Planta (2025) 262:72
https://doi.org/10.1007/s00425-025-04787-x

REVIEW

# Response of hidden architects to salt stress

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Received: 4 May 2025 / Accepted: 20 July 2025 / Published online: 5 August 2025


## Abstract

***Main conclusion*** **The molecular mechanisms involved in root architecture is crucial for developing crops with better salt stress tolerance are reviewed.**

**Abstract** Unraveling the intricate salt tolerance mechanisms is crucial to developing crop plants that can survive and produce superior yields. Soil salinity impacts predominantly root and shoot growth, thereby diminishing the final yields. Salt stress incites far-reaching consequences at the root meristem level. Hence it is essential to delineate the alterations in root anatomy resulting from salt stress and maintenance of the root meristem is essential for plants to achieve stress tolerance. This review addresses the contemporary comprehension of salinity and the adverse conditions under which plants thrive by regulating root tropism (halotropism), fluctuations in apoplastic pH, and their effects on root response outcomes, as well as the hormonal modulation of root growth and architecture. The complex interplay of auxin crosstalk with ABA and other hormones in conferring salt tolerance has been discussed. The position-dependent signaling events and feedback loops regulated through specific transcription factors that are critical for root remodeling and stress mitigation have been highlighted. The insights thus far generated may help to develop strategies for breeding crop plants with desired salt-tolerant traits with higher productivity.

Communicated by Gerhard Leubner.

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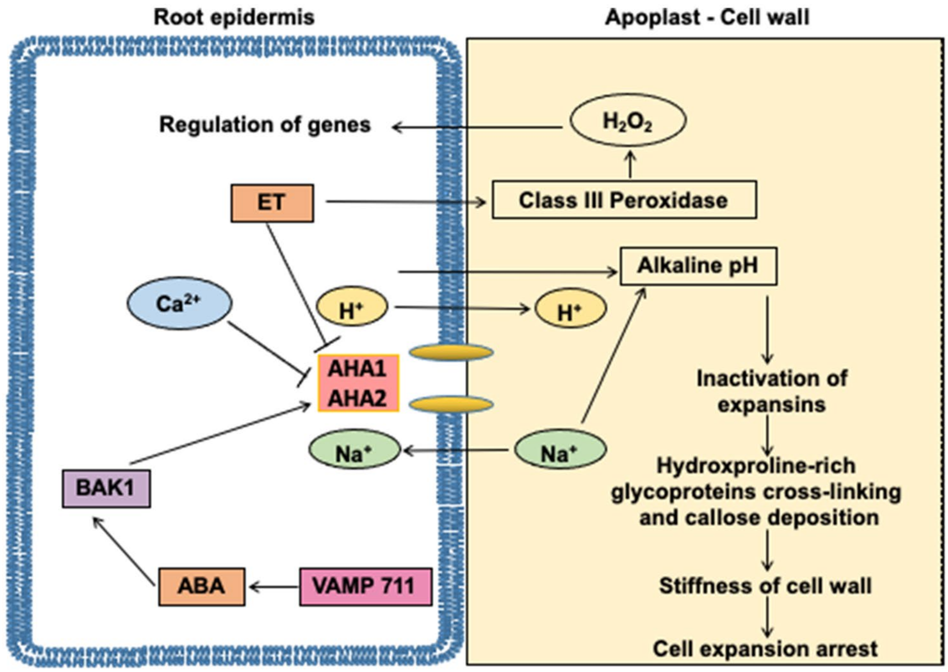
## Graphical abstract




**Root architecture as modulated by pH and autoinhibited $H^+$ ATPase (AHA) activities**

**Keywords** Extensins · Hormones · Root architecture · Salt stress · Wall-building enzymes

## Introduction

Optimized root architecture helps plants to take up water and nutrients properly and thus minimizes yield losses under salt stress conditions (Farooq et al. 2024). Variations in root system architecture exist in crop plants like in cotton. Optimizing the same has been found to enhance the mild water stress tolerance with minimal losses in the yields in cotton (Guo et al. 2024). Together, the spectrum of studies indicates that the root anatomy, root apex of the plants, and the ion accumulation patterns differ under salinized conditions in comparison with non-salinized conditions. In other words, root system remodeling is an important aspect of plant life for coping with salt and drought stresses (Julkowska et al. 2017). Reviews on root system architecture in response to salt stress have been published (Galvan-Ampudia et al. 2011). The articles mostly deal with the role of hormones on root system modulations in cereals and other plants (Harris et al. 2015; Lombardi et al. 2021; Maqbool et al. 2022; Jan et al. 2024; Yu et al. 2024). Epigenetic regulation of root responses to salinity have also been reviewed (Yun et al. 2024).

Halophytic species exhibit different morphology and novel mechanisms and tolerate better in comparison with glycophytes. Importantly, understanding the underlying salt stress responses and the associated physiological and molecular changes that take place at the root meristem, and root growth are highly critical for us to generate salt tolerant crop plants. In *Hordeum vulgare*, root growth was constrained at 100 and 200 mM NaCl treatment, and at 300 mM NaCl stress or above for 24 h, nuclear deformation was noticed leading to cell death (Katsuhara and Kawasaki 1996). The decline in shoot and primary root growth was also noticed in a wide number of taxa (Zidan et al. 1990; Geilfus et al. 2010; Nakamura et al. 2020). Root growth inhibition by cell wall acidification has been assessed by Zidan et al. (1990). An assay for root surface acidification indicated that roots exposed to salinized conditions are acidified with 1–2 mm behind the root tips, but not the remaining root surface. To reinforce this, a decrease in pH at the root surface from 6.0 to 5.1 was noticed over a 30 min time. Further, salt stress leads to the acidification of root cells and cell wall stiffening in the salt-sensitive lines of wheat (Shao et al. 2021). In contrast, in the salt tolerant line of wheat, a pH of 5.0 attenuated the cell wall stiffness resulted by salt stress (Shao et al. 2021). The results, therefore, elucidate a correlation between the pH of root cells, salt stress and cell wall stiffness. Such findings may have overarching implications in ameliorating the salt stress and enhancing crop yields. The apical one mm of the root apex was rich in $K^+$ ion accumulation and the ratio of Na:K was less than 2 (Hajibagheri et al. 1985). Such cellular $Na^+/K^+$ homeostasis is usually modulated by $K^+$ channels and anti-transporters under NaCl stress (Yang and Guo 2018; van Zelm et al. 2020; Kumar et al. 2024). Mitigating the harmful effects of $Na^+$ and $Cl^-$ ions, in addition to water deficiencies that influence root cell wall dynamics, and the protective mechanisms employed is critical. It is vital to exploit the architecture of roots in the crop plants, which might help to improve the yields under stress conditions (Lynch 2022).

Roots that are exposed to saline environments experience perturbations in the concentrations and distribution patterns of auxin, $Ca^{2+}$, $H^+$ fluxes, acidifications or alkalinizations in the apoplast or changes in the pH, accumulation of reactive oxygen species (ROS) and infiltration of $K^+$ and $Na^+$ ions (Jiang et al. 2019; Fu et al. 2019; Sachdev et al. 2021). The influx of $Na^+$ ions increases upon the exposure of root apex to saline conditions, depending on the concentration of NaCl. The growth of root apex seizes immediately after exposure to NaCl, but in a root tissue-dependent manner (Shabala et al. 2016). Concomitantly, mature cells efflux out tenfold higher $K^+$ than the apical region of the root. In other words, younger cells at the root apex retain more $K^+$ than mature cells. Higher efflux of $K^+$ and decreased intake and retention of $K^+$ in the mature root cells are because of lower $H^+$-ATPase activity and higher ROS production (Shabala et al. 2016). During salt stress, it is the root plasma membrane-bound cell-specific $H^+$-ATPase activities that modulate the transport of water and nutrients besides retention of $K^+$ ions (Siao et al. 2020).

The present review deals with a gamut of genetic components, the role of hormones, as well as gene modules that play a critical role in primary and secondary root architecture besides the root hair remodeling under NaCl stress. All these components are vitally important for a comprehensive understanding of the root system that occurs in response to salt stress to design saline tolerant crops.

## Morpho-physiological alterations with distinct molecular mechanisms in root growth contribute to differential salt tolerance in halophytes over glycophytes

### Root growth in halophytes

In general, halophytes tolerate high levels of salt concentrations due to their unique morphological, anatomical, physiological and molecular mechanisms. Effective root responses to salt stress also include proper maintenance of the cell expansion and allocation of sugars or carbon to the roots from the shoots (Li et al. 2023). Root responses, especially in halophytes, differ from that of glycophytes. Natural variation in *ZmNAC087* contributes to total root length regulation in seedlings of *Zea mays* (glycophyte) under salt stress (Zhang et al. 2023a). But this phenomenon has not yet been established in halophytes. Though the halophytic species *Schrenkiella parvula* does not have the ability to circumvent salt, suppression of growth under salinity stress is minimal. In *S. parvula*, roots accumulate higher ABA levels than the glycophytic species (Li et al. 2023). In *S. parvula*, salt stress triggers genes associated with sugar transport, cell expansion and suberization. Carbon partitioning and allocation to the roots of halophytes is appropriate, but sugar transport into the roots, root suberization and carbon partitioning are poor in a glycophytic species like *A. thaliana* (Li et al. 2023). Such experiments surmise that root growth is properly maintained in the halophytic species under salt stress conditions unlike that of glycophytes. Halophytic species such as *Suaeda salsa* display prolonged roots but with tiny root diameters, which might be useful to the plants to enhance the root surface area. On the contrary, in *Beta vulgaris*, a glycophytic species such altered root morphology was not observed. However, sugar beet activates rhizosperic processes to acquire higher nutrient levels (Wang et al. 2021a). Understanding these halophytic molecular mechanisms provides us with an avenue to improve root-specific traits in the crop plants.

