stress. The mutant *lrd2* presents an altered response to exogenous application of ABA, while ABA-deficient mutants and *lrd2* show an altered response to inhibitors of polar auxin transport (25-27) suggesting a joint interaction of the hormonal signaling pathway in the regulation of lateral root formation. Some authors propose a model where the promotion or suppression of hormonal signaling pathway and regulators as *LRD2* determine the type of lateral root primordium and coordinate the root system architecture in response to environmental stimuli (see (18)). In contrast, under drought stress conditions or osmotic stress, activation of the lateral root meristem is suppressed by ABA-mediated signals, producing few small lateral roots (9, 28). While auxins seem to be the main initialization hormone, pattern and emergence of lateral roots; ABA is the main hormone that controls the environmental effect (like drought and salt stress) over the root's architecture (29).

Ionic transport and abiotic stress

Root's epidermis is the first tissue that makes contact with salt; hence, it is the first to perceive osmotic and ionic changes in cells and the first one that triggers defense mechanisms. This can cause that stresses (drought and salt stress), were treated conjunctively in many cases, although it must not be forget the accelerated senescence of leaves in salt conditions by the ionic toxic accumulation. The accumulation of sodium in the cells and the resulting ionic imbalance is the main cause of inhibition of plant growth and decrease of yields (4). Therefore, maintaining low intracellular sodium is critical for plant adaptation to water and salinity stress. Plants use different strategies to fight against salinity damage in every organizational level, from cellular, biochemical, molecular to anatomic, morphological and phenological level. At cellular and molecular level, plants' cells keep a little cytosolic Na^+ content by compartmentalization and ionic transport regulation (3, 4). During salinity stress, processes of membrane transport play a very special role. Some transport mechanisms implied in the perception of salt stress are: 1) Water output of the cell by osmotic gradient. 2) Decrease of the availability of K^+ in root cells due to the reduced activity of this cation in soils' solution; sodium competes for binding sites for K^+ transporters in PM (plasma membrane) including low and high affinity. 3) Increased efflux of K^+ by selective and non-selective channels (30). 4) These ionic events initially evoked in the PM of epidermal root cells are propagated to intracellular organelles (mainly vacuole) and other plant tissues such as leaves.

Considering the entry of Na^+ and K^+ loss, preventing worsening of the K^+/Na^+ homeostasis is a key criterion for resistance to salt stress. Once the stress is perceived, the respective signalization triggers and changes in metabolism and genetic expression take place; all these are related with defense mechanisms (5, 30). For the response to osmotic changes in metabolic compartments, it occurs an immediate osmotic adjustment by synthesizing compatible osmolytes and inorganic ions capture (31), for the toxic component of stress is performed a compartmentalization of harmful ions and ion transport (32); and it generally occurs a restriction of unidirectional Na^+ entry by NSCC (non-selective cation channels) (32, 33) and high affinity potassium transporters HKT (34, 35), the Na^+ efflux from the cytosol by the Na^+/H^+ exchanger in the PM (4) or its capture by tonoplast (36); changes of metabolism and signalization by polyamines and ROS and the antioxidant activity (37, 38).

Signaling molecules

Practically all kind of abiotic stress, such as drought, salinity, heat and cold affect the cell's balanced metabolism, producing ROS (Reactive Oxygen Species) (39). The type of biological answer (e.g., a modification in root's architecture) to a particular kind of stress seems to be dependent of many factors: as production site, nature, stress response's signal's intensity (like with ROS), the development and nutritional state of the plant, as well as the modifications made by the plant before the stress occurred (stress acclimation) (10, 40). In virtually every study of the induction of stress in the proteome are a group of proteins typical of oxidative stress. Moreover ROS as superoxide radical and hydroxyl radicals accumulate during stress conditions and are kept under control to preserve the integrity of cellular macromolecules. The oxidation-reduction balance of the cells is controlled by a series of enzymes and intermediate metabolites. The accumulation of ROS during abiotic stress has long been considered as a collateral product of stress metabolism and as bio products of certain other non-beneficial aerobic metabolism. This view has now been modified. In particular, oxidative stress caused by drought and salinity, has been proposed that ROS production is an obligatory element of the response to induce an adequate acclimatization process (41). Therefore, the degree of accumulation of ROS is what determines whether it is a part of the signaling mechanism (low production) or a harmful event (high production) to plants, making the control of production and degradation of ROS the crucial element for plant resistance to stress (41-44). ROS is never completely eliminated, as it plays an

