INTEGRATION OF HORMONAL SIGNALS SHAPING ROOT GROWTH, DEVELOPMENT, AND ARCHITECTURE

EDITED BY: Javier Brumos, Javier Agusti and Eswarayya Ramireddy

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INTEGRATION OF HORMONAL SIGNALS SHAPING ROOT GROWTH, DEVELOPMENT, AND ARCHITECTURE

Topic Editors:
Javier Brumos, North Carolina State University, United States
Javier Agusti, Polytechnic University of Valencia, Spain
Eswarayya Ramireddy, Indian Institute of Science Education and Research, Tirupati, India

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EDITORIAL
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Editorial: Integration of Hormonal Signals Shaping Root Growth, Development, and Architecture

Javier Agusti[1], *Eswarayya Ramireddy*[2] *and Javier Brumos*[1,3]*

[1] *Institute of Molecular and Cellular Biology of Plants (IBMCP), Consejo Superior de Investigaciones Científicas (CSIC), Universitat Politécnica de Valéncia, Valencia, Spain,* [2] *Biology Division, Indian Institute of Science Education and Research, Tirupati, India,* [3] *Program in Genetics, Department of Plant and Microbial Biology, North Carolina State University, Raleigh, NC, United States*

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Editorial on the Research Topic

Integration of Hormonal Signals Shaping Root Growth, Development, and Architecture

Plants need to constantly modify their growth and development to adapt to the ever-changing conditions and thus optimize the use of available resources. Over millions of years of evolution, plants have developed sophisticated mechanisms that allow them to integrate the information from external stimuli with their own internal programs to generate appropriate developmental outputs. Plant hormones act as signals in this integration process and contribute to the extraordinary plant morphological plasticity. The root system is a key determinant of plant development, exploring uncharted territory in the soil and serving as an interface between plant and rhizosphere. The roots enable the selective uptake of water and nutrients whereas exclude phytotoxic compounds. All these functions are maximized by the root morphological plasticity. The root anatomy is defined by regular patterns originated by cell division in the root apical meristem and consecutive cell differentiation that result in the different tissues composing the root. Due to these remarkable regular patterns, the root is an exceptionally useful system to study the effects of hormones on growth and development. Changes in plant hormone homeostasis via synthesis, modification, catabolism, and transport as well as the modulation of signaling components are key for a tunable and resettable hormone response system that controls root growth and development. Additional layers of fine-tuning are achieved by the intense cross-talk between different plant hormones at various levels. Phytohormones affect every stage of plant development including agriculturally important processes. Therefore, understanding how particular hormones and gene expression networks interact to coordinate root growth and development in a dynamic environment is essential, not only for developmental biology but also for the design of the next generation of crops coping with current agricultural challenges such as increasing food demand and climate change.

The main objective of this Research Topic is to gather current works studying the integration of hormonal signals in the root, a key question in plant developmental biology. If we improve our understanding on how hormones coordinate root growth, development, and architecture we can then improve our crops.

In crops, especially those cropped intensively such as cereals, developing an optimal root architecture is crucial for yield enhancement and space optimization without disturbing proper nutrient absorption. Therefore, the original research done by Sun et al., "A strigolactone signal inhibits secondary lateral root development in rice" aims to understand the hormonal control of secondary lateral roots in rice. Based on previous knowledge indicating that strigolactone signaling regulates lateral root development, the authors investigated whether secondary lateral roots development is also regulated by strigolactone and what the relationship between strigolactone and

Edited by:
Laura Rossini,
University of Milan, Italy

Reviewed by:
Silvio Salvi,
University of Bologna, Italy
Raffaele Dello Ioio,
Sapienza University of Rome, Italy

***Correspondence:**
Javier Brumos
jabrufue@upvnet.upv.es

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auxin signaling could be. Following an approach combining genetic analyses and pharmacological applications the authors show that while auxin applications on rice mutants deficient in strigolactone biosynthesis and sensitivity increased the number of secondary lateral roots, adding strigolactone treatments to the experiment only reduced the auxin effect in strigolactone biosynthesis mutants, but not in strigolactone-insensitive mutants. Thus, Sun et al. work points out that auxin and strigolactone have opposing effects in the process, and that the regulation of their action is complex.

Another original research article in this Topic (Liang et al.) focuses on how the crop load influences growth and hormone changes in the roots of "Red Fuji" apple. Crop load represents a crucial factor for the shoot and root growth and development of apple trees. The authors analyze the effects of an extensive range of crop loads on hormone levels and growth in apple roots. Higher crop loads resulted in lower root growth and non-fruiting plants exhibit elevated root growth. During the root growth peaks, the levels of cytokinins, indole acetic acid, and gibberellic acid were also at their highest. Together with the increase of crop load, the hormone levels were gradually decreasing within each peak. The results of this work suggest that root growth is positively correlated with hormone levels during the fruit growth phase, and that the reduction in root growth caused by crop load might be regulated by the reduction on hormone levels.

A collection of reviews bringing together different levels of root development regulation is also present in this Research Topic.

Ramachandran et al. focus their review on how water limitations modulate xylem development. In normal conditions, correct xylem development depends on the balance between hormones such as auxin, cytokinin, brassinosteroids, jasmonic acid, and abscisic acid. Drought alters that balance leading to a reduction of cambial cellular proliferation accompanied by an increase of xylem vessels production. These vessels, however, are significantly thinner, enhancing water transport efficiency while protecting the plant from embolism. This developmental plasticity is key for acclimation to drought. However, to date, little is known about the molecular mechanisms underlying it. Data previously produced by the authors' lab indicate that abscisic acid is, most likely, at the center of this plastic response to drought. The authors elegantly explain why breeding for xylem developmental alterations emulating those induced by drought may improve agricultural systems sustainability by enhancing water usage efficiency. Finally, Ramachandran et al. also point out that a number of links between environmental factors and the molecular regulation of xylem development are still missing and that implementing new technological approaches such as single cell sequencing, sheet fluorescence microscopy combined with Growth and Luminiscence Observatory for roots (GLO-Roots) or natural variation analyses to the study of xylem development hold great promise in identifying them.

The review by Xu et al., hones in the integration of jasmonic acid and ethylene into auxin signaling and how these interactions coordinate root development through the activity of ERF and HD-ZIP transcription factor families. *ERF109* is induced by jasmonic acid. ERF109 induces local auxin production in the root stimulating lateral root formation. Recently, *ERF109* has also been associated with plant regeneration. Ethylene induces the expression of *ERF1* which activates auxin biosynthesis and transport that in turn inhibits the elongation of the primary root. Ethylene also upregulates the expression of *HB52*, a member of the HD-ZIP transcription factor family. HB52 regulates auxin transport, altering auxin homeostasis in roots and inhibiting primary root elongation. The examples discussed in this review represent key crosstalk nodes between ethylene, jasmonic acid, and auxin that regulate root development.

Cell fate determination and stem cells maintenance at the root apical meristem (RAM) are key for proper growth and organogenesis of the primary root. Many intrinsic gene regulatory networks that involve phytohormones, peptide signaling, microRNAs and transcription factors are integrating the information from the environmental cues to maintain the characteristics of the root stem cell niche. Recently, studies indicate the cellular redox status and the presence of ROS can also play a pivotal role in this complex process. In the current Research Topic, the work of Zhou et al. portraits the panoramic view of ROS, as a fine-tuner of plant stem cell proliferation and differentiation. Zhou et al. summarize the recent findings in the field of ROS and the role of ROS in root development with an emphasis on root stem cell differentiation and maintenance, root hair differentiation and during the cell-cycle progression. Further, Zhou et al. not only describe the crosstalk between known genetic factors, hormones, and peptides with ROS, but also its newly found role in aerenchyma formation.

Calleja-Cabrera et al. discuss the root growth adaptation to climate change in crops. Climate change is the biggest threat to crop productivity in the world. High temperatures caused by global warming have deleterious effects on plant growth and development. As mentioned above, roots are essential for water and nutrient uptake. Modifications of soil temperatures affect root growth restraining production. Root architecture is affected by warmer soils. Increasing temperatures trigger diverse physiological and metabolic responses in the plant coping with warmer soils. Different regulatory mechanisms control the plant responses that prevent root cell damage and root growth impairment. Increasing temperatures are accompanied by other abiotic and biotic stresses such as drought, salinity, nutrient deficiencies, and pathogen infections that affect hormone homeostasis and gene expression. The authors not only discuss the latest studies in the field but also future research paths.

In conclusion, these original and review articles discuss the large interest and substantial progress that has been made in the field of root biology, especially on shedding light on hormonal cross-talk in root development.

AUTHOR CONTRIBUTIONS

JB prepared the outline of the manuscript. All authors wrote and improved parts of the manuscript.

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ORIGINAL RESEARCH
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A Strigolactone Signal Inhibits Secondary Lateral Root Development in Rice

Huwei Sun[1], Fugui Xu[1], Xiaoli Guo[1], Daxia Wu[2], Xuhong Zhang[2], Manman Lou[2], Feifei Luo[2], Quanzhi Zhao[1], Guohua Xu[2] and Yali Zhang[2]**

[1] Laboratory of Rice Biology in Henan Province, Collaborative Innovation Center of Henan Grain Crops, College of Agronomy, Henan Agricultural University, Zhengzhou, China, [2] Key Laboratory of Plant Nutrition and Fertilization in Low-Middle Reaches of the Yangtze River, Ministry of Agriculture, Nanjing Agricultural University, Nanjing, China

Strigolactones (SLs) and their derivatives are plant hormones that have recently been identified as regulators of primary lateral root (LR) development. However, whether SLs mediate secondary LR production in rice (*Oryza sativa* L.), and how SLs and auxin interact in this process, remain unclear. In this study, the SL-deficient (*dwarf10*) and SL-insensitive (*dwarf3*) rice mutants and lines overexpressing Os*PIN2* (OE) were used to investigate secondary LR development. The effects of exogenous GR24 (a synthetic SL analogue), 1-naphthylacetic acid (NAA; an exogenous auxin), 1-naphthylphthalamic acid (NPA; a polar auxin transport inhibitor), and abamine (a synthetic SL inhibitor) on rice secondary LR development were investigated. Rice *d* mutants with impaired SL biosynthesis and signaling exhibited increased secondary LR production compared with wild-type (WT) plants. Application of GR24 decreased the numbers of secondary LRs in *dwarf10* (*d10*) plants but not in *dwarf3* (*d3*), plants. These results indicate that SLs negatively regulate rice secondary LR production. Higher expression of *DR5::GUS* and more secondary LR primordia were found in the *d* mutants than in the WT plants. Exogenous NAA application increased expression of *DR5::GUS* in the WT, but had no effect on secondary LR formation. No secondary LRs were recorded in the OE lines, although *DR5::GUS* levels were higher than in the WT plants. However, on application of NPA, the numbers of secondary LRs were reduced in *d10* and *d3* mutants. Application of NAA increased the number of secondary LRs in the *d* mutants. GR24 eliminated the effect of NAA on secondary LR development in the *d10*, but not in the *d3*, mutants. These results demonstrate the importance of auxin in secondary LR formation, and that this process is inhibited by SLs *via* the *D3* response pathway, but the interaction between auxin and SLs is complex.

Keywords: auxin, OsPIN2, rice, secondary lateral roots, strigolactones

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Javier Agusti, Polytechnic University of Valencia, Spain

Reviewed by:
Weiqiang Li, Riken, Japan
Kosuke Fukui, Okayama University of Science, Japan

****Correspondence:***
Huwei Sun
sunhuwei19431@163.com
Yali Zhang
ylzhang@njau.edu.cn

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INTRODUCTION

Plants have successfully colonized the terrestrial environment *via* the evolution of multicellular organs that absorb the nutrients and water required for their growth and development (Pires and Dolan, 2012). The root system is the main organ by which plants obtain nutrients and water from soil (Péret et al., 2009; Sun et al., 2018a, 2018b; Huang et al., 2019). Therefore, diversity and plasticity in root architecture may contribute to the survival strategies of plants.

Root systems consist of embryonic roots derived from the embryo and post-embryonic roots derived from existing roots or non-root tissues (Atkinson et al., 2014). Post-embryonic roots arising from existing roots are lateral roots (LRs), and roots arising from non-root tissues are adventitious roots (ARs) (Atkinson et al., 2014). LRs develop from founder cells in the pericycle, the outermost layer of the vascular cylinder (stele) of a root (De Smet et al., 2006). In contrast to the taproot system, the majority of monocot roots form a fibrous root system that is characterized by the formation of many seminal roots (SRs) and ARs. In monocots, the LRs develop from ARs and SRs (Osmont et al., 2007; Bellini et al., 2014).

Several lines of study have suggested that LR formation is regulated by genetic factors (Lavenus et al., 2015; Murphy et al., 2016; Fernández-Marcos et al., 2017). In addition to genetic factors, LR growth and development are also regulated by plant hormones, such as auxin. Previous studies have shown that auxin plays a key role in LR formation and growth in plants (Guseman et al., 2015; Xuan et al., 2016; Tang et al., 2017). Auxin is synthesized mainly in aboveground tissue, such as shoot apices, by *YUCCA* family genes (Zhao, 2012) and redistributed by auxin-influx carriers, such as AUX1/LAX family proteins, and auxin-efflux carriers, including ABCB/PGP and PIN family proteins in several plant species (Friml, 2003; Blakeslee et al., 2005; Wang et al., 2009; Zazimalova et al., 2010; Péret et al., 2012). The polar transport of auxin is very important for LR development in plants (Swarup et al., 2005; De Smet et al., 2007; Inahashia et al., 2018). For example, the roots of the *aux1* mutant bend constitutively in one direction, forming root coils with LRs distributed predominantly on the convex side of the curve, which differs markedly from the wavy pattern seen in the roots of *Arabidopsis* (Swarup et al., 2005; De Smet et al., 2007). The mutants of *pin2*, *pin3*, and *pin7* have an altered branching pattern, with closely grouped lateral root primordia (LRP)/LRs or fewer LRP/LRs, in *Arabidopsis* (Laskowski et al., 2008). Moreover, *AtPIN3* is part of an auxin reflux pathway that is transiently established during the early phases of LR formation (Marhavy et al., 2013). *OsPIN2*-altered auxin flow in the root tip region is responsible for LR growth and formation patterns in rice (Inahashia et al., 2018).

Besides auxin, newly identified phytohormones named strigolactones (SLs) are involved in the growth and formation of LRs in several plant species (Kapulnik et al., 2011; Ruyter-Spira et al., 2011; Mayzlish-Gati et al., 2012; Rasmussen et al., 2012; Sun et al., 2014; De Cuyper et al., 2015). Compared with WT plants, a SL-synthesis mutant (*more axillary growth4*) and a SL-signaling mutant (*more axillary growth2*) were found to have greater LR densities in *Arabidopsis* (Kapulnik et al., 2011; Kohlen et al., 2011; Ruyter-Spira et al., 2011). However, LR density did not differ between WT plants and *d* mutants in rice (Sun et al., 2014). In *Arabidopsis* and rice, application of GR24 (a SL analogue) decreased the LR density in WT plants and SL-synthesis mutants (*more axillary growth4/d10*), but not in SL-signaling mutants (*more axillary growth2/d3*) (Ruyter-Spira et al., 2011; Sun et al., 2014).

The interactions between SLs and auxin in the regulation of LR growth are closely linked (Ruyter-Spira et al., 2011; Sun et al., 2014). In *Arabidopsis* and rice, higher auxin levels in roots were recorded in SL-synthesis mutants than in WT plants. Application of GR24 to the roots of WT and SL-synthesis mutants inhibited LR formation by reducing auxin transport (Ruyter-Spira et al., 2011). PIN proteins are the major auxin efflux carriers in plants (Friml, 2003; Wisniewska et al., 2006). Application of GR24 decreased PIN1, PIN3, and PIN7 protein levels in the primary root tips of *Arabidopsis*. However, PIN levels were not affected when similar levels of GR24 were applied in the presence of exogenous auxin (Ruyter-Spira et al., 2011). The expression of most *PIN* family genes in roots was downregulated by application of GR24 in rice (Sun et al., 2014). These results indicate that SLs inhibit LR formation, perhaps by reducing the levels of PIN proteins.

Rice is an ideal model for the study of plant root growth because of its small genome and the availability of its complete genome sequence and well-characterized mutants (Feng et al., 2002; Sasaki et al., 2002). Relative to primary LR development, the formation of secondary LRs in rice has not been characterized in detail. We found that secondary LR formation was induced in *d* mutants and that exogenous GR24 inhibited secondary LR formation in *d10* plants, but not in *d3* plants. NPA treatment reduced the number of secondary LRs in the *d* mutants. However, application of NAA increased the number of secondary LRs in the *d* mutants, but not in WT plants. The effect of NAA on secondary LR development was eliminated by supplying GR24 to the *d10* plants, but this was not the case in the *d3* plants. These results demonstrate that auxin induced rice secondary LR formation in the absence of SLs.

MATERIALS AND METHODS

Plant Materials

The *d3-1* and *d10-1* mutants (Shiokari ecotype) (Sun et al., 2014), and lines overexpressing *OsPIN2* (OE1 and OE2) (Nipponbare ecotype), were used in this study.

Plant Growth

Rice seedlings were grown at day/night temperatures of 30/18°C under natural light in a greenhouse. Seven-day-old seedlings of uniform size and vigour were transplanted into holes in lids placed over the tops of pots (four holes per lid and three seedlings per hole). Nutrient solutions ranging from one-quarter strength to full strength were applied for 1 week, followed by application of full-strength nutrient solution for 2 weeks. The chemical composition of the International Rice Research Institute (IRRI) nutrient solution is (mM): 1.25 $(NH_4)_2SO_4$, 0.3 KH_2PO_4, 0.35 K_2SO_4, 1.0 $CaCl_2$, 1.0 $MgSO_4{\cdot}7H_2O$, 0.5 Na_2SiO_3; and (μM) 9.0 $MnCl_2$, 0.39 $(NH_4)_6Mo_7O_{24}$, 20.0 H_3BO_3, 0.77 $ZnSO_4$, and 0.32 $CuSO_4$ (pH 5.5).

The treatments applied were as follows: 10 nM 1-naphthylacetic acid (NAA), 2.5 μM GR24 (a SL analogue), 100 μM abamine (a SL-synthesis inhibitor) (Sun et al., 2014; Sun et al., 2015; Sun et al., 2016), and localized application of NPA (a polar auxin transport inhibitor). The latter was by dispensing diluted agar containing 20 μM NPA directly from a

pipette across the shoot base (Chen et al., 2012). All experiments included three independent biological replicates.

Measurement of Secondary Lateral Root and Primordia Numbers

As reported previously, SRs were significantly longer than ARs under our experimental conditions. Our preliminary experiment showed similar primary LR and secondary LR responses in SRs and ARs (Sun et al., 2014). Therefore, SRs were chosen as representative organs to study the mechanism of secondary LR formation. Primary LR density and the numbers of secondary LRs/primordia SR were analyzed in detail. SR length was measured with a ruler and LRs/secondary LRs were counted by eye. Primary LR density was calculated as LR number divided by SR length. All experiments included three independent biological replicates.

In this study, the stages of secondary LR development followed Malamy and Benfey (1997), with stages I–XII grouped here as unemerged primordia. The primordia of the secondary LRs were classified as unemerged and emerged. An emerged LRP longer than 0.5 mm (visible to the naked eye) was considered a LR, and was referred to as being activated (Song et al., 2013). To visualize the development of secondary LRs, we exploited *pDR5::GUS* transgenic rice plants. After the roots were stained in GUS buffer solution, the secondary LR primordia were easy to count. The experiments included three independent biological replicates.

*pDR5::*GUS Construct

To examine the distribution of indole-3-acetic acid (IAA) in rice plants, the *pDR5::GUS* construct was transformed into the WT plants a, *d* mutants, and lines overexpressing *OsPIN2* using *Agrobacterium tumefaciens* (strain EHA105) (Sun et al., 2014). The samples used for IAA analysis were also used for histochemical GUS staining. The stained tissues were photographed using an Olympus SZX2-ILLK stereomicroscope with a color CCD camera (Olympus).

GUS activity was examined according to Jia et al. (2011). Samples were homogenized in GUS extraction buffer (50 mM $NaPO_4$ (pH 7.0), 10 mM 2-mercaptoethanol, 10 mM Na_2-EDTA, 0.1% sodium dodecyl sulfate, 0.1% Triton X-100). After centrifugation, 20 µl of the supernatant was mixed with 180 µl of an assay buffer containing 1 mM 4-methylumbelliferyl-β--glucuronide. After incubation at 37°C for 1 h, the reaction was stopped by adding 1,800 µl 0.2 M Na_2CO_3. Fluorometer values were compared with those of a 4-methylumbelliferone dilution series. Protein content was determined with a Bio-Rad protein assay kit (Bio-Rad Laboratories, Shanghai, China) using bovine serum albumin as the standard. All experiments included three independent biological replicates.

Strigolactone Measurement

After 3 weeks growth, root exudates (approximately 500 ml) of the rice plants were collected at 24-h intervals, as described previously (Yoneyama et al., 2012; Xie et al., 2013). Root exudates adsorbed on charcoal were eluted with acetone. After evaporation of the acetone *in vacuo*, the residue was dissolved in 50 ml water and extracted three times with 50 ml ethyl acetate. The ethyl acetate extracts were combined, washed with 0.2 M K_2HPO_4 (pH 8.3), dried over anhydrous $MgSO_4$, and concentrated *in vacuo*. These crude extracts were stored in sealed glass vials at 4°C until use.

The 2'-*epi*-5-deoxystrigol concentrations in the root exudates were determined by liquid chromatography–mass spectrometry/mass spectrometry, as described previously (Xie et al., 2013). Data were acquired and analyzed using MassLynx software (ver. 4.1; Waters, Milford, MA). The experiments included three independent biological replicates.

Quantitative Reverse Transcription-Polymerase Chain Reaction

Total RNA was isolated from the roots of 7-day-old rice plants. The RNA extraction, reverse transcription, and quantitative reverse transcription-polymerase chain reaction (qRT-PCR) methods were as described by Jia et al. (2011). The experiments included three independent biological replicates.

Data Analysis

Data from the experiments were pooled to calculate the means and standard errors (SEs) and subjected to one-way analysis of variance (ANOVA), followed by an LSD test at $P < 0.05$ to determine the statistical significance of differences between treatments. All statistical evaluations were conducted using SPSS (version 11.0) statistical software (SPSS Inc., Chicago, IL, USA).

RESULTS

Tiller and Secondary Lateral Root Production Were Induced in the Rice *dwarf3* and *dwarf10* Mutants

As reported by Ishikawa et al. (2005), compared with wild-type (WT) plants, tiller numbers were increased in *d10* (SL-synthesis mutant) and *d3* (signaling mutant) plants (**Figures 1A**, **C**). Secondary LR formation was significantly induced in the *d* mutants relative to the WT plants (**Figures 1B**, **D–F**). These results imply that SLs induce branching of both shoots and roots.

Exogenous Application of GR24 Inhibited Secondary Lateral Root Formation in the *dwarf10* Plants, But Not in the *dwarf3* of Rice

As in a previous study, endogenous 2'-*epi*-5-deoxystrigol was detected in WT and *d3* mutant plants, but not in *d10* plants (Umehara et al., 2008). Primary LR density of SRs did not differ between the WT plants and the *d* mutants (**Figure 2A**). Application of GR24 decreased the primary LR density in the WT and *d10* mutant plants, but not in the *d3* plants (**Figure 2B**). These results are consistent with those reported by Sun et al. (2014). To determine whether SLs regulate the formation of secondary LRs in rice, GR24 was applied exogenously to WT plants and the two *d*

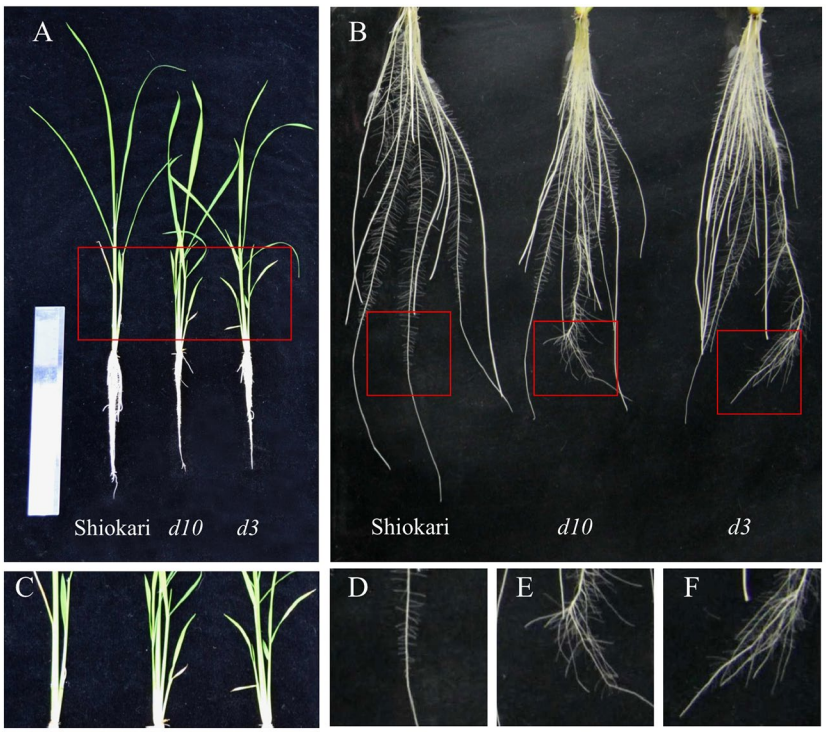

FIGURE 1 | The morphology of tiller and roots in wild-type (WT, Shiokari), strigolactone-synthesis (*d10*), and strigolactone-signaling (*d3*) mutants. Seedlings were grown in a hydroponic media for 21 days. **(A)** The morphology of the rice plants. **(B)** The morphology of roots. **(C)** Tiller. **(D–F)** Secondary lateral root (LR). All experiments included three independent biological replicates.

mutants (**Figures 2A**, **B**). Application of GR24 had no effect on the development of secondary LRs in the WT, but inhibited secondary LR formation in the *d10* mutants to the same level of the WT plants. However, the numbers of secondary LRs in the *d3* mutants were not affected by GR24 application (**Figures 2C**, **D**). Treatment with abamine had no effect on the development of secondary LRs in the *d* mutants, but induced secondary LR formation in the WT plants (**Figure 2E**). These results indicate that SLs inhibit secondary LR formation and the involvement of SL signaling (*D3* gene) in the SL regulatory pathway for secondary LR formation.

Higher Auxin Levels in the Rice Roots Were Not the Only Reason for Secondary LR Formation

In a previous study, endogenous IAA levels were higher in the roots of *d10* and *d3* mutants relative to WT plants (Sun et al., 2014). To assess whether higher auxin levels induce secondary LR formation in *d* mutants, the secondary LR primordia in the roots of rice plants were analyzed on application of exogenous NAA. A specific reporter was used that contains seven repeats of a highly active synthetic auxin response element, and changes in auxin levels *in vivo* were monitored *via* the expression of *DR5::GUS* (Ulmasov et al., 1997). Expression of *DR5::GUS* was subsequently examined in the WT plants and in the *d10* and *d3* mutants. GUS activity was higher in the roots of the *d* mutants than in the WT plants (**Figures 3A, B**), consistent with Sun et al. (2014). However, the numbers of secondary LR primordia were significantly higher in the *d* mutants, but not in the WT plants (**Figures 3A**, **C**). These results imply that higher auxin levels in roots increase secondary LR primordia production. Application of NAA to the WT plants increased expression of *DR5::GUS* in roots to levels similar to those in the roots of the *d* mutants (**Figure 3C**). However, the higher *DR5::GUS* levels did not induce secondary LR primordia formation in the WT plants. These results suggest that higher auxin levels in the roots of *d* mutants were not the only reason for secondary LR primordia formation.

Overexpression of *OsPIN2* Increased Auxin Levels in Roots But Did Not Induce Secondary Lateral Root Formation

Expression of *OsPIN2* was analyzed in the WT plants and in the *d* mutants. Compared with the WT plants, levels of *OsPIN2* were up-regulated in the *d* mutants (**Supplementary Figure 1**). To determine further whether secondary LRs were induced by auxin, lines overexpressing *OsPIN2* were used in this study. As reported by Chen et al. (2012), compared with the WT, plant height was significantly reduced in lines overexpressing *OsPIN2* (OE) (**Figure 4A**). The endogenous IAA content of roots is higher in OE lines than in WT plants (Chen et al., 2012). The secondary LR primordia in the roots of the OE lines were analyzed and expression of *DR5::GUS* in the rice plants was subsequently examined. GUS activity was higher in the roots of the OE lines

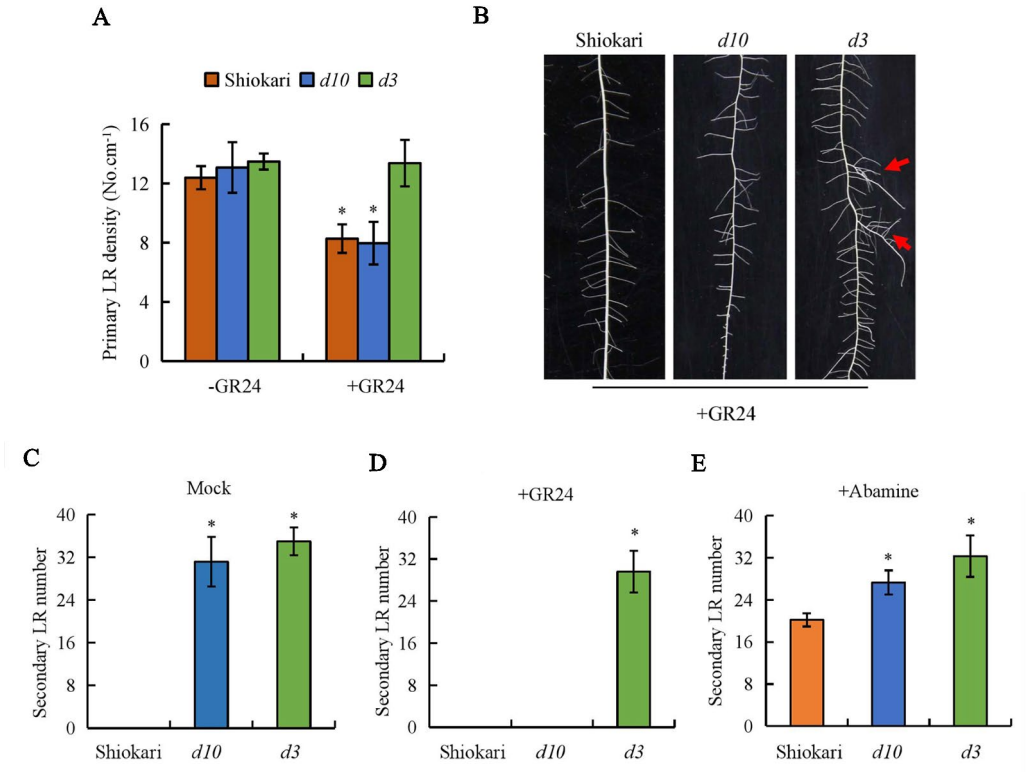

FIGURE 2 | The primary lateral root (LR) density and secondary LR number in wild-type (WT, Shiokari), strigolactone-synthesis (*d10*), and strigolactone-signaling (*d3*) mutants. Seedlings were grown in a hydroponic media with or without GR24 and Abamine for 21 days. **(A)** Primary LR density. **(B)** The morphology of secondary LR number. **(C–E)** Secondary LR number. Data are means ± SE. *$P < 0.05$ comparing the WT and other rice plants. The red arrow indicates the secondary LR. All experiments included three independent biological replicates.

than in those of the WT plants (**Figures 4F**, **G**), consistent with Chen et al. (2012). However, no secondary LRs or LR primordia were found in the OE lines (**Figures 4B-F** and **5B**). In addition, the primary LR density and numbers of secondary LRs did not differ between the WT and OE lines (**Figures 5A**, **B**). These results further imply that the higher auxin levels in the OE lines did not induce the development of secondary LRs.

Auxin Induced the Development of Secondary Lateral Roots in the Absence of Strigolactones

To analyze further the interaction between SLs and auxin in the regulation of secondary LR development, the numbers of secondary LRs in the WT plants and the *d* mutants were recorded on application of NAA, NPA, NPA+NAA, NAA+GR24, and NPA+NAA+GR24. In comparison with mock treatment, application of NPA significantly decreased both *DR5::GUS* levels in the primary LR region and primary LR density in the WT plants and in the *d* mutants (**Figures 6A**, **B**). The numbers of secondary LRs were reduced in the *d10* and *d3* mutants under NPA treatment relative to the mock condition (**Figure 7B**). The numbers of secondary LRs were increased in the *d* mutants, but not in the WT plants, on NAA supply (**Figure 7C**). Application of NAA restored the effect of NPA on the numbers of secondary LRs to levels similar to those induced by NAA treatment alone in the *d* mutants (**Figure 7D**), and supply of GR24 eliminated the effect of NAA on secondary LR development (**Figure 7E**). Treatment of roots with GR24 under the NPA plus NAA condition further inhibited secondary LR formation in the *d10* plants, but not in the *d3*, mutants (**Figure 7F**). These results imply that auxin induces secondary LR formation in the absence of SLs.

DISCUSSION

Development of optimal root morphology, including formation of LRs, is crucial for absorbance of nutrients and water and successful growth of transplants. In addition to providing anchorage, LRs contribute to water-use efficiency and facilitate extraction of micro- and macronutrients from soil (Casimiro et al., 2001; Péret et al., 2009). Most studies of LRs in plants have focused on primary LRs; the mechanisms of secondary LR formation remain largely unexplored. This study provides evidence of the regulatory roles of auxin and SLs in rice secondary LR development.

