Trends in Plant Science

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Review

Root-Apex Proton Fluxes at the Centre of Soil-Stress Acclimation

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Proton (H^+) fluxes in plant roots play critical roles in maintaining root growth and facilitating plant responses to multiple soil stresses, including fluctuations in nutrient supply, salt infiltration, and water stress. Soil mining for nutrients and water, rates of nutrient uptake, and the modulation of cell expansion all depend on the regulation of root H^+ fluxes, particularly at the root apex, mediated primarily by the activity of plasma membrane (PM) H^+-ATPases. Here, we summarize recent findings on the regulatory mechanisms of H^+ fluxes at the root apex under three abiotic stress conditions – phosphate deficiency, salinity stress, and water deficiency – and present an integrated physiomolecular view of the functions of H^+ fluxes in maintaining root growth in the acclimation to soil stress.

Highlights

Modulation of proton fluxes at the root apex plays roles in nutrient and water acquisition to overcome several types of abiotic stress conditions.

Enhanced plasma membrane (PM) H^+-ATPase activity in different root apex zones helps to maintain cell elongation, root hair formation, lateral root development, and the secretion of organic acids under phosphate-deficient conditions.

Auxin and blue-light signaling pathways are involved in the low-phosphate responses in roots that are tightly linked with regulation of the proton fluxes at the root apex.

PKS5- and PIN2-regulated PM H^+-ATPase activity at the root apex is essential for salt tolerance and the salt avoidance response.

Several signaling components that attribute to drought resistance and hydrotropic response control the proton fluxes at the root apex via ABA- and brassinosteroid-mediated pathways.

The Central Role of Root-Apex H^+ Fluxes

Plant roots growing in soil or other media, in their search for water and nutrients, encounter numerous unfavorable environmental situations, such as drought, salinity, pH challenges, flooding, hypoxia, and mineral nutrient deficiency. Since such abiotic stress factors often hinder the growth of plant roots, the mechanisms that allow roots to either 'weather' such conditions or keep growing towards less stress-challenged pockets of soil are a matter of survival.

Proton (H^+) fluxes at the root apex (i.e., the meristem, transition, elongation, and differentiation zones of primary roots [1–4]; Figure 1) have long been known to constitute an important component of the plant arsenal of mechanisms to mine the soil environment for nutrient resources and as an adaptive strategy to counter multiple stresses [5–9]. Along the root-apex longitudinal axis, the elongation zone, which varies significantly in size and distance from the root tip across species {e.g., *ca* 0.45–1 mm in arabidopsis (*Arabidopsis thaliana*) [1,2], 1.5–9 mm in maize (*Zea mays*) [10,11], and 0.5–3 mm in rice (*Oryza sativa*) [12–14]}, and which also varies according to stress-response signals, particularly reactive oxygen species (ROS)] [15,16], is the most active site for cell growth and where a shift to high rates of net H^+ efflux generally begins, driven mainly by members of the family of PM H^+-ATPases [2,6,17–19]. PM H^+-ATPases actively lower the pH in the extracellular matrix (the apoplast) and the rhizosphere and establish a H^+ gradient across the root PM (typically referred to as the 'proton motive force') to facilitate mineral nutrient uptake, given that most nutrient transport events in the roots of higher plants are coupled to, and driven by, H^+ gradients [17,20]. This in turn promotes water uptake to provide the turgor pressure to drive cell expansion. The extent to which 'strong ions' (e.g., K^+, Na^+, Ca^{2+}, Mg^{2+}, Cl^-), such as described in the 'Stewart model', can also affect compartmental pH should also be considered [21], although difficulties in quantifying apoplastic pool sizes and buffer capacities may limit its utility. H^+ fluxes are furthermore integral to the so-called 'acid growth theory', which links auxin, apoplastic pH, and cell elongation in a mechanistic framework (see below). Closely related are the tropic responses of roots either towards (positive tropism) or away from (negative tropism) external stimuli (e.g., gravitropism, hydrotropism, halotropism).

Although there have been many recent high-profile reviews on the molecular mechanisms underlying H^+-ATPase function and regulation [19,22] and root system architecture (RSA) and tropic

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responses to abiotic stress [23–27], this review aims to bridge these conceptual domains by focusing on the central role of root-apex H^+ fluxes in the context of root growth responses to abiotic stresses, namely phosphate (Pi) deficiency, salinity, and drought.

