Chapter 5

Root Development and Abiotic Stress Adaptation

L. Sánchez-Calderón, M.E. Ibarra-Cortés and
I. Zepeda-Jazo

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1. Introduction

As soon as plants became independent from homogeneous aquatic environments, root-like organs were developed. The interface between land and water bodies was probably the medium for the earliest land plants. Taking into account that those ancestral root-like organs did not face problems of water and nutrient acquisition, they were probably rather simple. As the earliest plants colonized this medium, the sandy substrate was replaced by heterogeneous soil, promoting more sophisticated vegetation and expanding the limits of land plant colonization. Therefore, to increase the efficiency of exploration of heterogeneous soil, during plant evolution the ancestral root-like organ was replaced by a complex root system (RS) as the one we now know [1-3]. Land plants nowadays present a wide diversity of root system architectures (RSA; spatial configuration of the root system) among species, from non-branched to highly complex branching patterns, achieving the most effective performance regarding anchorage and the acquisition of water and nutrients. Each kind of RSA is guided by a genetically controlled post-embrionary root developmental program (PERDP). This program is not rigid, and actually permits high phenotypic plasticity in response to stressing environmental conditions. PERDP is essentially driven by two cellular processes, cell division in the apical root meristem and new lateral meristems formed from the pericycle, and cell expansion performed in the root elongation area. This particular characteristic permits plants, which are sessile organisms, to change their root architecture to adapt to abiotic stress [4-6]. Soils provide plants with water and nutrients; however, nutrients and water are distributed in a heterogeneous or patchy manner. In order to enhance nutrient capture, plant roots have modified their root architecture to explore those nutrient-rich zones. In the last two decades, progress has been made understanding the physiological, molecular and biochemical basis of how the PERDP could be modified by abiotic environmental cues [5, 7]. The aim of this chapter is to provide a review of how abiotic stress modulates post-embryonic plant root development. We will begin with a discussion of origin, anatomy, morphology and kinds of RS. Then, we will review recent advances in the knowl-

edge of molecular, genetic and cellular processes that modulate post-embryonic root development in the model plant *Arabidopsis thaliana* making emphasis in the cell cycle. We will continue to focus on the modulation of PERDP in response to salinity and water. We will describe the changes in the RS induced by nutrients such as nitrogen, potassium and iron. The modulation of RSA by phosphorous will be discussed taking into account molecular, genetic and cellular responses. Finally, we will discuss how abiotic stress modulates apical root meristem activity.

2. Root system

Raven and Edwards (2001) define: "roots are axial multicelular structures of sporophytes of vascular plants which usually occurs underground, have strictly apical elongation growth, and generally have gravitropic responses which range from positive gravitropism to diagravitropism, combined with negative phototropism". The apical meristem of one (lower vascular plants) to many (all seed plants) diving cells produces a root cap acropetally and initials of stele, cortex and epidermis basipetally. The branching of roots involves the endogenous origin of new root apical meristems in the pericycle [2]. The most conserved functions of roots present in extant plants are anchorage to substrate, and uptake of water and mineral nutrients. The evolution of multicellular organs such as roots was necessary to successful colonization of land by early plants [1, 4].

2.1. Origin and evolution

Over 470 million years ago, in the mid-Palaeozoic era, took place one event with far-reaching consequences in the history of the life, the origin and early evolution of embryophytes (land plants). It appears that margins of drying pools were the place where early embryophytes evolved from algal ancestors. The earliest land plants probably presented a system of rhizoid-like filaments that performed the rooting functions (anchorage and uptake water and nutrients) helped by associated fungi. They grow in superficial soil produced for weathering of rock surface similarly to bryophytes (mosses). Their appearance started changes on energy and nutrient fluxes among terrestrial and freshwater ecosystems and consequently for the evolution of animal, bacteria and fungi groups that lives in those habitats. Roots as the ones we know now are present only in vascular plants (tracheophyta), they evolved in the sporophyte of at least two different lineages of tracheophytes, lycophytes (licopods) and euphyllophytes (ferns and seed plants), during the Early and middle Devonian. Roots of early Euphyllophytes started to penetrate deeper into substrate increasing the anchorage and funding the inorganic nutrients produced by rock leaching. In Euphyllophytes a fundamental difference in the anatomy of embryonic roots among seed plants and free-sporing monilophytes, suggesting that roots evolved independently. At this time root developed more branched axes and finer structures involved in the nutrient uptake, root hairs. In Carboniferous (300 millions of years ago) gymnosperms appear and their RS is highly branched and depth penetration, they break up rocks letting exposed mayor rock area exposed to weathering. By late Cretaceous (100-65 millions of years) angiosperms are presents showing similar root system as exant angiosperms [1, 2, 8].

During the Devonian period (415–360 million years ago) apparition and radiation of embryophytes with roots caused large changes to the global level. The early land plants with rhizoid-like filaments that penetrated the top few centimeters of soil, were replaced by plants with deep RS with complex structures. The apparition of those organs that actively penetrate the rock with the capacity of uptake and transport mineral nutrients permitted the development of structurally complex above-ground structures to photosynthesis, which increased the amounts of carbon fixed on the continent. The increase of primary production of early land plants changed the global carbon cycle and generates new complex soils which increased the border of land inhabited by plants. On one hand, the high rates plant production in this period allowed deposition of carbon on continental area from plant-drive organic matter, organic molecules secreted into the soil; on the other hand, the increase weathering rate of rocks by root penetration and secretion of organic compounds permitted the mining of rock-derived inorganic nutrients. Those changes in habitat turned up to be a part of a stimuli cycle in plant evolution, as themselves allowed the primary production to rise, which produced changes, and so on. The apparition of RS during Devonian allows that most of land surface was covered by plants, since Carboniferous forest (300 million of years ago), through late Cretaceous where basal angiosperms appeared (100-65 million of years ago) until days [1-3].

2.2. Classification and architecture

The RS consists of all roots that a plant has. It can be classified according to branch structure, root activity or development. The classification based on development is the more typical and useful to analyze the RS growth. This approach ontogenetically classified roots into three categories: primary root (PR), lateral root (LR) and adventitious root (AR; Figure 1 A). This classification reflects the differences between monocotyledonous and dicotyledonous RS. During germination PR is the first root to emerge from seed in both monocotyledonous and dicotyledonous, and is derived from embryonic root. In most of dicotyledonous LR are formed post-embryonically from pericycle cells (Figure 1 B-C) generating a branching system called primary root system. Depending on the length of LR relative to the primary axis (PR), the morphology of the RS will vary between tap rooted (Figure 1 A) and diffuse [3, 6, 9, 10]. Many monocotyledonous form PR and LR in a manner alike to dicotyledonous, in addition form nodal roots (AR) to generate a 'fibrous' adventitious roots system [6, 10, 11]. The morphology of the RS itself is very consistent, depends on the species, however, the spatial configuration of the RS (number, position and growth position of PR, LR and AR) called root system architecture (RSA) is highly variable, even among genetically identical plants. RSA is generated during post-embyonic root development and is guided by a plastic genetic program which is modulated by environmental cues [4, 9].