The SL pathway is involved in primary LR growth and development. In tomato (*Solanum lycocarpum*) and

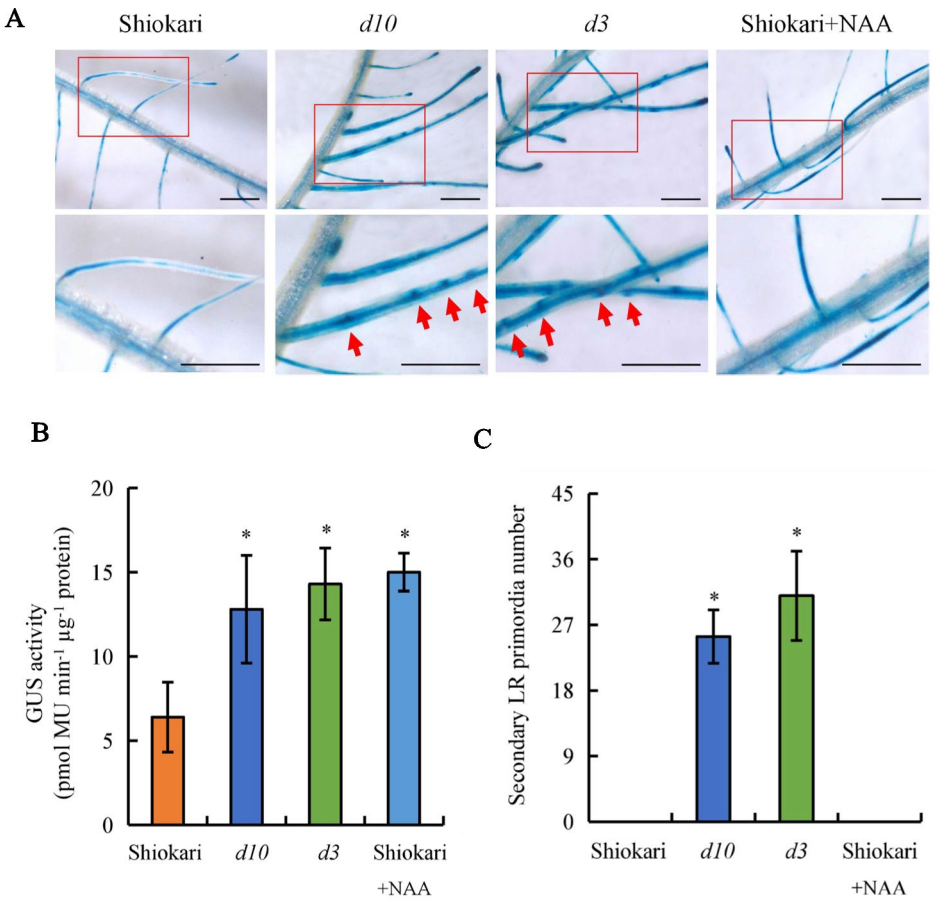

FIGURE 3 | *DR5::GUS* activity and secondary lateral root (LR) primordia number in rice plants. Seedlings were grown in a hydroponic media with or without 1-naphthylacetic acid for 21 days. **(A, B)** *DR5::GUS* activity in LR region. **(C)** Secondary LR primordia number. Bar = 1 mm. Data are means ± SE. *$P < 0.05$ comparing the WT and other rice plants. The red arrow indicates the secondary LR primordia. All experiments included three independent biological replicates.

Arabidopsis, the density of primary LRs was increased in SL mutants, implying that SLs inhibit LR formation (Koltai et al., 2010; Kapulnik et al., 2011; Ruyter-Spira et al., 2011). Application of GR24 reduced primary LR formation by suppressing the outgrowth of primary LRs in *Arabidopsis* and pea (Kapulnik et al., 2011; Ruyter-Spira et al., 2011; Rasmussen et al., 2012). The density of primary LRs was affected by GR24 in WT seedlings and SL-synthesis mutants, but not in SL-signaling mutants, implying that the effect of SLs on primary LR density is mediated *via* the *MAX2* gene (Kapulnik et al., 2011; Koltai, 2011; Ruyter-Spira et al., 2011). In contrast to findings in upland plants, primary LR density did not differ between WT plants and *d* mutants in rice (Arite et al., 2012; Sun et al., 2014). Application of GR24 reduced primary LR density, but the extent of the decrease did not change with increasing GR24 concentrations (Sun et al., 2014). The primary LR densities in the *d* mutants in the present study were similar to those reported by Sun et al. (2014). Correspondingly, the numbers of secondary LRs increased significantly in the *d* mutants relative to the WT plants. Application of GR24 reduced the numbers of secondary LRs in the *d10* mutants, but not in the *d3* mutants (**Figures 2C, D**). Treatment with abamine induced secondary LR formation in the WT plants (**Figure 2E**). These results indicate that SLs inhibit secondary LR formation and demonstrate the involvement of the *D3* gene in the SL regulatory pathway for secondary LR formation.

Accumulating evidence indicates that auxin regulates LR formation in plants (Goh et al., 2012; Xuan et al., 2016). Polar auxin transport is essential for LR formation, and an auxin-transport-independent pathway is involved in changes in LR formation in plants (Swarup et al., 2005; De Smet et al., 2007; Okumura et al., 2013; Inahashia et al., 2018). However, the mechanisms by which auxin regulates secondary LR formation are poorly understood. In this study, *DR5::GUS* levels were higher in the roots of the *d* mutants than in the WT plants (**Figures 3A, B**), consistent with a report by Sun et al. (2014). These results imply that the higher auxin levels in the roots of *d* mutants are not the reason for secondary LR formation. In addition, lines overexpressing *PIN2* showed increased auxin transport from shoots to roots in rice (Chen et al., 2012). Similar to the *d* mutants, higher *DR5::GUS* levels were found

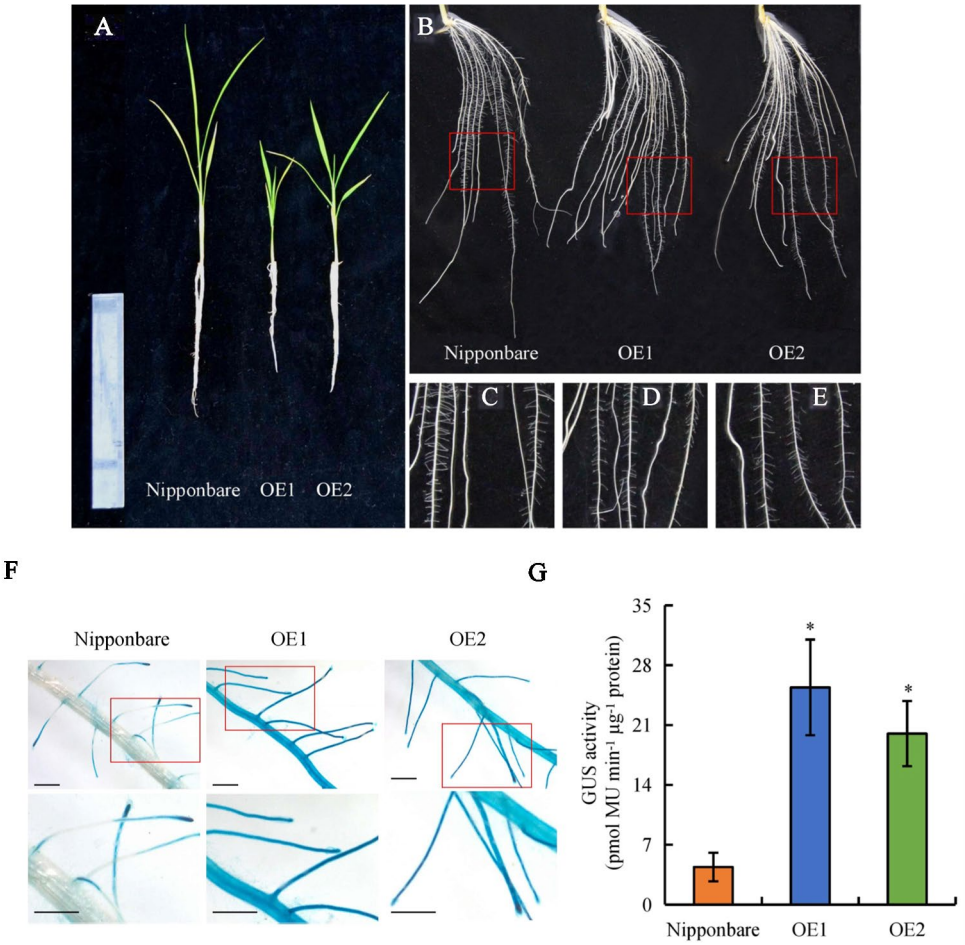

FIGURE 4 | The morphology and *DR5::GUS* activity in wild-type (WT, Nipponbare) and overexpression of *OsPIN2* lines (OE1/OE2). Seedlings were grown in a hydroponic media for 21 days. **(A)** The morphology of the rice plants. **(B–E)** The morphology of roots. **(F, G)** *DR5::GUS* activity in lateral root region. Bar = 1 mm. Data are means ± SE. **P < 0.05* comparing the WT and other rice plants. All experiments included three independent biological replicates.

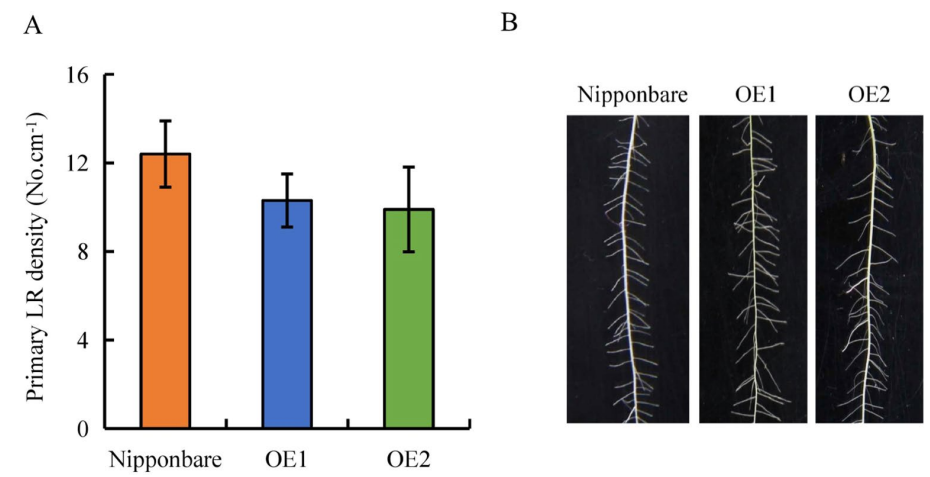

FIGURE 5 | Lateral root (LR) region in wild-type (WT, Nipponbare) and overexpression of *OsPIN2* lines (OE1/OE2). Seedlings were grown in a hydroponic media for 21 days. **(A)** Primary LR density. **(B)** The morphology of LRs region. Data are means ± SE. All experiments included three independent biological replicates.

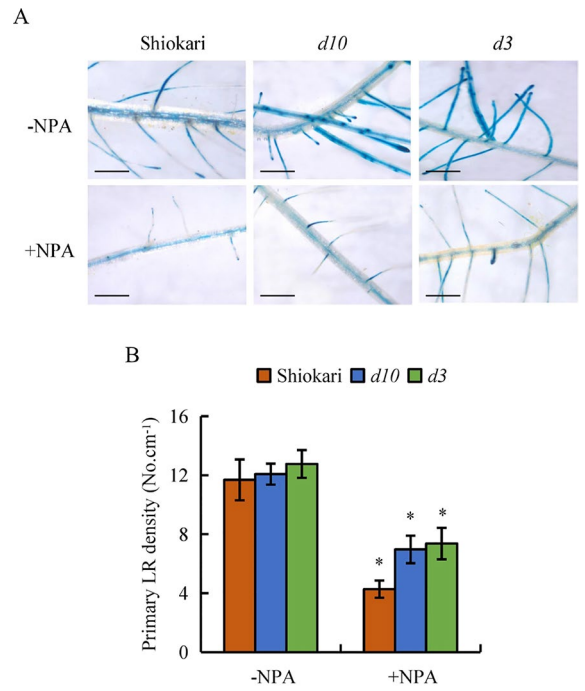

FIGURE 6 | *DR5::GUS* activity and lateral root (LR) region in wild-type (WT, Shiokari) and *d* mutants. Seedlings were grown in a hydroponic media with or without NPA for 21 days. **(A)**, *DR5::GUS* activity in LR region. **(B)** Primary LR density. Bar = 1 mm. Data are means ± SE. *$P < 0.05$ comparing the WT and other rice plants. All experiments included three independent biological replicates.

in roots in the OE lines relative to the WT plants (**Figures 4F**, **G**). However, no secondary LRs were induced in the OE lines (**Figure 5B**). These results further imply that higher auxin levels in roots may not be the reason for secondary LR formation in rice.

It has been suggested that SLs modulate auxin transport, thereby regulating primary LR growth (Ruyter-Spira et al., 2011; Sun et al., 2014). Polar auxin transport is mediated primarily by *PIN* genes. In *Arabidopsis*, Ruyter-Spira et al. (2011) suggested that SLs modulate local auxin levels and that the net result of SL action is dependent on the auxin status of the plant. Application of GR24 inhibited primary LR formation by decreasing auxin transport in roots, with the involvement of PIN protein (Ruyter-Spira et al., 2011; Sun et al., 2014). Experiments examining [^{3}H]IAA transport and *DR5::GUS* activity confirmed that application of GR24 markedly reduced auxin transport, indicating that *PINs* are involved in the auxin transport from the shoots to the roots that is downregulated by SLs in rice (Sun et al., 2014; Sun et al., 2018b). In this study, similar SL levels were recorded in WT plants and in lines overexpressing *OsPIN2* (**Supplementary Figure 2**). Although higher auxin levels were found in OE lines than in WT plants (Chen et al., 2012; **Figures 4F**, **G**), no secondary LRs were induced in the OE lines (**Figure 5**). Application of NPA significantly decreased *DR5::GUS* levels in the primary LR region and the density of primary LRs in the WT plants and in the *d* mutants (**Figures 6A**, **B**). However, the numbers of secondary LRs were reduced in the *d* mutants under NPA treatment (**Figures 7A**, **B**). Treatment with NAA restored the

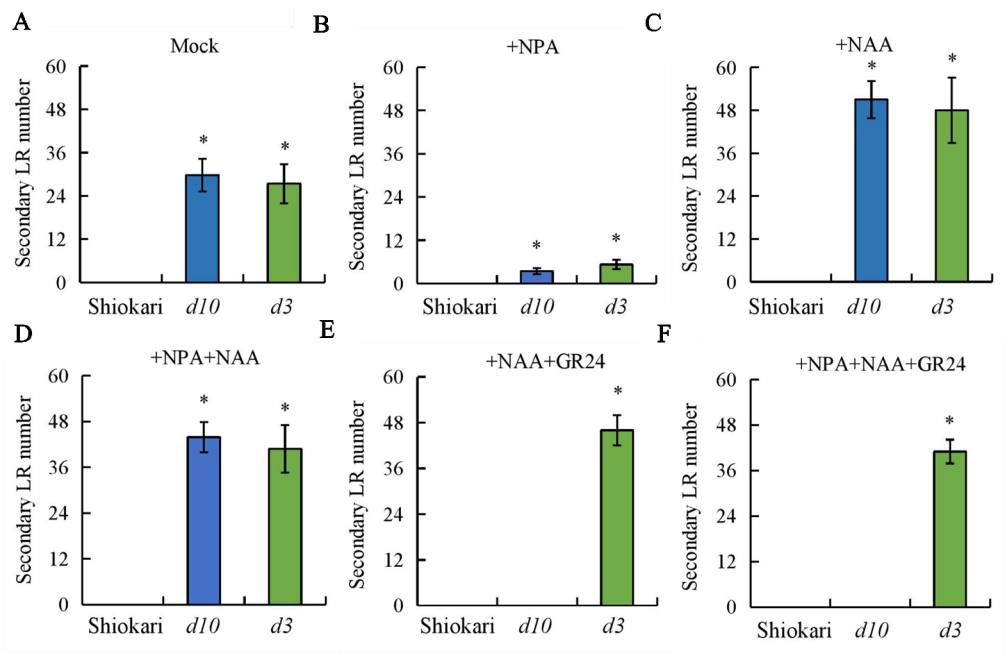

FIGURE 7 | The secondary lateral root (LR) number in wild-type (WT, Shiokari) and *d* mutants. Seedlings were grown in a hydroponic media in addition to NPA, NAA, NPA+NAA, NAA+GR24, and NPA+NAA+GR24 for 21 days. **(A–F)** Secondary lateral root number. Data are means ± SE. *$P < 0.05$ comparing the WT and other rice plants. All experiments included three independent biological replicates.

effect of NPA on the numbers of secondary LRs in the *d* mutants (**Figure 7C**). These results imply that auxin is involved in the development of secondary LRs. The effect of NAA on secondary LR development was eliminated in the *d10* mutants, but not in the *d3* mutants, by application of GR24 (**Figure 7E**). And a model for these signaling pathways is shown in **Supplementary Figure 3**. These results further demonstrate that secondary LR formation is inhibited by SLs *via* the *D3* response pathway, and the importance of auxin for secondary LR formation.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/ **Supplementary Material**.

AUTHOR CONTRIBUTIONS

HS performed experiments. FX, XG, DW, XZ, ML and FL assisted the experiment. QZ analyzed data. HS, GX, and YZ designed the experiment. HS wrote the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2019.01527/full#supplementary-material

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Integration of Jasmonic Acid and Ethylene Into Auxin Signaling in Root Development

Ping Xu[1], Ping-Xia Zhao[2], Xiao-Teng Cai[3], Jie-Li Mao[2], Zi-Qing Miao[2] and Cheng-Bin Xiang[2]**

[1] Basic Forestry and Proteomics Research Center, Fujian Agriculture and Forestry University, Fuzhou, China, [2] School of Life Sciences and Division of Molecular and Cell Biophysics, Hefei National Science Center for Physical Sciences at the Microscale, University of Science and Technology of China, The Innovation Academy of Seed Design, Chinese Academy of Sciences, Hefei, China, [3] Beijing Advanced Innovation Center for Tree Breeding by Molecular Design, Beijing University of Agriculture, Beijing, China

As sessile organisms, plants must be highly adaptable to the changing environment by modifying their growth and development. Plants rely on their underground part, the root system, to absorb water and nutrients and to anchor to the ground. The root is a highly dynamic organ of indeterminate growth with new tissues produced by root stem cells. Plants have evolved unique molecular mechanisms to fine-tune root developmental processes, during which phytohormones play vital roles. These hormones often relay environmental signals to auxin signaling that ultimately directs root development programs. Therefore, the crosstalk among hormones is critical in the root development. In this review, we will focus on the recent progresses that jasmonic acid (JA) and ethylene signaling are integrated into auxin in regulating root development of *Arabidopsis thaliana* and discuss the key roles of transcription factors (TFs) ethylene response factors (ERFs) and homeobox proteins in the crosstalk.

Keywords: *Arabidopsis thaliana*, root, auxin, jasmonic acid, ethylene, ethylene response factor, homeobox protein

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****Correspondence:***
Ping Xu
pingxu@mail.ustc.edu.cn
Cheng-Bin Xiang
xiangcb@ustc.edu.cn

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INTRODUCTION

Plant root systems represent the underground organs that provide mechanical support and uptake of nutrients and water. Depending on the species and environment, root systems show a high level of morphological diversity. Improved root architecture can increase the utilization of water and nutrients, which in turn helps increase crop yield. Most dicotyledons have tap root systems, while monocotyledons have fibrous root systems. The tap root system is composed of a developed primary root, lateral roots and adventitious roots, while the fibrous root system is mainly composed of adventitious roots (Martinez-de la Cruz et al., 2015; Zhang X. et al., 2019). The development of primary roots begins from embryonic development, whereas the lateral roots are initiated from asymmetrical divisions of the pericycle founder cell of primary roots. The root system morphology or architecture (RSA) is a highly plastic trait that is influenced by numerous biotic and abiotic factors (Osmont et al., 2007). An increasing number of studies in the model plant *Arabidopsis thaliana* have helped to address the underlying molecular mechanisms of this plasticity (Motte et al., 2019).

Root development occurs with the concerted action of multiple plant hormones (Petricka et al., 2012). Auxin has emerged as a core player on which other plant hormones integrate to regulate root development. Auxin synthesis, transport, and signaling pathways are important for plant root development. Indole-3-acetic acid (IAA) is the main naturally occurring auxin and the biosynthetic

pathway of IAA has been clearly understood (Zhao, 2018). L-tryptophan is the major precursor of IAA synthesis, and the rate-limiting step of tryptophan synthesis is catalyzed by anthranilate synthase (a heterocomplex consisting of ASA1/2 and ASB1) (Sun et al., 2009; Casanova-Saez and Voss, 2019). ASA1 and ASB1 are also named WEI2 (Weak Ethylene Insensitive 2) and WEI7, respectively, since they were characterized from ethylene insensitive mutants of root growth (Stepanova et al., 2005). The two-step indole-3-pyruvate (IPA) pathway is the only IAA biosynthetic pathway that has been fully elucidated, and it is also the main pathway for IAA synthesis (Zhao, 2012). TAAs (Tryptophan Aminotransferase of Arabidopsis) and YUCCAs (YUCs) are enzymes that catalyze these two steps (Mashiguchi et al., 2011; Zhao, 2012). TAA1/WEI8, like ASA1 and ASB1, was also identified from the ethylene insensitive mutant *wei8* (Stepanova et al., 2008; Tao et al., 2008). Polar distribution is characteristic of auxin, which is mediated by PIN-FORMED (PIN) and AUXIN1/LIKE-AUX1 (AUX1/LAX) family members under strict regulations (Band et al., 2014; Adamowski and Friml, 2015). Localized auxin biosynthesis has been shown to play critical roles in root development as well (Zhao, 2010, 2018). Besides, the auxin signaling pathway is intensively studies recently with a focus on the fine regulation mechanisms of the IAA (INDOLEACETIC ACID-INDUCED PROTEIN) -ARF (AUXIN RESPONSE FACTOR) network (Wang and Estelle, 2014). Briefly, the auxin receptor TIR1/AFB (TRANSPORT INHIBITOR RESPONSE1/AUXIN SIGNALING F-BOX) binds to auxin causing degradation of IAA proteins that interact with ARF transcription factors (TFs) (Leyser, 2018; Gallei et al., 2019). ARFs bind to the auxin response elements (AREs) in promoters of target genes to regulate gene expression (Gallei et al., 2019).

During the stage of embryogenesis, auxin distribution patterns determine the position around which the embryonic roots start growing. In a later stage, auxin distribution patterns in and around the meristem determine root meristem activity and lateral root spacing (Motte et al., 2019). The development of lateral root is closely related to auxin, including its synthesis, transport and signal transduction (Osmont et al., 2007; Motte et al., 2019).

The gaseous phytohormone ethylene is well-known for its functions in plant maturation and senescence. In addition, numerous studies have shown that ethylene is involved in various plant growth and developmental processes, including root growth (Ruzicka et al., 2007; Swarup et al., 2007; Lewis et al., 2011; Street et al., 2015; Mao et al., 2016; Miao et al., 2018). The function of jasmonic acid (JA) in plant injury and defense responses has been thoroughly studied, and its roles in growth and development has also been widely reported (Kazan and Manners, 2013; Cai et al., 2014; Ye et al., 2019). Like other hormone signaling pathways, ethylene and JA signaling are integrated into auxin in root development, largely through TFs acting as the key crosstalk nodes.

Ethylene-Auxin Crosstalk in Root Development

Ethylene is an important regulatory signal in regulating the process of root development (Ruzicka et al., 2007; Swarup et al., 2007; Street et al., 2015). Plants produce more ethylene when exposed to external stimuli (Wang et al., 2002). Ethylene binds to ETR1(ETHYLENE RESPONSE 1) receptor family on the endoplasmic reticulum (ER) membrane, leading to inactivation of the S/T protein kinase CTR1 (CONSTITUTIVE TRIPLE RESPONSE 1), which functions to repress EIN2 (ETHYLENE INSENSITIVE 2). After detaching from CTR1, EIN2 can be cleaved to release EIN2 C-terminal (EIN2C). The EINC has two levels of regulation of EBF1/2 (EIN3-BINDING F BOX PROTEIN 1/2). On the one hand, EIN2C binds to 3′-UTR of *EBF1/2* in the cytoplasm to inhibit its translation (Li et al., 2015; Merchante et al., 2015), and on the other hand, EIN2C is translocated into the nucleus to promote the degradation of EBF1/2 (Qiao et al., 2012; Dolgikh et al., 2019), both leading to stabilization of EIN3/EIL1 (ETHYLENE-INSENSITIVE3-LIKE1) to activate ethylene response genes. Although ethylene is best known for triggering fruit ripening, it also plays a crucial role in regulating root development. In response to ethylene or its precursor ACC (1-aminocyclopropane-1-carboxylic acid) treatment, the root of Arabidopsis seedlings shows three growth responses: rapid downregulation of cell elongation, increased root width, and induction of ectopic root hairs, which collectively will provide plants with greater anchorage and more dynamic regulation of root growth (Swarup et al., 2007).

Inhibition of root growth by ethylene depends on auxin biosynthesis, transport and signaling pathway (Ruzicka et al., 2007; Swarup et al., 2007). Ethylene up-regulates expression of auxin synthesis and transport-related genes in Arabidopsis roots, resulting in a high concentration of auxin that inhibits cell elongation (Ruzicka et al., 2007; Strader et al., 2010). Ethylene modulates the auxin transport machinery by directly or indirectly regulating the expression of auxin efflux (*PINs*) and influx (*AUX1*) carriers (Ruzicka et al., 2007). A subsequent study showed that ethylene can negatively regulate cell proliferation in addition to inhibiting cell elongation and SHY2 (SHORT HYPOCOTYL 2)/IAA3 mediated this effect in the root meristem (Street et al., 2015). It has been found that in Arabidopsis seedlings CTR1 transduces the ethylene signal to EIN2 in the root and then affects *PIN2* expression to modulate the root stem cell niche maintenance (Mendez-Bravo et al., 2019). The screening experiment on the ethylene overexpression mutant *eto1* identified a small molecule named L-kynurenine (Kyn), which could inhibit ethylene-directed auxin biosynthesis and root growth by inhibiting TAA1's activity (He et al., 2011). *POLARIS* (*PLS*), encoding a predicted functional 36-amino acid peptide, is required in ethylene-mediated root inhibition through regulating auxin transport and affecting microtubule cytoskeleton dynamics (Chilley et al., 2006). The *PLS* expression is activated by auxin and suppressed by ethylene, and PLS peptide in turn negatively regulates the ethylene signaling pathway (Chilley et al., 2006). It was reported that ethylene can induce an oxidase named MINE, which produces pyridoxal-5′-phosphate (PNP), and PNP acts as a cofactor in TAA1/TAR-dependent auxin biosynthesis, which in turn influences ethylene-auxin crosstalk in Arabidopsis root (Kim et al., 2018).

Ethylene is involved in regulating the growth and development of not only primary roots but also lateral roots. Increased endogenous ethylene or ACC treatment activates *PIN3/7* expression thereby enhancing auxin transport

and reducing lateral root formation (Lewis et al., 2011). Auxin signaling affects the cell division pattern of lateral root primordium by regulating the expression of the ERF (ethylene response factor) family transcription factor *PUCHI*, which is required for the proper pattern of early lateral root primordia (Hirota et al., 2007). PLS, the small peptide mentioned above, is also required in lateral roots initiation via ethylene-mediated auxin transport to the pericycle (Chilley et al., 2006).

Adventitious root initiation and development are also regulated by ethylene-auxin crosstalk. Ethylene was reported to inhibit adventitious rooting in Arabidopsis dark-grown seedlings by negatively regulating auxin biosynthesis (Veloccia et al., 2016). When applied together with IBA (indole-3-butyric acid), ethylene promotes the conversion of IBA to IAA and thus the development of adventitious roots (Veloccia et al., 2016). Ethylene-auxin crosstalk also regulates the initiation of adventitious roots near cut sites where the levels of auxin and ethylene both increase (Guan et al., 2019).

JA-Auxin Crosstalk in Root Development

Jasmonates are well-known lipid-derived compounds as key regulators in plant growth and development as well as in plant stress responses. JA participates in the regulation of root growth, seedling development, flower development, root regeneration, seed development, seed germination, tuber formation and senescence (Wasternack and Hause, 2013; Ye et al., 2019; Zhang G. et al., 2019). JA regulates root growth in many aspects, including inhibition of primary root (Chen et al., 2011), promoting lateral roots formation (Cai et al., 2014), negatively regulating adventitious roots (Gutierrez et al., 2012; Lakehal et al., 2019), and inducing root regeneration (Ye et al., 2019; Zhang G. et al., 2019). Most of these processes are achieved via cross-talking with auxin.

Root growth inhibition is one of the first discovered features of JA. By screening mutants insensitive to JA-mediated root inhibition, a number of regulatory factors in the JA signaling pathway were revealed, such as JAR1 (JASMONATE RESISTANT 1) (Staswick et al., 1992), MYC2/JAI1 (JASMONATE INSENSITIVE 1) (Berger et al., 1996), and COI1 (CORONATINE INSENSITIVE 1) (Feys et al., 1994). JA inhibits root elongation by reducing both cell counts and cell dimension, suggesting that JA-induced primary root growth inhibition is a complicated process involving diverse cellular processes in different root tissues (Chen et al., 2011, 2012). JA-mediated inhibition of root development is auxin-dependent (Wasternack and Hause, 2013). JA activates *MYC2*, leading to the repression of *PLT1* (*PLETHORA1*) and *PLT2* in root stem cell niche (Chen et al., 2011). *PLTs* encodes members of the AP2/EREBP transcription factor family and are key effectors for the establishment of the stem cell niche during embryonic pattern formation. They respond to auxin accumulation and this response depends on auxin-responsive TFs. Therefore, PLTs serve as a key node for JA-auxin crosstalk in regulating the maintenance of the stem cell niche in roots (Chen et al., 2011).

Jasmonic acid is also involved in regulating lateral roots development. In response to methyl jasmonate (MeJA) treatment, Arabidopsis wild type produces more lateral roots, while the mutant *asa1-1* does not produce lateral roots (Sun et al., 2009). The JA receptor COI1 plays a critical role in the formation and even distribution of lateral roots (Raya-Gonzalez et al., 2012). In the *coi1-1* mutant, the lateral roots displayed uneven distribution and JA failed to induce more lateral roots (Raya-Gonzalez et al., 2012). In the root, MeJA activates the transcription of *ASA1* and several other auxin biosynthesis-related genes, such as *YUCCA2* (Cheng et al., 2006), *ASB1* (Stepanova et al., 2005), and *NITRILASE 3* (*NIT3*) (Kutz et al., 2002). JA failed to increase lateral root initiation in mutants with disrupted auxin signaling, like *slr1* (*iaa14*) and *arf7/19* double mutant (Sun et al., 2009), which further supports that JA-induced lateral root formation is auxin-dependent. Activated expression of the transcription regulator *HDG11* (*HOMEODOMAIN GLABROUS11*) increases the level of JA in the roots by directly up-regulating the expression of several genes encoding JA biosynthetic enzymes, resulting in enhanced auxin signaling and lateral root formation (Cai et al., 2015). MeJA can also induce *YUC8* and *YUC9* expression and thus participate in auxin-mediated primary root growth and lateral root initiation (Hentrich et al., 2013).

Jasmonic acid can exert negative effects on adventitious root formation (Gutierrez et al., 2012). ARF6, ARF8, and ARF17 act upstream of *Gretchen Hagen3.3 (GH3.3), GH3.5*, and *GH3.6*. These three GH3s inactive JA by conjugating JA to amino acids Asp, Met, and Trp, and therefore promote adventitious rooting (Gutierrez et al., 2012). The effect of JA in adventitious root development depends on experimental conditions. At low sub-micromolar concentrations, MeJA has been shown to promote adventitious root development when applied together with IBA, and this process does not involve regulation of ARF6 or ARF8 expression (Fattorini et al., 2018).

It is well known that plants can regenerate tissues and even complete organs after damage. Recently, Zhou et al. (2019) reported that the synergy between jasmonate and auxin signaling pathways promotes root regeneration by activating root stem cells (Zhou et al., 2019). In this process, JA induces *ERF109*, *CYCLIN D6;1* (*CYCD6;1*), and *ERF115* expression to activate stem cell and promote tissue regeneration. Auxin also activates key regeneration regulators of this pathway (Zhou et al., 2019).

TFs Involved in JA-Auxin and Ethylene-Auxin Crosstalk

Transcription factors are specific implementers of numerous regulation processes. Each hormone crosstalk involves many important TFs. Here we focus on ERF family and HD-ZIP TFs in JA-auxin and ethylene-auxin crosstalk.

Ethylene response factor family TFs are plant specific and involve in a variety of plant development processes and stress responses. Many ERFs are responsive to ethylene. ERF1 negatively regulates primary root elongation in an auxin biosynthesis-dependent manner. Being downstream and a direct target of EIN3, ERF1 activates *ASA1* by binding to GCCGCC motifs (GCC-boxes) in the promoter of *ASA1*. The up-regulation of *ASA1* increases auxin biosynthesis, promotes auxin accumulation in root tip, and consequently suppresses root

elongation (Mao et al., 2016). Therefore, ERF1 acts as a critical crosstalk joint connecting ethylene and auxin in regulating primary root elongation (**Figure 1**).

HOMEOBOX PROTEIN52 (HB52) belongs to the HD-ZIP transcription factor family. The HD-ZIP transcription factor family only found in plants with 47 members in Arabidopsis. According to protein structures and functions, HD-ZIP family members can be divided into four subfamilies (I-IV), and HB52 belongs to the HD-ZIP I subfamily (Ariel et al., 2007). HD-ZIP I family genes are responsive to external stimuli like drought, high temperature, osmotic stress, and lights. HB52 was identified from the study of ethylene-mediated root inhibition (Mao et al., 2016). *HB52* is highly expressed in roots and is responsive to the ACC treatment as a direct target of EIN3. HB52 regulates primary root elongation through affecting auxin transport. HB52 binds to the homeodomain-binding *cis*-elements in the promoters of *PIN2* and *WAG1/2* to activate their expression (**Figure 1**). WAG1/2, closely related to PINOID, can phosphorylate PIN2 to increase its auxin efflux carrier ability (Willige et al., 2012). Therefore, HB52 serves as another important crosstalk node between ethylene and auxin to regulate root elongation (Miao et al., 2018). Together, ERF1 and HB52 constitute the ethylene-responsive modules for auxin biosynthesis and transport, respectively, in root elongation regulation.

