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Review

Root Involvement in Plant Responses to Adverse Environmental Conditions

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Abstract: Climate change is altering the environment in which plants grow and survive. An increase in worldwide Earth surface temperatures has been already observed, together with an increase in the intensity of other abiotic stress conditions such as water deficit, high salinity, heavy metal intoxication, etc., generating harmful conditions that destabilize agricultural systems. Stress conditions deeply affect physiological, metabolic and morphological traits of plant roots, essential organs for plant survival as they provide physical anchorage to the soil, water and nutrient uptake, mechanisms for stress avoidance, specific signals to the aerial part and to the biome in the soil, etc. However, most of the work performed until now has been mainly focused on aerial organs and tissues. In this review, we summarize the current knowledge about the effects of different abiotic stress conditions on root molecular and physiological responses. First, we revise the methods used to study these responses (omics and phenotyping techniques). Then, we will outline how environmental stress conditions trigger various signals in roots for allowing plant cells to sense and activate the adaptative responses. Later, we discuss on some of the main regulatory mechanisms controlling root adaptation to stress conditions, the interplay between hormonal regulatory pathways and the global changes on gene expression and protein homeostasis. We will present recent advances on how the root system integrates all these signals to generate different physiological responses, including changes in morphology, long distance signaling and root exudation. Finally, we will discuss the new prospects and challenges in this field.

Keywords: abiotic stress; drought; heat; high salinity; flooding; phytohormones

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1. Introduction

Abiotic stresses, including drought, low or high temperature, salinity, UV-B, light intensities, flooding, heavy metal toxicity, nutrient deficiency, etc., seriously affect plant growth and yield. According to the Intergovernmental Panel on Climate Change IPCC-2014 (http://www.ipcc.ch/), climate change is modifying intensity, frequency, and spatiotemporal extents of the extreme weather events. This, together with the rapid worldwide increase in human population, being 7.3 billion people nowadays, and expected to reach 9.7 billion by 2050, according to the estimation of the United Nations (reviewed in [1]), makes food supply as one of the major challenges to cope with in the near future.

Although most studies on abiotic stress resistance mechanisms focus on aerial organs, mainly because of the difficulty to study roots in their natural environment, it has been pointed out that aboveground and belowground organs have distinct responses (reviewed in [2,3]), and physiological and molecular mechanisms leading to stress tolerance can be complementary but not identical among tissues and organs [4]. Taking this into consideration, novel strategies for the development of crops with improved tolerance to abiotic stress conditions, based on targeting specific tissues or organs

(instead of the entire plant) are emerging (reviewed in [5]). Root is a key organ since it is involved in the uptake of water and nutrients, anchors the plant to the substrate and it is crucial for plant performance and crop productivity [6].

Perception of harmful conditions by different plant organs is the first step in the stress response. Abiotic stresses induce transcriptional changes in roots of many plant species [7]. It has been reported that antioxidant enzymes are upregulated in maize roots under water stress [8]. Under abiotic stress conditions, the synthesis of different metabolites (osmoprotectants, antioxidants, etc.) is induced to cope with the adverse conditions [9]. In addition, integration of environmental stimuli and physiological responses is mediated by an intricate network of plant hormones such as abscisic acid (ABA), jasmonates (JAs), salicylic acid (SA), or ethylene (ET) that modulate stress responses [10]. Auxins have a role in controlling root hair elongation and root branching under abiotic stress and have also been shown to participate in the positive regulation of drought stress tolerance through the arrangement of root architecture [11]. Stress perception, signaling and tolerance have been explored at the whole plant level (reviewed in [12]). However, the information related to the role of roots in these processes is much more limited. This study reviews recent findings in the biochemical, physiological and gene expression changes that take place in roots under different abiotic stress conditions, and the current progress in the recently developed platforms to achieve a global vision of plant stress response, which will be crucial in the future to develop breeding programs in a more targeted way.

2. Tools for the Study of Root Responses to Abiotic Stresses

Abiotic stresses affect roots at different levels and consequently, different tools to study root morphology and the regulatory networks that control root responses, including genomics, transcriptomics, proteomics, and metabolomics have been developed.

2.1. Phenotyping

Characterization of growth patterns is crucial since alteration in the root system architecture (RSA) is a critical adaptive strategy for crops to cope with abiotic stresses. As root phenotyping in the field is an important challenge, many works focus on root traits of plants grown in laboratories or under artificially controlled conditions, in gel medium or hydroponic solution [13,14].

Traditionally, root phenotyping has been achieved with 2D images, obtained from photographs or scans, and processed with informatic programs as WinRHIZO or free alternatives as SmartRoot or IJ-Rhizo macro for ImageJ, that allow the measurement of total and individual root length, root diameter, number of roots and the angles between primary and secondary roots [15]. An interesting tool for 2D phenotyping is the use of rhizotrons, growth chambers with transparent windows that allow continuous image acquisition while plant is growing, mimicking field conditions [16].