important role in signaling and growth regulation (45); ROS' quenching inhibits the roots growth (46), and overexpression in *Arabidopsis* of a peroxidase localized mainly in the elongation zone stimulates root elongation (47). Therefore, ROS fluctuations in time and space can be interpreted as signals to regulate growth, development, cell death and stress responses (48, 49). Understanding the mechanisms that control ROS signaling in cells in response to water stress and salinity could therefore provide a powerful strategy for increasing crop tolerance to these environmental stress conditions (41). Among the targets of ROS action at the cellular level, there are ion channels that mediate ion exchange in the PM. In the PM of roots and guard cells H_2O_2 , stimulates the channels activated by hyperpolarization that mediate the influx of Ca^{2+} and NSCC (46, 48, and 50) and inhibit the K^+ outward and inward rectifier currents (51). The stimulation of the influx of Ca^{2+} in guard cells appears to mediate the induction of stomata closure by ABA (50, 52-54). At the same time it was reported that the $\text{OH}\cdot$ activates a Ca^{2+} inward and K^+ outward currents in epidermal protoplasts derived from mature and growth zone of *Arabidopsis* roots (46). A larger stimulation of the inward current of Ca^{2+} in the growth zone may indicate that ROS are involved in growth regulation via Ca^{2+} signaling. Moreover, the $\text{OH}\cdot$ produced by NADPH oxidase in *Arabidopsis* root hairs activated a Ca^{2+} inward rectifier conductance causing an increase in cytosolic Ca^{2+} allowing the root elongation (48).

Recently it has been reported that under severe water stress autophagy programmed cell death occurs in the region of the root apical meristem (55). There is evidence that this defense mechanism is promoted by the accumulation of ROS in stressed meristematic cells of root tips. Analysis of the expression of BAX inhibitor-1 (AtBI1, apoptotic inhibitor) and the phenotypic response of the mutant *atbi1-1* under severe water stress indicates that AtBI1 and the pathway of endoplasmic reticulum stress response modulates the induction of PCD by water stress. As a result, thin and short roots induce an increase in their tolerance to stress. These authors also propose that under severe drought stress, plants activate the PCD program in the root apical meristem, removing the apical dominance; so they can remodel the root system architecture to adapt to stressful environments (56).

Conclusions and perspectives

There are many aspects to consider for fully understand the mechanism of perception and tolerance of plants to abiotic stress. However it is

truly accepted that these behavior underabiotic stresses are under complex trait responses that imply studying plant cell physiology, plant anatomy, genetics and biochemical and their associations.

ACKNOWLEDGMENTS

This work was funded by the Universidad de La Ciénegea del Estado de Michoacán de Ocampo, Avenida Universidad 3000, Fraccionamiento Lomas de la Universidad . CONACyTproject 204910