Root-Apex H^+ Fluxes and the 'Acid Growth Theory'

Plant cells are constrained by cell walls; thus, loosening of the cell-wall structure is essential to enable cell elongation and tissue growth [28]. The acid growth theory was formulated nearly 50 years ago to describe hypocotyl growth [29–32] and has been buttressed by numerous molecular-genetic characterizations in this system [33–35]. It relates the function of the phytohormone auxin to the induction of PM H^+-ATPase gene expression and to the functional (post-translational) stimulation of H^+-ATPases, which together result in the enhanced extrusion of protons and lowering of apoplastic pH. This, in turn, activates expansins and possibly other cell-wall-remodeling enzymes, resulting in cell-wall loosening and cell elongation (for recent reviews, see [25,36,37]).

Critically, however, this process does not seem to occur in this precise manner in roots, and thus has been the subject of continuous debate [37–41]. For example, in stark contrast to the model described above, H^+ extrusion from the elongation zone in *Brachipodium distachyon* roots was found to decrease in response to elevated cellular auxin levels; moreover, apoplastic acidification was shown to inhibit, rather than promote, cell elongation [40]. Whether these effects are unique

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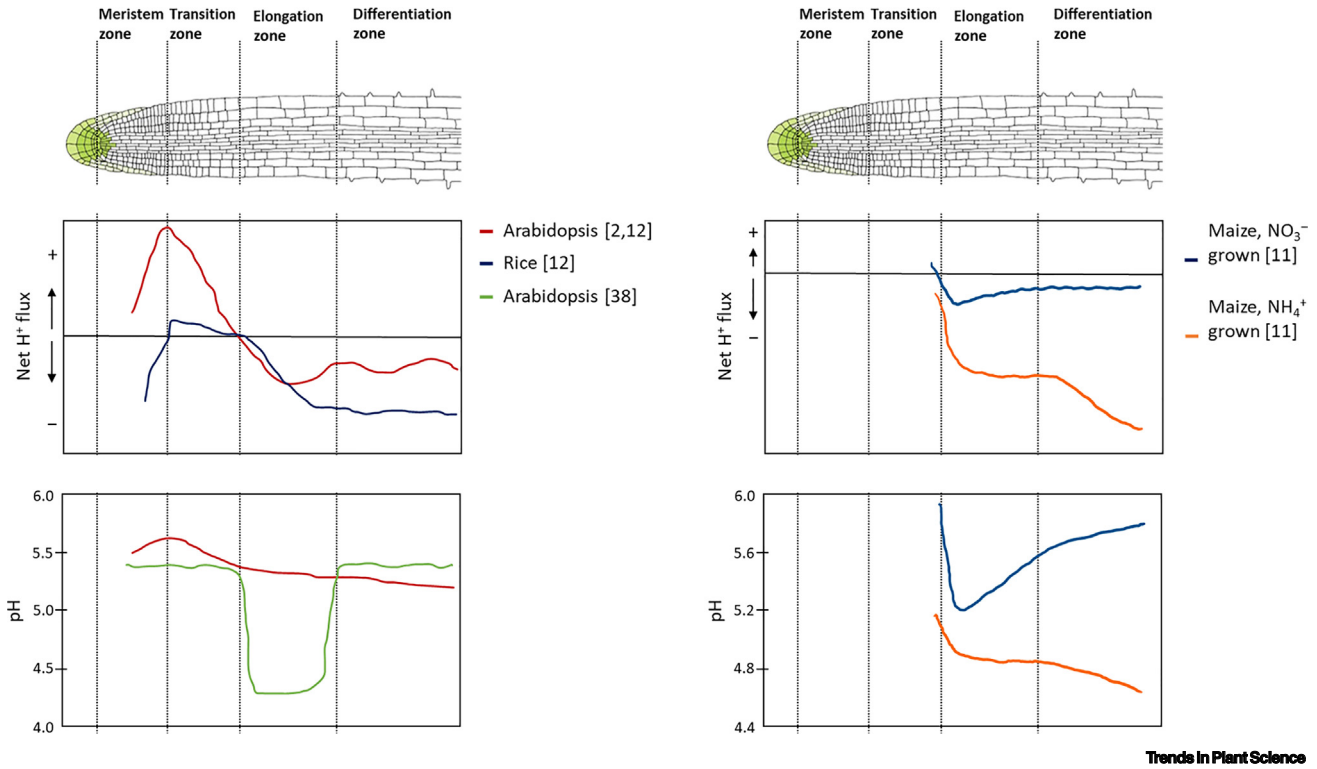