ERF109 is another member of the ERF family and responsive to the JA signaling pathway. ERF109 binds to GCC-boxes in the promoter regions of its target genes. Under normal conditions, *ERF109* is expressed at a very low level in roots. After MeJA treatment, the transcription level of *ERF109* was significantly induced in both roots and shoots, especially in the lateral root primordium region and the tip and base of lateral roots (Cai et al., 2014). Genetic analyses showed that ERF109 positively regulates lateral root formation through upregulating auxin biosynthesis. *In vitro* and *in vivo* experiments showed that ERF109 binds to the GCC-boxes in *ASA1* and *YUC2* promoters and directly activates their expression, leading to increased auxin biosynthesis and accumulation in the root (Cai et al., 2014). Thus, ERF109 serves as an important crosstalk node between JA and auxin signaling (**Figure 2**). Recently, three research groups independently reported that ERF109 has a novel function in plant regeneration depending on its roles in upregulating *ASA1* expression (Ye et al., 2019; Zhang G. et al., 2019) or activating *ERF115* and *CYCD6;1* (Zhou et al., 2019).

ERF1, ERF109, and HB52 are representative TFs involved in the crosstalk of JA-auxin and ethylene-auxin signaling pathways in regulating root development. Other TFs participated in the processes are yet to be identified.

CONCLUSION AND PERSPECTIVES

Crosstalk between hormone signaling are fundamental process in plant development, yet the underlying mechanisms are far from clear. In this review, we summarized recent advances on the understanding of ethylene and JA integration into auxin signaling in the regulation of root development.

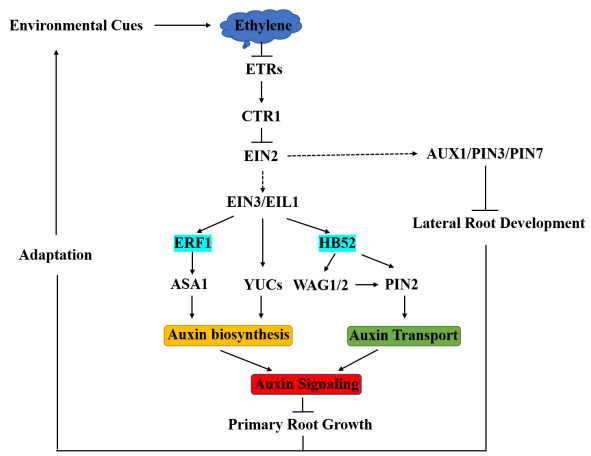

FIGURE 1 | Integration of Ethylene into Auxin Signaling in Arabidopsis Root Development. Environmental cues trigger the biosynthesis of ethylene in Arabidopsis, and then ethylene binds to ETR receptors to inactivate CTR1, which functions to repress EIN2. When EIN2 is released by CTR1, it can be cleaved and then helps to stabilize EIN3/EIL1, leading to the activation of downstream transcriptional cascades. Ethylene inhibits primary root growth by regulating auxin biosynthesis, transport, and signaling. ERF1 and HB52 function as crosstalk nodes between ethylene and auxin in this process. An increase in endogenous ethylene enhances auxin transport and reduces lateral root formation depending on AUX1, PIN3, and PIN7. The ERF1 and HB52 regulatory modules are part of the molecular mechanisms in the adaptive response of root growth to environmental cues.

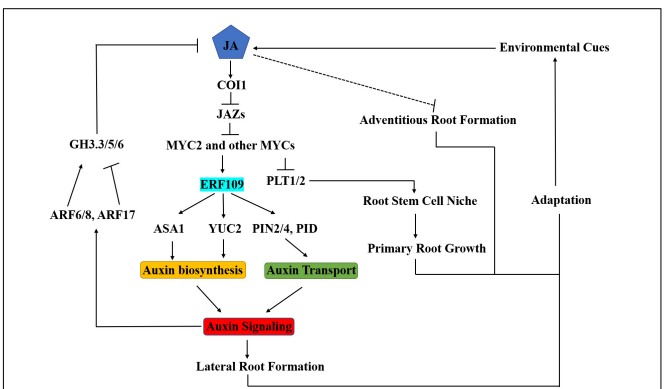

FIGURE 2 | Integration of JA into Auxin Signaling in Arabidopsis Root Development. Plants generate JA in response to environmental cues. COI1 receptor perceives JA, and then recruits JAZs subjected to degradation. Subsequently, MYC2 can activate transcription of early JA-responsive genes. JA promotes lateral root formation by regulating auxin biosynthesis (via ASA1 and YUC2) and transport (via PID and PIN2/4). Transcription factor ERF109 functions as a key crosstalk node in this process. JA inhibits primary root development by repressing the expression of *PLT1* and *PLT2*. Auxin modulates JA homeostasis by regulating GH3.3/5/6 through ARF6/8/17, then influences adventitious root formation. Therefore, the ERF109 regulatory module plays critical roles in the growth and development of lateral, primary and adventitious roots in the adaptive response of the root system to environmental factors.

Auxin plays the central role in regulating root development. Plant roots constantly perceive environmental cues and generate hormonal signals in order to adjust developmental programs for better adaptation to the changing surroundings. JA and ethylene are two representative hormones in plants responding to environmental changes. These two hormonal signals can be relayed to auxin signaling, the master regulator of root development. In the signal relay, TFs play critical roles to integrate other hormonal signal into auxin signaling through modulating auxin biosynthesis (for example, ERF1 and ERF109) or auxin transport (for example, HB52) to fine-tune the regulation of primary root growth and/or lateral root formation.

To unravel the complete network of JA-auxin and ethylene-auxin crosstalks in root development, we need to identify the more components involved in these processes, as well as understand the spatial-temporal relationships between these components. Some attempts have been recently made by identifying the root epidermis cells where the interaction between ethylene and auxin takes place (Vaseva et al., 2018; Mendez-Bravo et al., 2019). Moreover, local auxin biosynthesis is critical in ethylene-auxin crosstalk (Brumos et al., 2018). With the advance of new technology such as single-cell sequencing and high-resolution microscope, in-depth details in the crosstalk will be revealed.

AUTHOR CONTRIBUTIONS

PX and C-BX conceived the mini-review. PX wrote the mini-review. All authors contributed to the discussion and revision.

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REVIEW
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Root Growth Adaptation to Climate Change in Crops

*J. Calleja-Cabrera, M. Boter, L. Oñate-Sánchez and M. Pernas**

Centro de Biotecnología y Genómica de Plantas, Universidad Politécnica de Madrid – Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain

Climate change is threatening crop productivity worldwide and new solutions to adapt crops to these environmental changes are urgently needed. Elevated temperatures driven by climate change affect developmental and physiological plant processes that, ultimately, impact on crop yield and quality. Plant roots are responsible for water and nutrients uptake, but changes in soil temperatures alters this process limiting crop growth. With the predicted variable climatic forecast, the development of an efficient root system better adapted to changing soil and environmental conditions is crucial for enhancing crop productivity. Root traits associated with improved adaptation to rising temperatures are increasingly being analyzed to obtain more suitable crop varieties. In this review, we will summarize the current knowledge about the effect of increasing temperatures on root growth and their impact on crop yield. First, we will describe the main alterations in root architecture that different crops undergo in response to warmer soils. Then, we will outline the main coordinated physiological and metabolic changes taking place in roots and aerial parts that modulate the global response of the plant to increased temperatures. We will discuss on some of the main regulatory mechanisms controlling root adaptation to warmer soils, including the activation of heat and oxidative pathways to prevent damage of root cells and disruption of root growth; the interplay between hormonal regulatory pathways and the global changes on gene expression and protein homeostasis. We will also consider that in the field, increasing temperatures are usually associated with other abiotic and biotic stresses such as drought, salinity, nutrient deficiencies, and pathogen infections. We will present recent advances on how the root system is able to integrate and respond to complex and different stimuli in order to adapt to an increasingly changing environment. Finally, we will discuss the new prospects and challenges in this field as well as the more promising pathways for future research.

Keywords: climate change, root traits, crop yield, adaptation, increased temperature

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***Correspondence:**
M. Pernas
pernas.monica@inia.es

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CLIMATE CHANGE AND CROP YIELD

Effects of climate change are accelerating significantly since the last century. Changes in weather conditions and increases in the occurrence of extreme events are being felt more often. The Earth's climate continues to warm and, all the model simulations predict a global trend to warmer temperatures (Lean and Rind, 2009). Considering the temperature data, the northern hemisphere

is warming more rapidly than the southern hemisphere (Foster and Rahmstorf, 2011). Although long term weather changes are more difficult to predict, it is expected that, by 2050, the global mean temperature increase 1.5–2°C. These changes in the global temperature would cause further alterations in the climate leading to an increased frequency of heat-waves, fewer days of freezing temperatures, less rainfall but more intense precipitations and higher incidence of droughts and other weather extremes experienced across the globe that will negatively affect agricultural production (Easterling et al., 2000; Dempewolf et al., 2014). The global population is expected to reach nine billion by 2050, representing an additional two billion people to feed (Ray et al., 2013). The projections show that feeding world's population would require raising the overall food production by around 70% by 2050 (Global agriculture toward 2050. Rome, FAO, 2009a). However, current trajectory shows that the rates of global production in key crops would increase far below what is needed to produce enough food to meet the raising population demands (Ray et al., 2013). This widening mismatch between demand and supply is causing concern for future food security (Godfray et al., 2010). Further reasons for alarm are the yield losses predicted to be provoked by climate change (Lobell et al., 2011; Tai et al., 2014). Although climate changes will not impact crop production evenly according to geographical distribution, it will threaten food production globally (Thiault et al., 2019). For all those reasons, there is an urgent need to maintain and improve crop productivity under these climatic constrains (Bailey-Serres et al., 2019; Shan-e-Ali Zaidi et al., 2019).

Climate Change Impact on Crops

Climate change is a long-term challenge, but requires urgent action given the pace and the scale by which greenhouse gases are accumulating in the atmosphere and the risk of more than 2°C global temperature rise. Greenhouse gases (CO_2, O_3, and CH_4) driving climate change, affect directly crop productivity (IPCC, 2014). Higher concentrations of CO_2 are expected to act as a fertilizer by improving net photosynthesis rates and increasing water use efficiency (Long et al., 2004; Long et al., 2004; Deryng et al., 2016). This positive effect is higher in C3 plants such as wheat, rice and soybean, due to the limited photosynthetic output of photorespiratory carbon losses. Nevertheless, in the long term, the constant increment of CO_2 concentration will have a negative impact in the climate, thus counterbalancing the increase in crop yield (Specht et al., 1999; Long et al., 2004; Dong et al., 2018; Senapati et al., 2019; Wei et al., 2019). On the other hand, O_3 changes have significant negative effects on the yield of major agricultural crops. O_3 is one of the most highly reactive oxidants, provoking damage in plant tissues, which includes visible leaf injuries, decreased photosynthesis and accelerated senescence and cell death (Vandermeiren et al., 2009). But interestingly, there are pronounced differences in O_3 sensitivity between species (Mills et al., 2007). O_3 causes a decrease in crop biomass in wheat and soybean, more specifically root biomass, during reproductive and grain filling stages leading to a reduction of overall crop yield. Consequently, global production losses due to O_3 in these crops are expected to be higher than losses in rice and maize (Van Dingenen et al., 2009; Avnery et al., 2011; Tang et al., 2013; Feng Z. et al., 2019; Wang Y. et al., 2019).

Climate change is causing the shifting of the rainfall patterns. More intense rainfall producing flooding periods, the appearance of drought seasons and offseason precipitations are expected. In several prediction models, offseason rainfall during critical stages of crop growing could lead to a very significant reduction in crop yield (Lobell and Burke, 2008). In winter oilseed rape it has been reported that a more intense rainfall during autumn and winter periods may boost the appearance of diseases (Sharif et al., 2017). And in maize and soybean, more intense precipitations in spring provoke early damage in young plants (Urban et al., 2015). Another risk associated to more extreme rainfall is the intensification of flooding events. In China or Bangladesh much of the harvest areas are in the flooding threatened regions. Floods put in danger the food security of these countries by destroying cropping areas or delaying crop planting due to high soil moisture (Monirul Qader Mirza, 2002; Xu et al., 2013; Iizumi and Ramankutty, 2015). Moreover, in coming years the flooding risk of coastal regions will increase due to the rising of the sea-level and the alteration of climatology. Seawater flooding of coastal regions is becoming more frequent because waves and storm surges are getting stronger (Vitousek et al., 2017). Osmotic and anionic stress caused by the high salinity of seawater will become an additional problem to crops besides the low O_2 and CO_2 levels caused by anoxia. It has been shown that oilseed rape plants exposed to seawater flooding conditions suffer a reduction in plant biomass and a fall in productivity due to a lower number of siliques per plant and a lower seed mass (Hanley et al., 2019).

More frequent drought events are also expected due to longer periods without rain added to warmer temperatures. Although droughts restrict cropping areas, the decrease of agricultural productivity is mainly caused by a severe direct effect on crop yield (Saadi et al., 2015; Lesk et al., 2016; Zipper et al., 2016). The most damaging impact of drought stress on crop productivity occurs at reproductive or growing stages. The former produces pollen sterility (as observed in barley) or ovary abortion (as observed in maize) and the latter a reduction in kernel number and biomass (Boyer and Westgate, 2004). In general, a drought period causes a reduction of water consumption by the plant, leading to a stomatal closure and lower CO_2 intake. Following decrease in photosynthesis ratio provokes a final reduction of crop biomass (Garofalo et al., 2019). The water scarcity imposed by drought is frequently accompanied by salinity stress. The ion toxicity and the reduction of soil water potential contribute to a severe reduction of plant growth. Soil salinity reduces yield in highly tolerant crops as cotton, barley and sugar beet as well as in crops with high salinity sensitivity as sweet potato, wheat or maize (Zörb et al., 2019).

All these adverse climate effects together with elevated temperature will increase agriculture losses even further (Fuhrer, 2003; Lobell and Burke, 2008; Ainsworth, 2017; Tai and Val Martin, 2017). Numerous studies suggested that global warming will lead to substantial declines in mean crop yields in the next future, and that the most serious agricultural impacts will occur in the tropics, where the majority of the world's

food-insecure population resides (Battisti and Naylor, 2009). Furthermore, mean crop yield will decline and their variability will increase even if interannual climate variability remains unchanged (Tigchelaar et al., 2018). Adding up these and other effects, models show possible yield losses of 6–10% per 1°C of warming in the average temperature of the growing season (Guarino and Lobell, 2011). Moreover, climate variation is already causing a major effect on the stability of crop production. Yields of the top ten global crops–barley, cassava, maize, oil palm, rapeseed, rice, sorghum, soybean, sugarcane and wheat has been affected significantly in different regions all over the world (Ray et al., 2019). In this review we will focus on the effect and consequences of one of the major components of climate change, increased temperature and, in particular, its effect on crop roots (**Figure 1**).

Increased Temperature Impact on Crops

As a consequence of global warming, the yield increment that started in the last century is stagnant and even decreasing in some areas (Lobell and Field, 2007). High temperature response has been studied at extreme conditions characterized by the heat shock response. However, even small differences in ambient growth temperature can have profound effects on crop growth and yield. Although abundant literature is available on how plants tolerate extreme damaging heat less is known on how crops adapt to moderately increased or warmer temperatures (Quint et al., 2016; Vu et al., 2019b).

Prediction models reveal that the continuous increment in temperature would result in heavy losses in crop yield at medium latitudes (Liu et al., 2016), whereas less fertile soil areas located at extreme latitudes are getting a more appropriate climate for agriculture (Long and Ort, 2010; Lobell et al., 2011; Iizumi and Ramankutty, 2015; Sharif et al., 2017). Thus, warmer temperature could expand the areas potentially suitable for cropping, increase the length of the growing period, and crop yields may rise in these areas (How to Feed the World in 2050, Rome; FAO, 2009b). However, globally higher temperatures shorten the growth season, letting the crops with a much shorter period to perform photosynthesis even in the case of well irrigated and tolerant crops. Moreover, heat stress directly affects photosynthetic rate accentuating the effect of this shorter growth period. As a result, crops have less biomass to face the anthesis and the consequent grain filling. Warmer environments also affect post-anthesis stages reducing grain growth and promoting fruit senescence. Additionally, the increase in temperature promotes a higher evapotranspiration rate that, ultimately reduce soil moisture and the available water needed for grain filling. When plants suffer extreme temperatures of short duration these processes are even more severely affected (Asseng et al., 2011, 2015, 2019; Liu et al., 2014, 2019; Lesk et al., 2016). Accordingly, it has been reported that in wheat, rice and shorghum heat causes loss of grain yield by shortening its growth period, altering spikelet's development (number of spikes per plant and spikes size), grains per spike and reducing grain size (Prasad et al., 2006; Jagadish et al., 2010; Fahad et al., 2017). Similarly, in oilseed rape, *Brassica rapa* and *Brassica juncea* yield losses are produced by a decrease in seeds per silique and number of siliques per plant as well as defects in pod formation (Angadi et al., 2000; Morrison and Stewart, 2002). High temperatures also lead to a decrease in crop quality by changing seed composition. Thus, in cereals and oilseed crops heat stress reduces the oil, starch, and protein contents of seeds (Jagadish et al., 2015; Fahad et al., 2017). It has been shown that in wheat, increased temperatures reduce the levels of valuable protein whereas it causes the accumulation of proline and soluble carbohydrates (Qaseem et al., 2019). On the other hand, higher temperature also reduces oilseed rape seeds quality by reducing the amounts of oil and increasing the levels of proteins and glucosinolates (Aksouh et al., 2001). In rice, high temperatures during ripening led to the deterioration of grain quality including starch accumulation (Morita et al., 2016; Chen et al., 2017). In brief, crops are substantially but heterogeneously affected by temperature variability (Thiault et al., 2019). To remedy this effect, we need to evaluate and understand further the changes that crops undergo under the future climatic scenario.

ROOT RESPONSE TO INCREASED TEMPERATURE

Crops face rising temperatures by triggering a heat response, whose timing and effectiveness will determine if the plants overcome the stress. The effect of increased temperatures on aerial parts of the plants and their responses has been well studied, whereas their influence and response on roots (and root-to-shoot signaling) has been less explored (Wahid et al., 2007). If we attempt to enhance adaptation of crops to severer environments triggered by climate change, we need to take into account below ground traits. For that, first, we need to improve our understanding of the processes regulating the root response to increased temperature.

Plants have a greater water demand in warmer environments due to increased water loss by evapotranspiration and decreased water uptake by the root, causing an overall water deficit situation (Heckathorn et al., 2013). Water uptake takes place in the root either through aquaporins, membrane channels that facilitates water transport inside the cells, or by diffusion through plasmatic membrane (Maurel et al., 2015). Studies with several crops have shown different response of aquaporins and plasmatic membrane fluidity to higher temperatures in roots. Thus, in pepper and wheat, water uptake in warmer soil seems to positively correlate with aquaporin activity (Carvajal et al., 1996; Cabañero et al., 2004), whereas in broccoli (*Brassica oleracea* var. *italica*) and maize, warmer temperatures decrease aquaporin quantity and activity but increase membrane fluidity. When temperature is extreme, the membrane starts to rigidify heavily decreasing even more water uptake (Iglesias-Acosta et al., 2010; Ionenko et al., 2010).

Nutrient balance is also altered by changes in temperature. Similarly to water, temperature effect on nutrient uptake varies depending on the crop. In tomato, warmer soils limit root growth and decrease nutrient uptake causing a reduction in macro and micro-nutrient levels (Tindall et al., 1990; Giri et al., 2017). In *Agrostis stolonifera*, a grass species used as fodder for

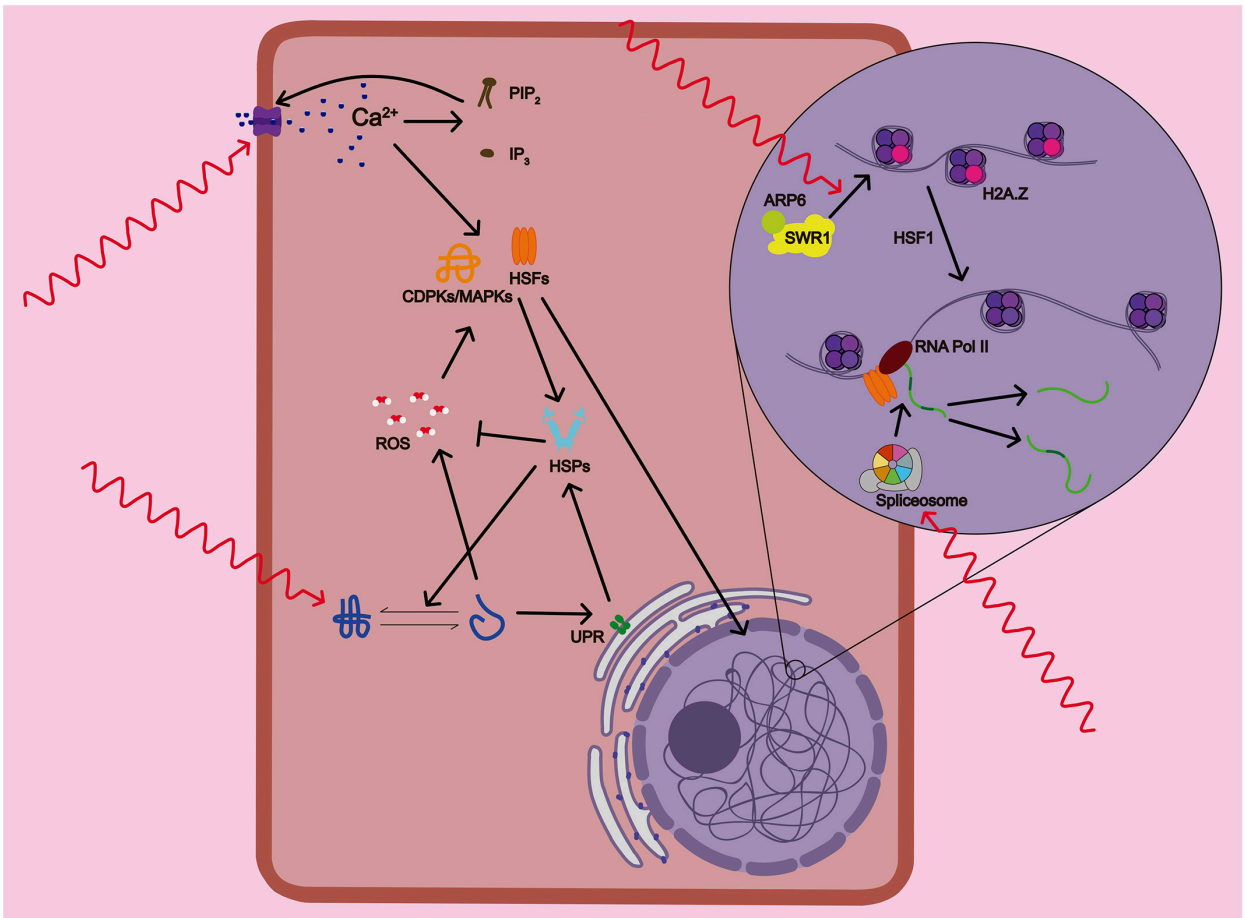

FIGURE 1 | Mechanisms of temperature sensing and response in plants. Plants sense variations in temperature that are translated into the activation of several physiological and signaling processes. Primary temperature-sensing events start with the alteration of membrane fluidity and composition that causes the activation of calcium (Ca^{2+}) channels. A feedback mechanism between the calcium and lipid signaling through accumulation of PIP_2 and IP_3, enhances even further the Ca^{2+} entry in the cell. Several heat shock transcription factors (HSFs) and calcium-dependent protein kinases (CDPKs and MAPKs) are activated by Ca^{2+} and ROS/redox signaling network. At the same time, the accumulation of unfolded proteins in the endoplasmic reticulum (ER) that are potentially toxic activates the ER stress that sets off the unfolded protein response (UPR), a cytoprotective signaling pathway. Subsequent activation of bZIP transcription factors induces the expression of Heat Shock Proteins (HSPs). HSPs protect proteins from misfolding and subsequent loss of functionality and help the detoxification of ROS. ARP6, a subunit of SWR1 complex, mediates the insertion of the variant histone H2A.Z in the nucleosome. At warmer temperatures, the antagonistic roles of H2A.Z and HSF1 seem to be required to activate heat response (HR) gene transcription. Lastly, the alternative splicing machinery allows the rapid adjustment of the abundance and function of key stress-response components.

livestock, the application of high temperature to roots results in a lower number of roots and an increase in the uptake and partitioning of nitrogen, phosphorous and potassium (Huang and Xu, 2000). In *Andropogon gerardii*, another plant used as fodder, supra-optimal root temperatures cause a decrease in root and shoot growth. Further higher temperatures moderately affects nitrogen uptake but its efficiency use is severely perturbed (DeLucia et al., 1992). In contrast, warm temperature does not alter nitrogen, phosphorus and potassium uptake in maize, but higher temperatures seem to only slightly decrease phosphorus and potassium uptake (Bravo-F and Uribe, 1981; Hussain et al., 2019).

All these negative root responses to increase temperature severely compromise water and nutrient uptake and the consequence is a dramatic reduction on crop yield. Cultivars better adapted to temperature will have to shape their roots to improve their water and nutrient efficiency if they aim to secure yield stability under this challenging environment. As we will ascertain during this review, root organization shows a high plasticity in response to soil changes providing high opportunities for improvement. Better comprehension of the physiological, genetic and molecular mechanisms regulating this plasticity will allow us to develop better adapted crops.

Temperature Sensing and Signaling in Roots

Although it has been proposed that thermomorphogenesis signaling could differs between roots and shoots, a common set of mechanisms of temperature sensing mediate organ response

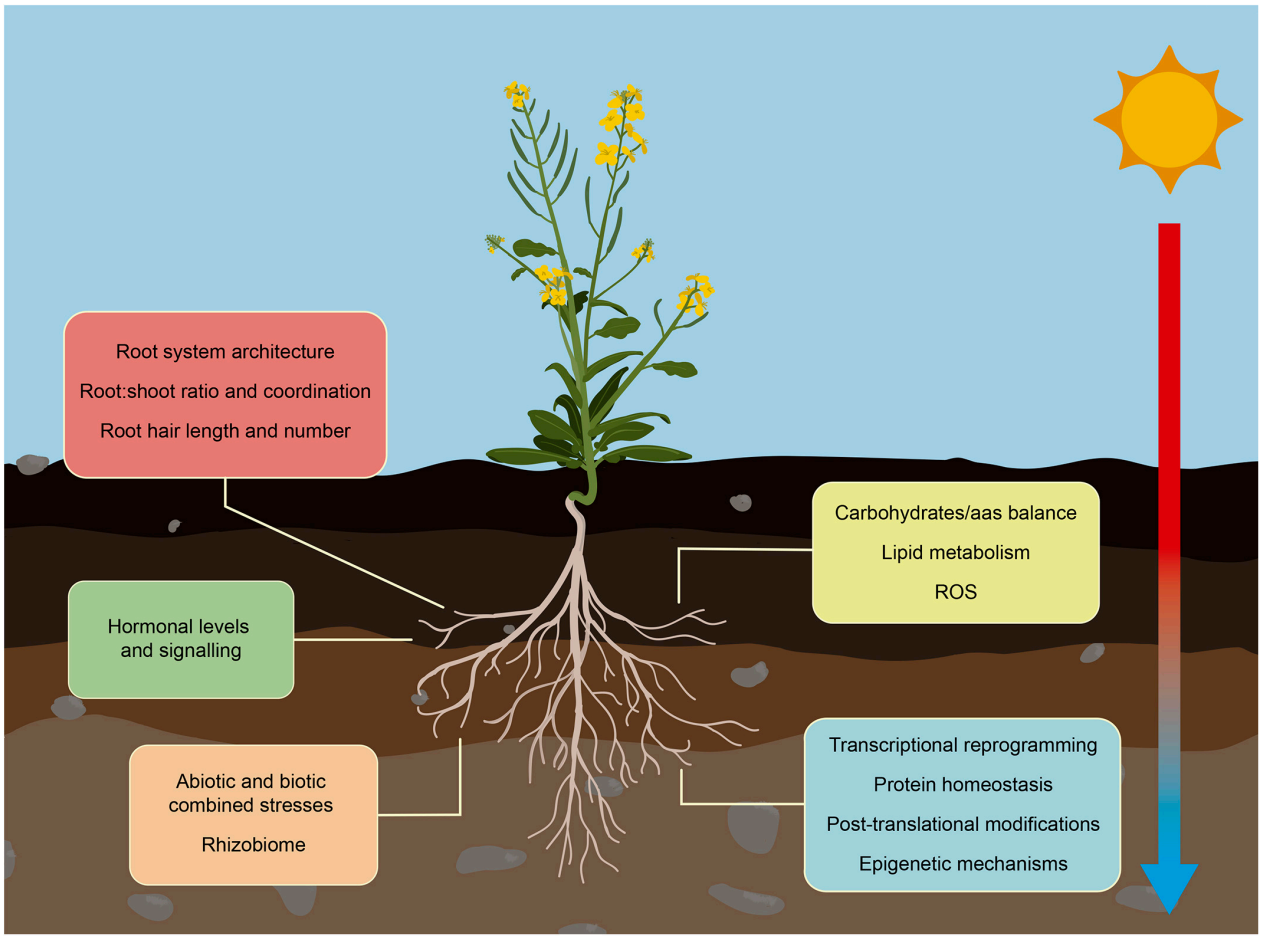

FIGURE 2 | Root response to increased ambient temperature. Climate change is increasing the ambient temperature altering crops growth. Crops adapt root development and functionality to maintain water and nutrients availability in this stressing environmental situation. These changes in their RSA, include alterations in lateral and primary root growth and root hair elongation, and adjustment of their interchange with aboveground organs. Roots also suffer changes in their metabolism affecting mainly carbohydrate/amino acid balance, lipid metabolism and the activation of heat and oxidative pathways to prevent disruption of root growth. Temperature-mediated alteration of hormone levels trigger signal transduction pathways that prepare plants to overcome the stress situation. Other significant molecular changes that regulate root adaptation include global transcriptomic reprogramming, changes in protein profiles, and activation of epigenetic and chromatin-based mechanisms. In the field, increasing temperature is usually accompanied with other abiotic and biotic stresses such as drought, salinity, nutrient deficiency and pathogen infections. Roots are able to integrate and respond to all these different stress situations to promote their survival and maintain their growth.

at a molecular and cellular level (Bellstaedt et al., 2019). Plants can sense small variations in temperature, and this sensing can be translated into activation of several physiological processes that are considered the primary temperature-sensing events (**Figure 2**; Penfield, 2008; McClung and Davis, 2010). Roots sense these thermal changes directly or indirectly. Indirectly sensing is either triggered by the shoot demand of water and nutrient or by the supply of carbon from the shoot to root (Plieth et al., 1999; Heckathorn et al., 2013). Warmer temperatures, and more sharply, high temperature, alter the stability of membranes and cystoskeleton components, as well as proteins and nucleic acids (Vu et al., 2019a). Temperature changes alter membrane fluidity and composition causing the activation of calcium (Ca^{2+}) channels. Increased intracellular Ca^{2+} triggers the lipid signaling through the lipid-modifying enzymes PLD and PIPK. Subsequent accumulation of PIP_2 and IP_3, in turn, enhances Ca^{2+} entry in the cell (Mittler et al., 2012). The Ca^{2+} influx can activate several heat shock transcription factors (HSFs) and calcium-dependent protein kinases (CDPKs and MAPKs) that control heat stress responses. The ROS/redox signaling network is also mediating plant sensing to high temperature due to direct activation of HSFs and heat related MAPKs. ROS accumulation might be produced as unwanted products of several metabolic pathways due to heat-mediated changes in the stability and activity of their enzymes or by calcium activation of ROS-producing enzyme RBOHD (Suzuki et al., 2011; Rasul et al., 2017).

Heat stress causes accumulation of unfolded proteins in the endoplasmic reticulum (ER) that are potentially toxic leading to what is known as ER stress. ER stress elicits the unfolded protein response (UPR), a cytoprotective response to mitigate and to protect from this damage (Howell, 2013). The UPR is signaled through two pathways: one involving the proteolytic

processing transcription factor bZIP28, and the other involving the ribonuclease IRE1, which mediates the splicing of the bZIP60 transcription factor mRNA (Neill et al., 2019). Both UPR pathways induce the expression of Heat Shock Proteins (HSPs) and activation of brassinosteroids (BRs) signaling (Che et al., 2010). These two pathways seems to be less sensitive than Ca^{2+} channels because only high temperatures are able to provoke a global unfolding of proteins (Liu and Howell, 2016). HSPs are actively translated during the onset of temperature stress response to protect proteins from misfolding and subsequent loss of functionality. But HSPs also improves membrane stability and detoxification of ROS by regulating several antioxidant enzymes therefore attenuating stress response (Ul Haq et al., 2019).

ARP6, a subunit of SWR1 complex, has been proposed as a histone themosensor. ARP6 mediates the insertion of the variant histone H2A.Z in the nucleosome. H2A.Z nucleosomes wrap DNA more tightly, which affects the ability of RNA polymerase (Pol) II to initiate transcription. At warmer temperatures, H2A.Z is evicted from the nucleosomes located at the transcriptional start of heat response genes (Kumar and Wigge, 2010). This process also required the recruitment of HSFA1 to the promoters of these genes to activate their transcription (Cortijo et al., 2017). Therefore, the antagonistic roles of H2A.Z and HSF1 seems to be require to activate gene expression rapidly and precisely in response to elevated temperature (Wigge, 2013). Lastly, warmer temperature could alter RNA unfolding, metabolism and structure (Su et al., 2018) as well as changes in small RNA expression (Liu et al., 2017). It also causes a recruit of alternative splicing (AS) machinery that will allow the rapid adjustment of the abundance and function of key stress-response components (Laloum et al., 2018). All these pathways trigger different sensing events that contribute to the activation of the overall heat response. This heat response includes a large number of morphological, physiological, metabolic and molecular changes altering root growth that we will describe in more detail.