3. Root system development

Root development can be divided in two main stages: a) embryonic development (ED) and b) post-embryonic development (PED). During the ED, through a suite of highly regulated and reproducible stages, the fertilized egg cell rises into an embryo. In the embryo, the primary

meristems, body axes and major tissue layers are established [12-15]. Unlike metazoans, almost all the body of the mature plant is generated during the PED. The PE begins during germination, when the mitotic activity of meristems commences. Primary root meristems occupy one end of the main body axis and originate the RS [9, 14, 16]. During the post-embrionary root development traits such a i) primary meristems activity, ii) cell elongation, where both determine the anatomy, length and trajectory of roots and iii) de novo formation of secondary meristems and organs increase the branching to explore new soil zones [5, 6].

In Arabidopsis, the root consists of a series of concentric cylinders of different tissues (Figure 1 B), and this pattern is formed by sequential and ordered cell divisions during embryogenesis [17]. The outer epidermal layer covers all root tissues, and by itself contains the trichoblasts, a cell lineage that produces root hairs by tip growth, providing the root with additional anchoring and nutrient uptake surface. Cortex layers give mechanical support and protection while the endodermis forms an ion barrier. Inwards the endodermis, the pericycle cells maintain meristematic properties that can give place to root primordia or diverge into vascular tissues or cambium during secondary root growth. This pattern is established during the embryogenesis by a series of asymmetric and formative divisions [18, 19].

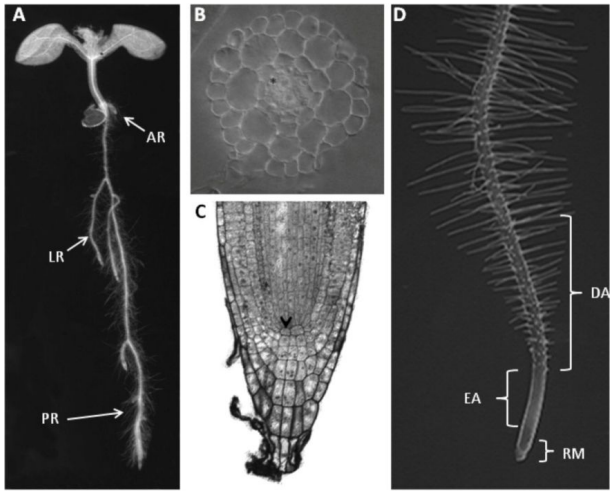

Figure 1. Arabidopsis root system. Typical tap root system of dicots (A). Transversal section of primary root (B). Longitudinal section of primary root meristem (C) and primary root tip. Primary root (PR), lateral roots (LR), adventitious roots (AR), pericycle cell layer (*), QC cells (arrow), root meristem (RM), elongation area (EA) and differentiation area (DA).

3.1. Cellular proliferation, elongation and differentiation

Root growth is produced by the biosynthesis of cell wall combined with cell division. In the root meristem (RM) (Figure 1C-D), the cell layers apart from the epidermal and root cap ones are originated around a region that consist of three or four slowly proliferating cells, the

quiescent center (QC) (Figure 1 C), which has a role organizing the meristem and is also involved in the stem cell identity maintenance QC removal results in the de novo formation of a new QC with adjacent initial cells and stem cells adjacent to the cortex and endodermal stem cells yield to epidermal initial cells and the lateral root cap [20-22]. Directly upwards from the QC the proximal meristem is located, as the distal meristem is located below, and within the meristems the forward growth is carried on as cells divide and grow there at a steady rate. When reaching certain distance from the meristem, in elongation area (EA)(Figure 1D) division is arrested and the cells start to elongate. Elongated cells are associated with endoreplication, a process of DNA replication without actual cell division which accumulates genome copies in the cell and uses part of the machinery associated with cell cycle, and involves the inactivation of mitotic CYC-CDK (Cyclin- Cyclin Dependent Kinase) complexes [23-25]. Pericycle and cambium cells, distanced from the root tip, maintain the potential to reenter division, forming LRs or transitional cells at the meristem end, depending on localized auxin responses [26] or oscillating gene expression [27].

3.1.1. Cell cycle

The cell cycle is a temporal regulator of proliferative cell division, and it is comprised of mitosis, cytokinesis, post-mitotic interphase (G1), DNA synthetic phase (S) and post-synthetic interphase (G2)[28]. The conjunction of all these is the key force driving organogenesis and growth in plants and other eukaryotes. The mitotic cycle is driven by the periodic activation of a multicomponent system that relies on CDKs as key regulators. CDKs combine with different CYCs to trigger the transition from the G1 to S phase and the G2 to M phase, and a wide variety of components control the activity of these kinases, thus becoming part of a complex molecular network that is still being studied [29-31]. In plants, a number of core cycle regulators have been revealed to exist [32, 33] and what appears to be distinctive in plants is that they appear to have many more CYCs and CDKs in comparison to animals and yeasts [21, 24]. The reason of this abundance of putative function overlapping components can be the one suggested in [34], postulating that that plants have evolved a combinatorial resource pool consisting of around ninety different CDK-CYC complex variants, thus explaining to an extent the plasticity of plant development regulation, as they provide with a strategy to recognize distinct stimuli and environments, and thus promote different phases of the cell cycle. Cell cycle progression and controlling mechanisms include transcriptional regulation, protein-protein interaction, phosphorylation-dephosphorylation and protein degradation [29, 30, 35, 36]. As recently reviewed [36], the evidence obtained from interaction studies suggests that Arabidopsis CDKA;1 primarily binds to CYCDs to promote the G1/S transition and to CYCA3 to drive the S phase progression while CDKA;1 pairs with CYCD3 to drive the M phase progression. In contrast, CDKBs presumably interact preferentially with CYCA2 and CYCBs to promote the G2/M transition and the M phase progression [37-39]. In Arabidopsis, the accumulation of the CYCB1;1 transcript is correlated with meristematic tissues [40], activated from early S phase in synchronized cells with no significantly increase during G2 phase [41]. Together with environmental and hormonal stimuli, the coordination of the different cell cycle control processes lead to a balance between cell division and expansion that ensures the correct embryonic and post-embryonic development. As part of the extensive toolset that plants

possess in order to finely tune the mitotic and endoreplicative cycles, the phase-specific activation of CYC-CDK complexes via temporal transcription is a mechanism that is evidently used but not completely understood in plants. In synchronized Arabidopsis cell cultures many cell cycle genes present highly specific expression windows during the mitotic cell cycle [41, 42]. For example, the expression of several CYCAs is dramatically upregulated at the G1/S transition and S phase, while others are accumulated at G2/M transition, as well as all CYCBs. Most of CYCDs are expressed during G1 and S phases, with the exception of a few ones, like CYCD3:1, expressed during G2-M. In the case of CDKs, CDKA;1 is expressed throughout the cell cycle, with constant transcript levels, the CDKB1s are present from S to M phase, and CDKB2s are detected specifically from late G2 to M phase.