Figure 1. H^+-Flux Profile along the Root-Apex Zones. Based on cell structure, development, and activity, unique zones along the longitudinal axis of the root apex have been delineated: the meristem zone, where cells undergo frequent cell division; the transition zone, with slow rates of cell division and elongation but high rates of endocytic vesicle recycling; and the elongation zone, where cells elongate at high rates; and the differentiation zone, where cells are fully elongated and finalize their differentiation and where root hairs begin to emerge [1,3,4]. Plotting net H^+ fluxes ('+' denotes net influx, '–' denotes net efflux) along the longitudinal axis of the root apex (by means of vibrating pH-sensitive microelectrodes) reveals that H^+ flux and root-surface pH generally correspond with one another but may differ across species and growth conditions, although discrepancies in pH profiles across studies may be the result of methodological differences (Box 1; see text for details). See also [2,11,12,38].

to this species or due to intricacies of the experimental methods has been speculated [37,38]. In another perplexing case, Barbez *et al.* observed that epidermal cells in the elongation zone of arabidopsis roots indeed had lower apoplastic pH (average pH 4.3) relative to neighboring meristem and differentiation zones (average pH 5.4; Figure 1) [38]; however, these cells did not follow an auxin response consistent with the model described above. Instead, short-term elevations in exogenous auxin [250 nM indole-3-acetic acid (IAA)] displayed a biphasic effect on apoplastic pH; namely, rapid apoplastic alkalinization (peaking at 25 min from the onset of treatment) followed by sizable acidification (after 8 h). It is unclear whether this was the result of changes to H^+-ATPase expression or activity (e.g., via phosphorylation status), as this was not directly tested. Nevertheless, the auxin-induced alkalinization resulted in an inhibition of cell elongation that preceded, and lasted beyond, the subsequent apoplastic acidification. The authors attributed this to a concentration-dependent effect of auxin. Although low levels of exogenous auxin (*ca* 10 pM) can promote root elongation in arabidopsis, concentrations above 1 nM can significantly suppress root growth, and this can occur as early as 45 s following exposure [42–44]. Auxin-dependent inhibition of cell expansion also appears to explain the gravitropic response, where root bending towards the gravity vector results in higher concentrations of auxin accumulating at the lower side of the root relative to the upper side, corresponding with higher and lower apoplastic pH, respectively, and cell growth restriction and elongation, respectively [43,45–47].

An initial auxin-induced alkalinization (following applications of 10 nM to 10 μM IAA) was also recently observed in arabidopsis root hairs in the differentiation zone, which coincided with membrane depolarizations and increased net H^+ influx, which the authors attributed to auxin influx via the AUX1 transporter (in a proposed 2 H^+/IAA^- symport) [48]. The effect on the activity of the PM H^+-ATPase was not explored here. Interestingly, in contrast to the root elongation zone, it is well established that auxin promotes cell growth of root hairs [49–51]. As far as we know, the reason for the differential growth effects of auxin between the elongation and differentiation (root hair) zones remains to be resolved.

Interestingly, the differential growth effect of auxin between roots and shoots was recently linked to the regulatory role of the SYP132 vesicle fusion protein in H^+-ATPase trafficking to the PM [52]. SYP132, a member of the PM-bound soluble *N*-ethylmaleimide-sensitive factor attachment protein receptor (SNARE) family, is essential for plant viability and is ubiquitously expressed in the plant, including at the root apical meristem, epidermis, cortex, endodermis, stele, and root hairs [53]. SYP132 was found to negatively regulate H^+-ATPase trafficking to the PM in both root and shoot epidermal cells by stimulating their internalization via endocytosis [52]. However, a high- (10 μM) auxin treatment resulted in a differential response in shoots and roots, with decreased *SYP132* expression in the shoot where growth was promoted and increased expression in the root where growth was inhibited. Whether such dynamics play out across the various root-apex zones and explain the differential auxin responses therewith remains to be seen.

Given the variability in auxin's effects on H^+ fluxes, apoplastic pH, and cell growth between tissues and root-apex zones (and the further complications and discrepancies across measurement techniques, growth conditions, and perhaps even species [40,46,54–64]; Box 1 and Figure 1), it is evident that the acid growth theory in roots is highly contentious and that more focus should be placed on the various distinctions described above before generalized models are adopted.

Pi Deficiency

Low soil Pi (LP) is a major constraint for plant growth and productivity in both natural and agricultural environments [65]. Plant-root responses to LP can be generally categorized into three main types, and in all of these root-apex H^+ fluxes play an integral part: (i) biogeochemical responses,