Morphological and Physiological Response

Roots need an optimal temperature range to have a proper growth rate and function. In general, optimal root temperature tends to be lower than optimal shoot temperature. Crop roots have different optimal root temperature depending on the species. Within this range, a higher temperature is usually associated to altered root:shoot ratio, and a further increase in temperature would limit root development and alter root system architecture (RSA) reducing root:shoot ratio (Ribeiro et al., 2014; Koevoets et al., 2016). RSA is defined as the organization of the primary, lateral, adventitious and accessory roots. Each RSA is determined by parameters such as length, number and angle of these root components. RSA is the main factor that controls nutrient and water uptake efficiency since it determines the soil volume that roots are able to explore at different environmental situations (Lynch, 1995). Generally, the exposure of roots to temperatures higher than the optimal causes a decrease in the primary root length, number of lateral roots and their angle of emergence. Moreover, the increase in temperature causes the initiation of second and third order lateral roots that are characterized by a larger diameter (**Figure 3**). The negative effect of increasing temperatures usually reduces the surface between root and soil, therefore decreasing nutrient and water uptake (Nagel et al., 2009). In cassava and sweet potato, high root zone temperature significantly decreases the total length of the adventitious roots and the number and total length of the first order lateral roots (Pardales et al., 1999). Seminal and crown roots retarded their emergence and elongation when wheat seedlings are grown at high temperature (Huang et al., 1991a). In maize adult plants, the increase in temperature slows down lateral root growth to promote the development of long axile roots to reach the water of the deeper soil layers (Hund et al., 2008). But in potato, the increase in temperature causes the inhibition of adventitious and lateral roots initiation and elongation. Other effects of the warmer soil in potato are the swelling of the root cap meristem and bending of the root tip. Alteration of root growth in these crops seems to be caused by a decrease in the cell division rate (Sattelmacher et al., 1990; Joshi et al., 2016). Similarly, in sorghum, high root zone temperature reduces the elongation and cell production rate in seminal roots (Pardales et al., 1992). Interestingly, in wheat the increase in temperature causes a decrease in the length and number of central late metaxylem in the root tip. This change has been interpreted as an adaptation to limit damage in the root by the changes in water viscosity and root hydraulic conductance produced by heat (Huang et al., 1991b; Morales et al., 2003).

Another strategy used by roots to cope with changing environmental conditions that affect water and nutrient availability is increasing the number of root hairs and their length. This increase enhances root surface area that in turn will improve soil exploration, and therefore, water and nutrient uptake (Pregitzer et al., 2000). Hence, the contribution of root hairs to total root surface area in two crops, oilseed rape and barley increases with temperature. This increase provides their roots with a greater surface area for absorption per unit root weight or length (Macduff et al., 1986). In Arabidopsis and soybean, the lack of root hairs produces reduction in heat adaptation competence suggesting a key role of root hairs in short-term adaptation to high temperatures (Tanaka et al., 2014; Valdés-López et al., 2016). Moreover, since genes that participate in early sensing and adaptation to high temperature are switched off in barley root-hairless mutant plants, it has been suggested a role of root hairs as sensors of environmental soil condition (Kwasniewski et al., 2016).

Communication between aerial and belowground organs seems to underlie heat tolerance and root response in some crops. Several studies made with tomato have shown that the more heat tolerant varieties are those that have a higher root activity or a larger RSA. Wider root system can access to more water and nutrient sources, increasing the water uptake and letting the leaves to increase its evapotranspiration rate, cooling their canopy temperature and improving the photosynthetic rate. This in turn allows that larger quantity of assimilates can be used to boost root growth (Shaheen et al., 2016; Zhou et al., 2019). On the other hand, it has also been observed that carbon translocation from shoots to roots is inhibited at high soil temperatures.

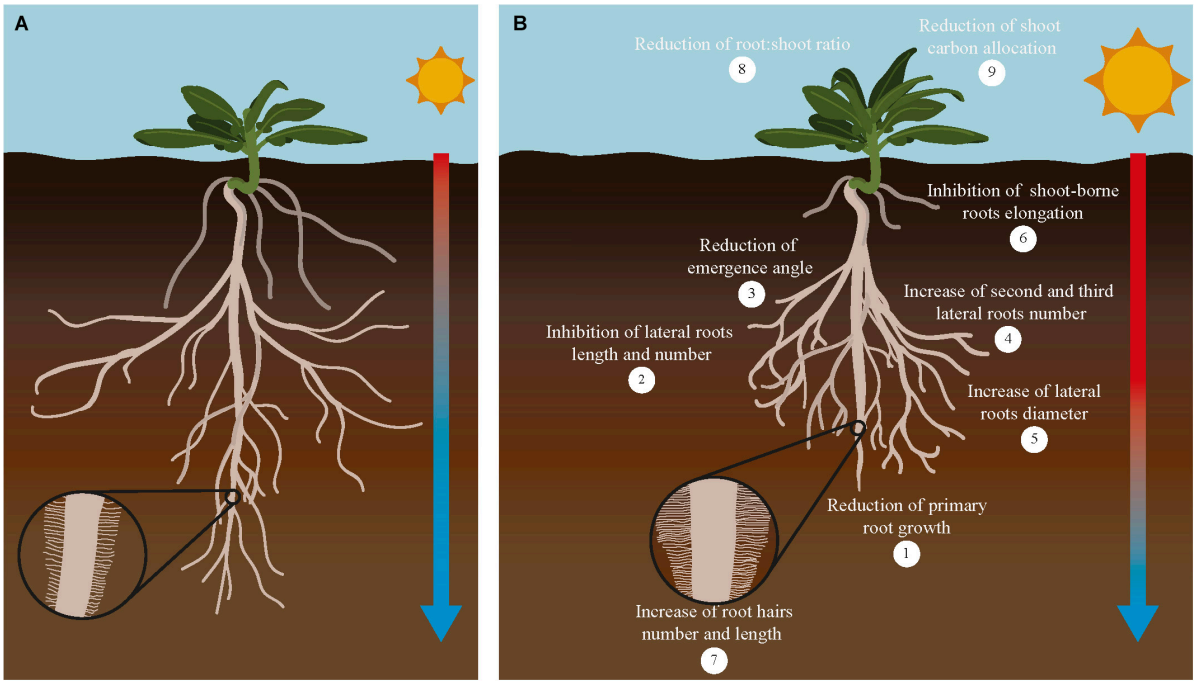

FIGURE 3 | Response of major root traits to increasing temperatures in crops. Increasing temperature of the soil affects root traits related with its organization, growth and function. Root system architecture defined as the organization of the primary, lateral, shoot-borne and lateral roots is drastically altered in response to increased temperature in the soil **(B)** compared to plants growing in optimal conditions **(A)**. Crops growing under higher temperatures show shorter primary roots (1), reduction of lateral roots growth and number (2) and their angle of emergence (3), higher number of second and third order roots (4) with larger diameter (5), inhibition of shoot-borne roots (adventitious and nodal roots) elongation and number (6) and increase of root hairs number and length (7). In addition, this overall reduction on root system growth causes a reduction of root:shoot ratio (8) and reduction of root carbon allocation (9). As a consequence of all these changes, nutrient and water uptake conducted by the roots for the whole plant is compromised and crop yield is severely affected. Although most of these effects are detrimental to root growth, some responses alleviate this situation by increasing root:soil surface [increase in number of second to third roots number (4) and number and length of root hairs (7)], improving water efficiency uptake [increase in diameter of roots (5)], or increase in root depth (lower root angle). Interestingly, these root responses coincide with root traits associated with cultivars more tolerant to high temperatures. A comprehensive evaluation of these traits and their impact on crops productivity will help to decide which root traits are more valuable to be incorporated to breeding programs designed to improved crop yield under climate change conditions.

Under high temperature field conditions, wheat root growth is diminished due to a reduction in the carbon partitioned belowground, and the number, length and diameter of roots are especially affected (Batts et al., 1998). Similarly, in grape, an increase in the temperature reduces root growth rate whereas shoot growth increases due to alteration of assimilate partition (Mahmud et al., 2018). This sink effect of the aerial part of the plants is mostly observed during the reproductive stage, when the carbon partitioning to the root decreases to help flowering and seed development. In summary, warmer soils cause alteration in RSA and root functionality triggering numerous changes in the whole plant in order to adapt to this climatic variance.

One more aspect of root adaptation that is being increasingly explored is the effect of gradient temperature on root architecture. As soil warming reduces downward, progressively deeper soil layers become better suitable for root growth affecting differentially the upper and lower part of roots (Parts et al., 2019). Thus, roots of barley seedlings exposed to uniform temperature or to a vertical gradient respond with significant differences in terms of biomass production and root architecture (Füllner et al., 2012). Other soil conditions associated with soil temperature that also differentially affect root architecture are soil compaction, nutrient composition and moisture. To respond to all these heterogeneous soil environments, crops produce compensatory effects regarding root system architecture and root growth dynamics. In order to capture the best root ideotypes, successful root mechanisms need to be identified by deep phenotyping in complex soil environments and climates. Ideally these ideotypes not only have to respond to specific growth locations but to different dynamics of the stress since increasing temperatures are to be expected as short heat waves or increase seasonal mean temperatures. Finally, farming practices, including plant density, and water and fertilization regimes that directly impact on root development could be crucial to mitigate the unfavorable effects on roots of higher soil temperatures (Pfeifer et al., 2014; Hecht et al., 2016). In this context, modeling of the root behavior under different scenarios including genotype, environment and management will be need to test root traits value for breeding new varieties adapted to increased temperatures.

Hormonal Response

Several plant hormones that take part in root development and growth have been described to mediate temperature stress response in this organ. In particular, a role of BRs

(Bajguz and Hayat, 2009; Anwar et al., 2018), salycilic acid (SA) (Dat et al., 1998), ethylene (ET) (Lin et al., 2009), abscisic acid (ABA) and cytokinin (CK) (Vishwakarma et al., 2017) has been reported in several crops. Temperature-mediated alteration of these hormone levels trigger signal transduction pathways that prepare plants to overcome the stress situation. Key phytohormones including ABA, SA, and ET increase their levels under heat stress, while others such as CK, auxin (AUX), and gibberellins (GAs), decrease (Talanova et al., 2003; Larkindale and Huang, 2004; Larkindale et al., 2005; Nolan et al., 2017, 2019).

Regulation of root response to temperature is mediated by BRs signaling in Arabidopsis. Increased growth temperature reduces the level of the BR receptor BRI1 to downregulate BR signaling and increases root elongation independently of auxin (Martins et al., 2017). Interestingly, it has been proposed that downregulation of BR signaling by temperature elevation could promote GA-dependent root growth. In contrast, in crops, different behavior of BRs has been reported. The application of 24-epibrassinolid (24-EBR), a functional BR, to tomato and oilseed rape seedlings inhibits root elongation in both species but increase their acquired thermotolerance. Molecular analyses of 24-EBR treated and untreated seedlings show that this thermotolerance is a result of increased levels of HSPs (Dhaubhadel et al., 1999, 2002). On the contrary, transgenic lines of oilseed rape overexpressing *AtDWF4*, an Arabidopsis gene encoding an enzyme that catalyzes a bottleneck step in BR biosynthesis, shows an increased root length and fresh and dry root weight. However, the transgenic plants show an increased thermotolerance, and consistent with the results in tomato and oilseed rape, the level of different HSPs gene family members were increased (Sahni et al., 2016).

Improved plant tolerance to heat stress mediated by SA has also been reported in crops (Khan et al., 2015; Nazar et al., 2017). In soybean, wheat, maize and chamomile, this tolerance seems to be mediated by the growth-stimulating effects of SA (Rivas-San Vicente and Plasencia, 2011). Additionally, exogenous SA has a protective role in mitigating extreme temperature-induced damages in different crops (Hasanuzzaman et al., 2017). In grape cultivars root-derived SA have a role in the response to aboveground high temperature. The increase in temperature did not affect free SA content in roots but reduced the levels of conjugated SA, a storage form of this hormone. It is proposed that the sensing of warmer temperatures causes roots to send its conjugated SA reserves to the aboveground parts of the plant where is transformed into free SA to promote the adaptation and resistance to heat stress (Liu et al., 2008).

ET also takes part in root adaptation to increased temperatures. ET production is increased under heat stress, although exogenous ET application cannot confer heat tolerance (Müller and Munné-Bosch, 2015). Nevertheless, thermotolerance is enhanced in rice seedlings under heat stress by an increase in the levels of ET (Wu and Yang, 2019). In sorghum, heat induced inhibition of root elongation and cell production rate is affected by ET levels (Prasad et al., 2008). Likewise, in lettuce, temperature promotes the synthesis of ET. Moreover, exogenous ET application to the root causes heat stress symptoms including reduced root length and surface area and increased root diameter. Application of ET biosynthesis inhibitors to plants exposed to heat alleviates the root growth inhibition. Interestingly, ET effect in this crop has been linked to a similar root-to-shoot communication mechanisms described for SA signaling. Higher ET biosynthesis produced by increased temperatures causes an efflux of ACC, the ET precursor, to the shoot via xylem. ACC then promotes thermotolerance in aboveground tissues by the reduction of oxidative damage and maintenance of chlorophyll content (Qin et al., 2007).

ABA is one of the main hormones to control tolerance to abiotic stress and its biosynthesis is promoted by these stresses also in roots. In cucumber, the application of higher temperature to the whole seedling increases the levels of ABA in both leaves and roots (Talanova et al., 2003). ABA seems to improve heat tolerance through exogenous application or by manipulation of ABA-related genes in some crops. This tolerance is achieved by increasing leaf photochemical efficiency and membrane stability or by induction of HSF (Abass and Rajashekar, 1991; Zhou et al., 2014; Wang et al., 2017). ABA also seems to increase root hydraulic conductance and promote root hair development during adverse environmental situations (Vishwakarma et al., 2017) and it has been suggested as a potential candidate of root-to-shoot communication (Talanova et al., 2003).

CKs are one of the key regulators of root system architecture and they have been implicated in heat stress. In contrast to their role in promoting growth in the shoot, CKs reduce root growth, by inhibiting primary root elongation and promoting cell differentiation in the root apical meristem (Dello Ioio et al., 2008). They are also regulators of root branching (Chang et al., 2015). A decrease in CK levels or a reduction in CK signaling can lead to an enlarged root system improving temperature root response (Bielach et al., 2017; Kieber and Schaller, 2018). Contrarily, stress driven alteration of *CKX1* levels in roots, a CK oxidase/dehydrogenase (CKX) enzyme that regulates CK degradation, results in enhanced drought and heat tolerance in tobacco. The enhanced stress tolerance of these plants has been correlated with raised bioactive CK levels during the early phase of the stress response (Macková et al., 2013).

In summary, several hormones are known to control root growth and are in charge of controlling this process during high temperature stress. Modulation of hormonal signaling in roots in response to heat not only prepares this belowground organ to respond to this stress but also the whole plant since some hormones like SA, ET and ABA could act as intercommunication signals between the root and the aboveground organs.

Metabolic Response

During heat stress, plant roots suffer large quantity of metabolic changes to maintain homeostasis and allow the plant to survive. It has been suggested that overall alteration of metabolic pathways probably depend on the sensitivity to high temperature of key metabolic regulatory enzymes. Different studies carried out in crops and fodder species shows a common pattern in the response of primary and secondary metabolism to heat stress in roots. Main carbohydrates such as glucose, fructose, galactose,

sucrose or xylose are usually lower after the root experience high temperatures, as well as the levels of several glycolytic cycle enzymes (Ribeiro et al., 2014; Aidoo et al., 2016; Sun et al., 2016). In, cassava, warmer soils inhibit starch biosynthesis through the direct decrease of enzymatic activity or down regulation of transcriptional levels of the main starch biosynthesis enzyme (Ma et al., 2018). Other sugars and polyols such as raffinose, galactinol, and glycerol that has been described as stress tolerance compounds increase its content during stress conditions (ElSayed et al., 2014; Salvi et al., 2018). In contraposition of down-accumulation of carbohydrates, some amino acids seem to be accumulated during heat stress. This negative correlation between sugars and amino acid appears to be provoked by the inhibition of carbon assimilates supply to the roots during heat stress. One of the accumulated amino acid is proline, an osmoprotective compound, used to avoid molecular and cellular damage during stress situations (Szabados and Savouré, 2010). Increase temperature also regulates significantly lipid metabolism probably associated to the cell membrane rigidity needed to counteract the fluidity provoked by warmer soils. Thus, fatty acids, phospholipids and glycerolipids shows a reduction in their accumulation after exposing the plant to heat stress together with TCA cycle intermediaries and related enzymes (Ribeiro et al., 2014).

There is fewer and fragmentary data concerning secondary metabolism response to rising temperatures in roots. In maize, increase in temperature causes a decrease in the level of secondary metabolism compounds such as fitosterols and terpenoids (Sun et al., 2016), but in castor bean, although β-sitosterol levels decrease, campesterol storage is increased. The levels of other metabolites like tocopherol, squalene and ricinine, also change in response to heat.

During heat stress, as with other stresses, the intracellular levels of ROS increase sharply. Although it could act as a signaling molecule, higher levels of ROS cause damage at cellular level and interfere with protein and enzymatic activities and gene expression. It has been reported in several crops that the high temperatures promote the expression of ROS scavenging enzymes such as catalases (CAT), peroxidases, superoxide dismutase (SOD) and ascorbate peroxidase to counteract ROS damage (Gill and Tuteja, 2010). Glutathione (GSH) has been described to take part in thermotolerance in eukaryotic organisms by scavenging ROS (Colville and Kranner, 2010). Under heat stress, roots use cysteine to synthesize GSH that could increase the thermotolerance of these organs (Nieto-Sotelo and Ho, 1986). NO and H_2S are two gaseous molecules that act as signaling compounds during different developmental processes, including root morphogenesis, and stress situations, like heat stress. It has been described for both molecules that its external application confers thermotolerance in both shoot and roots (Li et al., 2013; Singh et al., 2019).

Altogether, significant changes in metabolism in response to high temperature have been reported in different crops directed to alleviate the damage triggered by this stress. Although significant information in this process has been conveyed from several groups, the complete picture of how temperature regulates metabolism in roots is far from been complete. A substantial effort in the study of this regulation will be needed to understand how metabolic changes are integrated in the overall response of roots to this stress.

Genetic and Molecular Regulatory Pathways

High temperature triggers significant molecular changes in plants, including global transcriptomic reprogramming and changes in protein profiles, to adjust plant growth to this stressing environmental situation. A large number of transcripts and proteins alter their expression and levels in response to heat stress in roots. From these changes, a pattern of stress response reflecting the physiological, morphological and hormonal changes that we have previously described could be drawn. Thus, most of the differential transcripts and proteins represent genes that are involved in primary and secondary metabolism, such as genes related to ROS scavenging, as SOD or CAT and GSH synthesis to sugar and flavonoid biosynthesis; from calcium and signal transduction kinases to proteins related with the regulatory pathways of several hormones (such as ET, SA, JA, ABA, and CK); or from lipid signaling to heat shock proteins and factors (Bita and Gerats, 2013; Valdés-López et al., 2016; Jia et al., 2017; Carrera et al., 2018; Wang et al., 2018a,b).

Activation of *HSPs* and *HSFs* gene families seems to be a universal response to high temperature being found in all organisms from humans to plants. Consequently, several of these genes encoded proteins have been associated to thermotolerance in different crops. In wheat, *HsfA6f* overexpression enhances thermotolerance through the induction of several *HSP* and heat responsive genes. It also activates raffinose and galactinol biosynthesis enzymes and ROS scavenging enzymes by binding to the heat shock elements in the promoters of these genes (Xue et al., 2015). In many plant species, response to heat stress is particularly dependent upon induction of *HSP70* and *HSP101* (Queitsch et al., 2000). In maize, HSP101 regulates root elongation in both normal conditions and mild-heat stress and is needed during germination to balance growth and tolerance establishment (Nieto-Sotelo et al., 2002). Interestingly, it has been observed that differences in thermotolerance between rice cultivars could be mediated also by differences in HSP101 and HSA32 protein levels (Lin et al., 2014). Similarly, in pepper cultivars, HSP25.9, a HSP20, could also be mediating thermoresponse by reducing the accumulation of ROS, enhancing the activity of antioxidant enzymes and regulating the expression of stress-related genes (Feng X. H. et al., 2019).

Heat response encompasses different regulatory gene networks involving specific set of transcription factors, protein kinases and other signaling related proteins (Ohama et al., 2017). In several crops, specific families of transcription factors are candidates to mediate heat stress response in roots. Thus, HD-ZIP and NAC transcription factors are induced by heat stress in potato and radish (Karanja et al., 2017; Li et al., 2019). In batata, ABF4, an ABA-responsive element binding factor that is up-regulated under heat stress promotes the expression of several stress responsive genes and mediate root elongation response (Wang W. et al., 2019). In rice, ZFP350, a Zinc Finger

Protein (ZFP) transcriptional factor, is specifically expressed in roots and up regulated by heat. ZFP350 seems to control root response to high temperatures by promoting the expression of stress responsive genes like *HSP70* (Kang et al., 2019). In tomato, a GRF transcription factor, GRF6, is regulated by several stresses including heat through a hormonal mediated pathway (Khatun et al., 2017). Another group of important regulatory proteins that are induced after heat sensing are diverse kinases such as CDPKs or MAPKs (Wang et al., 2018a). A putative rice orthologue of Brassinosteroid insensitive 2 (BIN2), a glycogen synthase kinase3-like gene 1 (GSK1), that acts as repressor of BR signaling seems to mediate heat tolerance in roots (Koh et al., 2007). In pepper, WAKL20, a wall associated RLK-like (WAKL) kinases acts as a negative regulator of thermotolerance by down regulating ABA–responsive genes that in turn decrease plant ABA sensitivity during root growth (Wang H. et al., 2019). Other signaling pathways involving hormone responses are those related with Proline Rich Proteins (PRPs). This family of proteins has been described in several crops as part of root developmental and stress response processes. RCc3, a rice root specific PRP, improves RSA during heat stress by promoting auxin efflux, biosynthesis and accumulation in the roots (Li et al., 2018).

Stress response mediated by increased temperatures also alters several proteins levels through post-translational modifications (Ahmad et al., 2016; Wu et al., 2016; Kosová et al., 2018). These post-translational modifications included phosphorylation, sumoylation or ubiquitination events. For example, the differential phosphorylation levels of two isoforms of fructose-biphosphate aldolase seems to underlie the contrasting heat tolerance in roots of two C3 grass Agrostis species, *A. scabra* and *A. stolonifera* (Xu and Huang, 2008). Also sumoylation levels are altered in several crop roots under heat stress pointing to this protein modification as part of the root response to high temperatures (Augustine et al., 2016; Li X. et al., 2017). Finally, in tomato, ShATL78L, a RING finger protein, enhances multiple abiotic stresses tolerance, including heat, by interacting with a subunit of COP9 signalosome complex and therefore altering ubiquitin-mediated protein degradation (Song et al., 2016).

In recent years, several epigenetic and chromatin-based mechanisms have been implicated in the regulation of heat responsive genes and their function but few examples have been described in crop roots. These epigenetic mechanisms include DNA methylation, histone modifications, histone variants such as the previously mentioned H2A.Z variant, small RNAs and miRNA (Kim et al., 2015; Liu et al., 2015; Lämke and Bäurle, 2017; Saraswat et al., 2017). In rice, several microRNAs show a differential expression in roots of contrasting heat response cultivars. Similarly, in barley, a heat-induced increase in *miR160a*, down-regulates the expression levels of *ARF17* and *ARF13*, which could affect shoot morphology and root growth (Kruszka et al., 2014). In maize roots, the expression and acetylation levels (histone 3 lysine residue 9, H3K9; and histone 4 lysine residue 5, H4K5) of two genes related to lateral root development (*HO1* and *GSL1*), are decreased under heat stress suggesting a mechanism mediated by up-regulation of histone acetyltransferases (HATs) in the root response to this stress (Zhang et al., 2018).

In summary as we have described briefly, there are an increasing number of regulatory mechanisms that are being implicated in the control of heat response in root of different crops. Although there are still many gaps in our knowledge of how all these mechanisms work, all this mounting information will be crucial to expand the set of molecular targets that could be used to improve heat tolerance in crops.

Increased Temperature Associated Root Traits

Breeding of new cultivars able to overcome the challenging new environmental conditions driven by climate change must incorporate traits regarding root architecture (Koevoets et al., 2016). The potential of roots to boost crop productivity has been establish in several studies where correlations between root traits and yield have been determined (Bray and Topp, 2018; Robinson et al., 2018; Jia et al., 2019). This close relation is confirmed by the co-ocurrence of QTLs for root traits and grain yield and other agronomic traits associated to productivity in different crops (Maccaferri et al., 2016; Ju et al., 2018). Root traits like deep rooting or root angle seem to increase vegetative growth and subsequent grain filling but are also context dependent. Deep root systems developed in limiting water conditions increase grain yield by providing access to residual water in deeper soil layers (El Hassouni et al., 2018). Additionally, root length has been correlated with flowering traits in different crops but how this association takes place is not well known (Voss-Fels et al., 2018). Similarly, several above-ground traits are influenced by root behavior under different stress conditions including high soil temperatures (Batts et al., 1998; Arai-Sanoh et al., 2010). All these studies highlight the idea that a complete plant phenology has to be taken into account when root traits are selected for breeding for adaptation to avoid yield penalties.

As we have seen, roots are very plastic to environmental conditions and display a large range of highly variable physiological and morphological traits to adapt root architecture and functionality to disadvantageous conditions. Classical breeding trials were designed to select for cultivars with high yield using non-limiting nutrients and non-challenging environmental conditions which has often led to selection for smaller and less plastic roots (White et al., 2013). Moreover, modern cultivars have relied on the monitoring and selection of above-ground traits looking for increasing biomass into the shoots rather than into the roots, that it turns has selected for smaller root sizes and root:shoot ratios (Waines and Ehdaie, 2007; Friedli et al., 2019). As a result, root traits have been usually downplayed in breeding programs but numerous studies have shown the correlation of root traits with enhanced tolerance and productivity in different crops species (Den Herder et al., 2010). These studies highlight the potentiality of root traits as tools for breeding high tolerant crops (de Dorlodot et al., 2007). Heat stress tolerance as other abiotic tolerance seems to be a multigenic trait and the candidate genes are poorly known. Root traits are genetically complex and more difficult to measure (Wasaya et al., 2018). Everything considered, improving this stress tolerance in root crops is a very limiting

step in plant breeding. Roots are challenging to evaluate in the soil and this has been a major reason for the poor attention that they have been paid in breeding programs in the past. Numerous methods of phenotyping have been used, from laboratory-based methods including the use of soil-free media pots, rhizoboxes, hydroponics or semi-hydroponics media combined with high-throughput digital phenotyping or 3D imaging systems (Walter et al., 2015; Voss-Fels et al., 2018; Jia et al., 2019; Ma et al., 2019; Qiao et al., 2019) to field shovelomics (Trachsel et al., 2011). But still all these methods are generally expensive or/and time-consuming, so better and affordable tools to improve analysis of root traits are still needed. Nevertheless, significant information of root adaptation to changes in temperature has been provided by exploiting genetic variation associated to root traits.

Genome-wide association studies (GWAS) have been widely used during the last few years to identify loci on tolerance to extreme temperatures in crops (Hu et al., 2017; Maulana et al., 2018; Jamil et al., 2019; Jia et al., 2019; Oladzad et al., 2019) or root architecture (Li X. et al., 2017; Li Y. et al., 2017) but analyses focused on root response to temperature are still lacking. Similarly, QTL mapping has been used to narrow down regions of crop genomes related to root architecture (Gong et al., 2015). Although several studies has identified, mapped and predicted potential genes candidates for QTLs associated with heat or high temperature tolerance in several crops like tomato (Wen et al., 2019), maize (Van Inghelandt et al., 2019), barley (Arifuzzaman et al., 2014) and wheat (Sharma et al., 2017), very few have been focused on root related traits. Thus, in wheat, QTLs for cooler canopy temperature (QTL-CT) are associated to a higher number of superficial roots compared to deep roots (Pinto and Reynolds, 2015). QTL analyses also in wheat show a coincidence of a QTL for heat and drought tolerance suggesting a common genetic basis for adaptation to both stresses. This QTL seems to be associated with changes in root distribution to increase water availability (Pinto et al., 2010). Likewise, a later analysis in wheat to identify meta-QTL associated with adaptation to drought and heat stress, shows that a large number of QTLs are shared to both heat and drought response and two of them are associated to higher root length (Acuña-Galindo et al., 2015). Similarly, in rice, studies with recombinant inbred lines (RILs) obtained from crosses between heat tolerant and non-tolerant cultivars have identified QTLs associated with root length under heat stress (Ps et al., 2017; Kilasi et al., 2018), and in barley, two heat-stress QTLs are adjacent to a QTL reported for root length and root-shoot ratio (Gous et al., 2016). In maize, association mapping studies between inbred lines with different heat tolerance show a significant effect on lateral and axillary root elongation rates in these genotypes (Trachsel et al., 2010; Reimer et al., 2013). Interestingly, this change on root architecture coincides with the proposed maize ideotype for the root system which represents steep and deep roots, and reduction of the metabolic cost of soil exploration (Lynch, 2013; Gong et al., 2015). Altogether these analyses reinforce the idea that better developed roots help the plant to increase the water intake during heat stress that in turn increases the evapotranspiration rate and decreases the aboveground temperature allowing a better photosynthetic ratio and crop yield. However, the optimal RSA could be different in each targeted environment and breeding efforts have to account for these differences. Moreover, some of the adaptive root traits are only conveyed when roots are under specific stresses making phenotyping and evaluation of root traits even more challenging (Alahmad et al., 2019). Thus, drought induced deep rooting that reduces root growth in upper soil layers compare to shallow roots is an effective strategy when heat is combined with low moisture soil but has yield penalties in moisture rich soils (Comas et al., 2013; El Hassouni et al., 2018). Combination of context dependant or independent root traits has been proposed as solution for adaptation to target multiple environments. For that purpose, analysis of natural variation and wild relatives have been used to uncover some of the processes underlying either root growth or responses to temperature changes. New root trait alleles would be uncovered using this strategy but the effectiveness of these tools to analyze root response to increase temperature in crops is yet to be explored (Ristova and Busch, 2014; Blackman, 2017; Driedonks et al., 2018; Ristova et al., 2018; Wang et al., 2018c).

In summary, the information gathered from all these studies has been very useful to shed light onto some of the possible strategies adopted by the roots to confront temperature stress. These strategies include primarily alteration of RSA and adjustments of their interchange with aboveground organs. However, there are still many other avenues to extensively exploit the plasticity of the roots. In modern agricultural system, crops are highly densely planted and root traits related with root angle or root occupancy could be highly valuable (Meister et al., 2014; Hecht et al., 2016). In cereals, with a root system that changes during their lifespan (postembryonic root are different from embryonic roots), a multi-trait approach considering all root types will be needed to uncover useful genotypes. Lastly, root traits identifyed on multi environmental field trials considering complex and concomitant soil conditions seems a very promising approach to adapt root system of crops to climate change.

ROOT RESPONSES TO TEMPERATURE ASSOCIATED ABIOTIC AND BIOTIC STRESS

In field conditions, under the predicted climate change scenario, the increase in temperatures is usually accompanied by an enhanced evapotranspiration of soil and plants following by an increase in drought incidence and soil salinization. Additionally, higher temperatures could lead to an increased virulence and expansion of crop pathogens (Mahalingam, 2015). Therefore, in order to improve root adaptation in crops we need to consider how combined stress responses affect root growth (**Figure 4**; Koevoets et al., 2016).