### Distinct molecular mechanism confers salt tolerance in the roots of halophytes

Root meristem is an important tissue that absorbs minerals from the soil and helps root growth as well as whole plants. But the molecular mechanisms underlying the meristem maintenance under NaCl stress conditions are partly elusive. Roots grow mostly away from the saline areas, which is called halotropism. Such a tendency helps the plants to avoid areas affected by soil salinity (Galvan-Ampudia et al. 2013). Generally, the direction of root movement against gravity under a saline environment is due to the redistribution of auxin-by-auxin exporter PINFORMED2 (PIN2). Halotropism requires the activity of phospholipase D (PLDDf1/2) enzyme, which mediates not only the regulation of auxin polarity, but at the same time regulates $Ca^{2+}$ signal through the activity of PLDs with the release of phosphatidic acid, a signaling lipid molecule (McLoughlin and Testerink 2013; Han and Yang 2021), thereby alter the root movements (Galvan-Ampudia et al. 2013; Korver et al. 2020). This infers that root directional change is due to the redistribution of auxin and calcium signals. Phosphatidic acid moderates the auxin transporters, which help to maintain auxin levels in the roots (Jenness et al. 2019). Activation of the auxin transporters affects the proper maintenance of auxin levels in the cells and the growth of roots in a specific direction under salt stress (Han et al. 2017; Korver et al. 2020; Konstantinova et al. 2021). Roychoudhry et al. (2023) demonstrated that auxin drives the growth of lateral roots in a specific direction and further influences vertical growth by acting in the root columella cells. Auxin enhances the levels of protein phosphatase subunit ROOTS CURL IN NAPHTHYLPHTHALAMIC ACID1 (RCN1). Components like PINs and phosphatase subunit PP2A/RCN1 mediate the antigravitropic movement of roots. A shift in the localization of PIN3 protein basically causes lateral root growth at a range of angles. Roychoudhry et al. (2023) showed that manipulating auxin asymmetries leads to downward as well as upward movements of lateral roots in *A. thaliana*. ABA mediates the PIN1 protein, which then regulates the auxin movement in primordia of lateral roots, which is crucial. It appears that subtle shades of hormones fine-tune the growth of roots to survive under changing environmental conditions.

Besides halotropism, plants undergoing salt stress develop shallower roots with root angle modifications. In *A. thaliana*, gravitropism or gravity signaling pathway is dependent on the concentration of NaCl to modulate the growth direction of primary roots, which might involve SOS signaling (Sun et al. 2008). In the root tips, the uneven movement, distribution, and accumulation of auxin contribute generally to the halotropic movement of roots, thus avoiding areas of soils where the concentrations of salt are high (Wang et al. 2023). Two respiratory burst oxidases, *OsRBOHA* and *OsRBOHI* localized at the membrane play a vital role in systemic signaling and proliferation of lateral roots of rice under salt stress (Wang et al. 2023). It appears that in halophytes, the transcription factor bHLH is critical for reducing the development of root hairs, increasing osmotic resistance, and for imparting tolerance to salinity. *Limonium bicolor*, a halophytic species, displays high expression of *LbHLH* in response to NaCl treatment during salt gland development that helps to efflux the excess salts (Wang et al. 2021b). Over expression of *LbHLH* isolated from *L. bicolor* in the glycophytic species *A. thaliana* interacted with *GLABRA 1* resulting in enhanced trichomes, but with diminished tally of root hairs (Wang et al. 2021b). Taking together, it is concluded that bHLH reduces the development of root hairs but enhances salt tolerance.

## Changes in root anatomy in the salt tolerant and susceptible lines of glycophytes

In addition to the ion accumulation patterns at the root zone, deposition of polysaccharides, lignin, suberin in root endodermal and exodermal cells, orientation of microfibrils in the roots and cell wall modifying enzymes sharply differ in plants growing under saline conditions (Byrt et al. 2018). Such metabolite and anatomical changes in the roots determine the root elongation inhibition (Byrt et al. 2018). Changes that occur in the root anatomy are important in preventing water loss from the cells and for amending the transport of ions. Byrt et al. (2018) noticed that $Na^+$ ions bind to the cell wall components of roots and impact the passage of $Na^+$ and other ions. Such a phenomenon hinders the function of pectin in growing roots (Flowers and Hajibagheri 2001; Henry et al. 2015; Byrt et al. 2018). In *Sorghum bicolor*, root anatomical changes have been compared in contrasting genotypes under control (devoid of salt stress) and 200 mM NaCl stress. Root anatomy distinctly differs in the genotypes that are tolerant and susceptible. Roots of salt-tolerant plants displayed multilayered, lignified walls that constitute the hypodermis and endodermis (Karumanchi et al. 2023a). Roots of salt susceptible plants showed thin cell walled metaxylem elements with large lumen diameter. In contrast, thick-walled, narrow-lumen xylem elements have been noticed in salt tolerant plants. Significantly thin cuticles have been detected in salt susceptible *S. bicolor* cultivar in contrast to the salt tolerant cultivar. Upon exposure of salt tolerant plants, roots exhibited enhanced lignification in hypodermis cell walls, but not in susceptible ones (Karumanchi et al. 2023a). Corner regions of the cortical cells have been characterized by the deposition of the polysaccharides such as hemicellulose and pectin. These changes point out that root anatomy is important for imparting salt stress tolerance.

## Casparian strips and salt stress responses

Casparian strips act as fencing to the flow of ions, permitting ions to move into cytoplasm, rather than along the cell wall (Chen et al. 2011a). Casparian strips have developed close to the root apex more under saline conditions. Casparian strip thickness variation has conferred salinity tolerance in *Zea mays* and *Sorghum bicolor* (Wang et al. 2022; Karumanchi et al. 2023a). Defective Casparian strip enhanced the leakage of solutes and reduced root hydraulic conductivity in *A. thaliana* (Calvo-Polanco et al. 2021). While defective Casparian strip led to a decrease in rosette growth, ectopic suberin has been shown to partially compensate for defective Casparian strip phenotypes (Calvo-Polanco et al. 2021). *Salt-Tolerant Locus 1* (*STL1*) in *Zea mays* (*ZmSTL1*) produces ZmESBL protein which is localized to the Casparian strip domain and helps in lignin deposition. But *ZmESBL* mutants display impaired lignin deposition in maize leading to defective Casparian strip barrier, besides enhancing $Na^+$ transport via transpiration flow. Such a phenomenon escalates flow of $Na^+$ into shoots prompting salt hypersensitivity (Wang et al. 2022). Roots of *S. bicolor* (susceptible and tolerant genotypes) upon exposure to NaCl stress display thick lower tangential walls with Casparian strips in the endodermis. While higher lignin with thickened wall areas is the hallmark of salt tolerant roots, susceptible roots display tylosis in the metaxylem elements. In salt susceptible roots of *S. bicolor*, thin and deformed cell walls with large lumen metaxylem elements were noticed when treated with NaCl stress (Karumanchi et al. 2023a). Halophytic species *Suaeda maritima* shows higher degree of vacuolation in the cortical cells close to the root apex than in plants not exposed to saline conditions. Therefore, root anatomy sharply varies in salt tolerant lines. The above studies distinctly indicate that root anatomy is critical for salt stress tolerance. The work on Casparian strips in relation to salt stress responses is scanty, but genetic alteration leading to the modification of Casparian strip furnishes an important novel approach to develop salt-tolerant lines.

## Microtubule dynamics and halotropism

A close correlation exists between cytoskeleton and salt stress responses, but the role of microtubules is not completely clear. Salinity perturbs the organization of cortical microtubules [α-tubulin (TUA) and β-tubulin (TUB)] and the helical growth in *A. thaliana* (Shoji et al. 2006; Wang et al. 2007). But microtubules are necessary for carrying out diverse functions like proper deposition of cellulose polymer during cell wall formation (Bringmann et al. 2012; Chun et al. 2021). In-depth scrutiny of gene expressions in salt-adapted cells indicated that multiple genes like *FBA8*, *TUBs* and *CCoAOMT1* are involved in cell wall formation. Further, loss-of-function mutants such as *tub9* exhibit salt sensitivity in *A. thaliana* (Chun et al. 2021), indicating the importance of microtubules in lignin deposition and salt stress tolerance. Spiral 2-Like (SP2L)-dependent cortical microtubule reorientation is vital for halotropism of roots. It is an ABA-activated SnRK2 protein kinase which phosphorylates SP2L to modulate halotropism of the roots (Yu et al. 2022a). It appears that root twisting drives the haloptropism due to stress-induced microtubule reorientation (Yu et al. 2022a). The results thus far indicate that manipulation of microtubule-related genes over expressions is another intervention to generate salt tolerant plants.

## Role of reactive oxygen species (ROS) and iron (Fe) in root growth

*Reduced Root Elongation under Salt Stress 1* (*rres1*) mutant displays decreased root elongation, and shorter root meristem under NaCl, KCl, $NaNO_3$ and $KNO_3$ treatments which aligns well with diminished accumulation of auxin, higher levels of ROS, and low levels of sugars (arabinose and xylose) in the cell walls (Yu et al. 2022b). *Reduced Root Elongation under Salt stress* (*RRES1*) gene codes for a mitochondrial protein, mostly in leaves and roots. Mitochondrial protein plays a role in root elongation, piles up auxin, maintains integrity of cell walls and ROS homeostasis under NaCl stress (Yu et al. 2022b). Redox status in the root cells affects auxin distribution in the roots undergoing stress. Auxin induces redox balance in roots, and modulates *ASCORBATE PEROXIDASE 1* (*APX1*), thereby altering the levels of $H_2O_2$ at the site of roots and root system architecture (Correa-Aragunde et al. 2013). *IAA CONJUGATE RESISTANT 4* (*IAR4*, an auxin-responsive gene) regulates ROS-mediated auxin distribution during stress, thereby the formation of roots (Fu et al. 2019). In contrast, in *iar4* mutants, primary root growth is restricted but regained with exogenous supply of glutathione or auxin (Fu et al. 2019). Experiments carried out by Su et al. (2016) also underpin this view. They noticed that $H_2O_2$ causes highly branched primary roots, but more lateral roots (root system architecture) by regulating auxin transport. Accordingly, auxin concentrations decrease in the primordial cells of lateral roots and lateral root tips via AUX1 and PIN protein carriers (Su et al. 2016). Overall, these experiments infer that polar auxin transport is perturbed under stress conditions, $H_2O_2$ is generated which regulates the architecture of roots. In general, lower Fe and higher NaCl levels suppress root growth, but exogenous supply of Fe improves root growth under similar conditions (Hua et al. 2023). In *Triticum aestivum*, optimum concentrations of Fe, saline stress promoted ethylene and auxin accumulation (Hua et al. 2023), suggesting the pivotal role played by Fe under NaCl stress. Asymmetric stress causes an increase in cytosolic $Ca^{2+}$, and ROS in the root tips exposed to NaCl stress leading to systemic ROS signaling (stimulated by respiratory burst oxidase homologs, *OsRBOHA* and *OsRBOHI*) in the roots that are not exposed. Also, rapid proliferation of root growth has been noticed in salt stress free areas (Wang et al. 2023). If $Ca^{2+}$ signaling is blocked, it leads to inhibition of lateral root branching in the areas that are free from stress (Wang et al. 2023). Together, these experiments suggest that a cascade of events such as the activity of RBOH, coupled with ROS in the upstream and auxin signaling in the downstream results in rice root development to avoid localized stress.