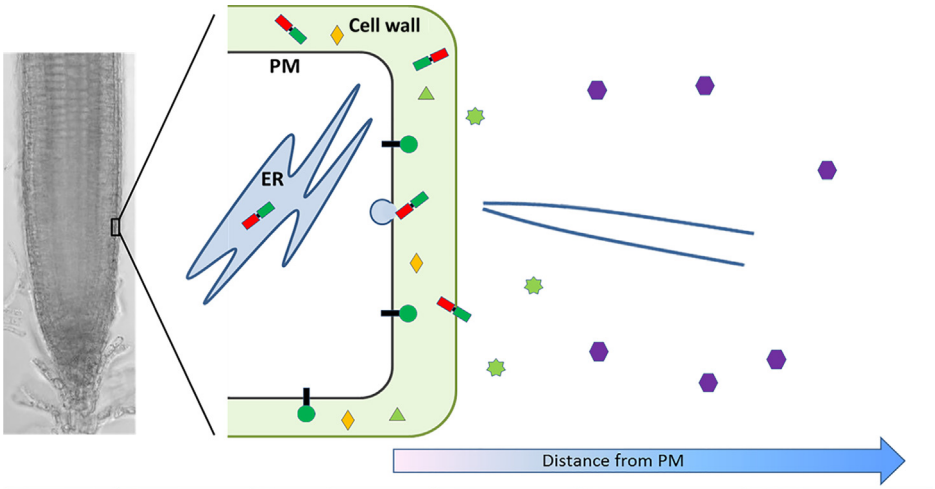
Box 1. A Methodological Note on Measuring Root-Apex H^+ Fluxes and pH

Root-apex apoplastic pH and concomitant H^+ fluxes can be measured over several orders of magnitude in distance, from the PM surface to the wider rhizosphere (Figure I). There are typically three approaches to estimating H^+ fluxes and pH in plant roots.

(i) Determination of the PM H^+-ATPase activity of isolated root PMs via physiological and biochemical methods to infer the extent of H^+ efflux (e.g., see [50]), since H^+ efflux is largely mediated by the PM H^+-ATPase. However, this method typically analyzes the overall activity in all cell layers of roots, which might not represent H^+ secretion out of roots, let alone root apices, specifically.

(ii) Measurement of the pH of the root apoplast or the surrounding medium. pH-sensitive fluorescent dyes or sensor proteins expressed in specific compartments are the two most common methods used to measure apoplastic pH [38,59,64]. Application of pH indicators to the medium (e.g., Bromocresol Purple-containing agar plates), quantification of H^+ extrusion by acid–base titration of the medium, and traditional pH-sensitive (micro)electrodes are also used to determine rhizosphere pH [46,60–63].

(iii) Detection of the H^+ fluxes at the root surface using scanning ion-selective microelectrode techniques, which can measure real-time net fluxes of protons in a specific region of the root surface [12,56]. The advantages and limitations of this method have been recently reviewed [58].



Indicator	PM-Apo	HPTS / Oregon Green / Fluorescein	Apo-pHusion	Microelectrode	Bromocresol Purple
Distance from PM	A few nanometers	A few to hundreds of nanometers	A few to hundreds of nanometers	A few to hundreds of microns	Up to a few centimeters
Refs	[59]	[38,64]	[57]	[54,56,95]	[60,61,63]

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Figure I. Detection of Extracellular pH at Various Distances from the Plasma Membrane (PM). See also [38,54,56,57,59–61,63,64,95] Abbreviation: ER, endoplasmic reticulum.

which include enhanced root exudation of organic acids and protons, facilitating Pi bioavailability in soils; (ii) physiological responses, which involve the induction of high-affinity Pi transporters and recycling and redistribution of internal Pi stores, thus optimizing Pi uptake and utilization; and (iii) developmental responses, which involve modifications to the RSA to improve topsoil foraging, where Pi tends to accumulate (Figure 2; for recent reviews, see [66–69]).

LP is both sensed and responded to predominately in root apices [67–70]. It is at the root apex that organic acids such as citrate, malate, and oxalate are exuded by many plants to mobilize