Abiotic Stresses

Water is one of the most limiting factors for crop growth and its availability is determined by weather, soil structure and root uptake. Root growth response to water deprivation usually

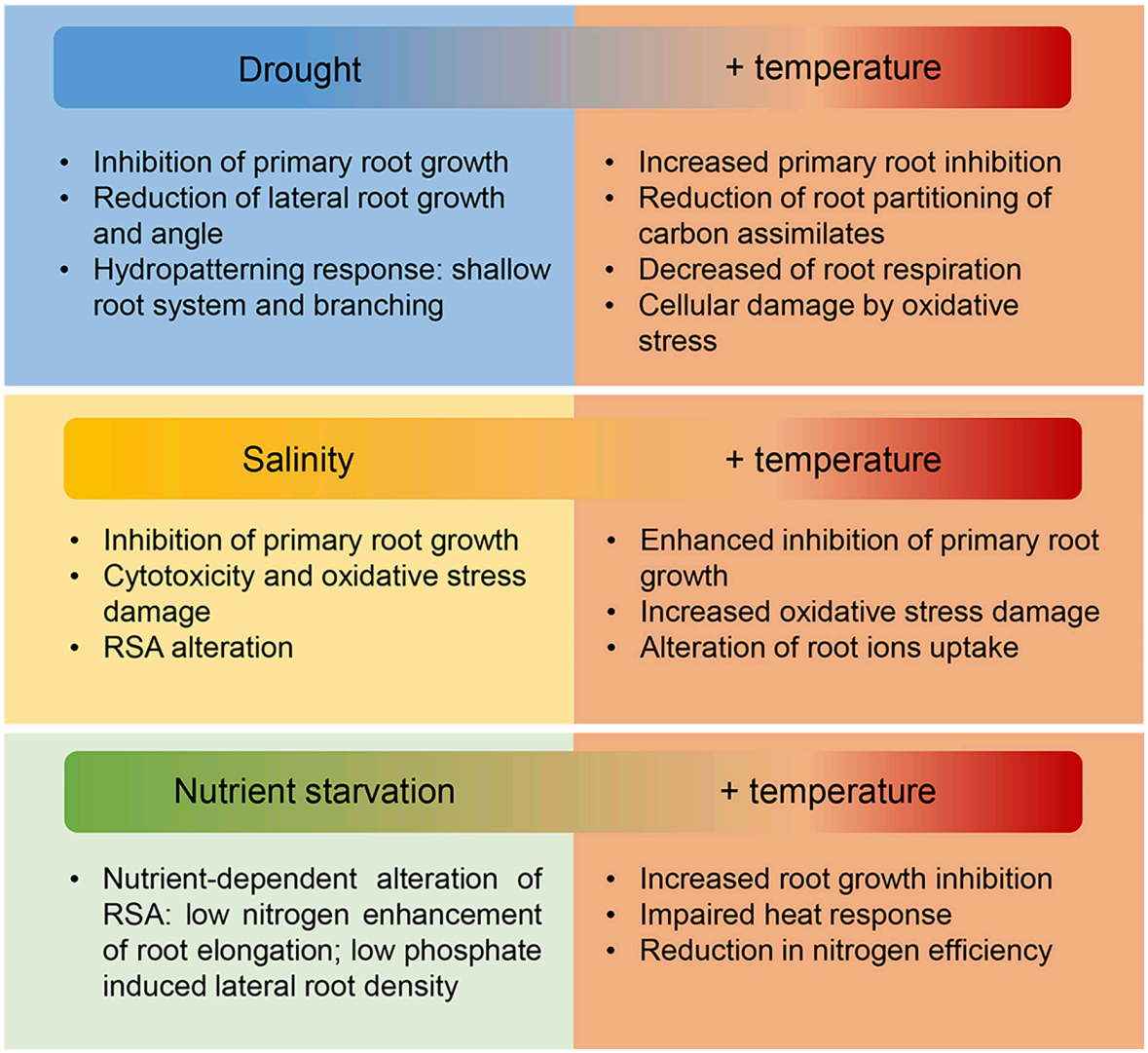

FIGURE 4 | Effect of increasing temperature and associated abiotic stresses on root growth. In the field, the increase in temperatures driven by climate change is normally accompanied by water deprivation provoked by enhanced evapotranspiration of the soil and plants. Moreover, increased soil salinization and changes in the nutrient composition of the soil further compromise plant growth. Roots are essential for water, ions and nutrient uptake therefore the adverse effects on roots of these combined stresses as is summarized in this figure, directly affects crop productivity on the field. New crops with improved root response to a variety of biotic and biotic stresses will be needed to maintain yield stability under the changeable environmental conditions driven by climate change.

includes inhibition of lateral root growth and enhancement of primary and secondary root growth. But when scarcity of water is more severe a drought avoidance program is deployed to direct root growth and branching into regions of soil where these resources are more abundant (Dinneny, 2019). ABA and auxins regulate this hydropatterning response (Orosa-Puente et al., 2018). Interestingly, a major rice QTL for the control of deep rooting, *DRO1*, modulates yield under drought stress by affecting root growth angle (Uga et al., 2013). Severe drought conditions, in addition to higher temperatures, provoke a strong inhibition on root respiration rate and growth as well as a reduction in the partitioning of carbon assimilates to the roots (Prasad et al., 2008). The root response to the combined effect of heat and drought could vary depending on the crop and the developmental stage. Thus, root growth seems to be directly affected by water deficit and temperature to a greater extent in C3 than C4 crops. Sunflower, a C3 plant, responds to the combined stress situation by partitioning carbon assimilates to the root to promote growth and ensure water availability. In maize, a C4 plant, increased temperature inhibits root elongation (Killi et al., 2017). In barley, plants at heading stage seem to be more sensitive to both stresses than plants during vegetative growth, and plants that show greater carbon assimilates partitioning to the root during heading also show lower yield and lower quality traits (Mahalingam and Bregitzer, 2019). In tomato, heat stress causes an increase in root activity that is translated into an increase in

water uptake. But this response is reversed when this stress is combined with drought. In addition, the combination of both stresses accelerates the harmful effects of each stress (Zhou et al., 2019). At cellular level, the combination of heat and drought causes oxidative stress (Zandalinas et al., 2018). Roots exposed to these conditions accumulate more proline and increased expression of antioxidant enzymes to suppress the potential molecular damage (Selote and Khanna-Chopra, 2010; Sekmen et al., 2014). Lastly, interesting information could be deducted from the ability of some plants such as members of the *Cactaceae* family to grow in arid desert that combine both stresses. Root traits from these plants includes the iterative senescence of the primary root tip, which facilitates rapid branching and shallow root system growth during the rare precipitation events occurring in the desert (Shishkova et al., 2013).

Soil salinization is a major threat that negatively affects crop productivity. Salinity impairs plant growth and development *via* water stress and cytotoxicity due to excessive uptake of ions such as sodium (Na^+). Additionally, salinity is typically accompanied by oxidative stress due to generation of ROS (Isayenkov and Maathuis, 2019). Contrary to what happen with heat, roots are more resistant to salt stress than leaves, but this stress still severely inhibits root growth and provokes damages and alterations in the RSA (Robin et al., 2016). These alterations seem to depend on the crop. Thus, in wheat, root elongation is promoted by the combination of heat and drought but high salinity alone inhibits root growth. Furthermore, when plants were treated with salt and heat, the inhibition caused by the salinity was stronger (Keleş and Öncel, 2002). Similarly, in barley, root growth is severely inhibited and ROS levels sharply increase. To counteract this response, plants accumulate a great quantity of proline and other osmoprotectants, and increase the expression and activity of ROS scavenging enzymes. SA may have a role in this tolerance process by promoting the biosynthesis of osmoprotectants and regulating the activity of several ROS scavenging enzymes (Torun, 2019). On the contrary, in tomato, heat seems to alleviate salinity damage by increasing evapotranspiration and photosynthetic rates. The combination of both stresses also seems to alter the uptake, transport and accumulation of Na^+ and K^+. So, under heat and salinity stresses, tomato accumulates Na^+ ions in the root in order to decrease the level of this ion in leaves and evict photosynthesis alteration (Rivero et al., 2014).

Nitrogen levels in soil also affect root viability, thereby higher or lower nitrogen levels than optimum negatively alters root growth. Additionally, proper N availability is important for plant resistance to stress conditions. In warm soils during spring, roots have to mobilize nitrogen reserves to respond to increased plant growth demand including enhanced root growth. Therefore, it has been suggested that supplying N to the soil could mitigate the effect of temperature on root growth in a similar way (Waraich et al., 2012). Application of nutrients like N, K, Ca, and Mg seems to reduce the toxicity of ROS whereas K and Ca improve intake of water and help to maintain high tissue water potential. One challenge to enhance nitrogen efficiency in crops is to understand how lroots respond to low nitrogen and how the modulation of root architecture is coordinated to maximize nutrient acquisition in variable ambient temperatures. Positive or negative coincidences between N uptake and heat tolerance have been observed in different species (Yan et al., 2012; Giri et al., 2017). Thus, N availability influences HSP levels in maize (Heckathorn et al., 1996) and in the perennial grass, *Agrostis stolonifera*. Combination of nutrient deficiency with higher temperatures in soils, further alters HSP synthesis (Wang et al., 2014).

A major constrain for crop productivity is the deficiency of resources, water and nutrients, in the soil surrounding the root system. As we have seen, roots alter their physiology and morphological traits to increase their efficiency when it is compromised by environmental conditions as increased temperature or a combination of stresses. This root multi-adaptive response need to be incorporated in the breeding of new cultivars to increase their adaptation to unstable climates.

Biotic Stress

Environmental conditions profoundly affect plant disease development; however, the underlying molecular bases are not fully understood. Weather plays a large role in determining the outcome of plant–pathogen interactions, and disease epidemics are more likely to occur when environmental conditions are detrimental for the plant. For example, it is known that temperature fluctuation is a key determinant for microbial invasion and host evasion. Thus, there is an observed pattern of movements driven by global warming effects on crop pathogens and pests, and/or on the availability of crops to cope with them (Bebber et al., 2013). Other outcomes of warming temperatures are that new pathogen strains better adapted to these temperatures may become prevalent and the rise of more aggressive plant disease vectors (Velásquez et al., 2018). High temperature enhances plant disease susceptibility, attenuating disease resistance and promoting pathogen growth (Fujita et al., 2006; Huot et al., 2017). Several mechanisms seem to be implicated in this effect. Increase in temperature causes a decrease in the elicitor detection by the plant and the breakdown of effector-triggered immunity (de Jong et al., 2002; Alcázar and Parker, 2011; Cheng et al., 2013; Hua, 2013). Examples of this effect in roots have been already described. Changes in weather conditions including increased mean winter temperatures have favored infection by several *Phytophthora* spp. species that are responsible for increasing amounts of root rot in forest trees (Jung and Burgess, 2009; Sturrock et al., 2011). Additionally, other soil-borne root diseases seem to be more severe under increased temperature conditions (Elad and Pertot, 2014). Plant response to pathogens and adverse environmental conditions is challenging. Since both responses share many components, plants need to trigger a balanced response between the tolerance and defense response. In fact, mounting evidence suggests that hormone signaling pathways regulated by ABA, SA, JA and ET, as well as MAP-kinase cascades and ROS signaling pathways, play key roles in the crosstalk between biotic and abiotic stress signaling such as heat (Chen et al., 2015; Zhai et al., 2017). In this context, stress caused by temperature has been shown to negatively affect the plant ability to respond to pathogens through changes in ABA levels that influence defense

responses involving SA, JA, or ET (Asselbergh et al., 2008). An emerging field in abiotic and biotic interaction is that involving plant–microbiome interaction. Disease-suppressive soils with enrichment in specific bacterial clades are able to protect against soil-borne pathogens including fungal root pathogens (Mendes et al., 2011; Philippot et al., 2013). But the alteration of the microbiome and the reduction in number and diversity caused by higher soil temperature could lead to the loss of pathogen suppression capacity of the rhizobiome (Mendes et al., 2011; van der Voort et al., 2016). Although much work is still to be made to understand the crosstalk between environmental conditions such temperature and pathogen interaction in plants, there is an urgency to produce disease-resistant crop plants that are resilient to climate change.

Crop breeding programs are incorporating the response to a combination of different stresses in the evaluation of new varieties. This type of analysis although challenging due to the requirement of multi-environment field trials, are becoming a necessary requisite to assess the real value of the traits to be integrated in the varieties. This is especially relevant in the context of root traits given the high plasticity of the RSA to changes in the environmental conditions and composition of the soil. Root traits aimed to improve the stability of crop productivity have to be able to respond favorably in all the environmental contexts.

CHALLENGES AND FUTURE SOLUTIONS

Humanity's main challenge of this century is to feed the growing population in a context of climate change. Between 2030 and 2050 the population will have increased to 9,000 million people whereas global temperature will have increased between 1.5 and 2°C. The alteration of climate and the more common appearance of extreme events, in addition to higher temperatures, will negatively affect crop yield. Global food security would be endangered resulting in the increase of food prices and food shortages, and in consequence increasing global hunger, poverty and inequality. So, it is of paramount importance the improvement of crop tolerance to abiotic and biotic stresses in order to confront climate change effects.

Root traits still withhold the potential to reach this goal, but first the extensive existing phenotypic variation in these traits must be studied and analyzed (**Figure 5**). Moreover, the improvement of root capability might help to mitigate the harmful effect of agriculture on environment. Better root performance could reduce the water used for irrigation during heat waves or the massive fertilization of fields. On the other hand, root development and capacity should be improved without sacrificing other traits regarding aboveground development or yield. How temperature related changes in root architecture might affect the aerial part of the plant is not well understood and in particular, the signaling from the root to the shoot (or vice versa) in order to prepare the whole plant for the heat stress. Having a better comprehension of the genetic and molecular regulatory pathways underlying root-to-shoot interaction under stress condition could be useful to improve root performance without altering shoot development related traits.

Another challenging aspect to consider is that the temperature of the soil is not uniform, but it maintains a gradient that decreases with depth. This gradient varies depending on the soil composition, a factor contributing to heat conduction and convection. Consequently, the temperature of the soil, and the root, decreases with depth increasing the complexity of root response to heat and its study. The complex relation between the root and the soil increases even more when the role of the rhizosphere is added to the analysis. The potential effect of the rhizosphere to defend or prepare the plant against biotic and abiotic stresses is little explored. Unraveling the complex interaction between the rhizobiome and the root, during heat stress at a molecular and cellular level is essential to understand whole-plant heat tolerance processes. As we have seen throughout this review, in the changing climatic condition, the different stresses do not occur separately but very often they appear together. How plants response to several stresses simultaneously is a poorly understood process especially in roots compared to the information gathered from aboveground tissues. Better understanding of plant response to each stress or its combination is primary to develop more tolerant crop varieties. In brief, there is still a lot of work to be done to obtain potential applications and improvements of root tolerance not only to heat stress but also to other biotic and abiotic stresses.

A first approach to tackle the effect of climate change on crops and at the same time lessen the impact of agriculture is the improvement of agronomic management practices and the use of precise farming. A more efficient use of nitrogen and phosphate fertilizers as well as water could reduce their use in the field. This strategy could help to alleviate the soil deterioration caused by these fertilizers and contribute to reduce water scarcity and pollution. In this context, the optimization of root efficiency in nutrients and water uptake and distribution could lead to a better fertilizer and water management. Better root systems provided by cover crops could be useful in managing and preserve soil quality and soil moisture. Moreover, the use of leguminous plants as cover crops could also be use as a fertilization method due to its symbiotic relationship with nitrogen fixation bacteria. Additionally, the use of better or new agronomic techniques could help to alleviate the increase in soil temperature. For example, no-tillage seems to be beneficial to avoid, or at least, decrease heat stress in root (Wang et al., 2007). Lastly as commented in the previous section, the tailored application of N to the soil could enhance root growth alleviating heat effects.

One of the emerging strategies to approach the use of root traits to fight global warming and its effects on crop yield is the use of the rhizobiome. Plants are able to adjust rhizobiome composition through root exudates that could stimulate the growth of beneficial microorganism in the rhizosphere (Vives-Peris et al., 2018). But changes in soil characteristics lead to a change in root exudates and, in consequence, a change in rhizobiome composition (Philippot et al., 2013). Specific bacteria have been described to enhance plant tolerance to biotic (Santhanam et al., 2015) and abiotic stresses (Rolli et al., 2015). In fact, increased temperature leads to alterations in root exudates

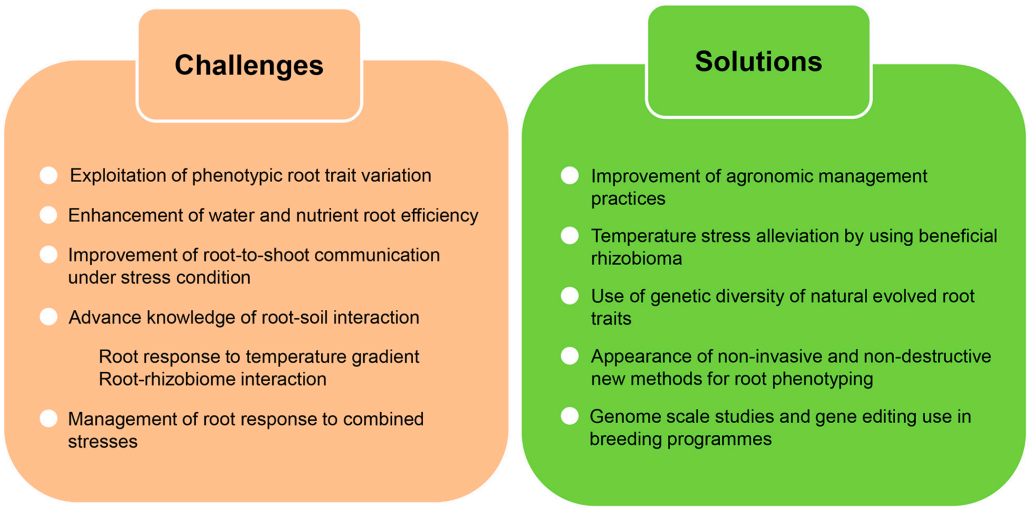

FIGURE 5 | Challenges and potential solutions to improve crop root adaptation to climate change. Global alteration of climate in addition to higher temperatures will negatively affect crop yield. There is an urgent need to improve and maintain crop productivity under these climatic constrains and root traits withhold the potential to reach this goal. In order to confront climate change effects we still have to overcome a few challenges, largely concerning the necessity to increase our knowledge of different aspects of the root adaptation process. New solutions bringing together technical and conceptual advances in the analysis of root traits will drive this advancement.

that promote some beneficial bacteria that could improve crop survival in this condition (Ali et al., 2011). Harnessing the beneficial interaction between the root and rhizosphere has the potential to improve crop tolerance to various stresses (Ahkami et al., 2017). Moreover, the use of symbiotic or non-symbiotic fungi isolated from plant species that grow in inhospitable environments to provide crops with tolerance to several stresses is also being explored (Singh et al., 2011).

Another focus of attention in the field of root adaptation is the use of temperature adapted wild relatives and landraces. During the domestication of crop species, the main traits selected were those related to a greater yield and quality. In this process the loss of root traits related with stress tolerance probably has happened. Crop wild relatives are a source of genetic diversity of natural evolved root traits including root adaptation to stresses. By analyzing the genome of these plants, the evolutionary pathways taken to gain these traits could be understood and applied in breeding programs. Analyses of crop wild relatives have already shown that their genetic variability is a great field to exploit in breeding programs centred on obtaining new crop varieties with tolerance to diverse stresses (Dempewolf et al., 2010, 2014). For example, wild relatives of pigeon pea (*Cajanus cajan*) and wheat has proven to be a source of genetic resources and traits to improve the tolerance of their related crops to stress conditions (Zaharieva et al., 2001; Khoury et al., 2015; Von Wettberg et al., 2018). In addition to wild relatives, crop landraces are a great source of genetic variability for their adaptation to specific ecosystems and climatic conditions (Cantalapiedra et al., 2017; Carvalho et al., 2017; Sani et al., 2018). On the other hand, latest studies with orphan crops have demonstrated that those crops are a powerful tool to improve their related global-traded crops due to its resistance against unfavorable conditions (Song et al., 2019; Tadele and Bartels, 2019).

Traditionally, one of the main bottlenecks to study root adaptation in crops and wild species has been the technical challenge to phenotype roots as a whole system and in their interaction with the soil. The progressive appearance of non-invasive and non-destructive new methods such as shovelomics, X-ray thomography and magnetic resonance imaging (MRI) to visualize the 3D-configuration of roots is allowing to deepen the study of root development during the whole life cycle of plants (Keyes et al., 2013; Walter et al., 2015). As a result, media that allow direct observation of root development, such as hydroponic culture or the use of gelled media, is being widely used to facilitate these studies. Still more problems arise when the goal is to analyze root soil interaction and specially to emulate soil temperature gradient (Füllner et al., 2012). Different sharing platforms and softwares specifically designed to analyze root traits are easing the study of the root system and the associations of different traits to different stages or root responses (Das et al., 2015; Tracy et al., 2020). Although a few challenges still remain to study root adaptation in crops, new methodologies and tools are constantly being developed. Thus, analysis like the transcriptional landscape of different roots types in wheat (Ramírez-González et al., 2018) or the development of expression tissue profiling similar to eFP browser (Winter et al., 2007) or Tomato Expression Atlas (Fernandez-Pozo et al., 2017) in roots of different crops will be immensely useful.

Once beneficial root traits have been defined and potential gene candidates are identified they must be incorporated into breeding programs. A critical challenge is the time it takes from research finding to implementation in agriculture. Complementary approaches and technologies are needed to accelerate downstream breeding. Between the most promising solutions, crop editing has the greatest potential to improve root

performance under various abiotic stresses in relatively short time (Butt et al., 2019). Gene editing driven by tailored strategies focused in specific crop species and stress situation, and a rational design and assembly of appropriated gene combination could result in the generation of new crop varieties able to respond to a particular or a combination of stresses without affecting their yield (Bailey-Serres et al., 2019). This approach, together with powerful genome scale analysis, genome wide association studies and molecular marker assisted breeding are a promiseful alternative to produce new elite varieties adapted to the incoming climatic situation.

AUTHOR CONTRIBUTIONS

MP and JC-C wrote the manuscript and draw the figures. LO-S and MB contributed in drafting and revising the manuscript.

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frontiers in Plant Science

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Coping With Water Limitation: Hormones That Modify Plant Root Xylem Development

*Prashanth Ramachandran, Frauke Augstein, Van Nguyen and Annelie Carlsbecker**

Department of Organismal Biology, Physiological Botany, Evolutionary Biology Centre and Linnean Centre for Plant Biology, Uppsala University, Uppsala, Sweden

Periods of drought, that threaten crop production, are expected to become more prominent in large parts of the world, making it necessary to explore all aspects of plant growth and development, to breed, modify and select crops adapted to such conditions. One such aspect is the xylem, where influencing the size and number of the water-transporting xylem vessels, may impact on hydraulic conductance and drought tolerance. Here, we focus on how plants adjust their root xylem as a response to reduced water availability. While xylem response has been observed in a wide array of species, most of our knowledge on the molecular mechanisms underlying xylem plasticity comes from studies on the model plant *Arabidopsis thaliana*. When grown under water limiting conditions, Arabidopsis rapidly adjusts its development to produce more xylem strands with altered identity in an abscisic acid (ABA) dependent manner. Other hormones such as auxin and cytokinin are essential for vascular patterning and differentiation. Their balance can be perturbed by stress, as evidenced by the effects of enhanced jasmonic acid signaling, which results in similar xylem developmental alterations as enhanced ABA signaling. Furthermore, brassinosteroids and other signaling molecules involved in drought tolerance can also impact xylem development. Hence, a multitude of signals affect root xylem properties and, potentially, influence survival under water limiting conditions. Here, we review the likely entangled signals that govern root vascular development, and discuss the importance of taking root anatomical traits into account when breeding crops for enhanced resilience toward changes in water availability.

Keywords: Arabidopsis, drought, root, development, xylem

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Javier Agusti,
Polytechnic University of Valencia, Spain

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Laura Ragni,
University of Tuebingen, Germany
Anthony Bishopp,
University of Nottingham, United Kingdom

***Correspondence:**
Annelie Carlsbecker
annelie.carlsbecker@ebc.uu.se

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ROOT XYLEM CHARACTERISTICS ARE INFLUENCED BY CHANGES IN WATER AVAILABILITY

Agricultural drought refers to conditions of insufficient water availability rendering conditions unsuitable for plant growth (Wilhite and Glantz, 2009). Understanding mechanisms of plant response to water limitation can help in the breeding of crops with enhanced survival under such conditions. For long, focus has been put on above ground traits or root system architectural properties, but recently more attention has been given to how anatomical parameters and, in particular, xylem structures of the roots influence water transport and drought resilience. The

tracheary elements of the xylem form hollow vessels or tracheids that are structurally reinforced with lignified secondary cell walls (SCW), providing the ability to withstand the strong negative pressure generated by the transpiration pull and promote bulk water movement from the roots to the shoot. The geometrical and physical properties of the tracheary elements influence water transport capacity and research in a wide array of species suggests that xylem traits are important for the ability of plants to withstand periods of reduced water availability (Lucas et al., 2013). The importance of root xylem characteristics for drought tolerance was recently underscored by a study identifying *Arabidopsis thaliana* (Arabidopsis) ecotypes with enhanced root hydraulic conductance (Tang et al., 2018). Through genome wide association studies this trait was linked to XYLEM NAC DOMAIN1 (XND1) (Tang et al., 2018), a well-known negative regulator of xylem differentiation (Zhao et al., 2008, 2017). The *xnd1* loss of function mutants in the Col-0 ecotype had increased root xylem area, and higher aquaporin activity, resulting in enhanced hydraulic conductance compared to wild type, and these plants also displayed enhanced drought tolerance on soil (Tang et al., 2018). Similar root anatomical traits were associated with enhanced hydraulic conductance, drought tolerance and increased yield in field grown soy bean (*Glycine max)* plants (Prince et al., 2017). Interestingly, wheat varieties bred to instead possess smaller xylem diameter displayed higher grain yield during drier growth periods because of improved use of subsoil water (Richards and Passioura, 1989). In line with this, drought exposed rice may respond with formation of smaller xylem diameter (Henry et al., 2012). This strategy is similar to what is observed in drought stressed poplar (*Populus nigra* L. × *Prunus maximowiczii*) trees, which adjust their xylem development to produce thinner but more xylem vessels in their wood (Arend and Fromm, 2007). Thinner xylem vessels increase resistance but reduce risk of embolisms, which occurs under water limiting conditions (Lucas et al., 2013). Thus, different species may benefit from different strategies, but the occurrence of xylem modifications under drought in different species grown under both lab and field conditions suggests these to be important adaptive responses to water limitation. Hence, the molecular mechanisms underlying these responses are potentially important targets for crop breeding programs. Here, we discuss a number of hormones and small molecules known, primarily from studies in Arabidopsis, to affect root xylem patterning and differentiation and how the current knowledge can be employed to optimize plant behavior under normal and drought conditions.

ABA REGULATES XYLEM DEVELOPMENT VIA MIRNA165

Under conditions of reduced water availability, *in vitro*-grown Arabidopsis responds with reduced root growth and suppressed lateral root development (Rowe et al., 2016). Recently, it was found that this also causes major changes to the root's internal anatomy (Jang and Choi, 2018; Ramachandran et al., 2018; Bloch et al., 2019). Normally, the Arabidopsis root stele has a diarch anatomy: a xylem axis traverses the stele with one strand of protoxylem with annular or spiral SCW at either end of the axis and metaxylem with pitted SCW in the center (**Figure 1**). When water availability is reduced, additional protoxylem strands form, both to widen the axis and to shift the identity of the xylem strands within the axis such that protoxylem develops in metaxylem positions (Jang and Choi, 2018; Ramachandran et al., 2018; Bloch et al., 2019). Identity changes were observed also under exogenous treatment with ABA, a well-known mediator of abiotic stress (Zhu, 2016), even below root growth-inhibiting concentrations (**Figure 1**). These phenotypic alterations were strongly attenuated when ABA signaling was compromised, suggesting that they are ABA mediated. Strikingly, inhibition of ABA signaling in the endodermis cell-layer, surrounding the stele, was sufficient to partially suppress xylem identity changes, indicating that ABA acts via a non-cell-autonomous signal (Ramachandran et al., 2018; Bloch et al., 2019). The microRNAs, microRNA165 (miR165) and miR166, are well-known signals moving from endodermis into the stele to determine xylem cell identity (Carlsbecker et al., 2010; Miyashima et al., 2011). These miRNAs are produced in the endodermis but move into the stele to target mRNAs of class III homeodomain leucine-zipper (HD-ZIP III) transcription factors (TFs). The lower levels of HD-ZIP III TFs in the periphery compared to the central stele determine protoxylem and metaxylem identity in the peripheral and central positions of the xylem axis, respectively (Carlsbecker et al., 2010; Miyashima et al., 2011). Hence, upon elevated miR165 levels or in HD-ZIP III loss-of-function mutants, protoxylem forms in the place of metaxylem, conspicuously similar to the phenotype observed under limited water availability or ABA treatments. Indeed, under water-limiting conditions miR165 production in the endodermis is enhanced and, consequently, HD-ZIP III TF levels reduced, explaining the observed shift in xylem cell identity (Ramachandran et al., 2018; Bloch et al., 2019). Intriguingly, if miR165/166 levels instead are strongly reduced throughout the Arabidopsis plant, by the use of an artificial miRNA-target that sequesters miR165/166 (STTM165/166), it results in elevated expression of ABA-related genes and enhanced drought tolerance (Yan et al., 2016). Similar approach conferred drought tolerance also in rice, however in rice miR166 is expressed only in the shoot and consequently only leaf and stem xylem number were affected (Zhang et al., 2018). Since the HD-ZIP III TFs can influence leaf morphology as well as root xylem development, further studies are needed to investigate if these factors could be differentially regulated in roots and shoot upon water stress, and how they may contribute to ABA homeostasis.

AUXIN-CYTOKININ INTERPLAY PATTERNS THE ROOT VASCULATURE

Under normal development, research on Arabidopsis embryos and roots has shown that auxin plays a key role in establishing vascular patterns where xylem and phloem are separated by intervening procambium (**Figure 1**; Bishopp et al., 2011). Central for this is the TF AUXIN RESPONSE FACTOR5

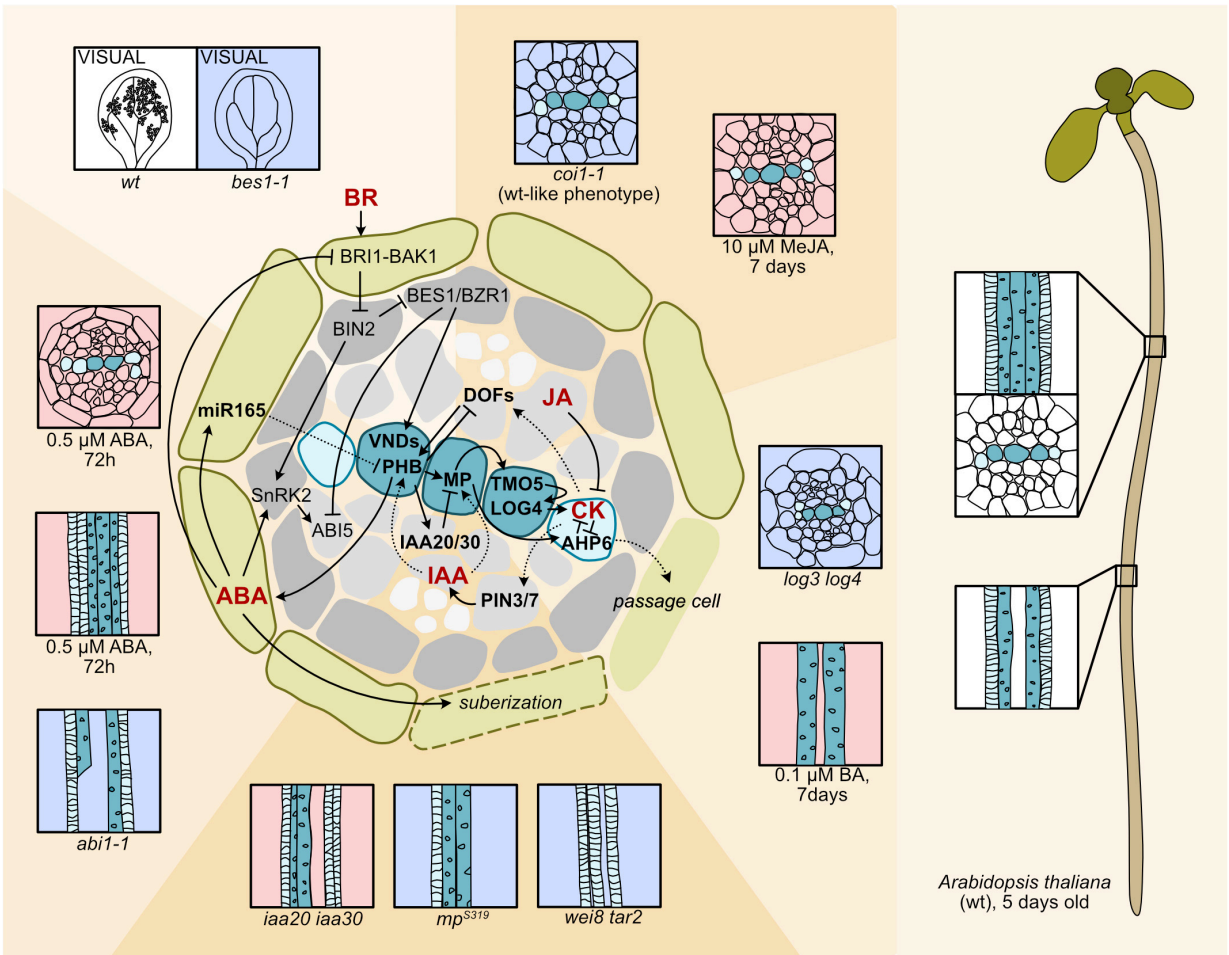

FIGURE 1 | Hormone circuits controlling root xylem development. In the Arabidopsis seedling root, to the right, spiral-walled protoxylem vessels (light blue-green) differentiate first followed by the pitted metaxylem vessels (dark blue-green). To the left a cartoon depicting a cross section focusing on the stele surrounded by the endodermis. Cell types are as indicated: endodermis (green), pericycle (dark gray), procambium (light gray), protoxylem (light blue-green), metaxylem (dark blue-green). Signaling pathways affecting xylem patterning and differentiation are shown on top of the cross section. Hormones are in bold red letters. Arrows indicate activation, bars inhibition. Dashed arrows indicate movement. Phenotypic consequences of hormone treatments or biosynthesis/signaling perturbations for selected experiments are displayed around the cross section. Decreased hormone levels/signaling (light blue background), enhanced levels/signaling (light red background). A PIN3/7 mediated lateral transport focuses auxin (IAA) to a central axis within the stele (Bishopp et al., 2011). Here, auxin-activated MP induces *TMO5* that activates *LOG3* and *LOG4* resulting in CK biosynthesis (De Rybel et al., 2014; Ohashi-Ito et al., 2014). MP also activates AHP6 which inhibits CK signaling (Bishopp et al., 2011). CK moves to the procambium and activates *PIN3* and *7*, and DOF TFs (Bishopp et al., 2011; Miyashima et al., 2019; Smet et al., 2019). MP is required for xylem formation, as the weak mp^{S319} mutant has discontinuous protoxylem and mutants defective in the MP repressors IAA20 and IAA30 result in additional protoxylem (Müller et al., 2016). The auxin biosynthesis mutant *wei8 tar2* lacks metaxylem because of reduced HD-ZIP III expression (Ursache et al., 2014). The cytokinin biosynthesis mutant *log3 log4* has extra protoxylem and a wider xylem axis (De Rybel et al., 2014; Ohashi-Ito et al., 2014), whereas treatment with the synthetic CK, 6-benzylaminopurine (BA) results in loss of protoxylem due to *AHP6* suppression (Argyros et al., 2008; Bishopp et al., 2011). JA activates *AHP6* expression and suppresses *PIN7* expression (Jang et al., 2017, 2019). Methyl-JA treatment results in extra protoxylem and a wider xylem axis, but mutation in the JA receptor COI does not affect xylem development (Jang et al., 2017). ABI1 mediated ABA signaling in endodermis induces miR165 and miR166, which move into the stele to restrict HD-ZIP III mRNA, exemplified with *PHABULOSA* (*PHB*) (Ramachandran et al., 2018; Bloch et al., 2019). ABA treatment results in protoxylem in place of metaxylem and extra protoxylem, while ABA signaling and biosynthesis mutants display xylem breaks (Ramachandran et al., 2018). Endodermal ABA signaling enhances suberization (Barberon et al., 2016). Mobile AHP6 represses suberization resulting in passage cells for water and nutrient uptake (Andersen et al., 2018). ABA signaling components interact with BR signaling resulting in antagonistic control of downstream targets. ABA signaling activates ABI5, while *ABI5* expression is repressed by BES1/BZR1 via BRI1-BAK1 receptor and BIN2 GSK3-mediated BR signaling, and BIN2 interferes with ABA signaling by activating SnRK2 kinases (Planas-Riverola et al., 2019). BR activates VND TFs that induce xylem differentiation. In the *in vitro* vascular cell induction system VISUAL, formation of ectopic xylem is inhibited in the BR signaling mutant *bes1−1* (Saito et al., 2018).