3.1.2. Cell cycle control in root meristem

The expression windows of cell-cycle control genes can be extrapolated to their expression in the actively dividing cells of the root meristems. In these and all dividing cells, The G1/S transition is generally controlled by the E2F-DP-RBR (E2F-Dimerisation Partner-Retinoblastoma Related) pathway. One of the three Arabidopsis-encoded E2F transcription factors forms dimers with one of the two DP proteins to bind to certain promoter sites in the transcriptional target genes to promote the G1/S transition, including those required for DNA replication and repair. In G1, CYCD-CDKA complexes phosphorylate RBR, releasing the E2F-DP dimers to allow them to bind to the transcriptional activation sites [43-46]. In the other hand, E2Fc-DPb dimers act as transcriptional repressors with yet unknown target genes, although their repressing mechanism appear to be independent from the RBR pathway [47]. Meanwhile, genes expressed during G2 and M phases contain M phase-specific activator (MSA) elements in their promoters, recognized by three Myb repeats (MYB3R) transcription factors, discovered for the first time in tobacco [48]. The Arabidopsis genome encodes five MYB3R proteins (MYB3R1-5), from which MYB3R1 and MYB3R4 are the closest homologs of the G2/M specific transcriptional activators NtMYBA1 and NtMYBA2, with the first having a stable transcript level through the cell cycle, and the latter having an expression peak during G2/M transition, suggesting that MYB3R1 is post-translationally regulated. The expression of many G2 to M specific genes possessing MSA elements in their promoters is visibly down-regulated in the *myb3r1 myb3r4* double mutant, but not completely abolished [49] suggesting an alternative mechanism controlling the transcription of G2 and M phase genes. Additionally to E2F and MYBs, there are other transcription factors that control cell cycle phase-specific gene expression, as the DNA-binding with one finger (DOF) transcription factor, OBP1, whose overexpression shortens the cell cycle with elevated expression of many other cell cycle genes, and that normally upregulates the expression of replication-specific transcription factors and CYCD3;3 [50]. Another form of controlling the activity of CYC-CDK complexes is through post-translational mechanisms, and among them, the ubiquitin-mediated degradation of cell cycle proteins is the most determinant for the correct timing in the progression of the cell cycle [51-53]. A number of ubiquitin-dependent degradation pathways have been associated with the mitotic cell cycle, and the E3 ubiquitin ligases participate in all cases, marking target proteins by polyubiquitination and subsequent proteolysis. The Skp-cullin1-F-Box (SCF) E3 ligase regulates primarily the G1/S transition while the Anaphase Promoting Complex/

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Cyclosome (APC/C), a Cullin-RING finger E3 ligase, is most active from the M phase to G1 phase. APC/C complex is composed by at least 11 subunits, and in the Arabidopsis genome, all APC/C components except for APC3/CDC27/HOBBIT are encoded by a single gene [54]. All APC/C subunit mutants studied so far accumulate mitotic CYCs in embryo sacs, suggesting that they're substrates of the APC/C [52, 54]. Apart from its core components, APC/C also pairs with co-activators, known as CDC20/FIZZY and CDC20 HOMOLOG1 (CDH1)/FIZZY-RELATED (FZR), which confer substrate specificity and are activated during distinct phases of the cell cycle with equally distinct activities. The Arabidopsis genome contains five CDC20 and three CDH1 genes, also called CELL CYCLE SWITCH 52 (CCS52), and even if their modification of the APC/C activity during the cell cycle is not fully established, CCS52A1 and CCS52A2 participate in meristem maintenance [55]. Notably, they act through different mechanisms and exhibit different expression patterns as well. The expression of CCS52A1 starts at the elongation zone of Arabidopsis roots and stimulates mitotic exit and an entry into the endoreplication cycle, whereas CCS52A2 is expressed at the distal part of the root meristem and is required to maintain the cell identity in the QC. The *ccs52a2* mutation activates the QC cell division, contrasting with the occasional division behavior normally presented, and when its promoter is switched with the one of CCS52A1, the expression of the latter rescues the phenotype in *ccs52a2*, suggesting homologous function. In vertebrates, negative regulators also modify the activity of APC/C. These regulators, called Early mitotic inhibitor1 (Emi1) and Emi2 directly bind to CCS52 and CDC20, inhibiting the APC/C activity. No direct plant orthologs are identified, but recent studies have shown that GIGAS CELL1 (GIG1)/OMISSION OF SECOND DIVISION 1 (OSD) and UV-INSENSITIVE4 (UVI4)/POLYCHROME (PYM) act as their functional homologs in plants [56, 57] by physically interacting with the APC/C activators CCS52 and CDC20. Their overexpression causes an accumulation of CYCB1;2 and CYCA2;3, respectively, by the inactivation of the APC/C, suggesting that it also could have an effect on root meristem maintenance by the inhibition of the APC/C-CCS52 complex activity. Another important way to control and modulate the CYC-CDK complexes activity involves said complexes binding directly to CDK inhibitors, proteins that interfere with the ability of CYC-CDK to phosphorylate their substrates. Plants have two classes of CDK inhibitors – KIP-RELATED PROTEINs (KRPs) and SIAMESE (SIM)/SIAMESE RELATED (SMR). The Arabidopsis genome encodes 7 KRPs, KRP1-7, and at least 13 SIM/SMRs. Recent analyses have shown that all 7 KRPs purify conjoined with CYCDs and CDKA [36] suggesting that they inhibit the activity of the CYCD-CDKA complexes, as it has been proposed previously [58], but not excluding the possibility of them inhibiting the activity of CYCD-CDKB complexes as well [59]. The seven KRPs display overlapping but distinct expression patterns in the Arabidopsis shoot apex, some of them present strongly in dividing cells, like KRP4 and KRP5, while KRP1 and KRP2 are present in differentiating cells [60]. KRPs have a role driving the endoreplication cycle as well, also by inhibiting CDK activities [61, 62]. The SIM/SMR family of CDK inhibitors is found only in plants, and is required to repress the mitotic cell cycle in trichomes via the interaction of SIM with the CYCD-CDKA complex [63]. Another member of the SIM family, SMR1/LGO, is implicated in the control of endoreplication in sepals [64], maintaining the presence of elongated, endoreplication-undergone giant cells in the sepals, which are lost in the *smr1/lgo* because they progressed through additional cell divisions instead of endore-

plication. Recent studies [34] show that both SIM and SMR/LGO are purified jointly with CDKB1;1 while other SMRs interact with CDKA;1, thus suggesting that CDKB1;1 could be directly inhibited by SIM/SMR1 leading to endoreplication onset.