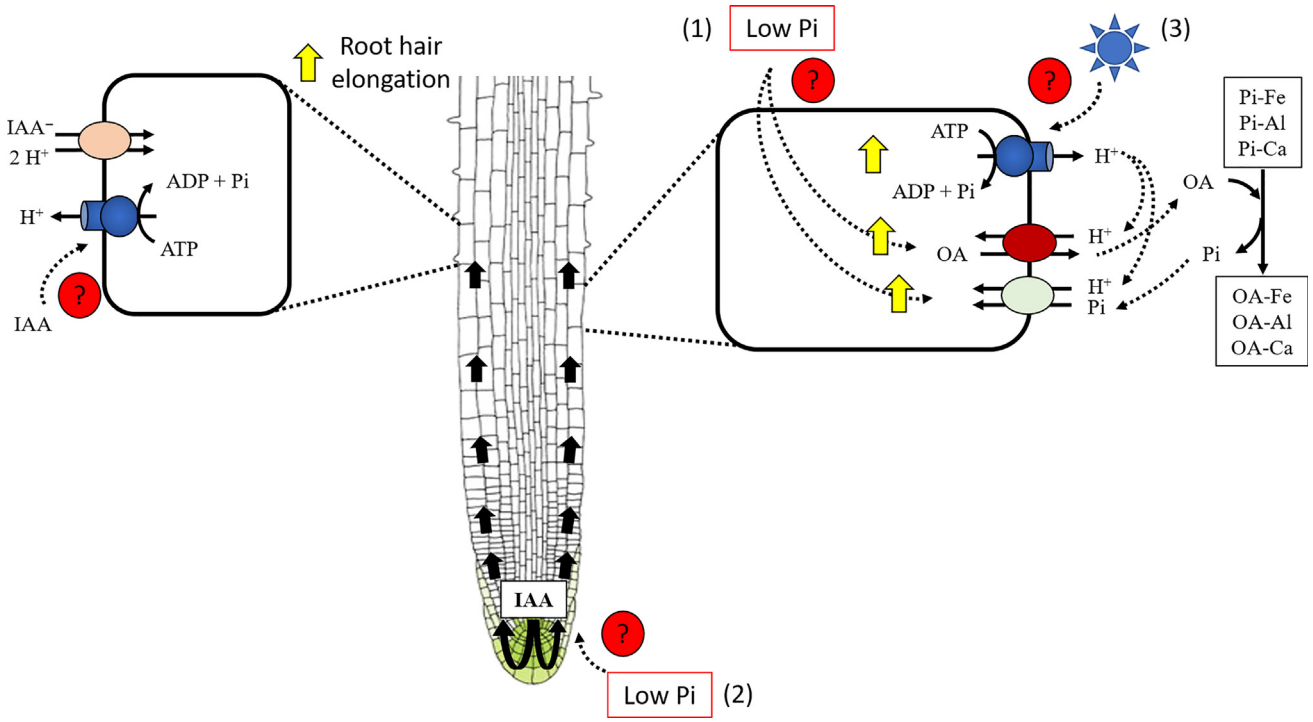

Figure 2. Root-Apex H^+ Fluxes and Growth Responses to Low-Pi (LP) Stress. LP stress is detected in root apices by unknown mechanisms but elicits numerous responses. (1) LP stimulates the genetic expression and post-translational activation of H^+-ATPases (e.g., AHA1, AHA2), organic-acid (OA) transporters (e.g., ALMTs, MATEs), and high-affinity Pi transporters (e.g., PHT) [67,76]. Both OA (specifically MATEs) and Pi transporters rely on the proton motive force generated by the activity of the H^+-ATPase [67,78,116]. Moreover, the OA released into the rhizosphere liberates Pi from fixed soil sources for root uptake. (2) LP elevates auxin levels in the root apex and polar auxin transport to the differentiation zone, where IAA induces the ARF19, RSL2, and RSL4 transcription factors that promote root hair elongation [84,85]. Auxin influx via AUX1 transporters is proposed to occur via a 2 H^+/IAA^- symport mechanism [48]. Whether elevated IAA stimulates or inhibits H^+-ATPase function under these conditions remains to be resolved. (3) A blue-light-induced effect potentially underlies many of the LP phenotypes with respect to RSA (namely, inhibition of primary root growth), as many studies utilize agar-plate-grown arabidopsis seedlings with roots exposed to light [83]. To what extent this artifact has affected LP studies is unclear, as is the case for blue-light-induced stimulation of H^+-ATPase function, which has been demonstrated in guard cells ([19], see references therein). Abbreviations: IAA, indole-3-acetic acid; Pi, phosphate; RSA, root system architecture

Pi from fixed soil sources such as Al- and Fe-oxyhydroxides [70,71]. H^+-ATPase activity at the root apex and organic-acid exudation appear to be positively correlated in many species, but the mechanistic link remains unclear ([72], see references therein). For example, plants with higher PM H^+-ATPase activity (e.g., as a result of genetic overexpression or pharmacological treatments such as fusicoccin applications) tend to exude more organic acids and show better growth and higher P content in LP culture [73–76].

Under LP conditions, stimulated absorption and translocation of Pi can be observed in root apices, particularly in the differentiation zone of primary roots [77,78]. This corresponds with LP-induced expression of high-affinity Pi transporters, particularly those belonging to the Pht1 family (Pi/$n$$H^+$ symporters, where $n > 1$) [78]. Root-apex H^+-ATPases are critical in maintaining the proton motive force necessary to drive these fluxes [79] and the activity of PM H^+-ATPases has furthermore been shown to be upregulated under LP conditions [72,73,80]. In arabidopsis roots, LP was found to induce the expression of the PM H^+-ATPase-encoding genes *AHA2* and *AHA7*, the former having been implicated in modulating primary root elongation by mediating H^+ efflux in the elongation zone while the latter is important in root-hair formation by mediating H^+ efflux in the differentiation zone [76].