(ARF5)/MONOPTEROS (MP) (Berleth and Jürgens, 1993; Bishopp et al., 2011). High levels of auxin, primarily within the xylem precursors, activate *MP*, which in turn induces *TARGET OF MONOPTEROS5* (*TMO5*) (Schlereth et al., 2010). TMO5 in complex with LONESOME HIGHWAY (LHW), controls procambial periclinal cell divisions (Ohashi-Ito et al., 2013),

by promoting cytokinin (CK) biosynthesis via the activation of *LONELY GUY3* (*LOG3*) and *LOG4* (De Rybel et al., 2014; Ohashi-Ito et al., 2014). Although CK is synthesized within the xylem domain, CK response is low here (Bishopp et al., 2011). Instead, CK is sensed in the neighboring procambial cells, where it activates several DNA-binding one finger (DOF) TFs to promote procambial periclinal cell divisions (Miyashima et al., 2019; Smet et al., 2019). CK also promotes the expression of auxin efflux carriers PIN3 and PIN7, which move auxin laterally into the xylem domain (Bishopp et al., 2011). Auxin, in the protoxylem positions, induces *HISTIDINE PHOSPHOTRANSFER PROTEIN6 (AHP6)* (Bishopp et al., 2011), a negative regulator of CK signaling (Mähönen et al., 2006), partially explaining the reduced CK response and limited periclinal cell divisions within the xylem axis. Within the central xylem axis, auxin biosynthesis promotes HD-ZIP III transcription (Ursache et al., 2014), and it is possible that these factors contribute to the suppression of CK signaling, as they can inhibit B-type response regulators (B-ARRs) under conditions of high CK levels (Sebastian et al., 2015). Modeling approaches have shown that the above described interactions are sufficient to generate *de novo* patterning, replicating both a diarch and more complex anatomical patterns that are seen in other plant species, primarily depending on the size of the stele (Mellor et al., 2017, 2019). The patterning factors are further intertwined, as the HD-ZIP III TFs both interfere with auxin signaling (Müller et al., 2016), and suppress expression of cytokinin induced DOF TFs, while certain DOF TFs move from the phloem to positively influence HD-ZIP III expression in intervening procambial cells (Miyashima et al., 2019). Hence, it is conceivable that, similar to ABA's influence on miR165/HD-ZIP III TFs, this complex network is targeted at multiple points by abiotic signals to alter xylem development. It remains to be examined if the formation of extra xylem strands, widening the xylem axis, observed under water limiting conditions, is the effect of ABA impinging on the delicate auxin-cytokinin balance that normally demarcates domains of low and high periclinal division activity. Multiple examples where abiotic stresses, and ABA specifically, intersect with and affect auxin and cytokinin can be found in other contexts for example in the regulation of seed germination, cell elongation and root growth (Verslues, 2016; Bielach et al., 2017; Huang et al., 2018). Such an intersection may therefore be anticipated also in the regulation of vascular patterning.

ABIOTIC STRESS AFFECTS ROOT XYLEM DIFFERENTIATION TO INFLUENCE DROUGHT TOLERANCE

The xylem precursor cells, patterned and specified by the auxin-cytokinin/HD-ZIP III regulatory networks, differentiate into functional xylem vessels through a differentiation program involving programmed cell death and SCW deposition (reviewed by Furuta et al., 2014). Apart from XND1, TFs of another NAC subfamily, VASCULAR NAC DOMAIN (VND), are master regulators of xylem differentiation, and overexpression of any of the seven VND-genes result in trans-differentiation of other cell types into tracheary element cells (Kubo et al., 2005; Endo et al., 2015). A hierarchical TF network with VNDs regulating two tiers of MYB domain TFs acts directly upstream of lignin and cellulose biosynthesis genes (Taylor-Teeples et al., 2014; Turco et al., 2019). Network perturbation analysis revealed that one of the HD-ZIP III TFs, REVOLUTA is a negative regulator of lignin biosynthesis, and that the network modulates xylem development under conditions of iron deficiency or salt stress (Taylor-Teeples et al., 2014). The increase in expression of lignin biosynthesis genes under iron deficient conditions is dependent on reduction in *REV* levels, while *MYB46* and *VND7* play crucial roles in enhancing xylem differentiation during salt stress (Taylor-Teeples et al., 2014). Thus, the presence of several upstream regulators of SCW biosynthesis allows the use of specific TFs in response to different types of stresses. Interestingly, in apple, MdMYB88 and MdMYB122 were found to influence hydraulic conductivity by affecting xylem density, diameter, and the expression of SCW biosynthesis genes (Geng et al., 2018). The activation of SCW biosynthesis genes to maintain root hydraulic conductivity during drought stress was found to be through their direct regulation of *MdVND6* and *MdMYB46,* suggesting that co-option of xylem development regulators maybe be evolutionarily conserved.

Intriguingly, low levels of ABA, even under non-stressed conditions, are required for the formation of continuous xylem strands, since both ABA-biosynthesis and signaling mutants have patches along the xylem strands that are either retained in an undifferentiated procambial state or are xylem cells with defective SCW formation (**Figure 1**; Ramachandran et al., 2018). Suppression of ABA signaling in cell-layers external to the stele, such as in the endodermis or epidermis also resulted in similar discontinuous xylem suggesting a non-cell autonomous effect of ABA. Indeed, inhibition of ABA biosynthesis or suppression of endodermal ABA signaling reduced *MIR165A* levels and consequently elevated the expression of certain HD-ZIP III genes (Ramachandran et al., 2018). ABA is also important during secondary development as ABA biosynthesis mutants exhibit delayed xylem fiber formation (Campbell et al., 2018). Contrastingly, exogenous ABA treatment induces protoxylem differentiation closer to the root tip in Arabidopsis and tomato (Bloch et al., 2019) suggesting that in addition to interfering with xylem identity ABA promotes differentiation. Interestingly, endodermal ABA signaling acts in a similar manner to promote suberization of the endodermis (**Figure 1**; Barberon et al., 2016). The movement of AHP6 from protoxylem precursors and neighboring pericycle cells to the endodermis represses cytokinin signaling allowing the formation of "passage cells" lacking suberization for the entry of water and nutrients into the stele. Increase in ABA levels enhances endodermal suberization and reduces passage cell number (Andersen et al., 2018). It will be important to further explore how the differentiation programs of xylem and endodermis are intertwined and how this may influence radial conductivity of water and nutrients. Furthermore, endodermal ABA signaling can also affect lateral root development (Duan et al., 2013), hinting toward the endodermis as a hub for multiple

developmental changes upon drought, from xylem patterning to root architecture.

BRASSINOSTEROIDS AND THERMOSPERMINES AFFECT XYLEM DIFFERENTIATION AND IMPACT ON ABIOTIC STRESS TOLERANCE

Use of Arabidopsis and *Zinnia in vitro* cell culture systems, where cells are triggered to trans-differentiate into xylem cells, have identified brassinosteroids (BR) as molecular cues that promote xylem differentiation (Yamamoto et al., 1997; Tan et al., 2019). The addition of BR or chemical inhibitors of BR signaling repressors to culture media containing auxin and cytokinin promoted xylem differentiation in a VND-dependent manner (Kondo et al., 2014; Tan et al., 2018). Although BR and ABA seem to act similarly with respect to promotion of xylem differentiation, there is substantial evidence for BR-ABA antagonism at several levels. BR and ABA responsive TFs, *BRI1 EMS SUPPRESSOR1* (*BES1*) and *RESPONSIVE TO DESICCATION* (*RD26*), respectively, share common targets but regulate them in opposing ways (Chung et al., 2014). Under normal conditions, BR signaling promotes growth in a BES1 dependent manner, however, upon exposure to stress the activation of RD26 inhibits BR mediated growth through the regulation of BES1 targets. Interestingly, while the application of BR promotes drought tolerance in a concentration dependent manner, genetic evidence indicates that loss of BR receptor function can also confer drought tolerance (reviewed by Nolan et al., 2020). Adding to the complexity, the overexpression of one of the BR receptors, BRASSINOSTEROID INSENSITIVE1 LIKE3 (BRL3) also conferred drought tolerance, without affecting growth, through the accumulation of osmoprotectant sugars in the root (Fàbregas et al., 2018). The antagonistic function of BR and ABA in growth modulation, but their similar effects in promoting xylem formation, raises the question of whether the two hormones might regulate similar sets of genes but under different conditions thus providing a frame work to regulate xylem development independent of growth inhibition. Also, other molecules need to be included into the equation: in the BR receptor mutant *bri1*, the root procambial cells differentiate into xylem, resulting in an increased number of xylem vessels in a BR independent manner. This is due to the positive effect that BRI1 exerts on phytosulfokine (PSK) signaling, and mutants defective in PSK signaling display similar ectopic xylem differentiation in procambial positions (Holzwart et al., 2018). The involvement of BRI1 in BR, ABA, and PSK signaling provides challenges to dissect the individual roles of these components in controlling xylem development and if they function together in stress mediated xylem modifications.

Another molecule with a capacity to regulate xylem differentiation is the polyamine thermospermine. This molecule represses xylem differentiation, as mutations in the thermospermine synthase gene, *ACAULIS5* (*ACL5),* result in earlier xylem differentiation (Muñiz et al., 2008). Furthermore, ACL5 influences procambial divisions as thermospermine affects the translation of the auxin induced SUPPRESSORS OF ACAULIS51 LIKE (SACL) group of bHLH TFs. The SACL TFs are paralogs to TMO5, and compete for dimerization with LHW, thereby restricting TMO5-mediated promotion of procambial divisions (Katayama et al., 2015; Vera-Sirera et al., 2015). Interestingly, the *acl5* mutant, which has excess xylem formation, is salt sensitive while mutations in the gene encoding a thermospermine catabolizing enzyme, *POLYAMINE OXIDASE 5 (PAO5),* or treatment with thermospermine which results in fewer xylem vessels, rendered the plant tolerant to salt stress (Shinohara et al., 2019). Thus, here fewer xylem strands correlate with an increased tolerance to salt stress, possibly by reducing the systemic spread of salt toxicity. However, *acl5* mutants displayed wildtype-like sensitivity when exposed to drought and mannitol treatments suggesting that different mechanisms are at play in mediating salt and drought stress tolerance. Interestingly, *pao5* mutants, which show elevated levels of thermospermine, spermine, and N'-acetyl spermine and have fewer xylem vessels in the root display tolerance to drought and reduced sensitivity to ABA thus indicating that the levels of these molecules can be modulated during stress to alter xylem development (Shinohara et al., 2019). A study in poplar revealed that thermospermine level established by a negative feedback regulation between ACL5, auxin and the HD-ZIP III TF ATHB8 is important for proper xylem differentiation (Milhinhos et al., 2013). Further investigations into the roles of these polyamines and how they function together with other xylem development regulators during stress will be important to understand how polyamine modulation can confer stress tolerance.

LONG DISTANCE SIGNALING COMPONENTS INFLUENCING XYLEM DEVELOPMENT

To cope with environmental stressors, plants have developed an array of long-distance signaling cascades that include hydraulic, electrical, and chemical signals (Huber and Bauerle, 2016). An example of how such long-range signals can impact root xylem development comes from experiments where wounding of Arabidopsis cotyledons resulted in hydrogen peroxide accumulation in the root causing root xylem differentiation closer to the root tip (Fraudentali et al., 2018). Jasmonic acid (JA), a wound induced signal, may be one such long-range signal as JA was found to cause hydrogen peroxide accumulation and early xylem differentiation (Ghuge et al., 2015). It has been suggested that JA and CK signaling pathways have antagonistic interactions (reviewed by O'Brien and Benková, 2013) and they play similar antagonistic roles in xylem development. Exogenous application of methyl-JA for long periods caused the formation of extra xylem strands by promoting xylem differentiation of procambial cells. This xylem promoting effect of JA was accomplished by interference with the auxin/cytokinin balance within the stele, through ectopic activation of AHP6, which suppresses cytokinin response, and repression of *PIN7* expression within the procambial domain (Jang et al., 2017, 2019). Further, reduced

water availability activated the expression of JA responsive genes, LIPOXYGENASE2 (*LOX2)* and JASMONATE INSENSITIVE 1 (*JAI1*/*MYC2)*, indicating that during drought stress JA signaling might be another pathway involved in xylem developmental plasticity (Jang and Choi, 2018).

A recent study identified the CLAVATA3/EMBRYO-SURROUNDING REGION-RELATED25 (CLE25) peptide to act as a mobile signal from the root to the leaves under dehydration conditions (Takahashi et al., 2018). Application of CLE25 to Arabidopsis seedlings, induced ABA biosynthesis and resulted in ABA mediated stomatal closure (Takahashi et al., 2018). The receptor BARELY ANY MERISTEM1 (BAM1) involved in CLE25 signaling, also associates with CLE9/10 to restrict xylem cell number. Mutants defective in *CLE9/10* display increased periclinal cell divisions within the xylem axis resulting in more xylem vessels (Qian et al., 2018). Interestingly, in cotyledons, CLE9 perception and signaling through a different receptor, HAESA-LIKE1, negatively affects the number of guard cells (Qian et al., 2018). Hence, the mobility of CLE peptides and their ability to control two aspects of plant development that are involved in hydraulic conductance warrants further investigation into how these peptides might coordinate drought stress responses in the root and shoot.

WHAT CAN WE LOOK FORWARD TO?

Studies on Arabidopsis have revealed how different regulatory components influence root xylem developmental. Existing evidences point toward the repurposing of core developmental regulators to bring about phenotypic alterations in response to environmental perturbations. However, there are missing links on how different environmental inputs are interpreted by the plant. Recent progress in single cell sequencing technologies will help identify how the developmental trajectories of specific cell types are altered by external stimuli and find components central to phenotypic plasticity (Rodriguez-Villalon and Brady, 2019; Ryu et al., 2019; Shulse et al., 2019). The understanding of plant response to water stress requires simultaneous monitoring of various physiological characteristics, such as modifications to the xylem vessel diameter and number, properties of the cell wall such as lignification or suberization and composition of the soil-root-microbiome interface (reviewed by Lynch et al., 2014). Plant imaging platforms such as *light* sheet fluorescence microscopy and Growth and Luminescence Observatory for Roots (GLO-Roots) allow not only the analysis of root system architecture and anatomical phenes but also the visualization of gene expression patterns, enabling the simultaneous characterization of responses at physiological and molecular levels (Rellán-Álvarez et al., 2015; von Wangenheim et al., 2020). In addition, computational simulation tools such as GRANAR, which facilitate studies on the effect of different monocot root anatomies on root hydraulic conductivity (Heymans et al., 2020) or OpenSimRoot, which can be used to reconstruct root systems, in combination with hydraulic models, will aid the study of anatomical parameters that influence water transport (Postma et al., 2017). One has to bear in mind, though, that varieties that constitutively employ theoretical water saving strategies are not always best suited for real world growth regimes (Skirycz et al., 2011). Rather, the future of agriculture likely lies in the generation of "personalized crops" that are designed to suit the climate, soil properties and microbiota of a certain region. To meet such a goal, multiple approaches will be needed, including further exploration into the extent of natural variation. Interestingly, the Arabidopsis C24 ecotype has been found to be tolerant to multiple stress factors and has a unique combination of low water use and high seed biomass (Bechtold et al., 2010; Bechtold et al., 2018), thus the underlying genetics of this and similar studies on naturally occurring stress tolerant populations of a species can guide approaches in crop breeding. Alternatively, available knowledge on regulatory networks such as those described in this review can be harnessed to alter phenotypes specifically and rationally.

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Crop Load Influences Growth and Hormone Changes in the Roots of "Red Fuji" Apple

*Bowen Liang†, Yu Sun†, Zhongyong Li, Xueying Zhang, Baoying Yin, Shasha Zhou and Jizhong Xu**

College of Horticulture, Hebei Agricultural University, Baoding, China

Crop load has a substantial impact on growth of the aerial and belowground parts of apple trees. Here, we examined the effects of different crop loads on growth and hormone levels in apple roots. A crop load of 1.5 (T1.5) fruits per cm^2 trunk cross-sectional area (TCSA) treatment resulted in lower root growth vigor, while non-fruiting (T0) and T0.4 conditions showed higher root growth vigor. In all treatments, dead roots increased in length 90 days after full bloom (DAFB), whereas live roots were more abundant at about 50 and 170 DAFB, showing a bimodal curve. During each root growth peak, levels of cytokinins (CTKs), indole acetic acid (IAA), and gibberellic acid (GA_3) were higher. Moreover, hormone levels gradually decreased with increasing crop load within each peak. Root turnover tended to decrease with decreasing crop load. These findings indicate that root growth and hormone contents were positively correlated during the fruit growth phase, and that the negative impact of crop load on root growth may have been caused by hormone level decreases.

Keywords: apple, root system, endogenous hormones, minirhizotron, fruit load

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***Correspondence:**
Jizhong Xu
xjzhxw@126.com

†These authors have contributed equally to this work

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INTRODUCTION

Alternate bearing is one of the greatest problems in apple production, resulting in unbalanced production and fruit quality. This issue can be alleviated by managing an appropriate crop load, which influences vegetative and productive growth (Smith and Samach, 2013). For instance, excessive crop load may reduce shoot elongation, leaf growth, and root development, which directly affect photosynthesis and carbon allocation. Root growth is of great significance for vegetative growth, because nutrients are necessary for the energy required for both photosynthesis and root uptake. Studies investigating the effects of fruits on photosynthesis, partitioning of assimilates, and dry matter accumulation have shown higher leaf photosynthetic efficiency in fruiting than in non-fruiting trees (Heim et al., 1979; Negi and Sharma, 2011). Both roots and fruits, non- or low-photosynthetic organs, act as sinks depending exclusively on photosynthetic products imported from leaves. Thus, root growth is much greater in non-fruiting trees than in fruiting trees (McClure and Cline, 2015). Unequal competition among sinks may cause a disequilibrium between vegetative and reproductive growth due to changes in carbon allocation, which may lead to a new source/sink balance and water and nutrient supplies. Carbon distribution plays an important role in root development. Despite studies on fruit and shoot growth, the effects of crop load on root growth and development remain unclear.

Phytohormones are endogenous substances that play vital roles in plant growth and development. Hormone signals transmit information about environmental and endogenous changes to integrate the physiological responses of the whole plant to optimize growth and development, and form new source–sink balances (Lemoine et al., 2013). The initiation and development of roots, which supply water and nutrients, are affected by the combined actions of endogenous phytohormones. Plant growth is modulated by sink strength, and cytokinins (CTKs) regulate the rate-limiting steps that determine nutrient availability by establishing local metabolic sinks (Werner et al., 2008). CTKs have an inhibitory effect on lateral root initiation and a stimulatory effect on lateral root elongation. Exogenously applied CTKs completely inhibit lateral root primordia formation and stimulate lateral root elongation by increasing cell length (Goodwin and Morris, 1979). Exogenously applied auxin counteracts the effect of CTKs on lateral root initiation and elongation, suggesting that CTKs act on lateral root elongation through an auxin-dependent pathway (Debi et al., 2003). Numerous studies have shown that auxin is necessary for lateral root initiation and subsequent growth (Blakely et al., 1988; Celenza et al., 1995; Reed et al., 1998). Exogenous application of auxin or enhancement of endogenous auxin synthesis results in a significant increase in the number of lateral roots (Kares et al., 1990; Boerjan et al., 1995; Laskowski et al., 1995). CTKs, together with auxin, play an essential role in plant morphogenesis, and have a strong influence on root and shoot formation and relative growth. CTKs act antagonistically to auxin and determine cell senescence by promoting shoot and root differentiation in callus culture (Laplaze et al., 2007).

Many studies have reported on the physiological functions of gibberellins (GAs) during root growth. Concentration-dependent stimulation of elongation growth by GA is important for regulating plant height and root length. In GA depletion experiments, either by inhibiting GA biosynthesis or using GA-deficient mutants, remarkable thickening of roots was observed, while slender roots were induced by GA treatment (Tanimoto, 1987, 1994). Furthermore, GA clearly stimulated root elongation under growth-suppressed conditions induced by a GA biosynthesis inhibitor (Zhang and Hasenstein, 1999). Finally, Tanimoto (2012) showed that endogenous GA content affected the root-to-shoot ratio.

The effects of hormones on root development have been well documented (Casimiro et al., 2003; Peret et al., 2009; Petricka et al., 2012). However, few such studies have applied minirhizotron methods. Despite the large body of experimental work on exogenous hormone application to roots, little is known about the effects of crop load on endogenous hormone contents, root growth, and their interactions. Therefore, to gain a better understanding of the effects of crop load on the belowground response, we conducted an experiment using minirhizotrons, which allowed for clear, accurate, and continuous observations of root growth. Plants were grown in pots for accurate observations, and the root growth dynamics and root hormone contents under different crop loads were determined. The minirhizotron observation method allowed us to compare root length, surface area, and volume under different crop load conditions during the observation period, revealing the changes in root growth dynamics and the relationship between root growth and root hormone contents. Our hypothesis was that crop load would have a negative effect on root CTK, GA_3, and IAA contents, thereby reducing root growth. To test this hypothesis, we assessed root growth dynamics and root hormone contents.

MATERIALS AND METHODS

Plant Materials

The trials were conducted at Hebei Agricultural University, Baoding, Hebei, China. We used 4-year-old Tianhong 2/SH40/Baleng crabapple potted plants. All plants were grown in cylindrical root limiter (30 cm × 30 cm) filled with loam in a greenhouse under natural temperature and light conditions.

Experimental Design

On April 19, 2018, plants of similar size (height, ∼1.5 m, trunk girth, 21 cm) were transplanted into cylindrical non-woven fabric pots (75 cm × 60 cm) filled with loam. The spacing between plants and rows was 1 m × 1.5 m. For root growth observations, two minirhizotrons (length, 60 cm; diameter, 7 cm) were installed 25 cm from the trunk on the east and west sides of each plant during transplanting. The experimental layout was completely randomized and we selected 24 plants and divided these into four crop load treatments. The plant material was thinned on May 18, and crop loads of 0 (T0), 0.4 (T0.4), 1.1 (T1.1), and 1.5 (T1.5) fruits per cm^2 trunk cross-sectional area (TCSA) were set up. Each treatment was repeated six times. Drip irrigation was used with two drippers per pot evenly distributed on both sides of the plant. Beginning at 50 days after full bloom (DAFB) on June 8, the roots were sampled with a soil sampler every 20 days to determine hormone contents. After sampling, the samples were transported to the laboratory and cleaned in distilled water, and then put into liquid nitrogen and stored at −80°C.

Root Data Acquisition and Analysis

The root Scanner-R root detection system was used to scan and collect root images every 20 days beginning 50 DAFB. Root analysis software was used to process the images, and the occurrence and death of new roots were observed and recorded. Relevant indicators were calculated based on unit soil volume (S × D), where S is the area of the cultivation matrix observed by a single minirhizotron ($S = 7\pi \times 22$ cm^2) and D is the observed thickness of the substrate ($D = 0.25$ cm). Roots that were un-suberized and white or changing to brownish in subsequent viewings were recorded as living. Roots were defined as dead when they turned black and produced no new roots on subsequent occasions (Wei et al., 2019).

Root length density ($mm \cdot cm^{-3}$) = L/(S × D), where L is the total length of a single minirhizotron. Root surface area density ($mm^2 \cdot cm^{-3}$) = SA/(S × D), and total root surface area (mm^2) of a single micro root canal. Root volume density

($mm^3 \cdot m^{-3}$) = V/(S × D), where V is the total volume of a single micro root canal (mm^3). Root number density ($\times 10\ m^{-3}$) = TN/(S × D), where TN is the total number of single micro root canals ($\times 10^3$). The annual mortality of fine roots was calculated by the total length of dead roots per unit volume of soil, and the number of live roots was calculated by the total length of living roots per unit volume each time we observed the roots. Root turnover was estimated by the ratio of total dead root length to average live root length for the entire observation period based on the method used by Majdi and Andersson (2005).

Determination of Hormone Content in Roots

The samples for hormones were collected under different crop loads at 50, 70, 90, 110, 130, 150, and 170 DAFB. Endogenous hormones, including indole acetic acid (IAA), zeatin riboside (ZR), dihydrozeatin riboside (DHZR), kinetin (KT), isopentenyladenine (IP), and gibberellic acid (GA_3) contents were extracted from root samples, using a high-performance liquid chromatography method described by Fang et al. (1998). Absorbance in each well was measured at 260 nm using a microplate reader (Infinite M200; Tecan, Vienna, Austria). The extracted phytohormones were separated by nano-flow reversed-phase liquid chromatography on a nano-LC system (1260 series; Agilent Technologies, Palo Alto, CA, United States) using a nano Acquity Eclipse Plus C18 column (0.5 μm, 250 × 4.6 mm; Agilent Technologies) at a flow rate of 0.7 $mL \cdot min^{-1}$ at 30°C in a mobile phase of 40% acetic acid in 0.7% or 5% acetonitrile and 55% methanol. The samples were measured at 254 nm on a VWD Chemstation (Agilent 1260 VWD), and the retention time was 10 min. The hormones were quantified based on standard curves and expressed as ng g^{-1} fresh weight. The standard curves for each hormone were as follows: ZR ($y = 0.0216x - 0.6876$, $R^2 = 0.9994$), DHZR ($y = 0.0253x - 0.419$, $R^2 = 0.9998$), IP ($y = 0.0225x - 0.0986$, $R^2 = 0.9998$), KT ($y = 0.0213x - 0.0987$, $R^2 = 0.9996$), IAA ($y = 0.0764x - 0.1301$, $R^2 = 0.9998$), GA_3 ($y = 0.4474x - 0.7624$, $R^2 = 0.9937$).

Statistical Analysis

Experimental data are presented as the mean ± standard deviation (SD). All data were analyzed by one-way analysis of variance followed by Tukey's multiple range test to detect differences among the groups. All statistical analyses were performed using SPSS 20.0 software (IBM Corp., Armonk, NY, United States). A p-value < 0.05 was considered significant.

RESULTS

Effects of Different Crop Loads on Live Root Development

To determine the effects of crop load on root development, we observed the roots every 20 days from 50 to 190 DAFB. Live root length density, live root surface area density (LRSAD), and live root volume density (LRVD) were determined (**Figure 1**). The results showed that root growth peaked at 150 DAFB under all crop loads. Among the peaks, root growth at the higher crop loads was significantly inhibited compared to that at lower crop loads. The growth peaks were less obvious after observing that the number of roots decreased from 50 to 110 DAFB. During this period, more roots were maintained under T0.4 than the other treatments. The root developing conditions of T0 differed markedly from all other treatments, showing a constantly increasing trend (**Figure 1A**). Root surface area and volume densities changed in a similar manner in all treatments, remaining relatively low from 50 to 110 DAFB, then increasing, and peaking at 170 DAFB. Among the peaks, LRSAD and LRVD at 130 DAFB were significantly higher in T0 and T1.5 showed the lowest levels ($p < 0.05$). The tendencies of the two parameters for each treatment were similar, although LRVD was higher than LRSAD for T0 and T0.4 (**Figures 1B,C**). Overall, T0 and T0.4 had longer roots than all other treatments, indicating the inhibition of root growth at higher crop loads.

Effects of Different Crop Loads on Dead Root Length Density and Root Turnover

The dead root length density (DRLD) in all treatments peaked at 90 DAFB (**Figure 2**), and then decreased gradually, but increased again 190 DAFB. At their peaks, T0, T0.4, and T1.1 had significantly higher DRLDs than T1.5 ($p < 0.05$). The DRLDs of T1.1 and T1.5 were significantly higher at 190 DAFB than those in T0 and T0.4, and the DRLD of T0 was significantly lower than those in the other treatments. Significant differences were observed in root turnover under different crop loads during the observation period (**Figure 3**). When compared with T0, the root turnover rate were increased by 66.67, 125.00, and 125.00% in T0.4, T1.1, and T1.5, respectively. Overall, root turnover presented an increasing tendency with increasing crop load.

Effects of Different Crop Loads on Root CTK Content

Crop load significantly affected endogenous hormonal levels in roots, and root CTK content exhibited a bimodal curve throughout the fruit development stages (**Figure 4**). At both 90 and 130 DAFB, the ZR contents were significantly higher in lower and non-crop load treatments than in higher crop load treatments. The first peak appeared from 70 to 90 DAFB, and the second peak appeared from 110 to 130 DAFB; those of the four treatments appeared at different periods (**Figure 4A**). The root IP content also exhibited a bimodal curve throughout the fruit development period, with two peaks appearing at 90 and 130 DAFB. At both 90 and 130 DAFB, the root IP contents were significantly higher in T0 and T0.4 than in T1.1 and T1.5. Lower crop load treatments showed higher IP content, which decreased with increasing crop load (**Figure 4B**). The DHZR contents in all treatments increased after 70 DAFB, with the first peak at 90 DAFB and the second peak at 150 DAFB. The DHZR content during the first peak was significantly higher in T0.4 than the other treatments, whereas T1.5 had the lowest level. The DHZR content decreased with increasing crop load, and T0 exhibited the highest level among the treatments during the second peak (**Figure 4C**). Root KT content also exhibited a

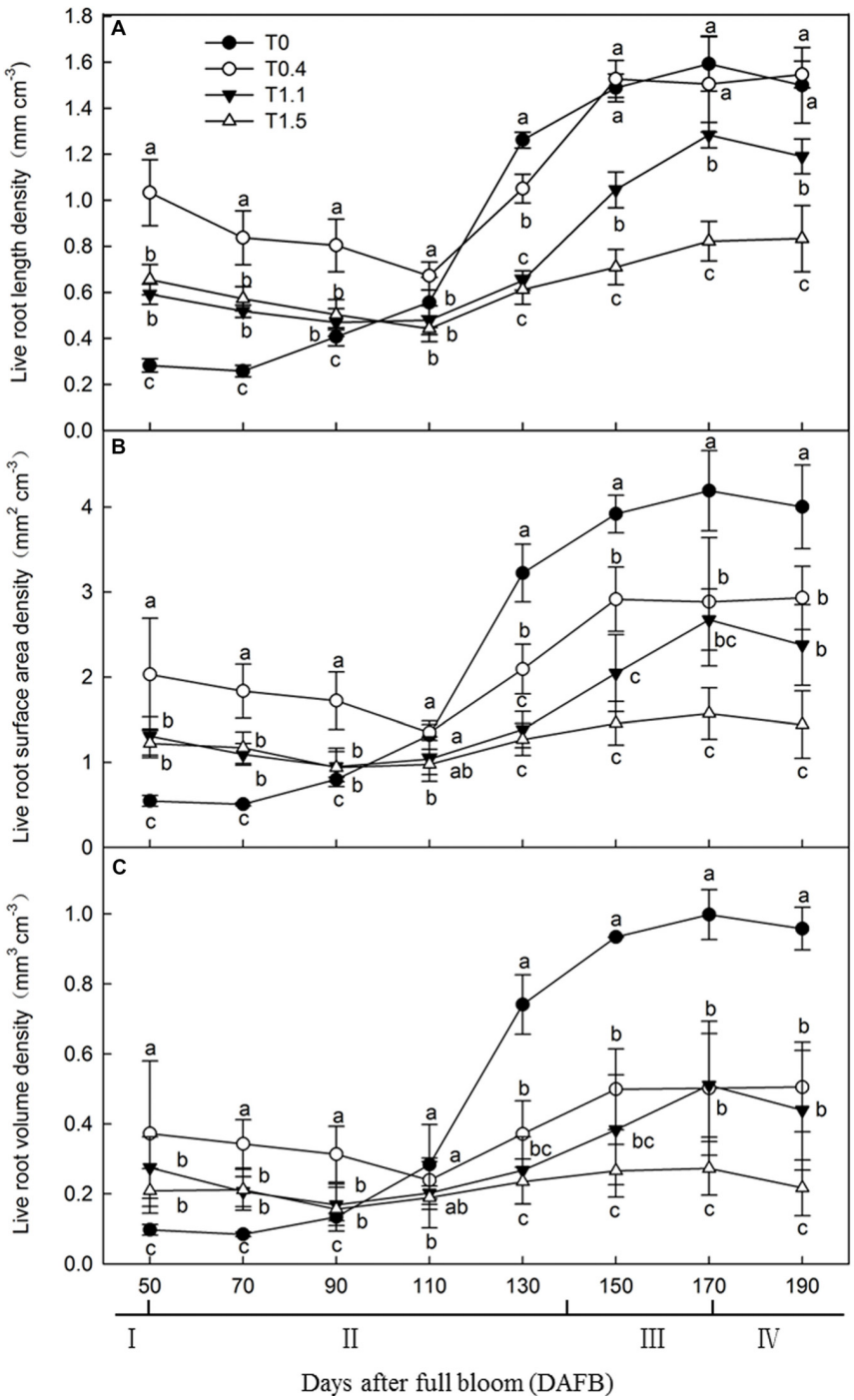

FIGURE 1 | Changes in the live roots length density [LRLD **(A)**], the live root surface area [LRSAD **(B)**] and live roots volume density [LRVD **(C)**] of "Red Fuji" apple under different crop load treatments from 50 days after full bloom (DAFB) to 190 DAFB. Data are means ± SD of three replicate samples. Treatments: T0, the crop load levels of 0 fruits cm^{-2} TCSA; T0.4, the crop load levels of 0.4 fruits cm^{-2} TCSA; T1.1, the crop load levels of 1.1 fruits cm^{-2} TCSA; T1.5, the crop load levels of 1.5 fruits cm^{-2} TCSA. I, fruit set stage; II, fruit growth stage; III, fruit ripening stage; IV, fruit harvest stage. Different letters indicate significant differences between treatments, according to one-way ANOVA followed by Tukey's multiple range test at $P_{0.05}$ level.

bimodal distribution, except for T0.4. The first peak appeared from 70 to 90 DAFB, and the second peak appeared from 130 to 150 DAFB. The KT contents in T1.1 and T1.5 at the first peak were significantly higher than those in the other treatments. However, after 90 DAFB, the KT content was significantly lower in T1.5 than in the other treatments (**Figure 4D**).