REFERENCES

1. Boyer JS. Plant productivity and environment. Science (New York, NY). 1982;218(4571):443-8.
2. Flowers T, Yeo A. Breeding for Salinity Resistance in Crop Plants: Where Next? Functional Plant Biology. 1995;22(6):875-84.
3. Zhu JK. Salt and drought stress signal transduction in plants. Annual Review of Plant Biology. 2002;53:247-73.
4. Zhu JK. Regulation of ion homeostasis under salt stress. Current Opinion in Plant Biology. 2003;6(5):441-5.
5. Chinnusamy V, Zhu J, Zhu JK. Salt stress signaling and mechanisms of plant salt tolerance. Genet Eng (N Y). 2006;27:141-77.
6. Termaat A, Passioura JB, Munns R. Shoot Turgor Does Not Limit Shoot Growth of NaCl-Affected Wheat and Barley. Plant physiology. 1985;77(4):869-72.
7. Munns R, Termaat A. Whole-Plant Responses to Salinity. Functional Plant Biology. 1986;13(1):143-60.
8. Munns R. Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. Plant, cell & environment. 1993;16(1):15-24.
9. Deak KI, Malamy J. Osmotic regulation of root system architecture. The Plant journal: for cell and molecular biology. 2005;43(1):17-28. Epub 2005/06/18.
10. Malamy JE. Intrinsic and environmental response pathways that regulate root system architecture. Plant, cell & environment. 2005;28(1):67-77.
11. Jovanovic M, Rielefevre, V., Laporte, P., Gonzales-Rizzo, S., Lelandais-Brière C, Frugier, F., Hartmann C. and Crespi, M. How the Environment Regulates Root Archyctecture in Dicots. Advances in Botanical Research. 2008;46.
12. Spollen WG, Sharp RE. Spatial distribution of turgor and root growth at low water potentials. Plant physiology. 1991;96(2):438-43.
13. Xiong YC, Li FM, Zhang T. Performance of wheat crops with different chromosome ploidy: root-sourced signals, drought tolerance, and yield performance. Planta. 2006;224(3):710-8.
14. Jaffe M, Takahashi H, Biro R. A Pea Mutant for the Study of Hydrotropism in Roots. Science. 1985;230(4724):445-7.
15. Takahashi H. Hydrotropism: the current state of our knowledge. J Plant Res. 1997;110(1098):163-9.
16. Sun F, Zhang W, Hu H, Li B, Wang Y, Zhao Y, et al. Salt modulates gravity signaling pathway to regulate growth direction of primary roots in *Arabidopsis*. Plant physiology. 2008;146(1):178-88.
17. Takahashi N, Yamazaki Y, Kobayashi A, Higashitani A, Takahashi H. Hydrotropism interacts with gravitropism by degrading amyloplasts in seedling roots of *Arabidopsis* and radish. Plant physiology. 2003;132(2):805-10.
18. Galvan-Ampudia CS, Testerink C. Salt stress signals shape the plant root. Current Opinion in Plant Biology. 2011;14(3):296-302.
19. Blilou I, Xu J, Wildwater M, Willemsen V, Paponov I, Friml J, et al. The PIN auxin efflux facilitator network controls growth and patterning in *Arabidopsis* roots. Nature. 2005;433(7021):39-44.
20. Munns R, Sharp R. Involvement of Abscisic Acid in Controlling Plant Growth in Soil of Low Water Potential. Functional Plant Biology. 1993;20(5):425-37.
21. Thomas JC, Bohnert HJ. Salt Stress Perception and Plant Growth Regulators in the Halophyte *Mesembryanthemum crystallinum*. Plant physiology. 1993;103(4):1299-304.
22. Talanova VV, Titov AF. Endogenous abscisic acid content in cucumber leaves under the influence of unfavourable temperatures and salinity. Journal of Experimental Botany. 1994;45(7):1031-3.
23. Kefu Z, Munns R, King R. Abscisic Acid Levels in NaCl-Treated Barley, Cotton and Saltbush. Functional Plant Biology. 1991;18(1):17-24.
24. Qi X, Wu Z, Li J, Mo X, Wu S, Chu J, et al. AtCYT-INV1, a neutral invertase, is involved in osmotic stress-induced inhibition on lateral root growth in *Arabidopsis*. Plant Mol Biol. 2007;64(5):575-87.
25. Xie Q, Frugis G, Colgan D, Chua NH. *Arabidopsis* NAC1 transduces auxin signal downstream of TIR1 to promote lateral root development. Genes Dev. 2000;14(23):3024-36.
26. Ljung K, Hull AK, Kowalczyk M, Marchant A, Celenza J, Cohen JD, et al. Biosynthesis, conjugation, catabolism and homeostasis of indole-3-acetic acid in *Arabidopsis thaliana*. Plant Mol Biol. 2002;49(3-4):249-72.
27. Dubrovsky JG, Sauer M, Napsucially-Mendivil S, Ivanchenko MG, Friml J, Shishkova S, et al. Auxin acts as a local morphogenetic trigger to specify lateral root founder cells. Proc Natl Acad Sci U S A. 2008;105(25):8790-4.
28. De Smet I, Zhang H, Inzé D, Beeckman T. A novel role for abscisic acid emerges from underground. Trends in plant science. 2006;11(9):434-9.
29. Ariel F, Diet A, Verdenaud M, Gruber V, Frugier F, Chan R, et al. Environmental regulation of lateral root emergence in *Medicago truncatula* requires the HD-Zip I transcription factor HB1. Plant Cell. 2010;22(7):2171-83.
30. Cuin TA, Shabala S. Compatible solutes reduce ROS-induced potassium efflux in *Arabidopsis* roots. Plant, cell & environment. 2007;30(7):875-85.
31. Shabala SN, Lew RR. Turgor regulation in osmotically stressed *Arabidopsis* epidermal root cells. Direct support for the role of inorganic ion