The (stereo)typical response of the RSA to LP is the reduction of primary root growth and the promotion of lateral root and root hair development, processes critically linked to root-apex proton fluxes [66,81–83]. Under LP conditions, auxin is mobilized from the root tip to the differentiation/root-hair zone, triggering Ca^{2+} signaling and gene-expression cascades that promote root-hair cell elongation [48,84,85]. The auxin influx carrier AUX1 is a key component of the auxin-dependent root-hair response to LP. The transient increase of proton influx induced by auxin application is elevated under LP conditions, suggesting that the activity of AUX1 is enhanced by Pi starvation [48]. Whether this rise of extracellular pH acts as a signaling component in concert with membrane depolarization and the calcium transient remains an open question.

Interestingly, a recent study demonstrated that perhaps the RSA response to LP, at least with respect to primary root growth in arabidopsis, may be an artifact of growth conditions; namely, growing seedlings on agar plates with roots exposed to light [83]. Here, the authors demonstrated that blue light was necessary and sufficient to explain the primary root growth inhibition typically observed under LP conditions. Another recent study demonstrated that AHA2 localization to the PM of root cells requires light; under dim light, AHA2 is sequestered into intracellular compartments of the transition zone, resulting in reduced H^+ fluxes and growth suppression [86]. Blue-light activation of H^+-ATPase function via phototropins (blue-light-activated protein kinases) has been demonstrated in guard cells ([19], see references therein); whether such mechanisms also operate in roots remains to be seen [87]. It has also recently been shown that buffered delivery of Pi eliminates some plant growth defects observed under traditionally unbuffered gel systems [88]. These findings may call for a reevaluation of the large number of studies that have employed such growth conditions (Figure 2).

Salinity Stress

Soil salinization is a major environmental problem limiting crop productivity globally [89,90]. While the cellular mechanisms and the physiological relevance to toxicity of Na^+ fluxes in and out of roots remain a topic of debate [91,92], it is clear that the root apex is a 'hotspot' for salinity stress and that H^+ fluxes at the root apex have the potential to alleviate stress by regulating Na^+ fluxes and cellular compartmentalization and contribute to the halotropic response (Figure 3).

Several genes involved in salt-stress responses in arabidopsis have also been shown to function in modulating the activity of PM H^+-ATPases. For example, arabidopsis *DNAJ HOMOLOG 3* (*J3*) mutants display reduced PM H^+-ATPase activity and H^+ efflux and are hypersensitive to salt stress, particularly under alkaline conditions, which often accompany saline conditions [93]. The chaperone protein J3 enhances PM H^+-ATPase activity by repressing SOS2-LIKE PROTEIN KINASE5 (PKS5). PKS5 phosphorylates the arabidopsis PM H^+-ATPase AHA2 and prevents the binding of 14-3-3 proteins to AHA2, leading to an inactivation of H^+-ATPase activity. Loss-of-function *pks5* arabidopsis mutants are also more tolerant to salt stress under alkaline conditions and display higher proton efflux activity [93,94]. Similarly, overexpression of the tomato 14-3-3 protein TFT4 in arabidopsis increases PM H^+-ATPase activity and H^+ efflux in the root elongation and differentiation zones and is associated with the maintenance of root growth under alkaline stress [95]. Saline–alkaline stress has also been shown to trigger Ca^{2+} signals and induce the Ca^{2+} sensor SCaBP3/CBL7 to dissociate from the autoinhibitory domain of AHA2 to enhance H^+-ATPase activity [96].

The auxin exporter PIN2 participates in PKS5-mediated alkaline-stress responses through regulating PM H^+-ATPase activity and proton fluxes from root apices. The primary roots of arabidopsis *pin2* and *pin2/pks5* mutants both secrete fewer protons and are hypersensitive to alkaline stress [18]. Thus, by acidifying the rooting environment, primary root growth can be maintained under