## Altered cell division and cell cycle genes inhibit growth under salinity

Primary cell walls of plants are heterogenous structures and help during environmental stresses, unlike that of secondary cell walls which are static structures. Secondary cell walls give strength to give a shape to the plant and act as pillars for providing architecture to the plants and water transport through them (Colin et al. 2023). Salt stress regulates metabolic activities, gene expressions that might lead to alterations in the composition of cell walls leading to changes in the root architecture. Multiples genes modulate the rate of cell division, growth of plant leaf and root, root branching, expansion of cell walls under saline conditions, or the dimensions of newly generated cells (Geilfus et al. 2010; Wolny et al. 2021). The results strongly indicate that salt-associated oxidative stress is the basis for genomic damage and epigenetic effects leading to the suppression of cell cycle genes besides the regulation of arabinogalactan protein (AGP) genes like *FLA1*, *FLA10*, *FLA11*, *AGP20* and *AGP26* in the roots leading to their reduced growth (Wolny et al. 2021).

## Auxin and other hormonal networks that influence primary root growth under salinity stress

The expression of *PINFORMED* (*PIN*) genes is suppressed, causing decreased auxin levels under saline stress. Suppression of *PIN* diminishes root meristem size on one hand and promotes the stability of the genes *AUXIN RESISTANT3 (AUR3)/INDOLE-3-ACETIC ACID17* (*IAA17*) on the other (Liu et al. 2015). In other words, salt stress strongly perturbs auxin distribution and signaling at the root level. Such a disruption in auxin concentrations in the root tissues steers suppression of root growth. It is auxin which regulates $H^+$ flux at the root level, leading to the alkalinization of apoplast. The interplay of TIR1/auxin-signaling (transport inhibitor response) F-box receptor (AFB) is essential for $H^+$ flux modulations (Li et al. 2021a, b). Such an $H^+$ flux is the primary cause for root growth inhibition. Also, while *tir1 afb2* and *tir1 afb3* mutants display tolerance to oxidative stress, *tir1 afb2* exhibit reduced accumulation of hydrogen peroxide and superoxide anion, higher ascorbic acid levels, better root elongation and resilience to salinity than the plants that are growing under non-saline conditions (Iglesias et al. 2010). Therefore, the overall inference is that auxin signaling is linked to oxidative metabolism which is vital for coping with oxidative stress and salinity tolerance. Further, the gene *IAR4* regulates ROS-mediated auxin distribution thereby modulates growth of primary roots (Fu et al. 2019). Contrarily, *iar4* mutants show stunted growth of roots under salinity, wherein the expression of PINs and the ability to scavenge the ROS was repressed. But auxin and glutathione supplementation restore the *iar4* phenotypes (Fu et al. 2019). Hence, redox regulations take active part during the growth of primary roots under saline conditions via auxin distribution/perturbation. Latif et al. (2024) have shown higher expression of *Dwarf and Runtish Spiklet1* (*DRUS1*, a receptor kinase), but not *DRUS2* under osmotic stress conditions. Enhanced *DRUS1* in *drus2* mutants under osmotic stress conditions repress the rice *OsIAA* repressors, ensuing a vigorous root growth. Contrary to this, decreased *DRUS2* in *drus1-1* mutants led to fewer weak and delicate adventitious and lateral root systems, making the plants susceptible to salinity (Latif et al. 2024). *DRUS1* and *DRUS2* seem to have different functions during stress but regulate root system architecture through auxin.

ABA INSENSITIVE 4 (ABI4) negatively regulates primary root growth by modulating cell divisions in root meristems (Luo et al. 2022). Nitric oxide (NO) plays a pivotal role in stress response (Shang et al. 2022). If NO production is blocked, root meristem size is not inhibited, thus clearly pointing out the important role that NO plays in salt-dependent growth of root meristem. Auxins and cytokinin play a role in root meristem growth under non-saline conditions (Ioio et al. 2008). Endogenous cytokinin levels are decreased under ABA, drought and NaCl stress conditions (Nishiyama et al. 2011), and cytokinin is associated with multistep phosphorylation and transduces the signals from receptors to the nucleus, thereby activating type-B response regulators. Cytokinin modulates auxin via ARABIDOPSIS RESPONSE REGULATORS (ARR1/12) which then activate SHORT HYPOCOTYL2 (SHY2/IAA3) to inhibit PINs. It has been demonstrated that overexpression of *CYP79A2* gene associated with benzylglucosinolate synthesis enhances lateral root formation via phenylacetic acid (Wybouw and de Rybel 2019; Zubo and Schaller 2020; Aoi et al. 2020). *GRETCHEN HAGEN 3* (*GH3*) genes in coordination with auxin-amido synthetases modify the ratio of IAA by regulating its biosynthetic pathway enzymes leading to dramatic changes in the auxin polarity (Ioio et al. 2008; Moubayidin et al. 2010; Di Mambro et al. 2017; Yan et al. 2017; Aoi et al. 2020). But suppression of the group II *GH3* genes bestows resilience to salt stress and drought conditions by exhibiting longer primary roots (Casanova-Saez et al. 2022). Thus, a complex network of genes operates either for positive or negative root growth under NaCl stress conditions. Auxin switches from the state of cell division to cell differentiation in the root (Moubayidin et al. 2010; Di Mambro et al. 2017). Both cytokinin and auxin cross talk in the root transition zone direct the growth of root under saline conditions (Ioio et al. 2008). Cytokinin deficient or defective mutants (Nishiyama et al. 2011; Hyoung et al. 2020), or genes like *AHKs*, or receptor *Arabidopsis thaliana Response Regulator* (*ARR;* the cytokinin receptor) (Mason et al. 2010; Abdelrahman et al. 2021) impart the tolerance to NaCl. Concomitantly, expression of *PIN 1/3/7* genes are suppressed under saline conditions, ensuing the reduction of auxin levels. Taken together, it appears that distribution of auxin and its transport including its efflux (PINs) and influx (AUX1/Like AUX1) porters greatly influence the primary root elongation and patterning (Yun et al. 2024). Inactivation of the gene *GH3*, an auxin-responsive gene, resulted in resilience to salt stress with longer primary roots (Casanova-Saez et al. 2022) indicating the importance of GH3 in root architecture.

### Accumulation of osmolytes, $Ca^{2+}$ signaling and root growth under salt stress

To maintain proper water relations, plants always regulate their internal water potential in such a way that helps plants facilitate water uptake under NaCl conditions. Upon exposure to saline environments, plants synthesize organic osmotic compounds like proline, glycine betaine, sugars and sugar alcohols and accumulate them in excess quantities that help them to absorb water and cope with stress (Rajasheker et al. 2019; Jawahar et al. 2019; Munns et al. 2020; Zhao et al. 2021). Meristematic cells of roots that harbor some or all the above components can act as salt sensors and trigger downstream genes (Wu 2018). As mentioned above, salt stress causes the bending of roots due to the asymmetric distribution of auxin (Galvan-Ampudia And Testerink 2011; Fu et al. 2019). Such an alteration is the principal cause of root growth inhibition. Either auxin or auxin-responsive genes modulate ROS accumulation and ROS-related auxin redistribution for the tropistic root movement and subsequent primary root growth under saline conditions (Fu et al. 2019). Salt stress has altered the root meristem organization in the salt-tolerant genotypes of *S. bicolor*. Further, a decrease in the length of primary roots along with the formation of ROS was noticed in the lateral roots (Peduzzi et al. 2024). Salt stress sensing is likely localized in the meristems of roots, which might lead to a spectrum of biochemical and genetic changes (Wu 2018). Under saline conditions, the levels of ROS and ROS-induced $Ca^{2+}$ ions increase within the cytoplasm. A $Na^{+}/Ca^{2+}$ exchanger (NCX)-like protein (AtNCL) is implicated in $Ca^{2+}$ flux repression (Wang et al. 2012; Li et al. 2016), but other players such as FERONIA (FER) receptor kinase, and cyclic nucleotide gated channels (CNGC) trigger the uptake of $Ca^{2+}$ and $Ca^{2+}$ signaling (Jiang et al. 2019; Zhao et al. 2021; Karumanchi et al. 2023b). Again, the growth promotion of lateral roots is tuned by the calcium signal CCaMK-MKK1/6 cascade in rice during stress; CaM-IQM disrupts the IAA-ARF interaction to regulate the growth (Yang et al. 2021; Zhang et al. 2022). The above experiments infer that several salt sensors act together and bring about changes in root growth under saline conditions.