3.1.3. Cell cycle control in post-embryonic root development

The cell cycle relies not only on its own molecular machinery to determine cellular fate. Post-embryonic plant development needs a highly precise coordination of cell cycle-directed signaling to correctly drive cells to form new tissues or cell types, as is evident in root development. Molecular genetic studies have uncovered several key regulators involved in developmental cell cycle control, and many of them have shown to be transcriptional regulators, but how are they linked to cell cycle control has not been well characterized. SHORTROOT (SHR) and SCARECROW (SCR) are members of the GRAS family of transcription factors required for the asymmetric division of cortex/endodermis initial cells (CEI) in the root apical meristem [65, 66]. This tissue-formative division generates two new cellular kinds- cortex and endodermis, making the CEI cell division control a key requisite for a proper root development. It has been demonstrated that both SHR and SCR directly regulate the expression of CYCD6;1, present at G1 and S phases, by binding to its promoter [67]. CYCD6;1 is expressed specifically in CEI and CEI daughter cells, and the asymmetric division of CEI is significantly decreased in the *cycd6;1* mutants. Additionally, when CYCD6;1 is expressed ectopically in the *shr* mutant background, it partially compensates the division defects presented by the latter, supporting the idea of CYCD6;1 being downstream of the SHR/SCR pathway. Other cell cycle genes, like CDKB2;1 and CDKB2;2, have their expression regulated by SHR and SCR, and when these CDKs are overexpressed in endodermal cells, the formative cell division of the CEI is promoted. However, they do not appear to be direct targets of SHR and SCR, implying that the activation of these CDK genes is linked by another control factor. Cell proliferation needs to be restored in the xylem-pericycle cells for the LR initiation and this process can be induced by auxin in many plant species, like Arabidopsis. LR development starts by the degradation of INDOLE ACETIC ACID 14(IAA14)/ SOLITARY-ROOT (SLR), dependent on auxin, that leads to the de-repression of two related AUXIN RESPONSE FACTORs (ARFs), ARF7 and ARF19 [68]. These ARFs are required for the subsequent expression of LATERAL ORGAN BOUNDARIES 18 (LBD18] and LBD33 transcription factors, which form a LBD18-LBD33 heterodimer that activates the expression of the E2Fa, one of the E2F genes induced at LR initiation, by binding directly to its promoter [69]. E2Fa expression is increased by auxin treatment at the LR initiation site and this auxin-dependent E2Fa expression is lost in the *iaa14/slr-1* mutant background. Expectedly, the number of LR primordial is decreased in the *e2fa* mutants, evidencing a requirement of E2Fa for LR emerging and establishing a link between auxin signaling and cell cycle progression during LR development. Another unrelated pathway that is also involved in the auxin-induced LR formation has KRP2 downregulated by auxin [70]. Under low auxin conditions, the CYCD2;1-CDKA activity is repressed by the presence of KRP2. Upon auxin treatment, both gene expression and protein accumulation of KRP2 is reduced, leading to an increase in the CYCD2;1-CDKA activity and subsequent enhancement of LR induction. A possible hyperphosphorylation of RBR resulting in the activation of E2Fb directly caused by the CYCD2;1-CDKA complex activity has been suggested [69]. A model on the basis of available information on the density and

orientation of auxin transporters, cell shape, and auxin transport parameters predicts a maximum auxin concentration in the QC and a steep auxin gradient in the proximal meristem, which drops according to the cell number from the quiescent center [71, 72]. This agrees with the auxin levels found in protoplasts derived from different apical cell types, as well as with the expression patterns of auxin responsive genes, such as members of the PLETHORA (PLT) family, in the different root tissues [73]. PLT 1 and PLT2 are known to be crucial for interpreting this gradient in the terms of root growth and development. They encode for AP2-domain transcription factors, and losing of their function results in the loss of stem cells, arrest of transit-amplifying divisions and reduction of cell expansion [74]. PLT pathway has other effects over cell cycle control. Histone acetyltransferase, a chromatin modifier and required to maintain the dividing ability in meristem cells, is also required to sustain PLT expression and support both transit-amplifying divisions and the root stem cell status at the root apex [75]. Moreover, the action of SUMO E3 ligase is vital to repress endoreplication in shoot and root meristems, and in the root, this SUMO E3 ligase acts in the PLT pathway [76]. It can be said then that the root tip is characterized by an auxin maximum, and auxin is required to support transit-amplifying divisions [77].

4. Root system development and abiotic stress

Abiotic cues as water and nutrient availability limit plant productivity in almost all ecosystems in the world. Typically, RS has to growth in media where the biotic and abiotic components are distributed heterogeneously. Soils are complex, a broad range of chemical a physical process occurs due to intrinsic soil characteristics and the action of biotic factors. Thus, this complexity presents several challenges to survive. As soon as the root makes contact with the soil must sense and integrate biotic and abiotic cues in order to adjust their genetic program of post-embryonic root development (PERD). This capacity to change their PERD allows them change their architecture to find the supplies of water and nutrients that could be limited and localized [3, 4, 12]. Environmental cues such as water, salinity and nutrient can modulate the ARS.

4.1. Regulation of root system architecture by water availability and salinity stress

Water and salinity can indirectly modulate the RSA because they can produce unfavorable changes in the nutritional composition of the soil, the distribution of said nutrients, the density and compaction of soil, and the type of soil particles [9]. Those interactions complicate the dissection of specific transduction pathways involved in root growth and development [78] The RS is the first to perceive the stress signals for drought and salinity, therefore its development is deeply affected by their availability in soil. In many agriculturally important species, the whole plant growth is inhibited during water starvation, however, RS is more resistant than shoots and continues growing under low water potentials that are completely inhibitors for shoot growth [79]. Notably, while growth of PR is not appreciably affected by water deficit, the number of LRs and its growth are significantly reduced [80]. It has been suggested that the reduction of the LR formation may be caused by the suppression of the activation of the lateral root meristems, not because of the reduction of the initiation in the LR per se, as primordia