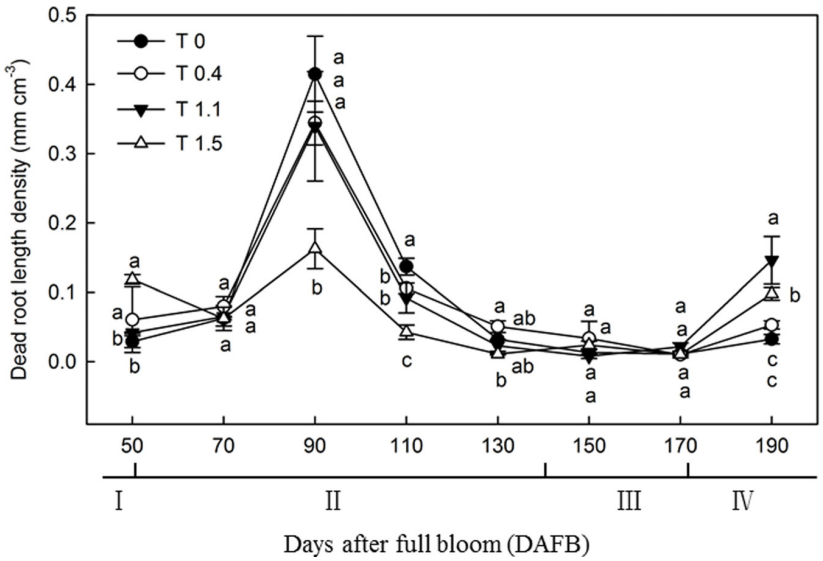

FIGURE 2 | Changes in the dead root length density (DRLD) of "Red Fuji" apple under different crop load treatments from 50 to 190 DAFB. Data are means ± SD of three replicate samples. Treatments: T0, the crop load levels of 0 fruits cm^{-2} TCSA; T0.4, the crop load levels of 0.4 fruits cm^{-2} TCSA; T1.1, the crop load levels of 1.1 fruits cm^{-2} TCSA; T1.5, the crop load levels of 1.5 fruits cm^{-2} TCSA. I, fruit set stage; II, fruit growth stage; III, fruit ripening stage; IV, fruit harvest stage. Different letters indicate significant differences between treatments, according to one-way ANOVA followed by Tukey's multiple range test at $P_{0.05}$ level.

Effects of Different Crop Loads on Root Auxin Content

The changes in IAA content were similar among the four crop loads, with unimodal curves peaking at 130 DAFB (**Figure 5**). At 130 DAFB, the IAA content was significantly higher in T0 than T1.1 and T1.5. No significant differences were observed in IAA contents between T0.4 and T0 or T1.1, but the IAA contents were significantly higher than that in T1.5 treatment ($p < 0.05$). The IAA content in T1.5 was significantly lower than that in the other treatments throughout the observation period ($p < 0.05$). At 110 DAFB, the IAA contents differed significantly among the four treatments. The IAA content was significantly higher in T0 than in the other treatments, and was significantly higher in T0.4 than in T1.1 and T1.5, whereas the IAA content was significantly lower in T1.5 than in the other treatments ($p < 0.05$).

Effects of Different Crop Loads on Root GA_3 Content

The root GA_3 content exhibited a bimodal distribution through the fruit development stage in T0.4 and T1.1, and a unimodal distribution in T0 and T1.5 (**Figure 6**). In T0.4 and T1.1, the first GA_3 content peak occurred at 90 DAFB; the GA_3 content was significantly higher in T0.4 than the other treatments, and was significantly higher in T1.1 than in T0 and T1.5 ($p < 0.05$). The GA_3 content also peaked at 130 DAFB. By contrast, the lowest GA_3 contents were observed at 110 DAFB for all four treatments. At 130 DAFB, the GA_3 content was significantly higher in T0.4 and T1.1 than in T0 and T1.5, and was significantly higher in T0 than in T1.5 ($p < 0.05$).

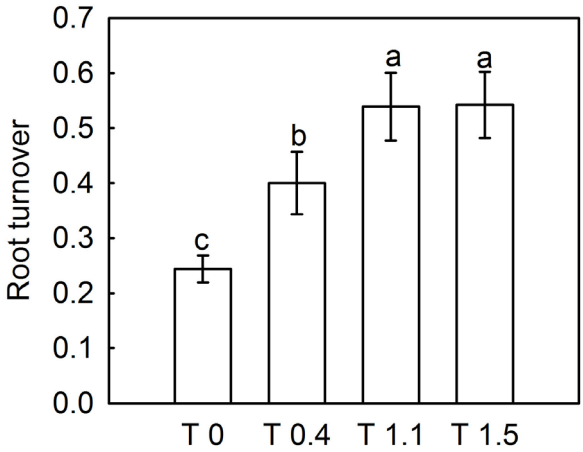

FIGURE 3 | Effect of different crop load treatments on the root turnover of "Red Fuji" apple. Data are means ± SD of six replicate samples. Different letters denote significant differences at $P_{0.05}$ by Tukey's multiple range tests. Treatments: T0, the crop load levels of 0 fruits cm^{-2} TCSA; T0.4, the crop load levels of 0.4 fruits cm^{-2} TCSA; T1.1, the crop load levels of 1.1 fruits cm^{-2} TCSA; T1.5, the crop load levels of 1.5 fruits cm^{-2} TCSA.

DISCUSSION

We examined the effects of crop load on growth and phytohormone contents in Fuji/SH40/Baleng Crabapple roots. Pome fruit trees exhibit irregular root growth patterns, with periods of active growth alternating with less active growth periods (Reig et al., 2013). In the present study, root growth dynamics exhibited bimodal curves, with decreases at 110 DAFB

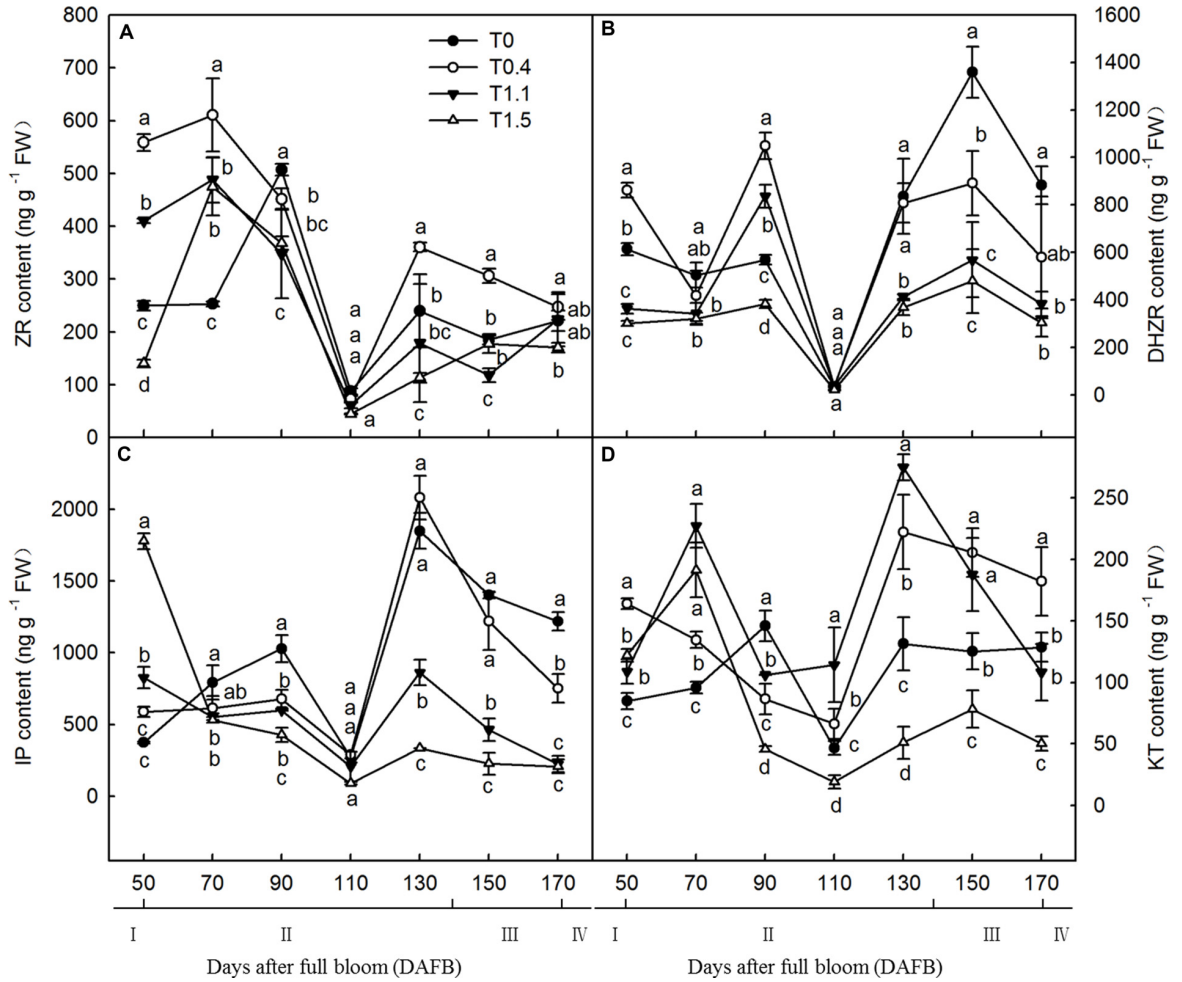

FIGURE 4 | Changes in the ZR **(A)**, DHZR **(B)**, IP **(C)**, and KT **(D)** content of "Red Fuji" apple roots under different crop load treatments from 50 to 170 DAFB. Data are means ± SD of three replicate samples. Treatments: T0, the crop load levels of 0 fruits cm^{-2} TCSA; T0.4, the crop load levels of 0.4 fruits cm^{-2} TCSA; T1.1, the crop load levels of 1.1 fruits cm^{-2} TCSA; T1.5, the crop load levels of 1.5 fruits cm^{-2} TCSA. I, fruit set stage; II, fruit growth stage; III, fruit ripening stage; IV, fruit harvest stage. Different letters indicate significant differences between treatments, according to one-way ANOVA followed by Tukey's multiple range test at $P_{0.05}$ level.

and a strong increase at 130 DAFB. Previous studies have shown that the fruit and vegetative growth of trees are affected by crop load, and that both shoot length and root growth are significantly restricted by excessive crop load (Pallas et al., 2018). These changes are induced by alterations in fixed carbon allocation to roots, because fruits are a major carbohydrate sink. Thus, during the most active period of fruit development, root growth parameters vary inversely with crop load. For example, Abrisqueta et al. (2017) reported that root growth activity was higher in non-fruiting trees than in fruiting trees. Similarly, decreases in root development were related to crop load in the present study; root growths was significantly higher in trees with low crop load than in those with high crop load. Thus, root growth was inhibited by crop load, possibly due to the absence of competition with fruit growth.

Cytokinins inhibit the initiation of root primordia but have a positive effect on root elongation, and IAA plays an important role in root initiation and elongation (Debi et al., 2005). GA has been shown to control root growth at a considerably lower concentration than is necessary for controlling shoot growth (Tanimoto, 1994). In the present study, increases in root growth corresponded with increases in hormones contents during the fruit development stage. Root development dynamics appear to have been mediated by hormones under different crop loads, such that the source–sink ratio and carbohydrate allocation affected hormone signaling during root development. High crop loads have been reported to decrease aerial part IAA content and basipetal transportation to roots, affecting root initiation and development (Casimiro et al., 2003; Van Hooijdonk et al., 2010). Our findings demonstrate that excessive crop load reduces root IAA content, thereby causing a decline in root growth. By extension, IAA content may also be positively correlated with root growth.

Reductions in hormone contents inhibits the development of root primordia, weakens growth vigor, and results in less root growth (Aloni et al., 2010). In the present study, the CTK and GA_3 levels in roots of the high crop load treatments were also the lowest among all treatments. CTKs and GA_3 in roots

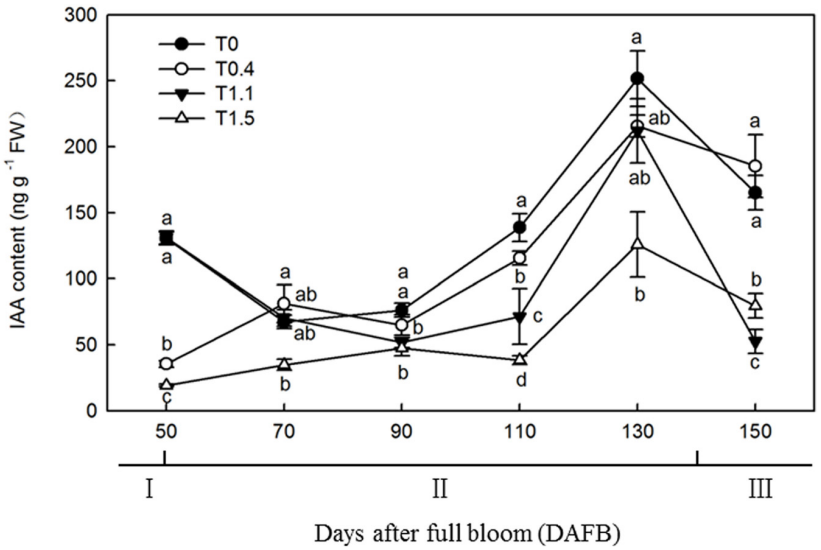

FIGURE 5 | Changes in the IAA content of "Red Fuji" apple roots under different crop load treatments from 50 to 150 DAFB. Data are means ± SD of three replicate samples. Treatments: T0, the crop load levels of 0 fruits cm^{-2} TCSA; T0.4, the crop load levels of 0.4 fruits cm^{-2} TCSA; T1.1, the crop load levels of 1.1 fruits cm^{-2} TCSA; T1.5, the crop load levels of 1.5 fruits cm^{-2} TCSA. I, fruit set stage; II, fruit growth stage; III, fruit ripening stage. Different letters indicate significant differences between treatments, according to one-way ANOVA followed by Tukey's multiple range test at $P_{0.05}$ level.

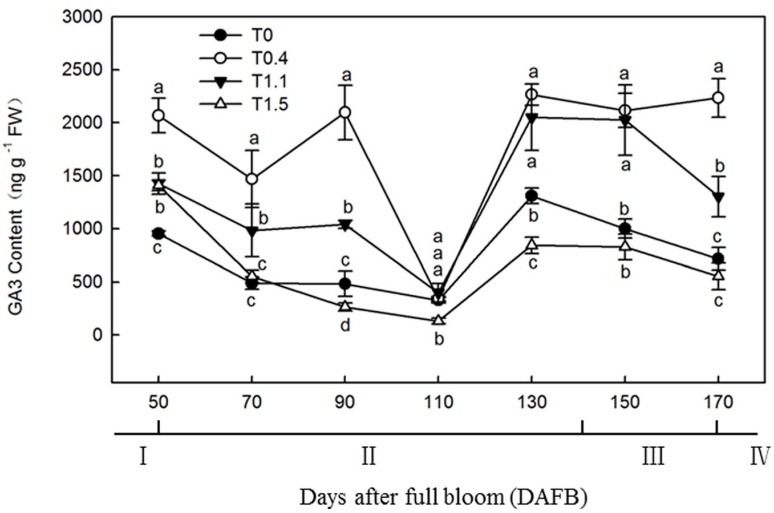

FIGURE 6 | Changes in the GA3 content of "Red Fuji" apple roots under different crop load treatments from 50 to 170 DAFB. Data are means ± SD of three replicate samples. Treatments: T0, the crop load levels of 0 fruits cm^{-2} TCSA; T0.4, the crop load levels of 0.4 fruits cm^{-2} TCSA; T1.1, the crop load levels of 1.1 fruits cm^{-2} TCSA; T1.5, the crop load levels of 1.5 fruits cm^{-2} TCSA. I, fruit set stage; II, fruit growth stage; III, fruit ripening stage; IV, fruit harvest stage. Different letters indicate significant differences between treatments, according to one-way ANOVA followed by Tukey's multiple range test at $P_{0.05}$ level.

may be regulated by IAA content and transport, considering that less vegetative growth affects the IAA level in both aerial and belowground parts of apple trees, resulting in less vigorous growth (Van Hooijdonk et al., 2010). Considering the relatively high levels of CTKs and GA_3 and the low quantity of roots in non-fruiting trees, an imbalance between hormone content and growth may be induced by undetected root growth in minirhizotrons. It can be assumed that the active growth in aerial parts provided abundant IAA to the roots, stimulating CTK and GA_3 synthesis. Studies have shown that exogenous CTKs enhance root elongation but have side effects on the initiation of root primordia, which differed from our study (Mao et al., 2018). However, unlike IP and DHZR, ZR, and KT did not correlate well with the root growth under different crop loads at 130 DAFB, but the highest crop load treatment did have the lowest root growth rate. It was reported that ZR and KT showed significant inhibitory effects on adventitious root formation (Kuroha et al., 2002). The inhibition of adventitious root formation by CTKs occurs during the induction phase of root cell division. During the induction phase, IAA induces adventitious root formation in apple cuttings

and seems to interact antagonistically with CTKs to control the initiation of adventitious roots (De Klerk et al., 1995). Endogenous CTKs along with IAA and GA_3 may work together to affect root development, masking the inhibitory effect of CTKs (Hayat et al., 2019). The regulation effect of phytohormones on root development is complex, and the functions of endogenous hormones are still need to be further studied.

Tworkoski and Miller (2007) reported that GA_3 negatively regulated radial growth of roots; thus, the higher concentration of GA_3 may have decreased radial root growth, resulting in a long and thin root phenotype. In this study, the low- or non-fruiting treatments resulted in a higher GA_3 content and higher root length density, which increased strongly after 130 DAFB; by contrast, root surface area and volume density did not increase as intensely as root length density. These differences may have been induced by the high root GA_3 content. We conclude that the differences in phytohormone levels could be responsible for differences in root growth vigor under different crop loads. In the present study, IAA, CTK, and GA_3 contents were positively correlated with root growth vigor in the different crop load treatments. The decline in root growth at 110 DAFB occurred when IAA, CTKs, and GA_3 reached their lowest levels, whereas hormone contents increased rapidly at 130 DAFB, and were subsequently maintained at relatively high levels. Root growth decreased after the root growth peak in fall along with the increase in crop load, which was positively correlated with hormone contents.

CONCLUSION

In conclusion, the results of this study confirm that fruit plays an important role in restricting root growth and hormone contents in apple. Trees with a low crop load showed more active root growth than trees with high crop loads. Excessive crop loads limited root growth and IAA, CTK, and GA_3 contents during the fruit growth phase. Our data also provided evidence that root growth dynamics and IAA, IP, DHZR, ZR, and GA_3 contents were positively correlated. We suggest that the decrease in IAA, CTK, and GA_3 levels in roots could be considered compliant with the root growth restriction caused by crop load.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

BL, YS, and JX conceived and designed the experiments. YS performed the experiments with assistance from ZL, XZ, BY, and SZ. BL performed the data analyses and wrote the manuscript. BL and JX provided financial support and helped to perform the analysis with constructive discussions.

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REVIEW
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Modulatory Role of Reactive Oxygen Species in Root Development in Model Plant of *Arabidopsis thaliana*

Xuemei Zhou[†], *Yu Xiang*[†], *Chenglong Li and Guanghui Yu*[*]

Hubei Provincial Key Laboratory for Protection and Application of Special Plants in Wuling Area of China, Engineering Research Centre for the Protection and Utilization of Bioresource in Ethnic Area of Southern China, College of Life Sciences, South-Central University for Nationalities, Wuhan, China

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***Correspondence:**
Guanghui Yu
yusheen@163.com
orcid.org/0000-0002-3174-1878

[†]*These authors have contributed equally to this work and share first authorship*

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Reactive oxygen species (ROS), a type of oxygen monoelectronic reduction product, have a higher chemical activity than O_2. Although ROS pose potential risks to all organisms *via* inducing oxidative stress, indispensable role of ROS in individual development cannot be ignored. Among them, the role of ROS in the model plant *Arabidopsis thaliana* is deeply studied. Mounting evidence suggests that ROS are essential for root and root hair development. In the present review, we provide an updated perspective on the latest research progress pertaining to the role of ROS in the precise regulation of root stem cell maintenance and differentiation, redox regulation of the cell cycle, and root hair initiation during root growth. Among the different types of ROS, $O_2^{\bullet-}$ and H_2O_2 have been extensively investigated, and they exhibit different gradient distributions in the roots. The concentration of $O_2^{\bullet-}$ decreases along a gradient from the meristem to the transition zone and the concentration of H_2O_2 decreases along a gradient from the differentiation zone to the elongation zone. These gradients are regulated by peroxidases, which are modulated by the UPBEAT1 (UPB1) transcription factor. In addition, multiple transcriptional factors, such as APP1, ABO8, PHB3, and RITF1, which are involved in the brassinolide signaling pathway, converge as a ROS signal to regulate root stem cell maintenance. Furthermore, superoxide anions ($O_2^{\bullet-}$) are generated from the oxidation in mitochondria, ROS produced during plasmid metabolism, H_2O_2 produced in apoplasts, and catalysis of respiratory burst oxidase homolog (RBOH) in the cell membrane. Furthermore, ROS can act as a signal to regulate redox status, which regulates the expression of the cell-cycle components CYC2;3, CYCB1;1, and retinoblastoma-related protein, thereby controlling the cell-cycle progression. In the root maturation zone, the epidermal cells located in the H cell position emerge to form hair cells, and plant hormones, such as auxin and ethylene regulate root hair formation *via* ROS. Furthermore, ROS accumulation can influence hormone signal transduction and vice versa. Data about the association between nutrient stress and ROS signals in root hair development are scarce. However, the fact that *ROBHC/RHD2* or *RHD6* is specifically expressed in root hair cells and induced by nutrients, may explain the relationship. Future studies should focus on the regulatory

mechanisms underlying root hair development *via* the interactions of ROS with hormone signals and nutrient components.

Keywords: reactive oxygen species, *Arabidopsis thaliana*, root-stem-cell maintenance and differentiation, root-hair development, cell cycle, aerenchyma formation

INTRODUCTION

In the Earth's distant past, the rapid accumulation of oxygen in the atmosphere was an important event for the evolution of multicellular molecular processes (Jeltsch, 2013). Oxygen is an essential element of life for all multicellular organisms including plants and animals especially some specific processes in animals (e.g., oxygen circulation blood vessels) and plants (e.g., cell survive in the deepmost position in roots). In the presence of oxygen, the cellular processes characterized by high-speed electron or energy transport inevitably result in the leakage of electrons or energy in the form of molecular oxygen (O_2), thereby producing reactive oxygen species (ROS) with a higher chemical activity than O_2. Consequently, ROS are continuously generated during the respiratory processes in aerobic organisms (Apel and Hirt, 2004). In addition, ROS are a primary product of several enzymatic reactions, which have emerged through cellular evolution. The main forms of ROS include singlet oxygen ($^1O_2$), superoxide anion ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($HO^{\bullet}$) (Mhamdi and Van Breusegem, 2018; Waszczak et al., 2018). Among these, H_2O_2 and $O_2^{\bullet-}$ are the most stable forms of ROS, having a long lifetime—from milliseconds to seconds, whereas the lifetime of singlet oxygen ($^1O_2$) and hydroxyl radical ($HO^{\bullet}$) is shorter, ranging from nanoseconds to microseconds (Waszczak et al., 2018).

ROS are highly reactive and may cause damage to cellular DNA, lipids, and proteins, and they are often implicated in the development of cancer and other diseases (Hossain et al., 2015). However, growing evidence indicates that ROS may play a critical regulatory role in blood-cell development in the larval lymph glands of *Drosophila melanogaster* (Theopold, 2009), resistance to drought stress and pathogen attack (Qi et al., 2018), and lateral root formation in plants (Biswas et al., 2019). Although ROS pose potential risks to certain processes, they also accumulate in plant root cells under normal growing conditions (Dunand et al., 2007). Furthermore, they are pivotal for the normal growth and development of the root. Recent research in the model plant *Arabidopsis thaliana* has provided strong evidence supporting the indispensable role of ROS in plant root development (Yu et al., 2016; Zeng et al., 2017; Kong et al., 2018; Yamada et al., 2018; Tian et al., 2018), and this research will provide reference for sustainable development of agriculture.

GRADIENT DISTRIBUTION OF ROS REGULATES ROOT STEM CELL DIFFERENTIATION

The roots form a key organ that anchors plants to the soil and provides the means to absorb the nutrients and water necessary for plant growth. In addition, roots can sense and respond to changes in the surrounding environment. Root growth relies on the balance of proliferation and differentiation in root stem cells (Petricka et al., 2012). Plant root systems can be divided into three zones along the longitudinal axis; namely, the meristematic, elongation, and maturation zones (Rodriguez-Alonso et al., 2018). The most characteristic stem cells of plants are in the shoot apical meristem and root apical meristem (Sarkar et al., 2007). Stem cells are defined as a specific group of cells with the capacity to self-renew and produce undifferentiated daughter cells, which can form new tissues. Such cells reside in a confined microenvironment known as the stem cell niche, and their characteristics are synergistically maintained by intracellular and extracellular signals (Sarkar et al., 2007). The potential molecular mechanisms underlying the formation and maintenance of plant stem cells have been extensively investigated (e.g., Sarkar et al., 2007; Yang et al., 2018). The role of the synergistic action of transcription factors, regulated by auxins and cytokinins, in the maintenance and differentiation of stem cells has been well established (Singh et al., 2017). Recent research has also revealed that the redox state and the presence of ROS can precisely regulate stem cell fate, and ROS are thus often referred to as a fine-tuner of plant stem cell fate (Tsukagoshi, 2016; Zeng et al., 2017; Yang et al., 2018; Qin et al., 2019). The root tips of *A. thaliana* exhibit complex redox potential patterns, and the quiescent center (QC) and cell regions adjacent to the meristem exhibit the strongest negative potential. The transition and elongation zones are in an oxidized state (Jiang et al., 2016). The implications, function, and regulation mechanism of ROS polarized gradient distribution at root tips are the present highlight research area. Among the different types of ROS, $O_2^{\bullet-}$ and H_2O_2 have been studied more extensively, and they exhibit different gradient distributions in the roots (**Figure 1**) (Dunand et al., 2007; Wells et al., 2010). Their gradient distribution is related to UPBEAT1 (UPB1). UPBEAT1, a basic helix-loop-helix (bHLH) transcription factor, that regulates the expression of a set of peroxidases which participate in the establishment of ROS (H_2O_2 and $O_2^{\bullet-}$) gradient distribution in the root meristem (Tsukagoshi et al., 2010; Perilli et al., 2012; Del Pozo, 2016). This distribution is affected by the nitrate nutrient (Trevisan et al., 2019).

The dynamic balance of ROS in the root apex also plays a key role in modulating cell distribution from the cell division zone to the elongation and maturation (differentiation) zones. $O_2^{\bullet-}$ and H_2O_2 accumulate in the meristematic and elongation zones, respectively (Dunand et al., 2007; Biswas et al., 2019). An imbalance will lead to a change in the size of the meristematic zone. UPB1 regulates the ROS (H_2O_2) content in the root apex by inhibiting the expression of class III peroxidases in the

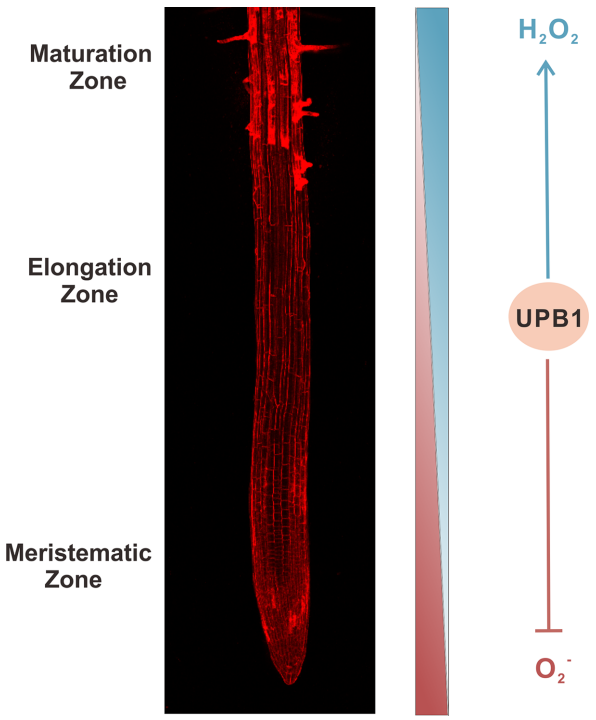

FIGURE 1 | Gradient distribution of superoxide anion ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2) in *Arabidopsis thaliana* roots. Nitro blue tetrazolium (NBT) staining showed the distribution of $O_2^{\bullet-}$ in the roots, from the meristematic to elongation zones. The gradients of reactive oxygen species (ROS) are regulated by peroxidases, which are modulated by the UPBEAT1 (UPB1) factor. The concentration of $O_2^{\bullet-}$ decreases along a gradient from the meristem to transition zones and the concentration of H_2O_2 decreases along a gradient from the differentiation to elongation zones. Arrow-head line indicates stimulation effect, and "T"-shaped line shows the inhibition.

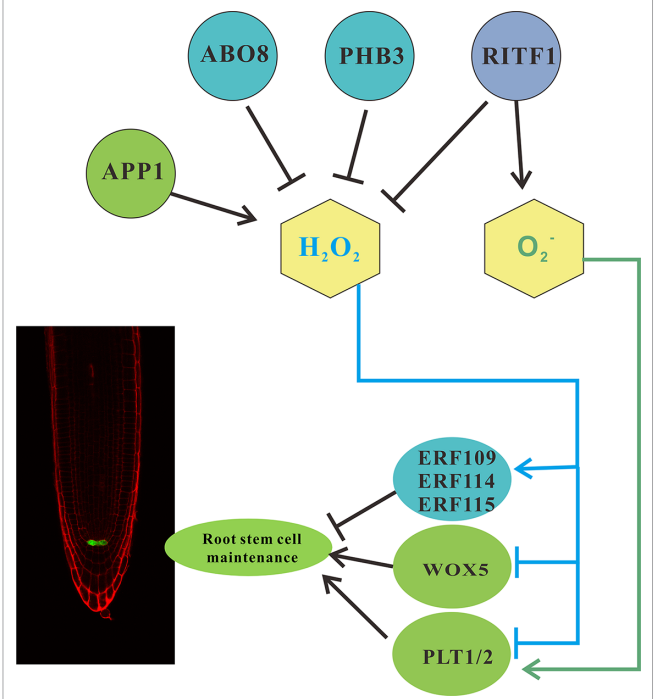

FIGURE 2 | Reactive oxygen species (ROS) mediate root stem cell maintenance. *pWOX5:GFP* marks the quiescent center (QC) in *Arabidopsis* roots. Multiple parallel signaling pathways integrate multiple transcription factors to converge as an ROS signal to regulate root stem cell maintenance. APP1 is upregulated, and ABO8 and PHB3 inhibit H_2O_2 signals, thus stimulating ERF109/114/115 or inhibiting WOX5. ERF109/114/115 negatively regulates root stem cell maintenance, whereas WOX5 positively regulates it. Another cascade pathway converges on RITF1 to regulate the level of H_2O_2 and $O_2^{\bullet-}$, and its downstream products regulate PLT1/2, thus controlling stem-cell fate. Furthermore, the brassinolide signaling pathway regulates the level of BRAVO and stem-cell fate in the roots. Arrow-head line indicates stimulation effect, and "T"-shaped line shows the inhibition.

elongation zone (**Figure 1**) (Tsukagoshi et al., 2010; Qi et al., 2018). The *upb1-1* mutant in *A. thaliana* presented longer meristems and a lower H_2O_2 level in the elongation zone, and the *UPB1* overexpression lines exhibited shorter meristems and a higher H_2O_2 level in the elongation zone than those in the wild type. Conversely, the peroxide level in the meristematic zone was higher in the *upb1-1* mutant but lower in the *UPB1* overexpression lines. Furthermore, the overexpression of a *UPB1*-targeted peroxidase resulted longer meristems than those in the wild type, and the overexpression of another peroxidase gene, *PER34*, resulted in a longer-root phenotype than that of the wild type (Tsukagoshi et al., 2010; Tsukagoshi, 2016).

ROS ARE KEY REGULATORS OF ROOT STEM CELL NICHE MAINTENANCE

There are multiple signal pathways mediated by ROS signals that may be involved in stem cell maintenance and cell fate determination (**Figure 2**). *APP1* encodes a mitochondria-localized P-loop NTPase involving ATP hydrolysis and ROS generation. Loss-of-function alleles of *APP1* caused lower level of ROS (both $O_2^{\bullet-}$ and H_2O_2) in the root meristem, and enhanced the expression of the two peroxidases genes *PER11* and *PER55*, which are involved in ROS detoxification (Del Pozo, 2016). This leads to an increase in the number of cells in the QC and promotes stem cell differentiation. However, *APP1* overexpression leads to defective stem cell niches and higher ROS (H_2O_2 and $O_2^{\bullet-}$) levels in the root meristem (Yu et al., 2016).

Another pathway involves the hormone abscisic acid (ABA). The ABA OVERLY SENSITIVE MUTANT (*ABO8*) gene, encoding a pentatricopeptide repeat domain protein, modulates ROS homeostasis in the root apex (Yang et al., 2014). In the *abo8-1* mutant, ROS accumulates excessively and hinders the expression of *PLETHORA1* (*PLT1*) and *PLT2*, both at the transcriptional and post-transcriptional levels. This leads to the establishment of a hypothetical relationship between ROS signals and *PLT*-mediated maintenance and regulation of the root stem cell niche (**Figure 2**) (Yang et al., 2014; Tsukagoshi, 2016). These results indicate that appropriate ROS levels and

gradients play a key regulatory role to preserve the stability of the root stem cell niche (Yu et al., 2016).

Recently, Kong et al. (2018) verified that PROHIBITIN3 (PHB3) maintains the root stem cell niche *via* regulating ROS homeostasis. Transcriptome analysis revealed that some downstream genes including ETHYLENE RESPONSE FACTOR 115 (ERF115), ETHYLENE RESPONSE FACTOR 114 (ERF114), and ETHYLENE RESPONSE FACTOR 109 (ERF109), which are responsible for maintaining the root stem cell niche, were induced by ROS (Yang et al., 2018) (**Figure 2**). In addition, ectopic expression of *ERF115*, *ERF114*, and *ERF109* were found in the *phb3* mutant root meristem, indicating that PHB3 limits the expression of *ERF115*, *ERF114*, and *ERF109* in the root meristem *via* ROS distribution (Kong et al., 2018). Kong et al. (2018) further confirmed that PHYTOSULFOKINE2 (*PSK2*) and *PSK5* are the direct targets of ERF115, ERF114, and ERF109 through ChiP-qPCR assay. Thus, ROS appears to modulate the proliferation of QC cells through the ERF-PSK module (Yang et al., 2018). However, the mechanisms of ROS regulating the expression of PLT1/2, ERF115, ERF114, and ERF109 are still unknown.