Recently, 3D imaging techniques have been developed and they allow phenotyping plant roots at field conditions. Some of these techniques are reviewed in [17] and also illustrated in Figure 1. The information obtained from phenotyping platforms has been used to obtain tolerant lines to abiotic stress, as maize plants resistant to drought [18] or *Arabidopsis* halotolerant lines [19].
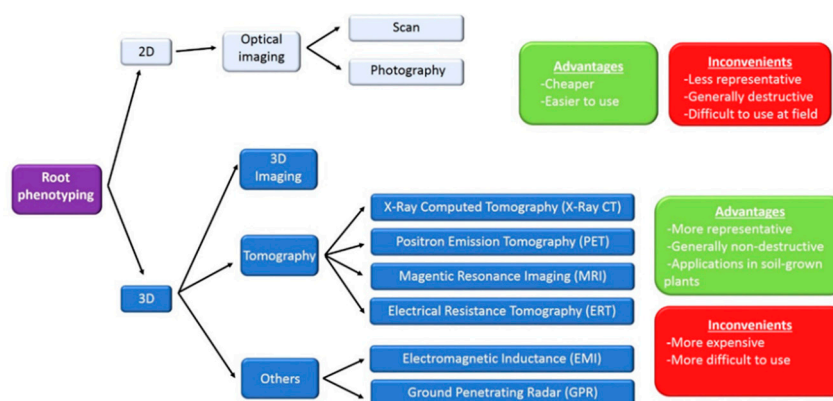
Figure 1. Technologies for root phenotyping. At the top of the figure, classical non-destructive 2D techniques, based on optical imaging, are indicated. Plant root systems are three-dimensional (3D) structures with many features, difficult to quantify in 2D. Advances for phenotyping root architecture in 3D imaging are nowadays available. Non-destructive 3D root phenotyping includes tomographic techniques [X-ray Computed Tomography (X-ray CT); Positron Emission Tomography (PET); Magnetic Resonance Imaging (MRI) and Electrical Resistance Tomography (ERT)]. More recently, two geophysical approaches, Electromagnetic Inductance (EMI) and Ground Penetrating Radar (GPR), have been developed. Advantages and inconvenients of the different technologies are indicated.

2.2. Genomics and Transcriptomics

The massive genome sequencing of many species has allowed to identify gene families related to abiotic stress tolerance. Although most of the works focus on plant aerial organs, some of them remark the importance of their expression in roots. Most of these gene families are related to phytohormone signaling pathways whereas other are transcription factors or final targets of the signals. Some examples are WRKY (which encode proteins with the conserved domain WRKYGQK) [20], Calcium-Dependent Kinases (CDPKs) [21], BURPs (which encode proteins with the BURP domain) or HSPs [22]. In addition, Quantitative Trait Loci (QTL) related with the resistance to drought [23,24] or soil salinity [25] have been found [26]. Recently, several studies have reported the use of next generation sequencing platforms (NGS) to characterize plant response to abiotic stress conditions in agronomically important crops, considering root organs [27].

MicroRNAs (miRNAs) are single-chain and non-coding fragments of RNA with a length of 21–24 nucleotides, which are involved in the post-transcriptional regulation of gene expression [28]. Different kinds of analyses are used for miRNA determination, including microarray, RNA sequencing, northern blot and RT-PCR [29]. miRNAs have been proposed as key regulators of several abiotic stress-related processes.

The information obtained from these analyses, together with metabolomic studies, facilitates the development of neural networks that reveal specific pathways which are induced or repressed in roots under abiotic stress conditions such as drought [30], salinity [31], or heavy metal toxicity [32].

2.3. Proteomics

Proteomics utilizes two-dimensional (2-D) gel electrophoresis, mass spectrometry (MS), matrix-assisted laser desorption ionization–time of flight (MALDI TOF), western blot, and ELISA techniques in combination with bioinformatics tools to identify proteins and map their interactions in a cellular context. MS-based methods in combination with computational tools are capable of processing hundreds of peptide transitions simultaneously (reviewed in [33]). The effect of abiotic stress conditions in root proteomic profile has been largely studied in several plant species under different adverse situations, including drought [34–36]; salt stress [37], high temperatures [38], waterlogging [39–41]; toxic metal ions [42,43], and nutrient starvation [44,45]. Under these conditions, profiles of protein families related to cell division and expansion, C and N metabolism, signal transduction and redox

balance are commonly altered. In addition, specific situations as heat stress or heavy metal ions induce the accumulation of specific protein families as Heat Shock Proteins (HSPs), or metallothioneins and phytochelatins, respectively [38,42]. Posttranslational modifications could be important for regulating protein activity under stress conditions [46].
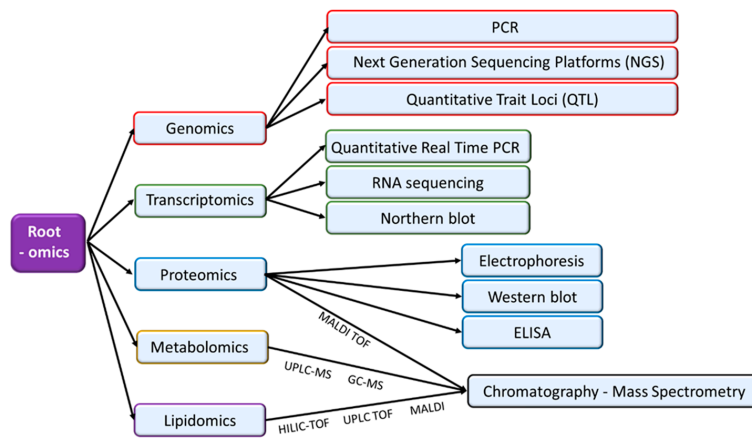
2.4. Metabolomics

Metabolomics allows the systematic identification and quantification of low-molecular-weight molecules present in a tissue/organ offering a direct approach to know the interaction of the plant genome with the environment. Although many methodologies are used (spectrophotometry, Fourier transform, infrared spectroscopy or immunoassays), chromatography coupled to mass spectrophotometry is the most extended technique to analyze the metabolome [47]. Matrix-assisted laser desorption/ionization (MALDI–MSI) technique has been used in the last years to study the spatial distribution of secondary metabolites and small molecules in roots under salt stress [46,48].