generation is unaffected [9, 80-82]. Mutants with alterations in the development of LRs respond differently to drought stress [80, 83]. Suppression of the growth of LR by drought has been widely accepted as an adaptive response to ensure the plant survival under unfavorable growing conditions [83]. Another factor that plays an important role in growing and development of plants to tolerate the drought stress is the hydrotropism [84, 85]. A recent study showed that a gradient of moisture generated by water stress causes an immediate degradation of amyloplasts in the columella cells of plant roots, producing a minor response to gravity and an increase of hydrotropism [86]. However, it is unknown how the gravity signals interact with other environmental signals to modulate the direction of root growth. Less known are the adaptations in root 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 [87]. Also it has been observed that Arabidopsis RS exhibit a reduced gravitropism under salt stress, growing against the gravity vector [88]. Arabidopsis RS 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 direct the root 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 PRs in Arabidopsis seedlings, although it has been reported that salt stress also modulates root gravitropism of PR in young seedlings. In vertical position, five day seedlings germinate normally in MS medium (Murashige and Skoog) containing different concentrations of sodium chloride (NaCl), however the direction of root growth changes according to the increase of NaCl concentrations, and the root curves in stressed plants with 150 mM NaCl in the medium [88].These results suggest that the salt stress and the induction of signal translations by stress modulate the direction of the root, despite of the gravity. Some reports suggest that the gravitropic signal and the answers in root apex are controlled, at least partially by Salt Overly Sensitive (SOS) signaling pathway. Therefore, this pathway might interact with the gravity sensor system in the cells of the columella to direct root growth in a coordinated way[88]. Abscisic acid (ABA) and auxins participate in a complex signal system that plays a very important role in the development of the RSA under drought conditions. These hormonal effects (levels) even though are considered as intrinsic [82] 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 [89], cytokinin and especially abscisic acid [90-92] have been proposed as potential chemical signals in response to water stress to modulate RSA. The decrease in water potential of roots caused by salinity is the factor that triggers the production of ABA in different species [93]. A condition of mild osmotic stress also inhibits the LR formation in a dependent way of ABA [80, 82, 83, 94]. In Arabidopsis, the reduced water availability dramatically inhibits the formation of LR, but not by the suppressing of initiation of LR at the lateral primordia. This inhibition does not occur

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in lateral root mutant 2 (*lrd2*) nor in two ABA deficient [80, 82]. Abscisic acid and a recently identified gen *LRD2* are linked to repression of LR formation in response to osmotic stress. It is very interesting to note that these regulators are also related to the establishment of RSA 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 [95-97] suggesting a joint interaction of the hormonal signaling pathway in the regulation of LR formation. Some authors propose a model where the promotion or suppression of hormonal signaling pathway and regulators as LRD2 determine the type of LR primordium (LRP) and coordinate the RAS in response to environmental stimuli [87]. In contrast, under drought stress conditions or osmotic stress, activation of the LR meristem is suppressed by ABA-mediated signals, producing few small LRs [80, 98]. While auxins seem to be the main initialization hormone, pattern and emergence of LRs; ABA is the main hormone that controls the environmental effect (like drought and salt stress) over the RSA [99].

4.1.1. Cellular responses

4.1.1.1. Epidermis

Root 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 rescue mechanisms. The accumulation of sodium in the cells and the resulting ionic imbalance is the main cause of inhibition of plant growth and yield decrease [100]. Therefore, maintaining low intracellular sodium levels 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 low cytosolic sodium (Na^+) content by means of compartmentalization and ionic transport regulation [100, 101]. During salinity stress, processes of membrane transport play a very special role. Some transport mechanisms implied in the perception of salt stress are: water output of the cell by osmotic gradient, the decrease of the availability of potassium (K^+) in roots due to the reduced activity of this cation in soil solution, where sodium competes for binding sites for K^+ transporters in PM (plasma membrane) including low and high affinity, also the increased efflux of K^+ by selective and non-selective channels [102] and finally that these ionic events initially evoked in the PM of epidermal root cells are propagated to intracellular organelles (mainly vacuoles) and other plant tissues such as leaves. Considering the entry of Na^+ and K^+ loss, preventing worsening of the K^+/Na^+ cytosolic relation 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 [102, 103]. For the response to osmotic changes in metabolic compartments, it occurs an immediate osmotic adjustment by synthesizing compatible osmolytes and inorganic ions capture [104], for the toxic component of stress is performed a compartmentalization of harmful ions and ion transport [105]; and it generally occurs a restriction of unidirectional Na^+ entry via non-selective cation channels (NSCC) [105, 106] and high affinity potassium transporters (HKT) [107, 108], the Na^+ efflux from the cytosol

by the Na^+/H^+ exchanger in the PM [100] or its capture by tonoplast [109]; changes of metabolism and signalization by polyamines and Reactive Oxygen Species (ROS) and the antioxidant activity [110, 111].

4.1.1.2. Reactive oxygen species

ROS fluctuations in time and space can be interpreted as signals to regulate growth, development, cell death and stress responses [112, 113]. 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 [114]. 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 [112, 115, 116] and inhibit the K+ outward and inward rectifier currents [117]. The stimulation of the influx of Ca^{2+} in guard cells appears to mediate the induction of stomata closure by ABA [116, 118-120]. At the same time it was reported that the OH• activates a Ca^{2+} inward and K+ outward currents in epidermal protoplasts derived from mature and growth zone of Arabidopsis roots [115]. 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 OH• 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 [112]. Recently it has been reported that under severe water stress autophagy programmed cell death occurs in the region of the root apical meristem [121]. 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 RSA to adapt to stressful environments [122].

A slight drought stress increases the expression of enzymes associated with root morphology (Xyloglucan endotransglucosylase) while other structural proteins (actin and tubulin) are downregulated, 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 of LR development that partially has an indirect effect on whole plant photosynthetic process [123]. 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 LR [124]. 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 LR growth under drought

stress conditions [124], these same authors found that overexpression of MYB96 promotes resistance to drought and reduced lateral root density.

4.2. Regulation of root system architecture by nutrients

In soil nutrients such as phosphorus (P), nitrogen (N), potassium (K) and iron (Fe), are distributed in a heterogenous patching pattern. As soon as the PR emerges from the seed, it has to grow. As growth goes on, *de novo* LR are formed to generate the particular RS morphology and architecture. These nutrients alter root patterning through particular signal transduction pathways. Thus, during their life plants change their PEDP in order to increase exponentially the root-soil interaction area and find the nutrient-rich regions [5, 125-129]. The changes in Arabidopsis root system are specific for each nutrient. P, N and K starvation dramatically alter primary root length (Figure 2).