### Implications of auxin in lateral roots and their development

Efflux-dependent dynamic auxin gradient at the tip of root primordia is necessary for organ formation (Benkova et al. 2003; Peret et al. 2009). Associated with this, INDOLE 3-ACETIC ACID INDUCIBLE14 (IAA14) performs an important role for the development of lateral roots. Lateral root formation can be inhibited by mutations in *SOLITARY-ROOT-1* (*slr-1/IAA14*) gene (Fukaki et al. 2002) indicating its key role in lateral root initiation. Formation of roots therefore needs the relocation of PIN1.11, PIN1.12 and phosphorylation by many genes (Michniewicz et al. 2007; Zhang et al. 2010, 2023b; Jia et al. 2016). Multiple auxin response factors (ARFs) like ARF7 and ARF19 and others help in the inception of lateral roots (Okushima et al. 2007). Further, salt stress triggered micro RNAs like *miR390*, and tasiRNAs together with ARFs regulate lateral root formation and growth. The suppression of the ARF activities by *tasiRNAs* leads to lateral root growth promotion. Salinity triggers the expression of *miR390* in *Populus* species, and its overexpression causes lateral root growth with improved resilience to salinity, while knockdown suppresses lateral root growth with no tolerance to salinity (He et al. 2018). *miR390* positively modulates the events necessary for lateral root formation and its growth under saline conditions. However, *ARF4* suppressed the signaling events involved in auxin response (He et al. 2018). Overall, it appears *ARFs* (ARF2, ARF3, and ARF4) module take a central stage in regulating *miR390* thereby the growth of lateral roots. Likewise, miRs such as *miR399* and *miR72c* have also been found to control growth of roots under stress (Sun et al. 2016; Sahito et al. 2017). Lateral root emergence and subsequent growth depends on ABA accumulation under salt stress. ABA promotes PIN1, which then reduces polar auxin transport, leading to inhibition of lateral root growth. ABA interacts with the transcription factor WRKY46 stimulating ABI4. This interaction results in lateral root initiation (Ding et al. 2015) (Fig. 1). ABI3 and ethylene response factor 1 (ERF1) module also suppress the PIN1 and AUX1 which represses lateral root emergence (Zhang et al. 2023b) (Fig. 1). Further, promotion of *AUXIN RESISTANT3* (*AXR3*)/*INDOLE-3-ACETIC ACID17* (*IAA17*), and suppression of PIN2 protein by NaCl results in root growth alterations including meristem development (Liu et al. 2015; Smolko et al. 2021). Saline stress leads to salt overly sensitive (SOS2) pathway phosphorylation and stabilization of PLETHORA 1 and PLETHORA 2 (PLT1/2) proteins, and the phosphorylated PLTs regulate root growth. Overall, it appears that upon exposure of plants to a saline environment, PLT1/2 promote lateral roots (Benfey et al. 2010; Hao et al. 2023).

## Regulation of root growth by phytohormones

### Dosage of abscisic acid (ABA) and its cross talk with other hormones differentially regulates root architecture under control and salinity stress

ABA biosynthesis is triggered under mild salt/water stress, but basal levels are maintained under well-watered conditions. ABA positively regulates the development of root

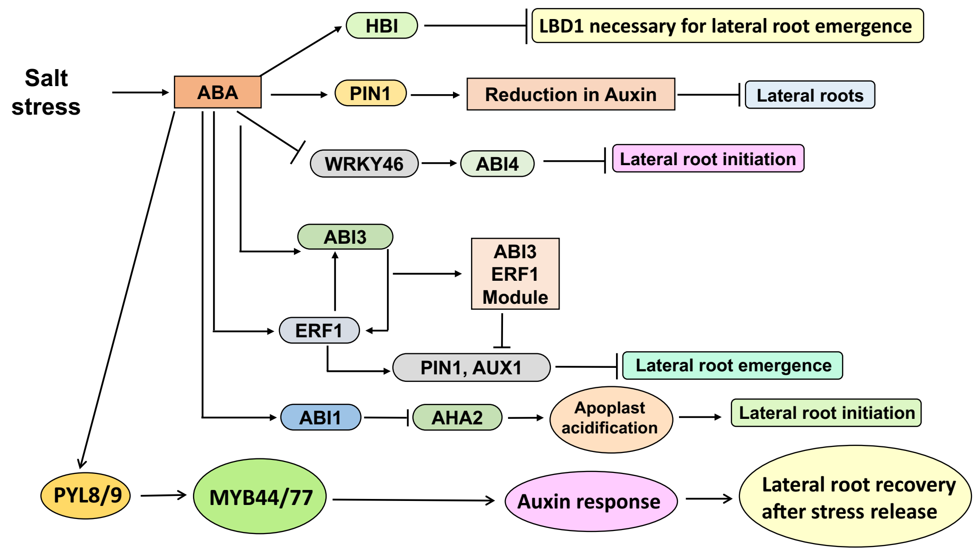



**Fig. 1** Growth of lateral roots as modulated by ABA. Salt stress or high ABA triggers the HD-Zip1 (HB1) transcription factor, which then negatively regulates the LATERAL ORGAN BOUNDARIES DOMAIN 1 (LBD1) transcription factor, which is required for lateral root emergence. Once the salt stress is relieved, ABA signals like PYL8/9 modulate MYB44/77 transcription factor, which then triggers auxin response for lateral root recovery. ABA-mediated PIN-FORMED 1 (PIN1) localization regulates auxin distribution in lateral root primordia. Therefore, auxin negatively regulates lateral root initiation. ABA negatively regulates WRKY46 to affect auxin concentrations and cell divisions via ABI4-mediated cell cycle genes, which then suppress the initiation of lateral roots and their emergence. ABA regulates Ethylene Response Factor 1 (ERF1) which in turn stimulates PIN1 and Auxin Influx Carrier (AUX1) which then negatively regulate lateral root emergence. But, ABI3, ERF1 module negatively modulates PIN1 and AUX1. ERF1 also promotes ABI3 and vice-versa. ABA promotes ABI1 which then negatively regulates Arabidopsis Plasma Membrane $H^+$ ATPase 2 (AHA2). AHA2 causes apoplast acidification to promote lateral initiation

architecture besides imparting stress tolerance (Orman-Ligeza et al. 2018; Kavi Kishor et al. 2022; Teng et al. 2023). PYR/PYL/RCAR-dependent route appears essential for the repression of lateral root formation by ABA (Orman-Ligeza et al. 2018). ABA-deficient mutants like *aba2* and *aba3* and the ABA-signaling mutants such as *abi4*, *abi8*, and *pyl8* vary in lateral root numbers under normal conditions in comparison with wild-type plants (Brocard-Gifford et al. 2004; Deak and Malamy 2005; Shkolnik-Inbar and Bar-Zvi 2010; Zhao et al. 2014). Further, ABA transporters like AtABCG17, AtBCG18, AtBCG40 in *A. thaliana* and MtABCG20 in *Medicago truncatula* regulate the development of lateral roots by controlling cell-to-cell transport of ABA under normal conditions (Pawela et al. 2019; Zhang et al. 2021). These experiments infer that ABA under basal level is necessary for lateral root growth under control conditions. Under water and salt stresses conditions, ABA and its signaling pathways and the 1-aminocyclopropane carboxylic acid synthase 2/5 (ACS2/5) involved in ethylene synthesis negatively regulates primary root growth. It appears that the function of ABA in lateral root emergence depends on the ABA concentration and the stage of plant growth. High ABA (under salt stress) induces HD-Zip 1 (HB1) transcription factor, which suppresses LATERAL ORGAN BOUNDARIES DOMAIN 1 (LBD1), necessary for the emergence of lateral roots. Once the salt stress is relieved, ABA and its signaling molecules PYL8/9 promote the MYB44/77 transcription factor, which then upregulate the expression of multiple auxin-responsive genes. The auxin helps in lateral root recovery once the plants are relieved from the salt stress (Teng et al. 2023). Such a phenomenon is termed as xerobranching (Orman-Ligeza et al. 2018; Teng et al. 2023). Auxin regulates ARABIDOPSIS RESPONSE FACTOR 2 (ARF2) which in turn triggers ABA response for modulating root meristem. ABA and auxin in a complex cross talk influences the development of roots such as lateral root emergence, root hair elongation and overall root growth under salt stress (Rai et al. 2024). Under conditions of salinity, ABA stimulates PINs (PIN1) at the tip of roots and powers the auxin distribution in lateral roots (Salazar-Henao et al. 2016; Promchuea et al. 2017). Upon exposure to salt stress, *CYCLIN B1;1* and *CYCLIN-DEPENDENT KINASE B2;2* genes associated with cell divisions are largely suppressed by ABA-mediated ABI4, causing primary root growth retardation (Luo et al. 2022). Besides, ABA-ASPARAGINE-RICH PROTEIN (NRP) expression is triggered by ABA under stress. NRP in turn facilitates the vacuolar degradation of PIN2 protein leading to root growth inhibition. The *nrp* mutant displays short root phenotype due to auxin over accumulation in the roots (Wu et al. 2022). Under stress conditions, root growth is subdued since ABA recruits this pathway (Wu et al. 2022; Teng et al. 2023). While this is one of the ABA-induced growth inhibition pathways, the second pathway is ABA INSENSITIVE 1 (ABI1)-dephosphorylated ARABIDOPSIS PLASMA MEMBRANE $H^+$-DEPENDENT 2 (AHA2) pathway. ABA INSENSITIVE 1 represses AHA2 ($H^+$-ATPase 2), and diminished ABA concentrations stimulate root growth besides hydrotropism (Miao et al. 2021). Protein phosphatase ABI1 dephosphorylates the protein AHA2 resulting in enhanced pH and decreased growth of root cells (Miao et al. 2021; Li et al. 2021a, b). ABA also downregulates WRKY46 which influences auxin concentrations and cell divisions and thereby restrict growth of lateral roots (Teng et al. 2023). Thus, ABA is vital for promoting root growth under normal conditions as well as for restricting the same when subjected to salinity.

## ABA regulates $H^+$-ATPase activity and $K^+$ homeostasis during salt stress

Salt stress promotes the accumulation of ABA, which inhibits the $H^+$-ATPase activity. ABA induces VESICLE-ASSOCIATED MEMBRANE PROTEIN 711 (VAMP711), which then interacts and inhibits plasma membrane $H^+$-ATPase activity (Xue et al. 2018) (Fig. 2). ABA activates BRASSINOSTEROID-INSENSITIVE 1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) which then stimulates AUTOINHIBITED $H^+$-ATPase 2 (AHA2) (Fig. 2). These events cause rapid efflux of $H^+$ ions, alkalinization of the cytoplasmic side and production of ROS leading to stomatal closure under stress (Pei et al. 2022). Cuin et al. (2008) noticed a high retention of $K^+$ ions in the young cells of roots, which correlate well with tolerance of wheat plants to soil salinity. Likewise, in salt-tolerant *S. bicolor*, roots accumulated higher levels of $K^+$ than the susceptible variety (Karumanchi et al. 2023a). Over and above, Shabala et al. (2016) also noticed higher levels of amino acids and sugar content in the meristematic zones of roots, especially in the apex but not in the mature cells of roots. Overall, cell-specific $H^+$-ATPase activity and retention of higher $K^+$ levels besides other metabolites in the younger cells of roots are the key components of salt stress tolerance.