In maize plants subjected to drought, root metabolism is not as altered as in leaves, indicating also that allocation of metabolites to shoots is reduced in sensitive lines [49]. High variation between organs was detected in the accumulation of sugars, amino acids and polyols in lentil plants under salt stress conditions, indicating distinct adaptation mechanisms [50]. Primary metabolism, including sugars, amino acids and organic acids is also induced in roots of other species such as soybean grown under water stress conditions [51]. This accumulation could contribute to an osmotic adjustment to avoid plant dehydration whereas secondary metabolites concentration, including phenolic compounds, is reduced in roots but increased in shoots, which is related to the high levels of antioxidants needed in leaves [52]. However, there is some controversy since it has also been reported that roots of soybean and tobacco plants highly induce their secondary metabolism under drought [53]. Roots of soybean plants subjected to salt stress accumulate high quantities of sugars, amino acids, fatty acids and organic acids, and the secondary metabolism of antioxidants is increased, revealing the importance of C and N metabolisms and the Krebs cycle in tolerant plants [54]. Sorghum plants grown under low N concentration reduced root content of phenylalanine, a precursor of SA, providing evidence of a reduced plant defense response under low N conditions [55].

2.5. Lipidomics

Lipidomics analyzes membrane lipid composition and has been used to decipher the role of lipids on tolerance to abiotic stress conditions [56]. Electrospray ionization tandem mass spectrometry (ESI-MS/MS) has been traditionally used for lipidomics although other mass spectrometry instruments such as HILIC-ESI-IT-TOF-MS/MS or UPLC-TripleTOF make lipid analyses more efficient and accurate [57]. Although this is a promising approach to study plant stress, its use in roots is limited. Yu et al. [58] reported changes in the levels of oxidized membrane lipids under salt stress conditions in barley. Recent studies have also analyzed the importance of glycosyl inositol phosphorylceramide (GIPC) sphingolipids of the plasma membrane in seedlings of salt-stressed plants by MALDI-MS [59].

Moreover, studies regarding root cell membrane have reported differences in plasma membrane viscosity and fluidity, highly influenced by plasma membrane/tonoplast intrinsic proteins [60]. Staining and microscope evaluation is usually used for these studies [61], as well as the analyses of K^+ and H^+ fluxes with selective electrodes [62]. Under osmotic and salt stress conditions, root cells exhibit a decrease of plasma membrane fluidity and an increase of its microviscosity [61,63] although at long term, there is an increase of membrane permeability induced by its degradation [62]. The most relevant analytical techniques used in each -omic approach are indicated in Figure 2.

Figure 2. Omic- approaches, including genomics, transcriptomics, proteomics, metabolomics and lipidomics, make possible active analyses of regulatory networks that control plant organ responses to adverse environmental conditions. In the figure, the most relevant analytical techniques used in each -omic approach are indicated.

3. Abiotic Stress Signaling

Signaling abiotic stress include mechanisms that should be able to link the sensing mechanism and the genetic response. Signal transduction pathways can be divided into four steps: signal perception, generation of second messengers (Ca^{2+}, inositol phosphate and reactive oxygen species -ROS-), activation of secondary sensor proteins (phosphorylation cascade), and activation of transcription factors (TFs) or stress responsive genes (Figure 3).
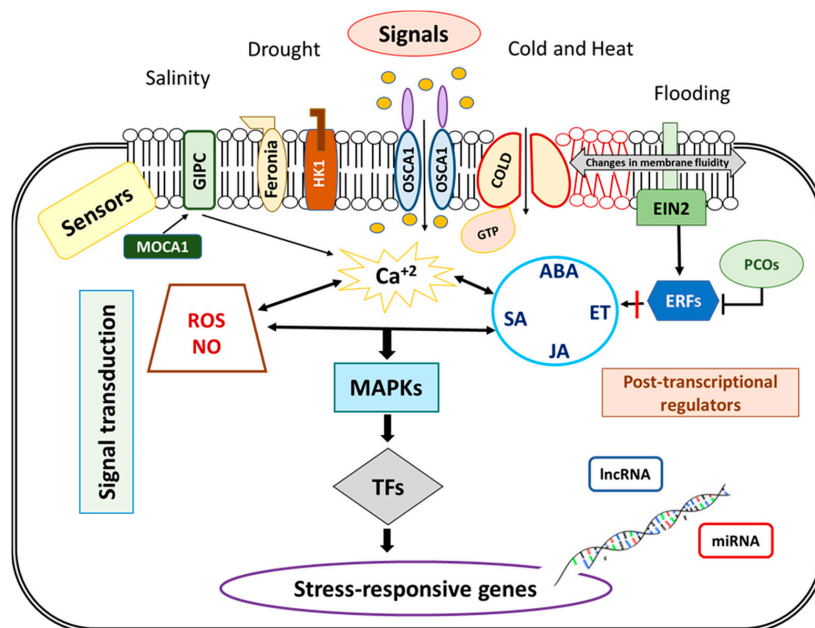
Figure 3. Abiotic stress signaling in roots. To activate adaptative responses, in a first step environmental signals should be detected by sensors located at plasma membrane (as ion channels and other transporters, membrane-anchored receptor like kinases). Then, second messengers (Ca^{2+}, inositol phosphate and Reactive Oxygen Species, ROS) amplify signals, and, in coordination with phytohormones (Abscisic Acid, ABA; Salicylic Acid, SA; Jasmonic Acid, JA, and Ethylene, ET) activate Mitogen-Activated Protein Kinases (MAPKs) signaling pathways and transcription factors (TFs) that modulate stress responsive genes expression. The expression of these genes is also posttranscriptionally regulated by non-coding RNAs (lncRNA and miRNA).