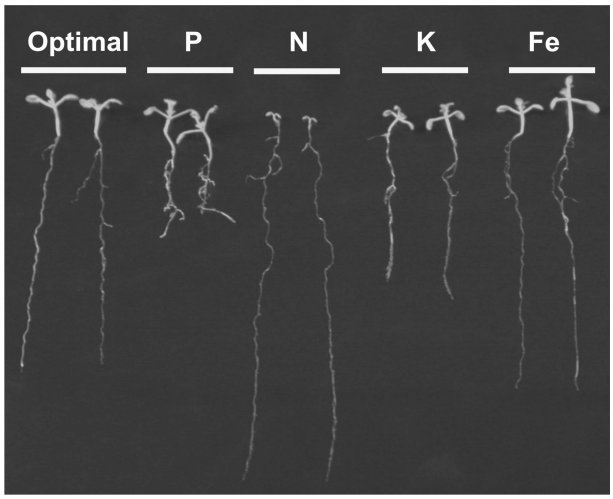

Figure 2. Changes in root system architecture of Arabidopsis seedlings when growth on media depleted of phosphorous (P), nitrogen (N), potassium (P) and iron (Fe).

4.2.1. Phosphate starvation

Root system in boot monocotyledonous and dicotyledonous plants, present a set of developmental modifications that tend to increase the exploratory capacity of the plant [130]. When Arabidopsis growth under limiting P conditions their RSA changes dramatically such as reduction in primary root length, increased formation of LRs and greater formation of root hairs [126, 128]. On optimal P conditions the newly formed root cells are added by the mitotic activity of primary meristem. These cells then get away from the meristem and increase their length, and the elongation process ends when the cells start to differentiate. When plants are P starved, cell division in the primary root meristems gradually reduces and the cells start to

prematurely differentiate until total inhibition of cell elongation and loss of meristematic activity occur (meristem exhaustion). At the end, root tips change their physiological characteristics and the exhausted meristem becomes a structure which takes part in P uptake. In this process, root tips locally detect P deficiency, this response being mediated by at least LPR multicopper oxidase genes [12, 131, 132]. Recently, iron (Fe) has been reported to play a role as well in the control of these PED reprogramming [133]. This change of root architecture is due to the fact that, in both meristematic and elongation areas, the content of ROS is reduced as long as the determined PED goes on [134].

In the past decade the changes in RSA evocated by P availability has been widely studied, several genes that regulates the root architectural changes has been idetified, trascription factor such as WRKY75, ZAT6 (ZINC FINGER 6), Pi-responsive R2R3 MYB (MYB62) and BHLH32 (BASIC HELIX_LOOP_HELIX 32) [135-138] are key regulators in this response. Mutants affected in the RSA changes induced P availability have been isolated: *pdr2* (*phosphate deficiency response 2*), *lpi* (low phosphorus-insensitive) *siz1* [SAP (scaffold attachment factor, acinus, protein inhibitor of activated signal transducer and activator of transcription) and *Miz1* (Msx2-interacting zinc finger), SIZ] [139-141]. It has been reported that ethylene is involved in modulating Pi-starvation-responsive root growth, it may restrict elongation of PR, but promote elongation of LRs [142] HPS4/SABRE (important regulator of cell expansion in Arabidopsis) antagonistically interacts with ethylene signalling to regulate plant responses to Pi starvation. Furthermore, it is shown that Pi-starved *hps4* mutants accumulate more auxin in their root tips than the wild type, which may explain the increased inhibition of their primary root growth when grown under Pi deficiency [143]. Gibberellins and ROS also trigger responses involving DELLAs proteins which control the rate and timing of cell proliferation and they will be dealt with in further sections.

4.2.2. Nitrogen

N is fundamental for biological molecules, such as nucleotides, amino acids, and proteins. Plants need to acquire nitrogen (N) efficiently from the soil for growth and development. In soil, nitrate (NO^{3-}) is one of the major N sources for higher plant and their concentrations vary in both time and space. Plants are able to sensing these variations of NO^{3-}, which is one of the most important environmental signals affecting plant physiology and development [144]. The effects of N supply on plant development have been particularly studied in Arabidopsis. NO^{3-}-free medium drastically reduces shoot biomass production and appears to have little effect on PR length (Figure 2). However, NO^{3-} has a dual role on LRs. On one hand, the uniform exposure of RS to high nitrate (>10 mM) inhibits lateral root growth at a specific developmental step corresponding to the activation of the meristem in LRP after their emergence[145-147]. As a high NO^{3-} supply on only one part of the RS is able to repress lateral root growth on the whole RS, it has been proposed that nitrate accumulation in the aerial tissues is responsible for this LRP arrest, suggesting that long-distance signals to the root are involved. On the other hand, when the entire RS is exposed to low nitrate concentration (10 μM) and only one part of the RS is exposed to a high nitrate, there is local proliferation of LR. NO^{3-} locally promotes LR growth and increased lateral root growth rate due to a higher cell production in the lateral root meristem [145, 146, 148]. The local stimulation of lateral root growth by nitrate-rich patches is a striking example of the

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nutrient-induced plasticity of PERDP. This stimulation could be dependent on NRT1.1 (Nitrate Transporter 1). This is partially due to the fact that NRT1.1 represses LRP emergence and growth of young LRs in the absence of nitrate. NRT1.1 transports nitrate and facilitates auxin transport in a concentration-dependent manner. NRT1.1 represses LR growth at low nitrate availability by promoting basipetal auxin transport out of the LRP, towards the parental root [149]. MADS-box transcription factor NITRATE REGULATED (ANR1) and Auxin signaling F-box protein 3 (AFB3) are key regulators of RSA in response to nitrate availability. The *Chlorate-resistant 1* mutant (*chl1)* is *ANR1* affected, and is less responsive to the localized NO^{3-}-rich patches similarly to transgenic plants in which ANR1 expression is down-regulated. In the tips of LR and LRP, ANR1 is expressed and is localize with NRT1.1 [150]. The *afb3-1* mutant shows altered root development response to nitrate. *AFB3* is an auxin receptor gene induced by nitrate in the primary root tip and pericycle; its mRNA is the target of miR393 that is induced by the products of NO^{3-} assimilation.

4.2.3. Potasium and iron

Contrasting with physiological and molecular responses to low K and Fe, changes in RSA have been scarcely described. Potassium deficiencies arrest LR and PR development in Arabidopsis (Figure 2) [129]. K^+ transporters play a crucial role in SRA changes in response to K^+ availability. Disruption of the root-specific K^+-channel AKT1 in the *akt1-1* Arabidopsis mutant causes reduced ability of plants to grow in low potassium media (100 μM)[151]. In Arabidopsis, changes in the gravitropic behavior of RS were also observed in low potassium media. The genes of the *KUP*/*HAK*/*KT* family are homologous to bacterial KUP (TrkD) potassium porters. The *trh1* (tiny root-hair 1) mutant, which is disrupted in *AtKUP4*/*TRH1* gene shows agravitropic behavior in its roots independently of K^+ concentration in the media when grown on vertical agar plates, and also, *ProTRH1:GUS* expression is limited to the root cap where gravity is sensed. Interestingly, agravitropic responses in *trh1* are complemented by exogenous auxin. This mutation is associated with the loss of auxin pattern in the root apex. Thus, TRH1 is an important part of auxin transport system in Arabidopsis roots [151-153].