## ABA hormone role in regulating root apoplastic pH, $H^+$-ATPases in root growth

Regulation of cellular pH is complex and needs multiple phosphorylation episodes, 14–3-3 proteins, maintenance of proper ion levels besides reactive oxygen species (ROS) (Cosse and Seidel 2021). Differential pH between the

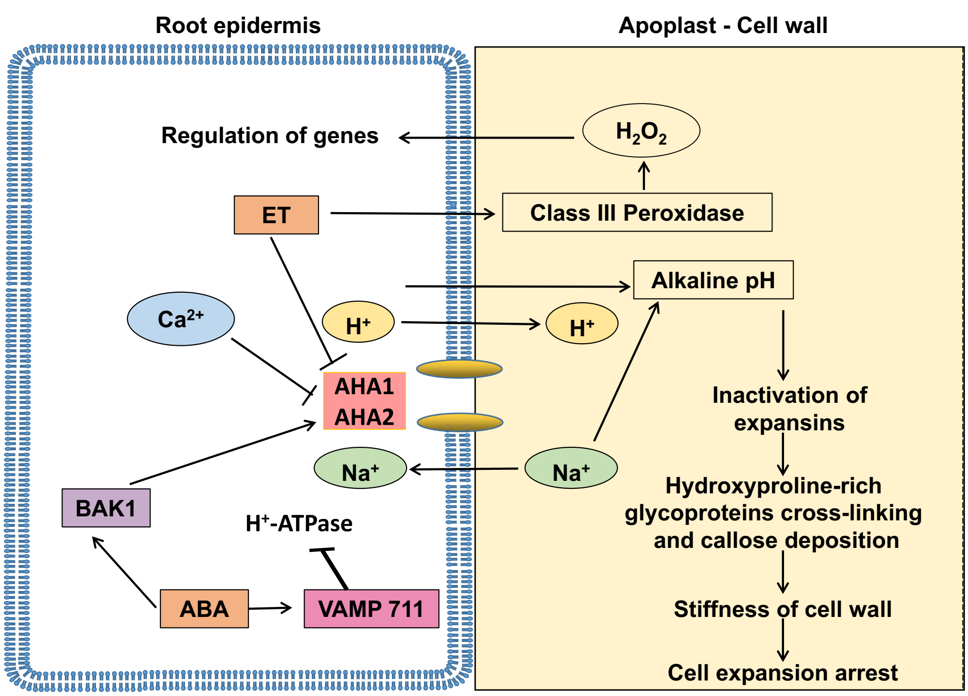



**Fig. 2** Regulation of pH, and stiffness of cell wall. While high ABA inhibits autoinhibited $H^+$-ATPase (AHA) activity, low ABA levels trigger its activity. Ethylene and $Ca^{2+}$ inhibit AHA activity, induce apoplastic alkalization, thereby inhibiting epidermal root cell growth. Ethylene regulates the activity of peroxidases which can lead to higher cell wall stiffness, arresting cell expansion during stress conditions. VAMP 711 is a Vesicle-Assiciated Membrane Protein 711, involved in vesicle trafficking, in the context of the response of the plants to ABA and drought stress. ABA signaling promotes Brassinosteroid-Insensitive 1 (BRI1) associated receptor Kinase 1 (BAK1) which in turn regulates AHA1 and AHA2 which create a proton gradient to facilitate the cellular pH, and also the uptake of water

cytosol and apoplast exists due to the extrusion of $H^+$ by the membrane-bound $H^+$-ATPases (Wegner and Shabala 2020), and the proton motive force (PMF) helps in driving water uptake under stress situations (Cosse and Seidel 2021). The activity of AUTOINHIBITED $H^+$-ATPases (AHAs) is regulated by many components, including hormones (Falhof et al. 2016). Low auxin levels enhance the AHA activity and lower pH. Such acidic pH levels induce cell wall loosening and regulate vacuoles for the water and nutrient uptake. ABA inhibits AHA activity, fosters epidermal pH and represses root growth (Planes et al. 2015). Receptors like TIR1/AFB and TMK1 promote shoot growth but display an opposite effect on roots (Lin et al. 2021). This indicates that localization of auxin in the specific tissue/cell type is also vital for root growth. Ethylene enhances auxin accumulation via AUX1 thereby regulates root growth (Vaseva et al. 2018). Further, class III peroxidases are regulated by ethylene, which in turn helps the plants to acclimate to soils affected by acidic pH, and modify the cell walls with callose deposition, which helps tolerance of plants to low pH (Gracas et al. 2021) (Fig. 2). Cytokinin is another important class of hormones, which regulates apoplastic pH by triggering AHAs and determining root meristem size (Pacifici et al. 2018). Likewise, brassinosteroids (BRs) also change root apoplastic pH, but the mode of action is largely obscure (Gamez-Arjona et al. 2022). Thus, root apoplastic pH is determined by redox-coupled reactions and, importantly, AHA activities. Besides hormones, Rapid Alkalinization Factors (RALFs, small signaling peptides) also interact with FERONIA (FER), a receptor kinase protein, and regulate apoplastic pH. Such manifold cross talks result in the phosphorylation of AHA2. Once AHA2 is phosphorylated by *TRANSMEMBRANE KINASE1* (*TMK1*), its activity diminishes by triggering $H^+$-ATPases which suppress root cell elongation (Haruta et al. 2014; Blackburn et al. 2020; Li et al. 2021a, b). Similarly, intracellular *TIR1/AFB*-associated signaling stimulates $H^+$-influx, with the result of alkalinization of apoplast. Such a contrasting phenomenon readies the root for fine-tuned growth (Li et al. 2021a, b). Overall, the results generated so far suggest that apoplastic pH variations locally in a cell or a tissue are a kind of response signals. So, pH alterations can be a predominant component to prepare the plant for the existing situations. Therefore, both pH and the membrane-bound $H^+$-ATPase activities are the determining factors for the root growth initialization under saline conditions.

## ABA role in regulating EXPANSIN genes and root growth

Analysis of the transcriptome revealed that ABA induces *EXPANSIN* genes through ABA signaling (Huang et al. 2021). The mechanism of cell wall stiffness and turgor during stress has been investigated in *A. thaliana* (Bacete et al. 2022). They demonstrated accumulation of ABA and the hormone-modulating turgor pressure and the reactions that occur due to drought are dependent on cell wall integrity. The authors discovered a wall integrity sensor named as *THESUS1* (*THE1*) which regulates ABA biosynthesis, accumulation, turgor changes, and wall integrity as a response to stress. They identified a *RECEPTOR-LIKE PROTEIN 12* as a key element that regulates the structure of the cell walls and helps in the accumulation of JA, but *THESUS1* harmonizes the cell wall changes such as stiffness. EXPANSINs have been found localized in root cap/columella or diverse root zones (Samalova et al. 2024). Overexpression of *EXPANSIN 1* (*EXPA1*) improved the cell wall stiffness, and triggered the genes such as *EXPANSINs*, *XYLOGLUCAN: XYLOGLUCOSYL TRANSFERASEs* (*XTHs*) and pectin methylesterification (Samalova et al. 2024). Root growth is perturbed due to stress and altered gene regulatory networks including *EXPANSINs* which open the doors for cell expansion and implicated in stress alleviation (Geilfus et al. 2010; Marowa et al. 2016; Samalova et al. 2022). Overexpression of *EXPANSINs* has been correlated with water retention, accumulation of osmoprotectants and proper lateral root growth in *Triticum aestivum* (Geilfus et al. 2010; Yang et al. 2020). These results indicate the key roles that EXPANSINs orchestrate in the rot cell walls and bring about root inhibition. Maize root growth is impeded since the cell divisions at the meristem region are stifled (Xing et al. 2023). In maize tap roots, *ZmmiR169/ZmNF-YA8* (micro-RNA and a Nuclear Factor Y module) tunes the growth of primary roots under saline conditions. Salt stress triggers the activity of *ZmNF-YA8* but suppresses the expression of *ZmmiR169q* (Xing et al. 2023). This in turn initializes an ethylene response factor *ZmERF1B*, provoking the upregulation of two anthranilate synthases (ASA1 and ASA2) involved in tryptophan biosynthesis, resulting in auxin over accumulation and root growth inhibition under salt stress (Xing et al. 2023). Such molecular insights certainly help us to understand the homeostatic regulation of primary and lateral root differentiation and subsequent development and therefore may be exploited in future for crop improvement.

## Role of ethylene and cytokinin in the growth of roots

Under conditions of salinity, ethylene inhibits the elongation of primary roots. Ethylene biosynthesis in rice is triggered by one finger 15 (*OsDOF15*), which moderates root meristem growth (Qin et al. 2019). At the same time, primary root growth is disrupted with the loss-of-function of *OsDOF15*. Under saline conditions, *OsDOF15* is downregulated, and therefore, root growth is controlled. Root growth is disrupted by cytokinin due to stiffening of cell walls but requires auxin transporter AUX1 (Liu et al. 2022a). Therefore, cytokinin's influence on root growth is mainly through AUX1.

### Gibberellic acid (GA) and root architecture

Biosynthesis of GA and GA 20-oxidation mostly occurs in the meristem and elongation zone of roots, and root elongation depends on the action of gibberellins (Barker et al. 2021). GA signaling-deficient mutants display diminished activity of PIN-FORMED (PIN) protein auxin transporters in Arabidopsis. The results infer the GAs are required for PIN protein functions and subsequent gravitropism modulation in roots via PIN2 stabilization (Willige et al. 2011) or promotion of xylogenesis (Yuan et al. 2019). In *Eucalyptus grandis* roots, GAs promote SUPERROOT2 (SUR2) involved in the auxin homeostasis (Liu et al. 2018a, b). Thus, the role of GA in root architecture appears by interacting with auxin.