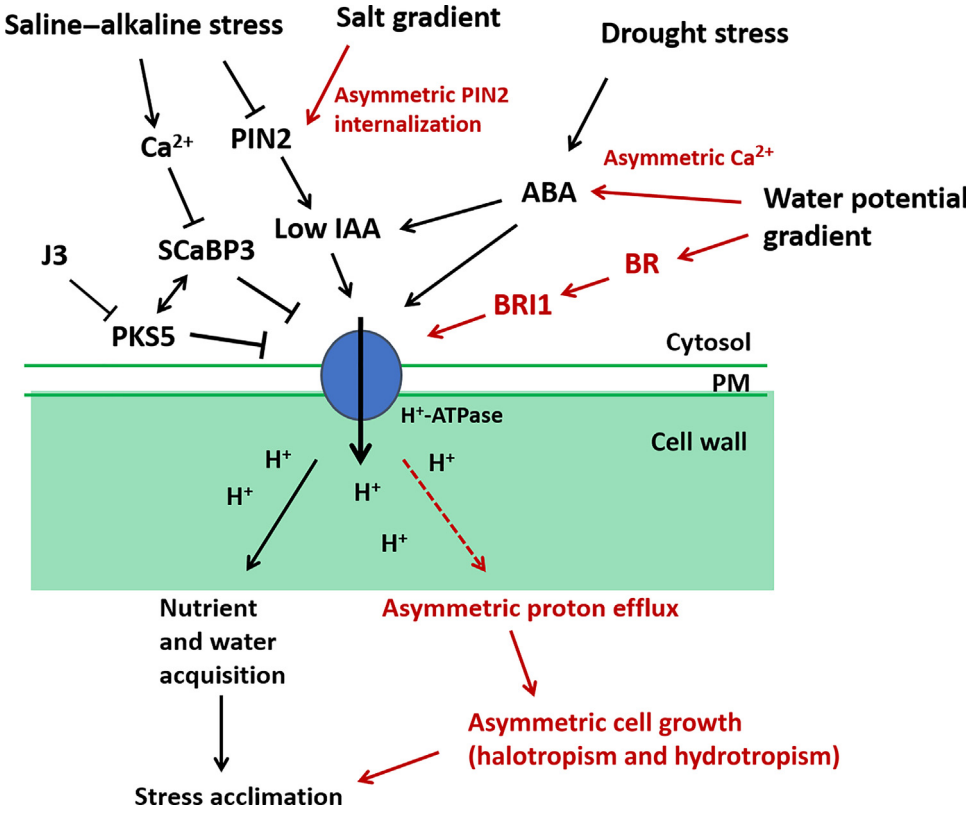

Figure 3. Regulation of Root-Apex Proton Fluxes in Response to Salinity and Drought Stress. High-salt and water-deficient conditions stimulate PM H^+-ATPases through the PKS5–J3 pathway, calcium signaling, phosphoregulation, and auxin transport [93–96]. The stress-induced cell-wall acidification mediated by proton efflux activates the processes of cell-wall loosening and promotes root growth. Asymmetric salt gradients result in a corresponding asymmetric internalization of PIN2 proteins in the two flanks of epidermal cells, leading to asymmetries in auxin flux, proton efflux, and ultimately cell elongation (i.e., root halotropism [99–101]). Hydrotropism (root bending towards areas of higher water potential) is driven by the asymmetric elongation of cortical cells and is controlled by calcium, ABA, and BR signals to PM H^+-ATPases [23,112,114,115]. Abbreviations: ABA, abscisic acid; BR, brassinosteroid; J3, DNAJ HOMOLOG 3; PM, plasma membrane; SCaBP3, SOS3-LIKE CALCIUM BINDING PROTEIN3.

alkaline stress. *PIN2* gene expression is reduced by salt treatment, and the primary roots of *pin2* mutants grow shorter under salt stress compared with wild-type arabidopsis [97]. Although *PIN1*, *PIN3*, and *PIN7* function in regulating root meristem growth under salt stress, *PIN2* does not function in salt-mediated inhibition of root meristem size [97].

Endocytic trafficking of PIN2 in roots is also a key regulator of the salt-avoidance response (i.e., halotropism) [98,99]. Salt stress inhibits PIN2 expression and alters the cellular localization of PIN2 [100], interfering with root gravitropism, a likely adaptive response to minimize salt stress [25,101]. Since the gravitropic response is controlled by PIN2-mediated redistribution of auxin that leads to the asymmetry of H^+ fluxes and cell elongation between the upper and the lower side of the roots [47,102], it is reasonable to expect that H^+ fluxes may also play a pivotal role in regulating root halotropism. The DII-VENUS and DR5::N7-VENUS auxin reporters reveal increased auxin levels in epidermal, cortical, and lateral root cap cells in arabidopsis at the side of the root opposite to the imposed salinity. Exposure to salinity has been shown to induce the internalization (endocytosis) of PIN2 auxin efflux carriers at the side of the root facing the higher salt concentration.

This response was triggered by phospholipase D activity controlling clathrin recruitment to the membrane [24,98]. Similar responses were not found for PIN1, PIN3, AUX1, or the PM H^+-ATPase PMA2. In summary, these studies all support a convergent role for PIN2 in saline-stress responses via control of H^+ flux and cell elongation.