Typically, the root architectural changes in response to low availability of Fe include ectopic formation of root hair due to modulation in their position and abundance [154]. Recently, Giehl et al. (2012) analyzed the changes in LR architecture in response to localized Fe supply in wild-type and Fe acquisition and translocation- defective mutant plants. They found that lateral root elongation is highly responsive to local Fe and that the symplastic Fe pool in LR favors local auxin accumulation. They identified the auxin transporter AUX1 as a major Fe-sensitive component in the auxin signaling pathway that mainly directs the rootward auxin stream into LRs that have access to Fe.

4.3. Meristematic activity regulation by abiotic stress

To cope with environmental changes, plants have to adapt their growth timing and pattern by altering rates of cell proliferation and differentiation. The expression of several cell cycle genes is increased or decreased upon external cues (Figure 3) [155] but it is poorly understood the full molecular basis supporting these transcriptional controls, and if the cell cycle control modifications happen to fall into the post-translational category, the current knowledge is also

very limited. However, there have been identified several key players in stress-induced cell cycle modifications that have cast the first light over the understanding the talk between environmental signals and the mitotic or endoreplication cycle. Gibberellins (GAs), plant hormones, promote cell expansion by disrupting growth inhibitory proteins named DELLAs [156] and also promote cell proliferation in Arabidopsis [157]. In the root meristem of GA-deficient mutants, cell division rate is decreased and the phenotype is rescued by GA treatment. DELLA proteins are also involved in this regulation, as non-degradable forms of DELLA inhibit cell proliferation. Low levels of GAs in GA-deficient mutants enhance the expression of certain CDK inhibitor genes – KRP2, SIM, SMR1 and SMR2- with a DELLA-related mechanism, and cell proliferation defects shown by these mutants can be recovered by overexpressing CYCD3;1. These findings tend to indicate that GA signaling drives cell proliferation by modulating the activity of CYC-CDK complexes, at least partially mediated by the DELLA-dependent expression of CDK inhibitors, and thus making DELLA a potential intermediate in the signal transduction channel connecting environmental signals and cell cycle progression. This is proposed to be a consequence of reduced cell expansion and associated division of the endodermis layer in the root apical meristem [158, 159], suggesting a role for the endodermis in controlling the growth rate in the root apical meristem. Another potential link is RICE SALT SENSITIVE 1 (RSS1), controlling the cell cycle progression under various abiotic stress conditions [160]. The *rss1* mutants do not present evident growth defects under normal conditions, but they display hypersensitivity to high salinity, ionic stress and hyperosmotic stress. Under these conditions, in *rss1*, shoot and root meristems are severely affected, showing a reduced population of proliferating cells, leaving RSS1 as a required factor for proliferative cell status in the meristem. RSS1 is expressed during the S phase of the mitotic cycle and its protein is degraded via APC/C during the M/G1 transition. RSS1 interacts with a Type 1 Protein Phosphatase (PP1), known in humans to inactivate Retinoblastoma (Rb) proteins through dephosphorylation, which is inhibitory to the G1/S transition [161]. Sugars can act as signaling molecules in assorted biological processes, and even that sucrose-dependent cyclin expression is known since a decade ago [162], LR formation through sucrose induction is a good example of sugar-dependent reactivation of cell proliferation [163]. This recent study shows that the expression of CYCD4;1 levels in root pericycle cells is dependent on the sucrose availability, and that reduced CYCD4;1 levels in *cyca4;1* mutants or wild-type (wt) roots grown in the absence of sucrose cause LR density to drop. It is not clear how sucrose upregulates CYCD4;1 in specifically in that kind of cells, but these findings suggest that the transcriptional effect has to do with sucrose-dependent regulation of LR density. Notably, auxin does not have an effect over the expression of CYCD4;1 in pericycle cells, and restores the reduced LR density phenotype of cyca4;1 mutants, suggesting that CYCD4;1 has no role in the auxin-mediated LR initiation pathway. CYCD3;1, is also responsive to sucrose availability, but the effects of this over CYCD3;1 activities are not clear [164]. Endoreplication progress is also affected by several environmental signals. E2F3/ DEL1, an atypical E2F present in Arabidopsis, and that functions as a transcriptional repressor, is one of the key regulators that negatively controls the entry into the endoreplicative cycle [165]. It has been suggested that the balance between the transcriptional activator E2Fb and repressor E2Fc controls light-dependent endoreplication through the antagonistic modification of the DEL1 expression [166]. E2Fb and E2Fc compete

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for the same DNA-binding site of the DEL1 promoter and enhances the DEL1 expression, respectively. Under light conditions, E2Fb is the preferred binding partner, enhancing DEL1 expression and consequently repressing the endoreplicative cycle [167]. In the dark E2Fb is degraded, allowing E2Fc to bind to the DEL1 promoter, repressing DEL1 expression. Ultraviolet-B (UVB) radiation damages DNA molecules by forming cyclobutane pyrimidine dimers (CPDs) which prevent DNA transcription and translation. Plants remove CPDs by photolyases, and these enzymes are encoded by a PHOTOLYASE 1 (PHR1) [168, 169]. It has been shown that in addition to CCS52A2, a known target of DEL1, DEL1 represses the transcription of the PHR1 gene and thereby coordinates DNA repair and endocycle triggering [167]. After UVB treatment, DEL1 expression is strongly downregulated, permitting the upregulation of PHR1 and thus leaving the cell able to repair its DNA.

Environmental and nutrient availability condition changes affect root apical meristem organization [170]. ROS and Reactive Nitrogen Species (RNS) have been reported to be rapidly induced by several kinds of environmental stresses in a variety of plant species to regulate the plant response to biotic and abiotic stresses. 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 [114]. 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 [114, 171-173]. ROS is never completely eliminated, as it plays an important role in signaling and growth regulation [174]; ROS quenching inhibits the root growth [115], and overexpression in Arabidopsis of a peroxidase localized mainly in the elongation zone stimulates root elongation [175]. This calls for redox control of the cell cycle, which is possibly linked to A-type cyclins, shown to be differentially expressed under oxidative stress in tobacco, resulting in cell cycle arrest [176]. It is also known that low temperatures [177, 178], metals [179] and nutrient deficiency [180] induce the presence of ROS and RNS in specific tissues. These forms of stress affect root morphology by reducing primary root growth and promoting branching, but the mechanisms of the redox generation-sensing are not well understood.