### Jasmonic acid (JA) and root growth

Perception of environmental stresses like salt stress stimulates the accumulation of JA (Riemann et al. 2015). In roots exposed to saline conditions, genes such as *AOC1*, *AOC2*, *AOS*, *LOX3* and *OPR3* involved in JA biosynthesis are triggered (Kilian et al. 2007). One of the JA biosynthetic pathway genes of wheat *OPR1* (*oxophytodienoate reductase 1*) improves ROS scavenging and reduces salt stress-mediated root growth suppression upon overexpression. The experiments infer that JA relates to root growth (Dong et al. 2013). A co-receptor CORONATINE INSENSITIVE 1, senses the accumulation of JA during salt stress and prevents the degradation of JAZ repressors. It is known that JA-responsive JAZ genes are activated by saline conditions and suppress cell elongation in primary roots. However, this depends on the JA signaling pathway gene *COI-1* (Valenzuela et al. 2016). Thus, it is the COI1 protein which regulates the growth of primary roots under NaCl stress conditions. Mutants of *coi1* have been noticed to be insensitive to jasmonate-dependent root growth suppression (Xu et al. 2002). This infers that *COI1* is vital for root growth under stress. While several of JAZ genes and spliced variants when overexpressed cause JA insensitivity, mutations in JAZ genes increase JA-induced root growth suppression. Such JA-insensitivity reduces the inhibitory effects JA on the development of roots (Thines et al. 2007; Thireault et al. 2015; Campos et al. 2016; Guo et al. 2018). Salinity causes upregulation of JA signaling in the root zone which is again controlled by JASMONATE RESPONSE LOCUS 1 (JAR1) and proteasome function. These results point out the critical role played by JA in root growth modulation under saline conditions. *ALLENE OXIDE CYCLASE 1* (*AOC1*), a salt-inducible JA biosynthesis gene triggers JA via *MYC2* and diminishes root growth but alleviates NaCl stress in wheat (Zhao et al. 2013). The basic helix-loop-helix (bHLH) and the JAZ repressor proteins play a critical role during stress. Therefore, JAZ-MYC coupling appears vital for responses of plants to NaCl stress (Chuquimarca et al. 2020). Other bHLHs (bHLH3 and 17) couple with JAZ proteins and repress root growth (Han et al. 2023). With interacting partners such as auxin and ethylene, JA modulates roots and root hair elongation (Han et al. 2020). However, JA-induced root hair development can be inhibited by JAZ proteins in association with *ROOT HAIR DEFECTIVE* genes (Han et al. 2020). The experiments indicate that the JAZ repressors control root hair growth.

### Involvement of brassinosteroids

Brassinosteroids in association with auxins regulate the initiation and growth of lateral roots under stress (Mahajan et al. 2014; Altamura et al. 2023). Brassinosteroids control the geometry of cells and the formation of root meristem (Fridman et al. 2021; Manghwar et al. 2022). On the other hand, overexpression of peptide signal Rapid Alkalinization Factor (*AtRALF1*) diminishes the size of cells and formation of lateral roots. *BRASSINOSTEROID-INSENSITIVE2* (*BIN2*) and *BIN-like* homologs (*BIL1* and *BIL2*) genes reduce brassinosteroid signaling (Yan et al. 2009). *BIN2* phosphorylates and improves the transcriptional activity of *AGAMOUS-LIKE 16* (*AGL16*) (Zhu et al. 2023). *agl16* restores root growth of *bin2-1* mutant. Further, overexpression of *AGL16* in the mutant background of *bin2 bil1 bil2* decreases resilience to saline stress. These experiments conclude that *BIN2* controls salt stress response and the suppression of root growth in an *AGL16*-dependent manner (Zhu et al. 2023). It has been noticed that under NaCl stress, brassinosteroids stimulate xyloglucan endotransglucosylase 19 (*XTH19*) and *XTH23* genes involved in lateral root growth (Xu et al. 2020). While the mutant *xth23* displays decreased root density, in the double mutant *xth19xth23* total inhibition of root initiation was recorded but stimulated by the brassinosteroid signaling (Xu et al. 2020; Fridman et al. 2021). In association with brassinosteroid signaling pathway, a tetratricopeptide-repeat thioredoxin-like (TTL) gene appears involved in lateral root emergence and its subsequent growth in Arabidopsis (Xin et al. 2022). In brassinosteroid-deficient mutants, interaction of brassinosteroids with auxin signaling triggers the root development (Bao et al. 2004). Brassinosteroids at super low concentrations cross talk with the auxin transporters and promote primary root apical meristem in Arabidopsis (Ackerman-Lavert et al. 2021). Primc and Maizel (2021) noticed that camalexin; an important component in stress tolerance occurs on the founder cells of lateral roots and permits their growth. Thus, a perfect link exists between stress tolerance, camalexin, and formation of lateral roots. However, lateral and adventitious root emergence and growth requires the involvement of nitric oxide, strigolactones, and spingolipids and their cross talk should be linked with brassinosteroids.

## Nitric oxide, strigolactones, sphingolipids, and prohibitin 3 in root formation

Formation of roots is associated with hormones, proteins and their interactions (Sun et al. 2015, 2022; Olah et al. 2020). Nitric oxide modulates the accumulation of auxin by acting upstream of its synthesis, degradation, conjugation, and signaling and therefore regulates the root growth (Liu et al. 2018a, b; Piacentini et al. 2020). Prohibitin 3 (PHB3), a mitochondrial protein controls lateral root initiation through nitric oxide (NO). NO degrades AUXIN/INDOLE-3-ACETIC ACID proteins and promotes GATA23, which triggers lateral root initiation and its growth (Li et al. 2022). Further, brassinosteroids control NO which then moderates root formation (Tossi et al. 2013; Hu et al. 2021). This aligns with the findings that exogenous supply of brassinosteroids promotes root formation by increasing NO levels (Della Rovere et al. 2022). Collectively, the information generated thus far illustrates that brassinosteroids cause an increase in NO signal which then stimulates the root growth.

Strigolactones are one class of phytohormones which are linked with salinity (Liu et al. 2022b). Further, strigolactones and the signaling molecule NO cross talk and foster the root growth (Olah et al. 2020). Strigolactones affect lateral root formation and root-hair elongation in Arabidopsis (Kapulnik et al. 2011a; 2011b). In transgenic tomato, low levels of strigolactones enhanced the root architecture and root hairs (Rasmussen et al. 2012; Kohlen et al. 2012). As opposed to this, strigolactones have been observed to decrease the auxin concentrations and stimulate lateral roots (Ma et al. 2020). In *Oryza sativa*, strigolactone mutants (deficient *d10* and insensitive *d3*) showed decreased adventitious root formation (Sun et al. 2015). External supply of strigolactones to the mutant lines of rice, dramatically improved the adventitious root formation per tiller. The results indicate the positive influence of strigolactones on root initiation (Sun et al. 2015, 2019). However, the complex signaling network of auxins, cytokinins, and strigolactones is paramount for root formation (Jiang et al. 2016).

Sphingolipids are abundant in plasma and endomembranes and are implicated in sensing saline stress and root development by triggering $Ca^{2+}$ influx. But interplay between very-long-chain fatty acids, ceramides and long-chain base are necessary for this purpose (Granrut and Cacas 2016; Jiang et al. 2019). Both auxin and sphingolipids are associated with lateral root formation, by interacting with very-long-chain fatty acids at the pericycle-endodermis (Lee et al. 2009; Shang et al. 2016). It appears that multiple genes like *APETALA2/ETHYLENE-RESPONSE FACTOR* (*AP2/ERF*) and *PUCH1* (an integrase-type DNA-binding superfamily protein) are involved in the regulation of roots (Hirota et al. 2007; Bellande et al. 2022). In callus cultures, *PUCH1* stimulates the biosynthesis of fatty acids which then help to the formation of lateral roots (Trinh et al. 2019). In turn, very-long-chain fatty acids modulate the activity of AUX/PIN1 auxin carriers and maintain the auxin levels essential for root initiation and growth (Della Rovere et al. 2013; Trinh et al. 2019; Boutte and Jaillais 2020). Any perturbations in the long-chain-fatty acids, especially C24 sphingolipids due to mutations in *puchi* gene results in the defective root development illustrating the importantance of *PUCHI* (Trinh et al. 2019). Auxin triggers MPK14 (mitogen-activated protein kinase), which then controls the development of lateral roots. It is *ETHYLENE RESPONSE FACTOR13*-orchestrated very-long chain fatty acids or their derivatives which act as the vital signals for the formation of roots (Shang et al. 2016; Lv et al. 2021; Guyomarch et al. 2021). Sphingolipids also impact brassinosteroid-mediated root development (Boutte and Jaillais 2020; Altamura et al. 2023). Hormonal regulation of genes implicated in root and root hair growth is shown in the Table 1.

## Regulators impacting root hair growth under salinity stress

Tap root emerges from the embryo first, and the lateral roots are formed later, which are often branched (Osmont et al. 2007; Atkinson et al. 2014; Bellini et al. 2014). Root hairs (modified epidermal cells) emerge from the trichoblasts and aid in enhanced anchorage, interaction with soil micro biota, acquisition of water as well as nutrients aside environmental interactions (Wang et al. 2008; Han et al. 2020; Vissenberg et al. 2020). Ion disequilibrium brings about differentiation of root hairs under salt stress (Wang et al. 2008). Root hairs sense the stress signals and respond accordingly (Cao et al. 1999; Muller and Schmidt 2004). NaCl stress hampers root hair development as well as their normal length (Jin et al. 2023). Root morphological plasticity prevents the accumulation of toxic ions; therefore absorption of water becomes normal (Schleiff and Muscolo 2011). But salt tolerant plants maintain better root hair growth in comparison with non-tolerant plants. Root hairs increase root penetration, contact with soil, and acquisition of nutrients thereby water and nutrient uptake improves under stressful environment (Haling et al. 2013). In *Bacoppa monniera*, at 5 g/l NaCl level, ample root hairs were noticed in comparison with 15 g/l NaCl stress (Ali et al. 1999). Density, diameter, and length of root hairs are critical factors that determine total root biomass under stress conditions. Root surface area has been found reduced in many species under saline conditions (Wang et al. 2008; Haling et al. 2013; Robin et al. 2016), but not under moderate stress conditions in *Silene*