In roots, environmental stress conditions trigger various signals for allowing cells to sense and activate the adaptive responses. Signaling processes during stress happen at the cellular level and some organs built common signals. However, root is constituted by many types of cells that follow radial (rhizodermis, cortex, endoderm) and longitudinal (cap, meristematic, elongated and differentiated cells) patterns and these cell types could have different sensing for stress.

3.1. Stress Perception

Stress perception is the first step for which external stimuli activate diverse receptors/sensors to trigger signal transduction cascades. Although the absence of clear ligands makes difficult to identify these sensors, they seem crucial for developing stress tolerance [64].

Abiotic stress causes disturbances mainly to plasma membrane fluidity and it can modify cell membrane components to maintain their integrity and optimal function [65]. Thus, integral membrane proteins (channels and other transporters) and membrane-anchored receptor like kinases can be potential sensors [66,67]. Root capacity to sense variation in osmotic potential is basic to achieve an appropriate response to drought and high salinity. By using several mutants, Yuan et al. [68] identified hyperosmolarity-gated calcium-permeable channels (OSCA1) as a potential osmosensor. A recent study describes *At*OSCA1 and *At*OSCA3 as mechanosensitive ion channels that are activated by a conformational change promoted by membrane tension during osmotic stress [69]. Histidine Kinase 1 (HK1) was identified as a unique osmosensor also in *Arabidopsis* [70] but recent studies question its role in this process [71]. Under high salinity, the Feronia receptor kinase seems to function as external sensor in cell walls of *Arabidopsis* roots [72]. In addition, a recent study highlights the importance of GIPC sphingolipids in the plasma membrane by using *monocation-induced Ca^{2+} increases 1* (*moca 1*) mutants. In *Arabidopsis*, MOCA1 was identified as a glucuronosyltransferase required for Ca^{2+} increase produced during salt stress signal transduction, related to GIPCs as monovalent-cation sensors [59].

Changes in the environment temperatures affect the fluidity of phospholipid membranes [73]. In rice, *Chilling tolerance divergence* (*Cold 1*) is associated with G-proteins and mediates Ca^{2+} fluctuation induced by cold, indicating their role in sensing adverse conditions [74]. Phytochrome B has been described as a thermosensor in leaves but it is reasonable to propose a different sensor mechanism in roots, given that phytochrome B requires light to be activated [75,76]. These root sensors could be found among the new elements (DNA/chromatin structures, mRNAs, protein conformation changes) that have been recently proposed as thermosensors in plants [77].

3.2. Phytohormone Signaling

Abiotic stress induces changes on phytohormone levels in roots and these changes can be different from that observed in leaves. Moreover, as observed in Table 1, various phytohormones could participate in the responses to different stress conditions. This accounts for the complexity of the signaling process.

The importance of ABA in plant tolerance to drought is widely accepted but recent studies also show that a complex network of plant phytohormones performs with it [92,93]. In the past decade, core ABA signaling components were broadly characterized but only a few works addressed organ-specific signaling mechanisms. For instance, a high number of ABA receptors operate in tomato roots [94] whereas ABA treatment increased only the transcripts of *ZmPYL1*, *ZmPYL2* and *ZmPYL3* in maize roots [95]. In rice, the expression of *OsPYL10* is upregulated by ABA treatment but downregulated under cold stress [90]. Therefore, additional species-specific characterization is required to understand the complexity of core ABA signaling [96].

Table 1. Changes in hormonal content in roots of plants under different abiotic stress conditions.