The typical response of the Arabidopsis radical system to low phosphorous (P) availability is an example to illustrate how complex these processes are. A recent study showed that ROSs are involved in the developmental adaptation of the RS to low P availability [181]. Rapidly growing roots of plants within a normal P medium synthesize ROS in the elongation zone and QC on the root, whereas seedlings within low P mediums showed a slow growth of the PR, and the ROS normally found in the QC relocate to cortical and epidermal tissues. In a previous study [131], it has been indicated that Arabidopsis plants under low P conditions show a decreased number of cells in the root apical meristem, and it decreases until it is depleted. In these roots, all root apical meristem cells differentiate and the QC is almost indistinguishable. A possible cause of this response to P starvation could be the cell cycle arrest modulated by ROS and CYCAs, but it is more complicated, as the response is also modulated by auxin [170, 182] and gibberellin-DELLA pathways [183]. Interestingly, DELLAs promote survival by reducing the levels of ROS [184], suggesting a link between the gibberellin-DELLA cell cycle

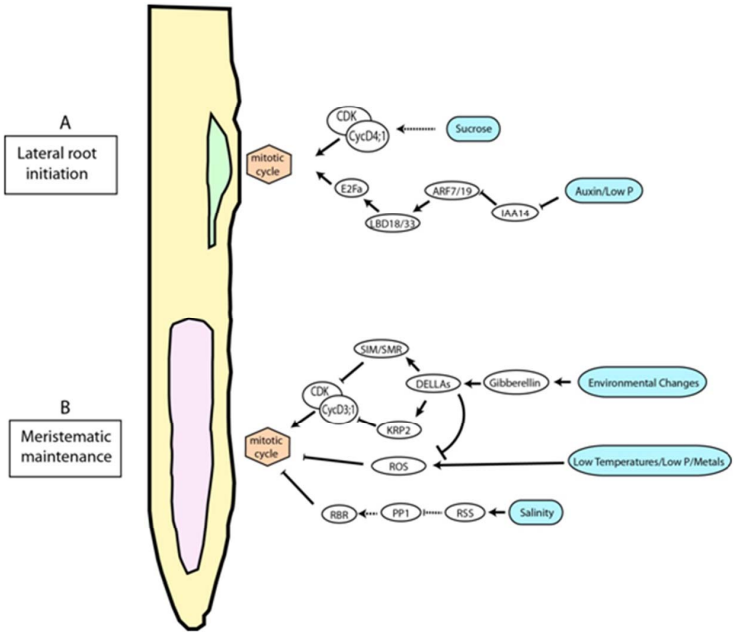

Figure 3. Abiotic Stress affects root mitotic cycle. A) Lateral root formation responds to sucrose availability in medium through an unknown link that enhances CycD4;1 expression in pericycle cells, allowing them to proliferate; it also responds to low P availability through the activation of the auxin pathway. Auxin controls lateral root initiation through the E2F mechanism, promoting the degradation of IAA14 and thus activating ARF7/18 transcription factors, subsequently activating LBD18/33 factors which in turn bind and activate the promoter of the cell cycle-enabling E2F transcription factor. B) Meristematic maintenance also responds to diverse environmental changes. Through the gibberellin pathway, DELLA proteins inhibit cell cycle progression by enhancing the accumulation of CDK inhibitors. DELLAs are influenced by various environmental factors including light and temperature. These factors, as well as metals and nutrient deficiency as in low P, promote the accumulation of ROS, known for inhibiting cell cycle in tobacco cells. Interestingly, DELLAs promote survival by lowering the levels of ROS, indicating a novel pathway to maintain cell cycle in the meristems. Salinity affects it by activating RSS1, required to maintain the mitotic cycle in the meristem. The putative mechanism comprises RSS1 interacting with a type 1 protein phosphatase (PP1), regulating its activity at the G1/S transition.

control pathway and ROS pathway in the developmental adaptation to the RS to low P availability It requires further study to precise the way these signals crosstalk and determine the developmental adaptation of the RS to low P availability by means of cell cycle progression control, as well as additional efforts to reveal the manners by which other regulatory pathways responding to abiotic stress interact with and influence the cell cycle control mechanisms.

5. Conclusion

Sensing and responding to environmental cues by roots enable plants to overcome the challenges posed by their sessile lifestyle [10]. As we mentioned above, RS is important to

plants due to a wide variety of processes, including nutrient and water uptake from soil, which is a complex medium with high spatial and temporal environmental variability. Thus, it is not surprising that RSA is highly influenced by environmental cues [9, 148]. The importance of RSA in plant productivity stems from the fact that many soil resources are unevenly distributed or are subject to localized depletion, so that the spatial deployment of the RS will largely determine the ability of a plant to exploit those resources [4].The PERDP which regulates the changes in RSA, can be considered as an evolutionary response to medium with high spatial and temporal variability in resource supplies [148]. The genetic controls regarding root deployment (PERDP) are still largely unknown. A great effort has been made to understand the molecular components that regulate the formation, proliferation and maintenance of meristems, either being embryo or pericycle-originated. Nevertheless, the facts behind their regulation by environmental factors still leave many questions to be solved.

Plants are important to humans, as they provide food, fuel, fibres, medicines and materials. As the global population is projected by the UN to rise to over 9 billion by 2050, the improvement of crops is becoming an increasingly pressuring issue. The new challenge arisen is to solve the current and future obstacles to the maintenance of food supply security through higher crop yields [10]. Water and nutrient availability limit the productivity in most agricultural ecosystems. In all environments characterized by low water and nutrient availability, RSA is a fundamental aspect, the acquisition of soil resources by RS systems is therefore a subject of considerable interest in agriculture [4]. RSA and PERDP are important agronomic traits; the right architecture in a given environment allows plants to survive periods of water of nutrient deficit, and compete effectively for resources [9]. Most of drought-resistant rice varieties have a deeper and more highly branched RS than sensitive varieties [9].

Understanding the RSA and the PERDP holds potential for the exploitation and opening of new options for genetic manipulation of the characteristics of the root, in order to both increase food plant yield and optimize agricultural land use. Improved access to deep soil water, inherently reducing the need for irrigation, is one potential benefit that could be achieved by exploitation of RSA. Increase in root branching and root hair in crops may enable plants to make more efficient use of existing soil nutrients and increase stress tolerance, improving yields while decreasing the need for heavy fertilizer application [9, 10]. Understanding which structures and environmental cues that regulate proliferation and elongation of the RS cells will allow us to develop strategies to generate crops that possess greater soil exploration capacities in order of a more efficient usage of nutrients and water present in the soil.

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Author details

L. Sánchez-Calderón[1], M.E. Ibarra-Cortés[2] and I. Zepeda-Jazo[1,3]

1 Unidad de Ciencias Biológicas, Universidad Autónoma de Zacatecas. Zac, México

2 Instituto Tecnológico de Monterrey Campus Querétaro Celaya, Gunajuato, México

3 Current Address: Trayectoria Genómica Alimentaria Universidad de La Ciénega del Estado de Michoacán de Ocampo. Mich, México

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