**Table 1** Hormonal regulation of genes associated with root growth and root hair elongation/inhibition

| Name of hormone | Associated gene(s) or components | Effect of hormone on root growth | Reference |
|---|---|---|---|
| Auxin | Apoplast alkalinization through auxin receptors TIR1/AFB | Primary root growth inhibition | Scheitz et al. (2013) |
| Auxin | WRKY modulates IAA conjugation | Lateral root inhibition | Ding et al. (2015) |
| Auxin | Production of ROS via ARF5, RSL4/RSL2 | Root hair elongation | Mangano et al. (2017) |
| Auxin | *ARF7*, and *ARF19* associate with CrRLK1L kinase ERULUS during root hair tip growth | Root hair elongation | Schoenaers et al. (2018) |
| Auxin | Mutation in *IAA-CONJUGATE-RESISTANT 4* (*IAR4*) | Inhibition of primary root growth | Fu et al. (2019) |
| Auxin | Activation of plasma membrane $H^+$-ATPase for apoplast acidification by TRANSMEMBRANE KINASE 1 (TMK1) | Fine-tuned root growth modulation | Li et al. (2021a, b) |
| Auxin | Negative regulation of PLT2 by ARF2 and inhibition of quiescent cell divisions | Root growth inhibition | Marzi et al. (2024) |
| ABA | ABI4 regulates ABA and cytokinin leading to lateral root formation | Inhibition of lateral root initiation | Shkolnik-Inbar and Bar-Zvi (2010) |
| ABA | Endodermal signal | Inhibition of cell cycles in lateral root primordia and post-emergence growth | Duan et al. (2013) |
| ABA | WRKY46 modulates the growth of lateral roots via ABA signaling (ABI4) and auxin homeostasis | Inhibition of lateral root emergence | Ding et al. (2015) |
| ABA | Inhibits the expression of *ROOT HAIR DEFECTIVE SIX-LIKE* (*RSL2*) transcription factor by promoting OBF BINDING PROTEIN4 (OBP4) | Suppression of root hair growth | Rymen et al. (2017) |
| ABA | Through ABA-promoted auxin biosynthesis | Inhibition of primary root elongation in rice | Qin et al. (2023) |
| Brassinosteroids (BR) | Low levels of BR increase acropetal auxin transport | Promotion of lateral root initiation | Bao et al. (2004) |
| BR | Negative regulation of BIN2 which then downregulates WER-GL3/EGL3-TTG1. Negative regulation of RHD6/RSL1 | Promotes root growth through the control of meristem size | Gonzalez-Garcıa et al. (2011) |
| BR | BR-deficient mutants (*brd2*) | Higher number of root hairs | Cheng et al. (2014) |
| BR | Low BR inhibition of transcription factor complex WER-GL3/EGL3-TTG1 | More root hairs | Cheng et al. (2014)<br>Wei and Li (2016) |
| BR | High BR promotes WER-GL3/EGL3-TTG1 | Inhibition of root hair growth | Cheng et al. (2014)<br>Wei and Li (2016) |
| Cytokinin | Loss-of-function of ZINC FINGER PROTEIN 5 (*zfp5*) mutant | Exhibit a short root hair phenotype | An et al. (2012), Zhang et al. (2016) |
| Cytokinin | Promotion of CAPRICE (CPC) gene by ZFP5 | Positive root hair growth | An et al. (2012), Zhang et al. (2016) |
| Cytokinin | Supplementation of cytokinin to the wild-type plants | Increased root hair length | An et al. (2012), Zhang et al. (2016) |
| Cytokinin | Altered auxin distribution via ARR1, ARR12, Tryptophan Aminotransferase of Arabidopsis 1 (TAA1), and also through TIR1/AFB | Inhibition of primary root growth | Yan et al. (2017), Tiwari et al. (2023) |
| Ethylene | Loss of ETR1 and EIN2 function results in ethylene insensitivity | Inhibition of root hair growth | Masucci and Schiefelbein (1996), Rahman et al. (2002) |
| Ethylene-related activity | OsSIT1-MAPK3/6 cascade promotes ethylene, and ROS production | SIT1 is expressed in root epidermal cells and regulates salt tolerance | Li et al. (2014) |

**Table 1** (continued)

| Name of hormone | Associated gene(s) or components | Effect of hormone on root growth | Reference |
|---|---|---|---|
| Ethylene | Ethylene induces MAO HUZI5 (MHZ5) (OsCRTISO [CAROTENOID ISOMERASE])- and MHZ4 (OsABA4 [ABA-DEFICIENT4])-mediated ABA biosynthesis | Inhibition of root elongation | Ma et al. (2014), Yin et al. 2015 ) |
| Ethylene or its precursor aminocyclopropane (ACC) | Ethylene or ACC supplementation triggers RHD6, RSL4 and RSL2 genes | Stimulation of root hair growth | Pitts et al. (1998), Zhang et al. (2016) |
| Ethylene | Coordinated activities of EIN3/EIL1 and RHD6/RSL1 modules | Promotion of root hair growth | Feng et al. (2017) |
| Ethylene | Activation of ETHYLENE INSENSITIVE3 like1 (EIL1) on YUC8 transcription and auxin biosynthesis | Inhibition of root elongation in rice | Qin et al. (2017) |
| Ethylene-related activity | *OsDOF15* modulates ethylene biosynthesis | Positively regulates primary root elongation under salt stress | Qin et al. (2019) |
| Ethylene | Through ABA- and auxin-mediated mechanisms | Inhibits rice root elongation | Huang et al. (2022) |
| Ethylene | Interaction of EIL1 with IAA modulate tryptophan aminotransferase (TAR) (involved in auxin synthesis) MHZ10)/ OsTAR2 | Root growth regulation in rice | Zhou et al. (2022) |
| Gibberellic acid (GA) | Through DELLA | Root hair elongation in *Agrostis alba*, *Datura innoxia* | Devlin and Brown (1969), Ohkawa et al. (1989) |
| GA | Interaction with DELLA proteins | Negative regulation of root apical meristem size and the number of lateral roots | Fonouni-Farde et al. (2019) |
| GA | GA biosynthesis (GA20ox activity) in a tissue dependent manner in the root elongation zone | Promotes cell production in the root meristem and cell expansion in the elongation zone | Barker et al. (2021) |
| Jasmonic acid (JA) | ANTHRANILATE SYNTHASE 1 (ASA1) is crucial for jasmonate-mediated regulation of auxin synthesis and its transport | Lateral root formation | Sun et al. (2009) |
| JA | Repression of *PLT2* by MYC2 that inhibits division of quiescent cells | Inhibition of root growth through interaction with auxin | Chen et al. (2011b) |
| JA | Activation of jasmonate signaling pathway | Inhibition of primary root cell elongation | Valenzuela et al. (2016) |
| JA | JA inhibits auxin-induced lateral roots independent of CORONATINE INSENSITIVE1 (COI1) | Inhibition of lateral roots | Ishimaru et al. (2018) |
| JA | JAZ proteins interact with RHD6 and RSL1 | Promotion of root hair formation | Han et al. (2020) |
| JA | JASMONATE RESISTANT 1 and boron deficiency | Negative regulation of root growth | Huang et al. (2021) |
| JA | CORONATINE INSENSITIVE 1 (COI1)-JASMONATE ZIM-DOMAIN (JAZ) co-receptor trigger the degradation of JAZ repressors and JAZ-binding factors act additively with MYC2, MYC3 and MYC4 | Stimulation of primary root growth inhibition | Han et al. (2023) |
| JA | Suppression of RHD6 and RSL4 by JAZ8 | Suppression of root hair formation | Han et al. (2023) |
| Strigolactones (SL) | Supplementation of SL (GR24) act through MAX2 F-box proteins | Enhanced root hair elongation | Kapulnik et al (2011a, b) |

**Table 1** (continued)

| Name of hormone | Associated gene(s) or components | Effect of hormone on root growth | Reference |
|---|---|---|---|
| SL | Loss-of-function mutants of *max2/3/4* | Short root hair phenotype | Kapulnik et al (2011a, b) |

*vulgaris* (Franco et al. 2008). In barley, fewer root hairs were noticed in salinized seedlings than in non-saline environment (Shabala et al. 2003). Length and density of root hairs have been found superior in plants exposed to NaCl stress, in comparison with control conditions (Arif et al. 2019). Under salinity, expansion of root surface area has been noticed (20%), which may participate in better absorption of minerals and water (Arif et al. 2019). Divisions are symmetric in rice root hair development unlike that of *Brachypodium* (Kim and Dolan 2011). Root hair development is fine-tuned by not only hormones and proteins but also by *GLABRA2* (*GL2*), a transcription factor (Ohashi et al. 2003), *GTPase* (Denninger et al. 2019; Liu et al. 2023) and *ROOT HAIR DEFECTIVE/ROOT HAIR DEFECTIVE SIX LIKE* (*RHDs/RSLs*) genes (Vijayakumar et al. 2016; Zhang et al. 2023c). Also, in *A. thaliana*, under NaCl stress phosphorylation of RhoGDI1 (a guanine nucleotide dissociation inhibitor) modulates the formation of root hairs (Liu et al. 2023). It has been found that OBF BINDING PROTEIN4 (OBP4) binds to the promoter region of the *ROOT HAIR DEFECTIVE6-LIKE* (*RSL2*) and suppresses the expression (Rymen et al. 2017) (Fig. 3). RHD6 also called as bHLH83, a member of bHLH VIIIc subfamily member is repressed by the homeobox gene *GL2*, and regulate RSLs and expression of many downstream genes to inhibit formation of root hairs in the non-root hair forming cells called as atrichoblasts (Masucci et al. 1996; Bruex et al. 2012; Lin et al. 2015) (Fig. 3). Overall, it appears that *RSL2* along with *RSL3/4* and *Lj-RHL1-LIKE3* (*LRL3*) are necessary for the formation of root hairs (Yi et al. 2010; Bruex et al. 2012; Han et al. 2020). Ethylene has also been found necessary for root hair growth along with ETHYLENE INSENSITIVE 3 (EIN3) and its homolog EIN3-like 1 (EIL1) also (Feng et al. 2017). ABI1 negatively regulates AHA2, thereby causes apoplast acidification, inhibiting lateral root initiation (Fig. 3).