Stress	ABA	SA	JA	IAA	SLs	ET	References
Drought	↑	↑	↑		↑		[78–82]
Salinity	↑				↑		[80,83]
Waterlogging	↓		↓			↑	[84,85]
	↑		↑				[83,86]
Trace elements	↓		↓				[87]
	↓	↑	↓	↑			[88]
Heat	↓		↓				[89]
Chilling/cold stress	↓						[90]
Heat + water stress	↑						[91]

In citrus and *Arabidopsis* roots, a transient increase of JA was recorded before ABA accumulation in response to water deficit [78,79]. In tomato roots, an interaction between ABA and SA was observed under water stress, where ABA seems to negatively regulate SA levels [82]. By using a split-root system in *Gossypium hirsutum*, it was showed that ABA signal could jump from salt-stressed to non-stressed roots. Saline roots could send through shoots some signals that increase *9-cis-epoxycarotenoid dioxygenase* (*NCED*) expression and decrease that of cytochrome P450 family (*CYP707A*), enhancing ABA levels in non-stressed roots. This phytohormone could induce *NADPH-Oxidase C* (*RBOHC*) expression to produce H_2O_2, which downregulates *NCED* genes to prevent higher ABA accumulation in the non-salt-stressed roots [83]. In addition, JA biosynthesis rice mutants showed that uptake of Na^+ in rice depends on jasmonates [97]. In tomato, *JA-deficient mutant defenceless-1* (*def1*) increased levels of Na^+ and reduced N levels in salt-stressed roots indicating a possible role of JA in N homeostasis. An increase in oxidative stress was also observed in this mutant, demonstrating that JA is involved in the protection response of plant during salt stress [86].

Ethylene is a key hormone mediating numerous important biological processes, including responses to abiotic stresses [98]. The membrane protein Ethylene Insensitive 2 (EIN2), a central regulator of ET signaling, controls the transduction of the ET signal from the endoplasmic reticulum membrane to the nucleus in Arabidopsis, and its phosphorylation inhibits ET signaling. After the signal cascade mediated by different EIN proteins, ET signals are delivered to ET Responsive Factors (ERFs), the last downstream components of the ethylene signaling pathway, which lead to the regulation of ET-controlled gene expression [99]. Hypoxia modifies transcript profiles of Group-VII ERFs (reviewed in [100]), which are part of a large family of proteins. Most of the VII-ERFs in plant species are degraded by N-end rules pathway in a process regulated by Plant Cysteine Oxidases (PCOs). These PCOs oxidize the amino terminal cysteine of ERF, in a way dependent on the intracellular oxygen levels, indicating the fate of the protein for degradation by proteasome [101]. Therefore, PCOs could be oxygen sensors under waterlogging stress [102].

Auxin mediates ET signaling to control root growth [103] and a recent study reveals that ET regulates organic acid secretion through auxin signaling in vine roots under alkali stress [62], indicating that ET is involved in responses to different stress conditions.

3.3. Signal Transduction and Stress-Induced Gene Expression

Second messengers as calcium and ROS are key elements to amplify signaling and the ROS/Ca^{2+} waves together with phytohormones coordinate pulses of gene expression regulating plant responses to stress (reviewed in [104]).

Calcium plays a critical role in signaling nutrient availability [105] and cold stress response in plants [106]. Several studies have shown how Ca^{2+} signaling and its crosstalk with nitric oxide (NO), ROS and Mitogen-Activated Protein Kinases (MAPKs) signaling pathways are responsible for

establishing cold tolerance in plants (reviewed in [107]). Interestingly, phytohormones act and regulate some of the genes and transcription factors needed for the stress response [27,108]. For example, the regulation of lateral root growth under drought stress seems to directly depend on the interaction of ABA and RBOHI in Arabidopsis roots [109].

Under high salinity conditions, the Salt Overly Sensitive (SOS) signaling pathway is the most important point to control ion homeostasis in roots and has been extensively studied. Briefly, influx of Na^+ induces an increase of cytoplasmatic Ca^{2+} activating different transporters, increasing ROS levels and triggering ABA biosynthesis (reviewed in [110]). In *Arabidopsis*, *At*ANNEXIN 4 functions as a Ca^{2+} permeable transporter generating a calcium signal by interaction with SOS2-SOS3-like calcium-binding protein complex triggering the SOS pathway in response to salt stress [111]. A recent work, establishes that the calcineurin-B like protein 10 (CBL10)-interacting protein kinase 8 (CIPK8) complex regulates the plasma membrane Na^+/H^+ antiporter SOS1 in *Arabidopsis* roots, suggesting an additional branch of the SOS signaling pathway [112].

NO acts as a secondary messenger in plants, regulating protein function through a variety of different mechanisms [113]. In NH^{4+} treated rice plants an early NO burst in response to water stress, that promote the activities of antioxidant enzymes, has been described [114]. In addition, NO seems to be important in plant responses to heavy metal intoxication. For instance, Cd treatment in *Arabidopsis* induced an increase in NO levels, inhibiting auxin transport and root growth [115]. In addition, a recent work in cucumber roots determined that Cd treatment increases hydrogen sulphide (H_2S) and H_2O_2 levels although their function under vascular H^+-ATPase activity is opposite, indicating a different role during Cd stress for both signaling molecules [116].

Cold stress signaling is mostly regulated by the expression of *Cold Responsive* (*COR*) genes although the transcriptional cascade by temperature stress included other two components: *C-repeat Binding Factors* (*CBF*) and *Inducer of CBF Expression* (*ICE*) (reviewed in [117]). In wheat, *ICE/CBF* and *COR* genes were characterized and analyzed, showing that *CBF* genes are upregulated during different developmental stages in roots [118]. In *Hevea brasiliensis*, levels of *HbCBF1* and *HbCBF2* transcripts increased quickly after cold stress and JA treatment enhanced cold tolerance, indicating a possible role of this hormone in temperature signaling [119]. On the other hand, heat stress signaling is principally modulated by ROS and NO regulatory systems together with Heat Shock transcription Factors (HSFs), ABA and SA (reviewed in [120]) but more studies are necessary to explain hormone interaction in root responses to high temperature stress.