It is worth noting that, in addition to the free cytoplasmic auxin sensors DR5 and DII-VENUS, microelectrode techniques are powerful tools for measuring auxin fluxes along the root apex *in vivo*. The DR5 and DII-VENUS auxin sensors pick up only free cytoplasmic auxin and are blind to vesicular, endoplasmic-reticular, and vacuolar auxin. This is why, although there is an auxin maximum recorded in the root apex transition zone with respect to auxin fluxes when measurements with auxin-sensitive electrodes are undertaken [103–106], there is an auxin minimum in the same zone when assayed with the DR5 and DII-VENUS auxin sensors [107].

Water Stress

Drought is one of the major limiting factors for plant growth, and several studies have recently converged on the central role of root-apex H^+ fluxes in regulating root growth and development under drought stress. A key phytohormone in this response is abscisic acid (ABA) [108,109]. Enhanced accumulation of ABA in the root apex has been shown to maintain primary root elongation under drought stress, in part by regulating cell-wall loosening [110]. Using rice and arabidopsis, we found that moderate water stress increases ABA accumulation and signaling in root apices, resulting in enhanced auxin transport and activation of H^+-ATPases [12]. Moreover, He *et al.* suggested that GRF9, a 14-3-3 protein in arabidopsis, was involved in plant root responses to water stress by allocating more carbon from the shoot to the root system and enhancing H^+ efflux in the root elongation zone, critical for water uptake in drought-afflicted soils [111].

Hydrotropism is a pivotal mechanism directing root growth towards moisture patches in soils for water acquisition. The ABA signaling pathway is involved in regulating root hydrotropic bending, which is mainly directed by the differential elongation of cortical cells in the elongation zone [23,112]. The ABA-biosynthesis mutant *aba1-1* and ABA-signal-transduction mutants *abi2-1*, *pp2c*, and *pyr/pyl* all display altered hydrotropic responses [113,114]. In addition, the application of exogenous ABA, which is nondirectional, to the roots of *aba1-1* has been shown to rescue the hydrotropic response, indicating that the ABA gradient across roots may not be the cause of directional growth [23,114]. We have recently shown that brassinosteroid (BR)-associated H^+ efflux is also critical for root hydrotropism [115]. In the presence of an inhibitor of BR biosynthesis, the normally strong hydrotropic response, root H^+ efflux, and root growth in the arabidopsis ecotype Ws were all reduced. Moreover, the BR-insensitive arabidopsis mutant *bri1-5* displayed stronger inhibition of root growth and root curvature on moisture gradients in both vertical and oblique orientations compared with the wild type. The BR receptor BRI1 was shown to interact with AHA2 to modulate H^+ fluxes in root apices and regulate root growth for water acquisition. Using apo-pHusion, a pH marker for the apoplast in transgenic arabidopsis plants (Box 1), we found that, under moderate water stress in sand culture, roots grew longer in their search for water, and H^+ efflux at the root apex corresponded with the hydrotropic responses in both vertical and horizontal orientations (our unpublished results).

Concluding Remarks and Future Perspectives

Over the past several years, a clearer picture has begun to emerge with respect to the critical role of H^+ fluxes in regulating root growth in response to abiotic stress. Protons secreted into the rhizosphere, in coordination with organic-acid exudates, have been shown to facilitate the release of bound minerals such as Pi from soils. Moreover, H^+ fluxes, in conjunction with phytohormone

Outstanding Questions

Why is it that in some cases the acid growth theory, in concern with the auxin responses and the changes of the apoplast pH in hypocotyl cells, cannot be applied to the root cells in different root zones?

Can the changes in apoplast pH in root cells serve as a signaling component in response to stress stimuli?

Do the elevated IAA levels enhance or inhibit the activity of PM H^+-ATPases under LP conditions?

Does the elevation of PM H^+-ATPase activity in the root cells under LP conditions result from blue-light illumination?

What are the dynamic changes in the apoplast pH of the root cortex cells during the root hydrotropic response?

(e.g., auxin, ABA, BR) fluctuations, clearly play critical roles in cell-wall loosening and cellular expansion (albeit with several caveats, as discussed above) as well as in tropic responses, which are essential for plant acclimation to stresses such as nutrient deficiency, drought, and salt stresses (Figure 3). Overall, our improved understanding of the role of H^+ fluxes at root apices in response to abiotic stresses is expected to greatly benefit crop breeding aimed at improving the ability of plants to maintain root growth in stressful soil environments (see Outstanding Questions).

Acknowledgments

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