The expression or repression of *GLABRA 2* (*GL2*) depends on the cell types in which it is working, for example on H-type and N-type of root hair cells (Song et al. 2011; Schiefelbein et al. 2014; Balcerowicz et al. 2015). A suite of transcriptional regulators particularly *WEREWOLF* (*WER*) and *CAPRICE* (*CPC*) code for MYB transcriptional factors which then promote the outcome of nonhair and root hair cells respectively (Song et al. 2011). They noticed that overexpression of *WER* gene, via *GL2* promotes epidermal cells to produce nonhair cell fate. It appears that *WER* acts together with *GL3/ENHANCER OF GLABRA 3* (*EGL3*) to trigger *GL2* expression. Moreover, CPC represses the *WER* overexpression phenotype, indicating competition between the two. Differential expression of these genes in both space and time involves complex interactions governing root epidermis cell fate (Schiefelbein et al. 2014). Such complex regulatory interaction mirrors the need for robustness and also ensures proper root hair development once the decision

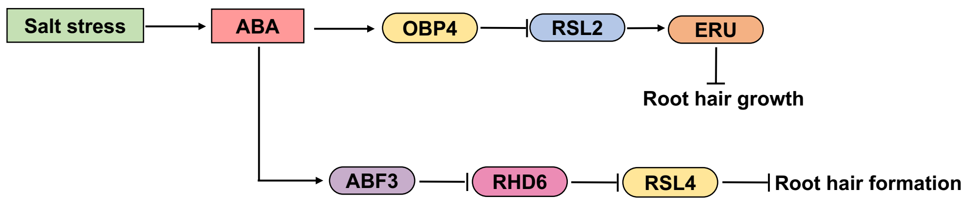



**Fig. 3** ABA-modulated inhibition of root hair formation and its growth. ABA triggers DNA-binding-with-one-finger (DOF) transcription factor 1 (OBF1)-binding protein 4 (OBP4), which negatively modulates ROOT HAIR DEFECTIVE SIX-LIKE 2 (RSL2). RSL2 in turn promotes ERULUS (ERU, a receptor-like kinase). ERU inhibits root hair growth. Further, ABA promotes abscisic acid response elements-binding factor 3 (ABF3), which negatively regulates RHD6 and RSL4, thereby inhibit root hair formation

for cell fate is made by the cells. Also, *GL2* represses the expression of *RHD6*, thereby prevents the development of root hair in N-type cells (Lin et al. 2015; Jin et al. 2023). For salt stress suppression of RHD6-mediated root hair development, ABF (abscisic acid-responsive element binding factor) proteins are necessary (Choi et al. 2000). Specifically, it has been shown that ABF3 interacts with RHD6 and inhibits its transcription activation to *RSL4* expression (Choi et al. 2000). *RHD6* and *RSL1*, stimulate *RSL2*, and *RSL4* to initiate root hairs (Bruex et al. 2012; Shibata and Sugimoto 2019). *RSL2* regulates ROS accumulation as multitaskers and helps in the growth of root hairs, and *RSL4* regulatory network stimulates elongation of root hair (Zhu et al. 2020) (Fig. 4). Overall, the studies conducted by Jin et al. (2023) evidence that ABF proteins repress *RHD6* to diminish the root hair aggregate number and elongation when exposed to NaCl stress. Besides the above genes, overexpression of *bHLH85* reversed it through the signaling pathways of ABA and auxin (Song et al. 2022). It appears that *RHD6* is a key node that integrates root hair formation under stress conditions. The hormone ethylene promotes EIN3/EIL1 activity which in turn regulates RHD6/RSL1 EIN3/EIL1 complex and promote root hair initiation (Fig. 4). EIN3/EIL1 RHD6/RSL1 complex then contrls the expression of RSL2 and RSL4 which in turn promote root hair elongation. Further, JA and Jasmonate ZIM-domain (JAZ) negatively regulate RHD6/RSL1 EIN3/EIN1 complex (Fig. 4). ABA produces hydrogen peroxide ($H_2O_2$) which activates OXIDATIVE SIGNAL INDUCIBLE 1 (AtOXI1), a Serine Threonine Kinase. At OXI1 promotes root hair initiation and growth. Also, a Rho GDP dissociation inhibitor RhoGD11 (SUPERCENTIPEDE1 or SCN1) regulates root hair formation. The

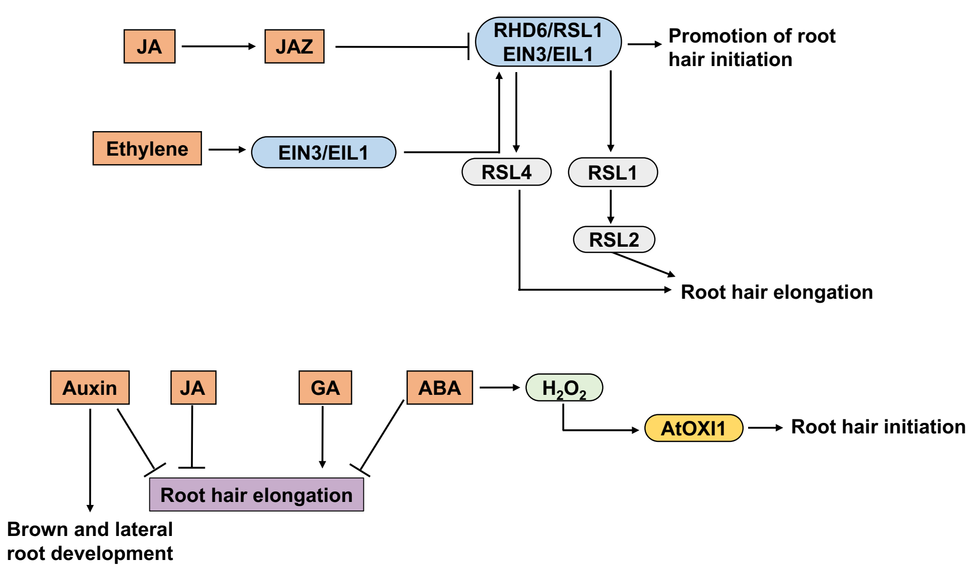



**Fig. 4** Regulation of lateral roots and root hairs by different hormones under stress. Ethylene promotes EIN3/EIL1 activity which in turn regulates RHD6/RSL1 EIN3/EIL1 complex and promote root hair initiation. EIN3/EIL1 RHD6/RSL1 complex promotes the expression of RSL2 and RSL4 which in turn promote root hair elongation. High phosphate levels suppress both RSL4 and RSL2, and inhibit root hair initiation and growth. But JA and JAZ negatively control RHD6/RSL1 EIN3/EIN1 complex. ABA produces hydrogen peroxide ($H_2O_2$) which activates OXIDATIVE SIGNAL INDUCIBLE 1 (AtOXI1), a Serine Threonine Kinase. At OXI1 promotes root hair initiation and growth (bottom of the figure)

mutant *scn1* displays many bulges in one trichoblast under NaCl stress and a stubby root hair phenotype (Carol et al. 2005; Liu et al. 2023). But, studies on how root hair recognizes abiotic stress signals are few (Zhang et al. 2023d). Taken together, it appears that a dynamic-module gene network modulates root hair development under NaCl stress (Benitez And Alvarez-Buylla 2010). Future studies therefore should focus on breeding programs related to root trait plasticity.

## Regulators influencing root branching under salinity

Lateral roots (LR) generally contribute to the growth of mature roots (Du and Scheres 2018). Soil salinity stimulates AUXIN RESPONSE FACTOR 7 (*ARF7*) and helps in bending of roots in the direction of water availability (Orosa-Puente et al. 2018). Factors such as positioning of LR, initiation and emergence of LR determine spatial and temporal distribution of LR growth pattern as guided by auxin signaling (Du and Scheres 2018). At the site of LR initiation, LR formation occurs due to the action of PECTIN METHYLTRANSFERASEs (PMEs) as well as PME INHIBITOR 3 (PMEI3). Besides cell wall-loosening proteins, vesicular trafficking, root clock genes activate the initiation of LR (Wachsman et al. 2020). Auxin stimulates MAPK cascade which is necessary for cell wall remodeling during the initiation of LRs (Kumpf et al. 2013; Zhu et al. 2019). Several other factors like nitrate-responsive DOF transcription factor OBP4-XYLOGLUCAN ENDOTRANSGLUCOSYLASE 9 (XTH9) and XTH23 regulatory modules control the LR development via auxin signaling pathways (Kumpf et al. 2013; Xu and Cai 2019). Therefore, several cellular events including wall modifications appear important for the emergence of LRs under salt stress (Teixeira and Ten Tusscher 2019; Vangheluwe and Beeckman 2021). Due to suppression of auxin signaling under NaCl stress, *ZINC FINGER OF ARABIDOPSIS THALIANA 6* (*ZAT6*) moderates the activity of *LATERAL ORGAN BOUNDARY DOMAIN16* (*LBD16*) and promotes LR growth (Zhang et al. 2024). The experiments infer that LR growth depends on salt-operated auxin-independent pathway intersecting LBD16 activity. In *A. thaliana LBD16* regulates lateral root formation without any stress. But Zhang et al. (2024) identified an alternative pathway that modulates the activity of *LBD16* under high NaCl stress. Salt stress promotes the activity of ZINC FINGER OF ARABIDOPSIS THALIANA 6 (ZAT6) which then triggers *LBD16*. *LBD16* then contributes to the growth and development of lateral roots under NaCl stress (Zhang et al. 2024). These experiments indicate that auxin-independent, but salt-stimulated pathways operate for the regulation of root branching under elevated salt stress conditions.

## Concluding remarks and future perspectives

Due to global warming the rise in sea levels leads to contamination of salinity in the coastal areas which will negatively impact the final yields and nutritional quality of grains. Therefore, well-orchestrated and complex network of physiological and gene networks linked to salinity stress must be unraveled, including the architecture of roots. Several players such as phytohormone signaling, transporters, regulation of redox, dynamics of $Ca^{2+}$ signaling, pH, root architecture, and cell wall protein networks play pivotal roles in controlling root system architecture under NaCl stress conditions. Genotypic variations for root system architecture need to be explored in diverse crops using multi-omics studies including the single-cell multi-omics studies of root meristem under salinity stress exposure (Depuydt et al. 2023). Importantly, epigenetic studies involving salt stress responses should also be taken into consideration while aiming to evolve crops for stress tolerance. There is a need for (a) unraveling the crosstalk of root and shoot growth from the salt-tolerant lines within glycophytes under prolonged salinity stresses including reproductive phase to minimize yield losses under salt and water stresses, (b) apply the molecular knowledge gained from halophytes of hormonal cross-talks conferring salinity tolerance to be applied to cereals and legumes. Some of the molecular leads gained thus far for understanding root system architecture are crucial for us to evolve crops with better yields under saline environment.

**Acknowledgements** PBK is grateful to the Head, Department of Genetics, Osmania University, Hyderabad for providing facilities.

**Author contributions** PBK has prepared the first draft, and NS edited the manuscript. VJS prepared the figures. All authors have analyzed the data, added lateral text, reviewed, refined the manuscript and improved its quality.

**Funding** This research is not funded by any internal or external funding agency.

**Data availability** Data sharing was not applicable to this article, as no new data were generated or analyzed during the preparation of this review paper.

## Declarations

**Conflict of interest** The authors declare no conflict of interests. All authors have read and approved the final manuscript.

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