Flooding signal transduction is mainly modulated by VII-ERFs. In *Arabidopsis*, five groups have been described: Related to *APETALA 2 12* (*RAP2.12*), *RAP2.2*, *RAP2.3*, *hypoxia responsive 1* (*HRE1*) and *HRE2* (reviewed in [102]). The VII ERFs are regulated by continuous proteasomal degradation in normoxia [121]. *Hypoxia-Response Attenuator1* (*HRA1*) function under low O_2 levels has also been analyzed [122]. The observed repression of *RAP2.12* by a fast induction of *HRA1* in young tissue could be related to the prevention of excessive expression of anaerobic genes. In addition, the study of *universal stress protein 1* (*hru 1.1*) mutant in *Arabidopsis* determine that HRU1 interactions with other proteins are important for the regulation of ROS production under anoxia, probably through an interaction with RBOHD [123]. As a result, the coordination network of HRU1 and HRA1 proteins is fundamental for the flooding response. As in other stresses, Ca^{2+} is a key signaling molecule in *Arabidopsis*, maize, rice, and wheat under hypoxic conditions (reviewed in [102]). A recent study has revealed that ET could prevent VII-ERF proteolysis by increased production of the NO-scavenger Phytoglobin 1, preparing the plant for the response to hypoxia conditions, although the induction of the core hypoxia genes and second messengers as ROS or Ca^{2+} is necessary to induce a response [124].

MAPKs have an important role in the transduction of hormone signals and abiotic stresses but the relation between ROS and MAPKs activation is confusing. In tobacco, overexpression of the *Populus trichocarpa MAPKK4* enhanced the activity of antioxidant enzymes, improving tolerance to salt stress [125]. A recent work in maize roots described that Cd treatment induced a rapid and transient ROS production following *Zm*MAPK6-1 and *Zm*MAPK3-1 activation, indicating that ROS

accumulation may activate MAPKs cascade [126]. A comparative study between *Arabidopsis* and *Brassica juncea* under Ni treatment showed a different redox response, suggesting that increased Ni tolerance of *Brassica juncea* may be linked to reduced redox signaling [127].

Transcription factors are key components of signal transduction [128]. Under abiotic stress, different TFs, such as AP2/ERF and WRKY groups, mediate processes involved in tolerance to high salinity, cold and drought (reviewed in [129]). In citrus, Vives-Peris et al. [20] identified 50 putative WRKY TFs with particular expression patterns under different abiotic stress situations. In grapes, *VvWRKY30* was shown to have a positive role in stress signaling [130]. Knockout plants of the *NAC transcription factor* (*SlTAF*) showed an increased sensitivity to salt stress, indicating a role of this NAC in signal transduction of salinity stress [131]. Overexpressing *ABA-responsive element binding factors of sweet potato* (*IbABF4*) in transgenic *Arabidopsis* seedlings enhanced salt and drought tolerance [132]. A novel stress responsive bZIP transcription factor (*OsbZIP62*) that seems to be regulated by ABA has been described [133]. In common bean, several *PvDREB* genes that increase their transcript levels after different abiotic stresses have been identified. *PvDREB1F* and *PvDREB5A* responded to salinity, cold and dehydration whereas *PvDREB2A* and *PvDREB6B* were only induced by cold and dehydration [134]. In rice, the overexpression of *histone gene binding protein-1b* (*OsHBP1b*) reduced ROS levels and modulated stress-related transcripts, increasing plant tolerance to multiple abiotic stresses [135]. Additional work is needed to elucidate the specific role of many TFs in roots.

Other genes codify proteins to remove harmful compounds (as antioxidant enzymes) or to protect the cell (as chaperones), whereas other transcripts are involved in coordinating a specific response. Under water stress, a comparative study between roots of two chickpea genotypes with different tolerance showed a remarkable induction of ABA-dependent (*ABI5*) and ABA-independent (*DREB1A* and *DREB1C*) genes in the tolerant genotype, as well as increased expression of many antioxidant enzymes and genes related with JA and ABA biosynthesis, indicating an adaptative response [136]. In wheat, water supply limitation induces the expression of *lateral root density gene* that decreases gibberellin levels by activating their catabolism, reducing lateral root growth, and improving plant response to drought [137]. In roots of soybean, some *Calmodulin Binding Transcription Activator* (*GmCAMTAs*) are important during early response to water stress and the overexpression of *GmCAMTA12* in roots of *Arabidopsis* enhance drought survival [138]. Concerning to phytohormones, *LeNCED1* overexpression, a key gene in ABA biosynthesis, improved salinity response [139] and the knockout of *ABA 8'hydroxylase* (*OsABA8ox2*), involved in ABA catabolism, enhanced drought tolerance [140]. In soybean, *Salt induced1* (*GmSIN1*) overexpression induced *GmNCED3* and *GmRbhoB*, improving salt tolerance, suggesting *GmSIN1* gene could work as a modulator between ABA and ROS signaling [141]. A comparative analysis of roots and leaves of *Thellungiella* under cold stress has allowed to identify cold responsive genes that seem to be closely related to environmental adaptations [142]. In rice roots, common genes in response to Cd and As stress related with redox control, glutathione metabolism and transport activity have been identified [143].