The ROOT MERISTEM GROWTH FACTOR 1 (RGF1)-RGFR1/2/3 signaling pathway maintains the characteristics of the root stem cell niche by maintaining the PLT gradients in the proximal meristem (Ou et al., 2016). However, the molecular mechanisms involved in promoting the PLT1/2 protein stability *via* the RGF1-RGFR1/2/3 pathway remain unclear. In a recent study, Yamada et al. (2018) provided evidence that the RGF1-RGFR1/2/3 signaling pathway modulates ROS distribution and enhances PLT1/2 stability. Moreover, PLT2 localization is related to ROS distribution, and transcriptome data analysis of RGF1 treatment revealed that RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1 (RITF1; AT2G12646) is one of the downstream mediators of the RGF1-RGFR1/2/3 pathway (Yamada et al., 2018). This is consistent with the observations in similar ROS distribution phenotypes between *RITF1* overexpression and RGF1-treated roots. The aforementioned results indicate that the RGF1-RGFR1/2/3 signaling pathway maintains the characteristics of the stem cell niche by regulating the ROS levels and distribution by RITF1, and thereby maintaining PLT1/2 stability in the meristematic zone (Yang et al., 2018) (**Figure 2**).

One plausible explanation is that the PLT1/2 stability may be related to ROS-induced post-translational modification. ROS may rapidly modulate the target proteins such as PLT1/2 *via* post-translational modifications, which include phosphorylation, glycosylation, and ubiquitination (Yang et al., 2018). The ROS-sensitive proteins undergo oxidative modifications targeted at sulphur atoms in cysteine and methionine residues in an H_2O_2-dependent manner. Research has revealed that H_2O_2 treatment of plant cells leads to sulphur oxidation in approximately 100 types of cytosolic proteins (Hossain et al., 2015). Tian et al. (2018) have reported the redox regulation of brassinosteroid (BR) signals, and this process is related to ROS-induced protein modification. BRs induce the generation of H_2O_2 in the root meristem, particularly in the root stem cell niche, in a BRASSINOSTEROID INSENSITIVE 1 (BRI1)-dependent manner, and this is required for BRs to promote QC cell division (Yang et al., 2018; Surgun-Acar and Zemheri-Navruz, 2019). *In-vitro* and *in-vivo* studies have confirmed that cys-63 and cys-84 residues are the conserved oxidization sites in BRASSINAZOLE-RESISTANT 1 (BZR1) and BRI1-EMS-SUPPRESSOR 1 (BES1), respectively (Tian et al., 2018). During the oxidative modification of BZR1, the transcriptional activity is enhanced by promoting interactions between BZR1 and key transcriptional regulators of the auxin and light signaling pathways, such as AUXIN RESPONSE FACTOR 6 (ARF6) and PHYTOCHROME INTERACTING FACTOR 4 (PIF4) (Tian et al., 2018).

Mutations in the oxidation sites in the proteins aforementioned such as BZR1 and BES1, or a reduction in endogenous ROS content can significantly impair the functions of BZR1 and BES1 in regulating gene expression and various biological processes, including QC cell division in the roots (Vilarrasa-Blasi et al., 2014; Yang et al., 2018; Surgun-Acar and Zemheri-Navruz, 2019). Furthermore, Vilarrasa-Blasi et al. (2014) indicated that the BRAVO/BES1 signaling model, rather than BZR1, plays a role in BR-mediated stem cell quiescence regulation in plants. In the future, it is worth investigating whether the oxidative modification of BES1, which regulates root stem cell quiescence, leads to changes in BRAVO-BES1 interactions and BRAVO expression.

BALANCE OF THE INTRACELLULAR REDOX STATE FINE-TUNES CELL-CYCLE PROGRESSION

While there is evidence to suggest that ROS regulate the animal cell cycle (Burhans and Heintz, 2009), direct evidence for the role of ROS in the plant cell cycle is still limited. The utilization of exogenous H_2O_2 has been reported to inhibit the expression of genes related to cell-cycle inhibition and reduce the size of the root meristem (Tsukagoshi, 2012; Tsukagoshi, 2016). A potential scenario for the accumulation of ROS and prevention of cell proliferation following DNA damage has been reported (Tanaka et al., 2006; Roldán-Arjona and Ariza, 2009). H_2O_2 accumulation occurred in the root elongation zone after treatment with zeocin, a double-strand DNA break-inducing agent. The *sog1* mutant was not sensitive to zeocin treatment, and it did not accumulate H_2O_2 (Yoshiyama et al., 2009). SUPPRESSOR OF GAMMA RESPONSE 1 (SOG1) is a master transcription factor regulating the response to double-strand DNA break induction (Yoshiyama et al., 2009; Yoshiyama et al., 2013). ChiP-qPCR showed that defense-related genes were the target genes of SOG1, suggesting the involvement of SOG1 in plant immunity (Ogita et al., 2018). *FMO1*, directly controlled by SOG1 under DNA damage conditions, encodes a flavin-containing monooxygenase that is associated with the production of ROS (Chen and Umeda, 2015). Therefore, ROS homeostasis is pivotal in root meristem size modulation following DNA damage. H_2O_2 also influences cortex proliferation (Cui et al., 2014).

The redox state regulates the maintenance of the root meristem in plants (Tsukagoshi, 2016). As ROS are highly reactive, the accumulated ROS in cells will oxidize proteins,

chemical substances, and metabolites. To prevent such oxidative damage, the cells regulate redox balance through small antioxidant molecules, such as glutathione (GSH) and thioredoxin (TRX) (Hernández et al., 2015; Sevilla et al., 2015). γ-Amino butyric acid (GABA) could function as an antioxidant to scavenge ROS under stress conditions (Liu et al., 2011). In plants, *ROOT MERISTEM LESS 1 (RML1*) encodes the first enzyme in GSH biosynthesis, and active root meristem formation was inhibited in *rml1* mutant plants (Vernoux et al., 2000). The regulatory role of the GSH levels in the G1/S transition of cycling cells has been demonstrated. Glutathione reductase (GR) catalyzes GSH reduction and regulates root meristem maintenance (Schippers et al., 2016). *Arabidopsis thaliana* contains two GR genes, *GR1* and *GR2* (Marty et al., 2009). Based on the T-DNA insertion and homozygous and heterozygous phenotype screening and observation, the complete loss of function of *GR2* leads to embryonic lethality (Tzafrir et al., 2004), severe growth defects were observed in seedlings of *gr2* mutants (Yu et al., 2013).

GSH and TRX also participate in the regulation of root meristem size. Mutants of TRX reductase (*ntra* and *ntrb*) exhibit small meristem phenotypes (Reichheld et al., 2007; Bashandy et al., 2010). These findings provide strong evidence of the key role of cellular redox regulation in maintaining the meristem activity. Redox regulation is a crucial mechanism involving ROS, GSH, GR, and TRX, and it plays an important role in the regulation of plant growth and development. With such a mechanism, hormonal control, energy metabolism, and bioenergetics can be linked to plant growth and development (Schippers et al., 2016). It is highly likely that cell proliferation and differentiation regulated by ROS are affected by the regulation of cell-cycle progression and/or proteins and enzymes involved in cell differentiation, by the coupling of TRX with GSH/GR.

Cell-cycle phases are highly conserved throughout eukaryotic cells; they comprise the G1 phase, which involves DNA unzipping and the start of RNA and protein synthesis, followed by the S phase (DNA synthesis), and G2 phase (lipid synthesis) (Schippers et al., 2016). In these consecutive, dynamic, cellular events, oxygen consumption, energy metabolism, and cellular redox state are closely related with the cell-cycle progression in eukaryotic cells (Burhans and Heintz, 2009; Schippers et al., 2016). Bursts of $O_2^{\bullet-}$ and H_2O_2 activate cell signaling pathways, thereby activating the G0/G1 transition (Kovtun et al., 2000; Diaz Vivancos et al., 2010).

During DNA replication and mitosis in yeast, oxygen consumption and relevant metabolic processes are reduced to their lowest levels. However, it is unclear whether the redox regulation of shoot apical meristematic cell proliferation in plants is similar to relevant mechanisms observed in other eukaryotes. A mechanism conserved in plants and animals is the nuclear localization of GSH during the cell cycle (Diaz Vivancos et al., 2010; García-Giménez et al., 2013). This may be due to reduced auxin polar transport (Bashandy et al., 2010). For instance, reduced polar transport and a weaker auxin response were observed in *grxs17* mutants (Benitez-Alfonso et al., 2009).

The cellular entry of apoplastic H_2O_2 is mediated by intrinsic membrane proteins. Although there is no direct evidence of the influence of protein oxidation on cell-cycle components (e.g., cyclins and cyclin-dependent kinases), redox regulation occurs in cell-cycle transcriptional regulators (Schippers et al., 2016). For instance, transcriptional factors, NF-YC (Nuclear Factor-Y subunit C) and TCPs (TEOSINTE BRANCHED/CYCLOIDEA/PCFs) are deactivated *via* cysteine oxidation, and the presence of GSH and GR can reduce such proteins and restore their activity (Schippers et al., 2016). TCPs stimulate the expression of *CYCA2;3*, *CYCB1;1*, and retinoblastoma-related protein (RBR), thereby directly regulating the cell cycle (Schippers et al., 2016). The initial GSH pool may also be induced by the plant hormone jasmonate, and TCPs are negative regulators of jasmonate biosynthesis (Schippers et al., 2016). Therefore, their function will lead to the consumption of the GSH pool, and ultimately causes TCP deactivation through oxidation. In addition, prohibitin is necessary for the coordination of mitochondrial function in the meristem. Lastly, the ROS generated in non-green plastids negatively influence intracellular communication by promoting callose accumulation at plasmodesmata. In the non-green plastids of meristems and organ primordia, the main function of TRX-m3 is to prevent excessive ROS formation (Schippers et al., 2016).

ROS REGULATION DURING ROOT HAIR DIFFERENTIATION

Root hairs, which are tubular structures formed by root epidermal cells, facilitate the uptake of nutrients, interaction with microbes, and anchoring of roots to soil (Molendijk et al., 2001). Root hair development comprises four stages: cell specialization, root hair initiation, tip growth, and root hair maturation (Grierson et al., 2014). Epidermal cells are regulated by multiple genes during the specialization process. SCRAMBLED (*SCM*), a leucine-rich repeat receptor-like kinase, allows epidermal cells to sense their location and select the correct cell fate and gene expression patterns. Mutations in this gene disturb the distribution of root hair and non-hair cells (Kwak et al., 2005).

In *A. thaliana*, WEREWOLF *(WER*), TRANSPARENT TESTA GLABRA (*TTG*), and GLABRA3 (*GL3*) simultaneously promote non-hair cell differentiation and inhibit root hair cell differentiation (Galway et al., 1994; DiCristina et al., 1996; Bernhardt et al., 2005). The products of these genes form the WER-GL3/EGL3-TTG complex through physical interactions to positively regulate the expression of GLABRA2 (*GL2*) (AT1G79840) (Bernhardt et al., 2003). *GL2* encodes a homeodomain transcription factor that determines non-hair-cell differentiation by promoting the expression of genes related to non-hair-cell differentiation (DiCristina et al., 1996; Schiefelbein and Lee, 2006) (**Figure 3**).

CAPRICE (*CPC*) encodes a nuclear-localized R3-type MYB transcription factor, which can positively regulate root hair-cell differentiation (Tominaga-Wada et al., 2017). Mutations in this gene result in fewer root hair cells (Wada et al., 1997). CPC can bind with GL3/EGL3-TTG to form an inactive complex, which inhibits *GL2* expression and ultimately promotes epidermal cell differentiation into root hair cells (Tominaga et al., 2007;

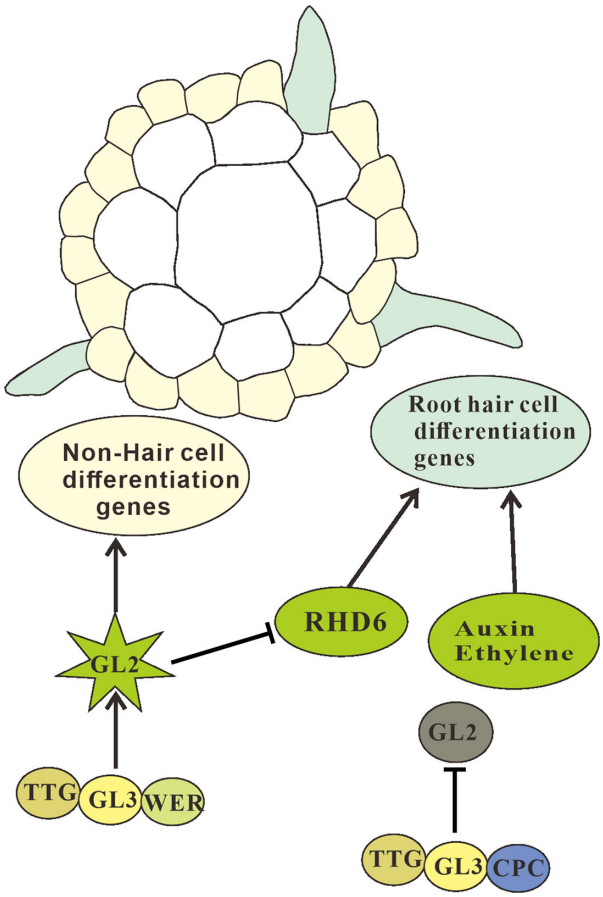

FIGURE 3 | Regulation of crucial components in root-hair development. Transverse section of *Arabidopsis* root showing the relative position of the epidermis and cortex. The epidermis cells are in the H cell position and emerge to form hair cells, and the epidermal cells beneath the cortex cells are in the non-hair cell (N) position and do not form root-hair cells. The root (H) and non-hair cell (N) positions have different components that participate in root-hair formation. Some components shuttle to different types of cells to converge at ROOT HAIR DEFECTIVE (RHD6), a bHLH factor, which when activated, controls the differentiation and formation of root-hair cells, and when non-activated, regulates non-hair-cell formation. Meanwhile, plant hormones such as auxins and ethylene play a positive role in root-hair formation *via* reactive oxygen species (ROS). Arrow-head line indicates stimulation effect, and "T"-shaped line shows the inhibition.

Song et al., 2011; Kang et al., 2013). Besides *CPC*, other genes that encode R3-MYB proteins include TRIPTYCHON (*TRY*) and ENHANCER OF TRY AND CPC1 (*ETC*) with functions that are partially redundant with those of *CPC* (Schellmann et al., 2002; Kirik et al., 2004; Simon et al., 2007; Serna, 2008; Wang et al., 2016; Tominaga-Wada et al., 2017).

ROOT HAIR DEFECTIVE 6 is a crucial gene encoding a bHLH transcription factor (Menand et al., 2007). Mutations in this gene result in root without root hairs, a condition which can be alleviated with the addition of 1-amino-1-cyclopropanecarboxylic acid or indole-3-acetic acid (IAA) in the medium (Masucci and Schiefelbein, 1994). RHD6-like 4 (RSL4) and MEDIATOR 25 (MED25) also promote root hair elongation and function in the auxin-regulated transcriptional pathway (Foreman et al., 2003; Sundaravelpandian et al., 2013; Mangano et al., 2017).

Polarized growth of root hairs is an ideal model to study the regulation of ROS. NADPH oxidase (NOX), which catalyzes ROS production, and is an effective protein regulating root hair development. NOX, also known as Respiratory Burst Oxidase Homologs (RBOH), plays an important role in plant development (Choudhary et al., 2020; Hu et al., 2020). *RBOHC* (AT5G51060), a member of the Arabidopsis RBOH family, was specifically expressed in Arabidopsis root hairs (Chapman et al., 2019). The study of root hair cells shows that the polarized growth of cells depends on the local accumulation of ROS produced by NADPH oxidase (NOX) (Foreman et al., 2003). Root hairs of ROS mutants without *AtRBOHC*/*RHD2* did not elongate (Foreman et al., 2003).

During root hair formation, owing to changes in the acid environment of the cell wall, cell protrusion is localized to a small disc-shaped area in the cell wall facing outward, approximately 22 μm across, in a process known as root hair initiation (Grierson et al., 2014). Accumulation of large amounts of ROP (Rho of Plant) proteins, which are GTP-binding proteins unique to plants and related to the small GTPases that control the morphogenesis of animal and yeast cells (Vernoud et al., 2003), occur at root hair growth sites (Molendijk et al., 2001). The localization of the ROP proteins is the first marker of root hair formation, and these proteins remain at the tip of developing root hairs throughout root hair growth (Molendijk et al., 2001; Grierson et al., 2014). RHO-RELATED PROTEIN FROM PLANTS 2 (*ROP2*) activates ROS generation through the NADPH oxidase gene ROOT HAIR DEFECTIVE 2 (*RHD2*), which encodes a respiratory burst oxidase homolog (RBOH) or NADPH oxidase (Jones et al., 2007; Gu and Nielsen, 2013). Mutations of this gene impair the ability of ROS to accumulate in the tips of root hairs, thereby inhibiting the development of root hair initials (Foreman et al., 2003). In addition, treating wild-type *A. thaliana* with the NADPH oxidase inhibitor diphenyleneiodonium (DPI) also impairs ROS accumulation in the root tips and leads to the failure of root hair development.

In addition to RHD2 (also called RBOHC), there are nine other respiratory burst oxidase homologs (RBOH), named as RBOHA-RBOHJ (**Table 1**). The isoforms of RBOH regulate all aspects of plant development. For example, *RBOHB*, *RBOHC*/*RHD2*, and *RBOHG* are specific to, or at least relatively highly expressed, in the roots. RBOHC participates in root hair formation and primary root growth, and the mutants of *RBOHC*/*RHD2* exhibit defective root hair phenotypes (Mhamdi and Van Breusegem, 2018). The other RBOH homologs control primary root elongation and lateral root emergence (e.g., RBOHD, RBOHE, and RBOHF) or pollen tube growth (e.g., RBOHH and RBOHJ). The mutants of *RBOHE* and *RBOHH* exhibit reduced fertility and disrupted pollen tube growth (**Table 1**).

Root hair tip growth is closely related to ROS signaling. ROS accumulation activates calcium channels in root hair cells, increasing the calcium ion levels (Wymer et al., 1997). The Ca^{2+} gradient at the tip of root hairs is a part of the mechanism

TABLE 1 | Summary of the role of the respiratory burst oxidase homolog (RBOH) isoforms in plant development.

Gene	Locus tag	Relative expression level	Function(s)	Mutant phenotype
RBOHA	AT5G07390	Specific, highly expressed in the roots and 6–7-week-old siliques	Unknown	Unknown
RBOHB	AT1G09090	Specific, highly expressed in the roots	Seed after ripening	Faster germination of fresh seeds
RBOHC/RHD2	AT5G51060	Specific, highly expressed in the roots	Root hair formation;primary root elongation and development	Root hair defective
RBOHD	AT5G47910	Specific, highly expressed in the cotyledons, hypocotyl, rosette leaves (2–12), cauline, and senescent leaves	Stomata closing, lateral root emergence, and primary root elongation and development	Atypical tubulin formation; early emergence of lateral roots (LRs), and enhanced density of LRs
RBOHE	AT1G19230	Specific, highly expressed in 6–10-week-old of siliques	Anther and pollen development and lateral root emergence	Aborted pollen and reduced fertility
RBOHF/SGN4	AT1G64060	Specific, highly expressed in the stamens and sepals	Stomata closing, lateral root emergence, and primary root elongation and development	Early emergence of lateral roots (LRs) and enhanced density of LRs
RBOHG	AT4G25090	Relatively highly expressed in the roots	Unknown	Unknown
RBOHH	AT5G60010	Specific, highly expressed in mature pollens	Pollen tube growth	Defective root hairs, reduced fertility, and impaired pollen tube growth
RBOHI	AT4G11230	Highly expressed in the roots, and relatively highly expressed in the shoot apex and mature pollens	Unknown	Unknown
RBOHJ	AT3G45810	Specific, highly expressed in mature pollens	Pollen tube growth	Dfective root hairs, reduced fertility, and impaired pollen tube growth

Data were comprehensively analyzed using AtGenExpress eFP, and the excerpt from Mhamdi and Van Breusegem (2018) was obtained with permission granted by the Copyright Clearance Center.

that regulates growth direction in root hairs, promotes the fusion of vesicles with plasma membranes of root hair tips, and provides raw material for cell wall expansion (Ridge, 1995; Pei et al., 2012). The calcium gradient is maintained in the root hair tips throughout tip growth (Wymer et al., 1997). These results indicate that ROS accumulation in the root hair tips is necessary for normal root hair development (Tsukagoshi, 2016).

GENERATION OF ROS AND MODIFICATION OF CELL WALLS IN ROOT ELONGATION

The ROS are essential for root growth and development, and one of their major functions in the development of the root system is cell wall modification (O'Brien et al., 2012; Kärkönen and Kuchitsu, 2015). In the root system, the ROS are generated by NADPH oxidases (RBOH) in the plasma membrane or through mitochondrial and plastid respiration (Suzuki et al., 2011; Lázaro et al., 2013; Serrato et al., 2013). The RBOH isoforms may also be key producers of ROS in the apoplast (**Table 1**).

$O_2^{\bullet-}$ is formed in O_2 reduction by the catalytic activity of NADPH oxidases (Tsukagoshi, 2016). As the catalytic domain of NADPH oxidases is positioned toward the apoplast, $O_2^{\bullet-}$ is released into the apoplastic space (Suzuki et al., 2011). Subsequently, $O_2^{\bullet-}$ is degraded into H_2O and O_2 by the catalytic activities of enzymes such as superoxide dismutase (Bowler et al., 1992), apoplastic oxalate oxidases, diamine oxidase, and peroxidase (Federico and Angelini, 1986; Caliskan and Cuming, 1998; Cosio and Dunand, 2009). The H_2O_2 generated in the apoplast is then degraded by peroxidases secreted into the apoplastic space (Trevisan et al., 2019).

The shape of plant cells changes with the modification of their cell walls (Grierson et al., 2014). Peroxidases promote the conversion of H_2O_2 into H_2O and O_2. During this conversion, an electron is also produced and is used to modify the primary and secondary cell walls (Francoz et al., 2015; Tsukagoshi, 2016). The modification process involves electron transfer to lignin monomers, which are subunits of polymeric lignin, in cells in the maturation zone. Upon activation by electrons, lignin monomers will trigger the lignin polymerization process and bind to secondary cell walls during the process of secondary cell wall formation (Novo-Uzal et al., 2013). Lignin in the secondary cell walls provides substantial mechanical strength, which is essential for vascular plants (Ros Barceló, 2005). In addition, NADPH oxidases, peroxidases (e.g., Peroxidase 64 (PER64)), and other enzymes catalyzing ROS metabolism are recruited to form lignin polymerization machinery in the formation of casparian strips (Kamiya et al., 2015), which are bands of lignin that act as diffusion barriers in the endodermal cells of plant roots (Lee et al., 2013; Tsukagoshi, 2016). To facilitate the formation of casparian strips, the casparian strip domain proteins, which are specifically expressed in the endodermis, guide the localization of the aforementioned enzymes into the plasma membrane of endodermal cell walls (Lee et al., 2013; Geldner, 2013).

ROS INTERACT WITH OTHER SIGNALING HORMONES TO REGULATE ROOT DEVELOPMENT

The ROS act as key signaling molecules under conditions of stress and increasing attention has been paid to the role of ROS in plant stress resistance (Jia, 2011; Gill et al., 2015; Wang et al.,

2016). Different environmental stresses, including drought, salt, ultraviolet radiation, and light, can cause an increase in cellular ROS levels (Perez and Brown, 2014; Gururani et al., 2015). ROS accumulation can influence hormone signal transduction, and vice versa (Xia et al., 2015). Auxin, one of the most important plant hormones, influences systematic root development (Bustillo-Avendaño et al., 2018), and participates in meristem maintenance and lateral root formation (Vilches-Barro and Maizel, 2015). Notably, all RBOH transcripts are auxin inducible (Mhamdi and Van Breusegem, 2018).

PLETHORA (PLT) is a key regulator of auxin-induced stem cell niche activity (Aida et al., 2004), and *PLT* expression was altered in *miao* mutants (one kind of Glutathione reductase (GR) mutant) (Yu et al., 2013). Although *PLT2* overexpression in the *miao* mutants does not lead to the recovery of small meristem phenotypes, it increases meristem size in the wild type. Despite the understanding that auxin induces ROS production to regulate cell elongation (Schopfer, 2001) and root gravitropism (Joo et al., 2001), the molecular relationship between ROS and auxin remains largely unknown. Recent study revealed the potential feed-forward loop between ROS and auxin signaling to control lateral root formation (Biswas et al., 2019). It was confirmed that production of reactive oxygen species (ROS) *via* the hormone-induced activation of respiratory burst oxidase homologous NADPH oxidases facilitates lateral root (LR) formation, and that the auxin-induced production of ROS and their downstream products RCS (reactive carbonyl species) modulate the auxin signaling pathway in a feed-forward manner. RCS are key agents that connect the ROS signaling and the auxin signaling pathways (Biswas et al., 2019).

The hormone ABA is a major contributor to the response of plants to abiotic stresses (Nakashima et al., 2014). The accumulation of ABA under abiotic stress conditions reduces root growth. As mentioned above, the production of ABO8 is responsible for splicing NADH dehydrogenase subunit 4 (NAD4) in the mitochondrial complex, and *abo8* mutants were associated with ROS accumulation and ABA production. ROS accumulation was enhanced in the root tips of *abo8* mutants treated with ABA, and this inhibited root growth (Yang et al., 2014). Moreover, auxin distribution and PLT protein levels in the root tip cells of *abo8* mutants were altered. Therefore, ABA-induced ROS accumulation in the mitochondria reduces the root-system growth *via* changes in auxin distribution and PLT levels.

These findings clearly illustrate the complex interactions between plant hormones and ROS in the modulation of root system growth. Other plant hormones such as brassinolide (BR), gibberellin, ethylene, strigolactones, salicylic acid, and jasmonate also participate in hormonal crosstalk (Xia et al., 2015), which in association with ROS, regulate plant growth (Biswas et al., 2019).

Pharmacological and genetic experiments have indicated that auxin and ethylene promote root hair cell differentiation in *A. thaliana*. Treating the roots of *A. thaliana* seedlings with 1-amino-1-cyclopropanecarboxylic acid induced ectopic root hair formation (Tanimoto et al., 1995). In addition, in the ethylene signaling pathway, the CTR1 Raf-like kinase encoded by CONSTITUTIVE TRIPLE RESPONSE (*CTR1*) acts as a negative regulator of root hair formation (Kieber et al., 1993), with mutations in *CTR1* leading to ectopic root hair formation (Dolan et al., 1994; Ikeda et al., 2009). This is consistent with evidence indicating that epidermal cells in the root hair position (H) are more sensitive to ethylene induction than epidermal cells in the non-hair position (N) (Casson and Lindsey, 2003). Besides ethylene and auxin, other hormones also influence root hair development (Konno et al., 2003; Boisson-Dernier et al., 2013). During the early stages of root hair initiation, BRs can influence the fate of root hair cells (Kuppusamy et al., 2009); strigolactones can increase root hair length by interfering with the regulation of cell expansion by auxin, indicating that strigolactones play a role in the late stages of root hair formation (Kapulnik et al., 2011). Similarly, methyl jasmonate promotes root hair growth in a dose-dependent manner, involving the participation of the ethylene and auxin pathways (Zhu et al., 2006).

NUTRIENT STRESS REGULATES ROOT HAIR DEVELOPMENT

The major function of root hairs is to expand root surface area, and thus, facilitate water and nutrient uptake from the soil (Grierson et al., 2014). More or longer root hairs are advantageous to plants under low-nutrient conditions. For instance, a high density of long root hairs was more efficient in acquiring phosphate in *A. thaliana* Co and C24 accessions (Narang et al., 2000). Furthermore, under low phosphorus conditions, phosphorus was more efficiently taken up by wild-type plants than the mutants of *rhd6* and *rhd2* (Bates and Lynch, 2000). Enzymes and nutrient transport proteins in root hairs participate in nutrient uptake (Böhme et al., 2004). For example, the activity of ferric chelate reductase (FCR) in wild-type plants was two-fold higher than that in hairless mutants (*rm57/rhd7*), suggesting that this enzyme is localized in the root hairs (Moog et al., 1995).

Root hair development is influenced by nutrient concentrations, and root hair density and length are generally increased under nutrient-deficient conditions (Grierson et al., 2014). Phosphate (Bates and Lynch, 1996), iron (Schmidt et al., 2000), manganese (Konno et al., 2003), and nitrate can increase root hair density in *A. thaliana* (Canales et al., 2017). The density of root hairs in *A. thaliana* 'Columbia' grown under low-phosphorus (1.0 μM) conditions was five times greater than that in plants grown under high-phosphorus (1000 μM) conditions (Bates and Lynch, 1996; Savage et al., 2013; Grierson et al., 2014). Under low-phosphorus conditions, the number of root hair-forming files was increased from 8 to 12, and more of the cells in these files formed root hairs than in plants grown under high-phosphorus conditions (Ma et al., 2001; Grierson et al., 2014). Furthermore, the root hairs in *A. thaliana* grown under low-phosphorus conditions were three times longer than those in plants grown under high-phosphorus conditions (Bates and Lynch, 1996). The bHLH transcription factor ROOT HAIR DEFECTIVE6-LIKE4 (RSL4) promotes root hair growth. Thus, the length of root hairs increases in plants grown

under low-phosphorus conditions (Yi et al., 2010; Grierson et al., 2014). The same phenomenon was also observed under iron deficiency, which was accompanied with an increase in root hair density and length. In iron-deficient roots, ectopic hairs were produced, and root hair length was doubled (Schmidt et al., 2000). The mechanisms by which different nutrients modulate root hair development differ. For instance, auxin and ethylene signaling is crucial for the responses of plants to iron deficiency, but it has no effect on low-phosphorus responses (Schmidt and Schikora, 2001). Currently, data about the relationship between nutrient stress and ROS signals in root hair development are limited. However, the genes specifically expressed in root hair cells, such as *ROBHC*/*RHD2* and *RHD6*, which may be induced by nutrients, seem to validate this relationship (**Table 1**). A recent study further confirmed that nitrite could affect the expression of UPBEAT1 and localization of ROS in *Zea mays* L. roots (Trevisan et al., 2019).

ROS FUNCTIONS IN AERENCHYMA FORMATION

The parenchyma tissue with a large number of intercellular spaces is called aerenchyma. Aerenchyma is the evolutionary result of plant adaptation to flood-submerged and waterlogged growth environments (Bailey-Serres et al., 2012; Nishiuchi et al., 2012; Kato et al., 2020), and the classical view is that it is the channel for oxygen to enter the root. For hydrophytes and hygrophytes, aerenchyma forms in their rhizomes; however, terrestrial plants could also differentiate to produce or accelerate the development of aerenchyma in an anoxic environment. In this situation, ROS and ethylene signaling are involved in this adaptation regulation (Yamauchi et al., 2014; Sasidharan and Voesenek, 2015; Singh et al., 2016; Choudhary et al., 2020; Hong et al., 2020). Lysigenous aerenchyma contributes to the ability of plants to tolerate low-oxygen soil environments by providing an internal aeration system for the transfer of oxygen from the shoot. However, aerenchyma formation requires Programmed Cell Death (PCD) in the root cortex (Drew et al., 2000; Bartoli et al., 2015; Fujimoto et al., 2018; Guan et al., 2019). Interestingly, both the aerenchyma formation and PCD in waterlogged sunflower stems are promoted by ethylene and ROS (Steffens et al., 2011; Petrov et al., 2015; Ni et al., 2019). In the root, during lysigenous aerenchyma formation under oxygen-deficient conditions, the precise balancing of ROS production and scavenging serves a crucial role (Paradiso et al., 2016; Yamauchi et al., 2017a; Yamauchi et al., 2017b).

CONCLUSIONS

Root system growth depends on maintaining the balance between root-tip cell proliferation and differentiation (Petricka et al., 2012). In the meristematic zone, the cells exhibit higher rates of cell division, but they do not elongate; in the elongation zone, the cells cease to proliferate, become elongated, and start to differentiate (Beemster and Baskin, 1998). The maturation zone is characterized by fully elongated cells that undergo differentiation to form different types of cells, including root hairs (Caño-Delgado et al., 2010; Mendrinna and Persson, 2015). More importantly, the lateral roots are developed from primary roots in the maturation zone. These newly formed organs are important for the branching structure of the root system (Vermeer and Geldner, 2015). Research on the components that regulate such a balance is crucial to understanding plant growth and root development (Tsukagoshi, 2016). After decades of research, several pivotal plant hormones involved in root development have been identified (Ubeda-Tomas et al., 2009; Vanstraelen and Benková, 2012; Yamada and Sawa, 2013; Schaller et al., 2015). Recent studies have shown that ROS can function as signaling molecules to regulate root system growth (Mhamdi and Van Breusegem, 2018; Waszczak et al., 2018; Biswas et al., 2019; Chapman et al., 2019; Trevisan et al., 2019). ROS are especially important in maintaining the balance between cell proliferation and differentiation. The hypothesis that ROS have a hormone-like function by acting as signaling molecules is supported by a substantial amount of evidence (Yang et al., 2018; Mhamdi and Van Breusegem, 2018; Waszczak et al., 2018). From these results, ROS appear to be key to vital processes, including stem-cell maintenance, cell-cycle progression, and root hair initiation in the maturation zone of roots. Future research should aim to further elucidate the involvement of ROS in these processes. This will advance our understanding of the role of ROS in root development (Boisson-Dernier et al., 2013).

AUTHOR CONTRIBUTIONS

XMZ carefully revised and edited the manuscript and replot the figures. YX wrote the draft of the manuscript and CLL performed a part of the experiments in the manuscript, and GHY revised, guided, and improved the manuscript.

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