- uptake as revealed by concurrent flux and cell turgor measurements. *Plant physiology*. 2002;129(1):290-9.
32. Demidchik V, Davenport RJ, Tester M. Nonselective cation channels in plants. *Annual Review of Plant Biology*. 2002;53:67-107.
 33. Amtmann A, Sanders D. Mechanisms of Na⁺ Uptake by Plant Cells. In: Callow JA, editor. *Advances in Botanical Research: Academic Press*; 1998. p. 75-112.
 34. Laurie S, Feeney KA, Maathuis FJ, Heard PJ, Brown SJ, Leigh RA. A role for HKT1 in sodium uptake by wheat roots. *The Plant journal: for cell and molecular biology*. 2002;32(2):139-49.
 35. Rus A, Lee B-h, Muñoz-Mayor A, Sharkhuu A, Miura K, Zhu J-K, et al. AtHKT1 Facilitates Na⁺ Homeostasis and K⁺ Nutrition in *Planta*. *Plant physiology*. 2004;136(1):2500-11.
 36. Blumwald E, Aharon GS, Apse MP. Sodium transport in plant cells. *BiochimBiophysActa*. 2000;1465(1-2):140-51.
 37. Chen Z, Pottosin II, Cuin TA, Fuglsang AT, Tester M, Jha D, et al. Root plasma membrane transporters controlling K⁺/Na⁺ homeostasis in salt-stressed barley. *Plant physiology*. 2007;145(4):1714-25. Epub 2007/10/30.
 38. Sairam R, Tyagi, A. Physiology and molecular biology of salinity stress tolerance in plants. Bangalore, INDE: Current Science Association; 2004. 15 p.
 39. Mittler R. Oxidative stress, antioxidants and stress tolerance. *Trends in plant science*. 2002;7(9):405-10.
 40. Mittler R. Abiotic stress, the field environment and stress combination. *Trends in plant science*. 2006;11(1):15-9.
 41. Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R. Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant, cell & environment*. 2010;33(4):453-67.
 42. M. C.J. Hydrogen Peroxide and Plant Stress: A Challenging Relationship. In: Books GS, editor. *Plant Stress: Global Science Books*; 2007. p. 11.
 43. Garg N, Manchanda G. ROS generation in plants: Boon or bane? *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*. 2009;143(1):81-96.
 44. Mortimer JC, Laohavisit A, Miedema H, Davies JM. Voltage, reactive oxygen species and the influx of calcium. *Plant signaling & behavior*. 2008;3(9):698-9.
 45. Carol RJ, Dolan L. The role of reactive oxygen species in cell growth: lessons from root hairs. *Journal of Experimental Botany*. 2006;57(8):1829-34.
 46. Demidchik V, Shabala SN, Coutts KB, Tester MA, Davies JM. Free oxygen radicals regulate plasma membrane Ca²⁺- and K⁺-permeable channels in plant root cells. *J Cell Sci*. 2003;116(Pt 1):81-8.
 47. Passardi F, Tognolli M, De Meyer M, Penel C, Dunand C. Two cell wall associated peroxidases from *Arabidopsis* influence root elongation. *Planta*. 2006;223(5):965-74.
 48. Foreman J, Demidchik V, Bothwell JH, Mylona P, Miedema H, Torres MA, et al. Reactive oxygen species produced by NADPH oxidase regulate plant cell growth. *Nature*. 2003;422(6930):442-6.
 49. Gechev TS, Van Breusegem F, Stone JM, Denev I, Laloi C. Reactive oxygen species as signals that modulate plant stress responses and programmed cell death. *Bioessays*. 2006;28(11):1091-101.
 50. Pei ZM, Murata Y, Benning G, Thomine S, Klusener B, Allen GJ, et al. Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. *Nature*. 2000;406(6797):731-4.
 51. Köhler B, Hills A, Blatt MR. Control of Guard Cell Ion Channels by Hydrogen Peroxide and Abscisic Acid Indicates Their Action through Alternate Signaling Pathways. *Plant physiology*. 2003;131(2):385-8.
 52. An Z, Jing W, Liu Y, Zhang W. Hydrogen peroxide generated by copper amine oxidase is involved in abscisic acid-induced stomatal closure in *Vicia faba*. *Journal of Experimental Botany*. 2008;59(4):815-25.
 53. Lee S, Choi H, Suh S, Doo I-S, Oh K-Y, Jeong Choi E, et al. Oligogalacturonic Acid and Chitosan Reduce Stomatal Aperture by Inducing the Evolution of Reactive Oxygen Species from Guard Cells of Tomato and *Commelinacommunis*. *Plant physiology*. 1999;121(1):147-52.
 54. Kim TH, Bohmer M, Hu H, Nishimura N, Schroeder JI. Guard cell signal transduction network: advances in understanding abscisic acid, CO₂, and Ca²⁺ signaling. *Annual Review of Plant Biology*. 2010;61:561-91.
 55. Cao M, Li X. Die for living better: plants modify root system architecture through inducing PCD in root meristem under severe water stress. *Plant signaling & behavior*. 2010;5(12):1645-6.
 56. Duan Y, Zhang W, Li B, Wang Y, Li K, Sodmergen, et al. An endoplasmic reticulum response pathway mediates programmed cell death of root tip induced by water stress in *Arabidopsis*. *New Phytol*. 2010;186(3):681-95.
 57. Sengupta D, Reddy AR. Water deficit as a regulatory switch for legume root responses. *Plant signaling & behavior*. 2011;6(6):914-7.
 58. Seo PJ, Park CM. Auxin homeostasis during lateral root development under drought condition. *Plant signaling&behavior*. 2009;4(10):1002-4.