Long non-coding RNAs (lncRNA) affect the expression of other genes [144]. In *Arabidopsis*, a nucleus-localized lncRNA DRIR is a positive regulator, enhancing plant responses to drought and salt stress [145], and the root-specific AtR8 increases accumulation under hypoxic conditions [146]. In rice, one hundred forty four lncRNA affect root development at early stage in response to Cd stress [147], and recently it has been reported that lncRNAs are involved in the regulation of key metabolic pathways in response to water stress in maize root tips [148].

miRNA are post-transcriptional regulators, essentially inhibiting gene expression [149]. miRNA analyses have been performed in roots of plants under drought or high salinity [150,151]. In salt-tolerant rice cultivars, miRNAs associated with maintenance of cellular homeostasis and development of root during salt stress have been identified [152]. The overexpression of eight miRNAs in *Arabidopsis* roots subjected to low oxygen conditions have been also reported [153]. Under hypoxic stress, *miRNA72a* was downregulated in maize roots [154] whereas in lotus it was upregulated [155]. Therefore, its expression was correlated to the species tolerance to waterloging (much higher in *Lotus*).

Specific miRNAs were identified in maize under heat stress [149]. Gao et al. [156] provided new insights for the functional characterization of miRNAs, showing that *Zma-miR393b* and *Zma-167f* are key in auxin signaling under Cd^{+2} treatment in maize roots. A study in an apple rootstock evidenced that adventitious root formation is regulated by miRNAs [157].

4. Physiological Changes

Changes at molecular level induced by stressful situations lead to physiological responses such as the modification of root architecture (Figure 4) and root exudation pattern.
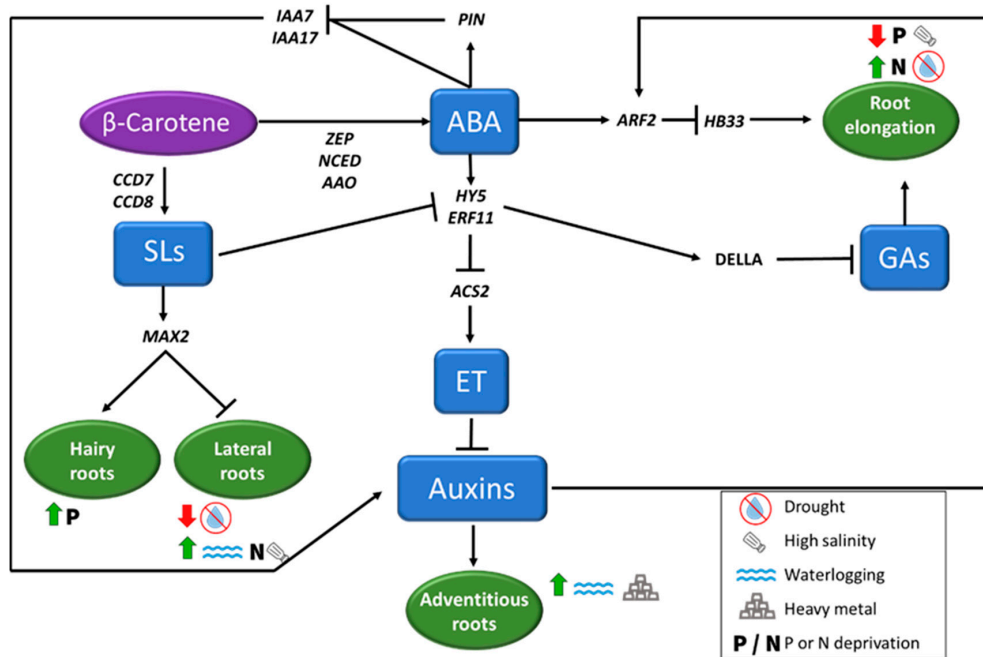
Figure 4. Root architecture (considering root elongation, and hairy, lateral, and adventitious roots formation) under abiotic stress conditions is regulated by phytohormones, that induce or repress the process depending on the adverse condition. Abscisic Acid (ABA) plays a key role in regulating root cell elongation in different ways, repressing Gibberellins (GAs) through an increase of DELLA proteins concentration or inhibiting auxins biosynthesis. Auxins and Strigolactones (SLs), also play important role in root architecture, inducing or repressing the formation of new roots depending on the adverse environmental situation, as indicated in the figure.

4.1. Root Architecture

Plants are able to sense soil physicochemical parameters and consequently adjust their development in order to adapt to environmental adverse situations [158], adjusting their genetic program to post-embryonic root development, following different strategies depending on the applied stress [159]. Under water stress, the development of lateral roots is inhibited, but not its initiation, and the development of primary roots increased depending on hydrotropisms, being this adaptation highly modulated by ABA [159]. Under high salinity conditions, it is essential to keep low contents of cytosolic Na^+ and Cl^- ions to ensure plant adaptation and survival, having an important role the compartmentalization of these ions and their transport through membranes [160]. Under waterlogging conditions, the formation of lateral roots and aerenchyma in the root cortex to increase the internal concentration of O_2 has been widely reported in species such as rice or maize, which is induced by ET and also regulated by ROS [85].

When plants face nutrient starvation, root morphology is also affected, and its area usually increases. However, specific effects depend on the element supplied in lower quantities, as the root response is focused on the assimilation of the specific nutrient [161]. One of the most studied deficiencies

is P, which decreases the growth of the primary roots, while induces the expansion of secondary roots, hairy root growth and the formation of cluster roots, due to variations in endogenous levels of sugars and phytohormones [162]. New studies with 3D scanning under low N concentrations reveal the enhancement of the number of cells in root meristematic zone, an increase in cell elongation [163], and an increased growth of lateral roots, being this highly influenced by strigolactones (SLs) [161].

Most of the changes in root architecture are regulated by auxins and SLs, inducing or repressing the formation of new roots depending on the adverse environmental situation [164]. Both groups of plant hormones are closely related, being *PIN*, *MAX2*, and *SHY2* some of the genes involved in this crosstalk. The role of ABA in root architecture is clearly important under abiotic stress conditions but with a changing role depending on the endogenous content, regulating root length, and lateral root development [165]. Among the mechanisms of root cell elongation inhibition, ABA is involved in different interactions, including the repression of *ACS2* expression through *HY5* and *ERF11* [8]; the increase in the concentration of DELLA proteins (gibberellin repressors, [166]); or the inhibition of auxin biosynthesis through inhibiting *IAA7* and *IAA17* and inducing the expression of *PIN* gene family (Figure 4, [167]). In contrast, ABA is known to be an inducer of *ARF2* expression that inhibits root cell elongation through *HB33* inhibition [168]. Under osmotic stress, ABA is also involved in root xylem differentiation to protoxylem and metaxylem and inhibition of lateral root formation [169].

4.2. Root Exudation Pattern

Abiotic stress conditions can modify root exudation patterns, through mechanisms like direct diffusion through root membranes, the transport through ionic channels, vesicles transport, or membrane transporters as ABC or MATE, depending on the chemical properties of the exuded metabolites [170]. Among genes involved in this process, *PDR2*, *PDR6*, *MRP2*, *PGP4-1* and *ABCG30* are the most studied in the ABC family whereas in MATE family, *FRD3*, among others, is responsible for citrate root exudation in response to Al stress as a mechanism to chelate the toxic ion [171].

The exudation rate generally increases under abiotic stress conditions as occurs with primary metabolites as amino acids and sugars, which are released to the rhizosphere when plants are subjected to drought [172], high salinity [173] or Pb toxicity [174]. Compounds from the secondary metabolism are also exuded in response to drought [172], salt stress [175], heat stress [176], Al toxicity [177] and flooding [178]. Nutrient deficiencies also affect exudation rates of primary metabolites. Carvalhais et al. [179] concluded that while N starvation does not affect exudation at large grade, K deficiency reduced carbohydrate exudation and P starvation had the opposite effect.

However, it has been reported that root exudate composition may vary depending on the stress duration, severity, and plant tolerance. Therefore, under short-term drought, relative C exudation increased but at the long-term, exudation was highly variable and even decreased [180]. In addition, some metabolites as proline are usually exuded under drought conditions [181] and can be used for the detection of plant stress [89,181].

All these metabolites can also lead to microbiota recruitment, stablishing mutualistic relationships between plants and mycorrhizal fungi or plant growth promoting rhizobacteria [170]. This microbiota can induce a large variety of benefits for the plants through different mechanisms, including biofilm formation, that favors humidity retention around roots and protects the plant; production of phytohormones; fixation of atmospheric N; soil nutrient solubilization due to the release of organic acids; siderophore production; etc. [182].

An important aspect which is beyond the scope of this review is communication between roots and aerial organs [183]. Role of hormones and RNA molecules as signals among aerial and underground organs under abiotic stress conditions has been extensively studied [183–188].

5. Conclusions and Perspectives

Plants respond to environmental adverse conditions through specific pathways including stress sensing, signal transduction, the activation of several stress-responsive genes and regulating specific

metabolite synthesis. Roots play a key role as the site of unique metabolic activities and, in many cases, as major contributors to secondary metabolites production in the whole plant. However, the underground location of this organ has hindered its study for decades. Consequently, the root phenotypes obtained from hydroponic and gel/agar systems do not really reflect the exact growth and development in soil. Recently, new non-destructive phenotyping approaches to study the root system architecture in natural soils and in complex environments make possible more reliable measurements of root traits.

In the past years, -omic technologies have provided relevant information on the genes and biochemical pathways that control plant responses to abiotic stresses, first in model plants, and more recently in agronomically important crops. The integration of data obtained from transcriptomic, proteomic, metabolic, phenotypic and physiological studies will provide relevant information for a better understanding of complex molecular networks underlying the mechanism of abiotic tolerance in plants Although the combination of all these approaches will help in the deciphering of stress resistance mechanisms, this will generate a large amount of data whose handling, interpretation and analysis will be a major challenge in the near future.

Under adverse conditions, the induction of myriad proteins occurs. Identifying these elements, that could be target for future breeding programs, including transformation methods and CRISPR/Cas9 gene editing techniques would lead to plants more resistant to the increasingly severe abiotic stress conditions to which they are subjected.

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