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REVIEW

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Root osmotic sensing from local perception to systemic responses

Lucille Gorgues[†] , Xuelian Li[†] , Christophe Maurel , Alexandre Martinière* and Philippe Nacry*

Abstract

Plants face a constantly changing environment, requiring fine tuning of their growth and development. Plants have therefore developed numerous mechanisms to cope with environmental stress conditions. One striking example is root response to water deficit. Upon drought (which causes osmotic stress to cells), plants can among other responses alter locally their root system architecture (hydropatterning) or orientate their root growth to optimize water uptake (hydrotropism). They can also modify their hydraulic properties, metabolism and development coordinately at the whole root and plant levels. Upstream of these developmental and physiological changes, plant roots must perceive and transduce signals for water availability. Here, we review current knowledge on plant osmotic perception and discuss how long distance signaling can play a role in signal integration, leading to the great phenotypic plasticity of roots and plant development.

Keywords: Drought, Water deficit perception, Local signaling, Long distance signaling, Local water deficit, Adaptive development

Introduction

Like some prokaryotic and most fungal cells, plant cells are wall-encapsulated. Although it provides important advantages such as a robust exoskeleton and a protection of cells from adverse abiotic or biotic factors, the wall creates a direct restriction for cellular expansion. This important constraint can be overcome by intracellular turgor that in response to cell wall loosening allows growth. The cell turgor, that can be up to 10 bars in certain cell types, is actually built from the osmotic gradient between cell interior and the external media. This gradient triggers a flux of water into the cell that leads to a compensatory hydrostatic pressure, called turgor. Any change in the osmotic gradient by for instance an increase/decrease in water potential in the external

media or changes in the internal solute concentration, leads to a direct change in turgor that can modify cell volume and tissue rigidity. To allow localized expansion growth or prevent wilting, cells have therefore to maintain a constant dialog between cell wall mechanical properties, solute concentration and turgor.

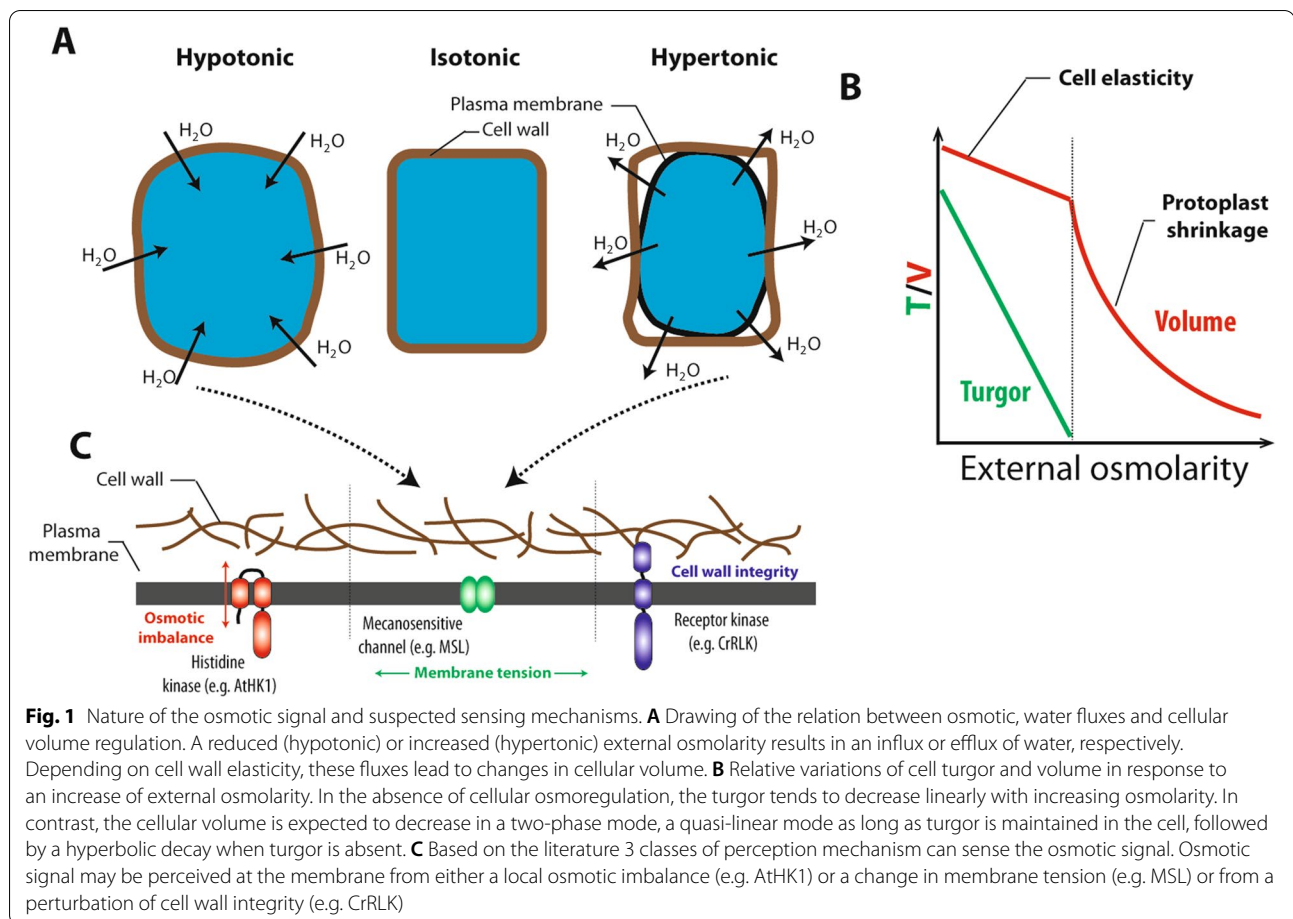
Whereas plant aerial parts are protected from air drying by specialized waxes deposited on their surface, the root system is in direct contact with its surrounding environment and therefore has to cope with dramatic changes in water potential. Soil is a complex porous medium with marked differences in its composition and structure e.g. air pockets and hydrated soil particles. Thus, root systems are continuously facing contrasted water availabilities during soil exploration. In addition to a local perception of water availability, followed by signal transduction and responses at cellular level, long-distance signals are produced. These so-called systemic signals coordinate responses at the multicellular scale, to

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modulate integrative traits, such as root system architecture (RSA).

In this review, we will focus on recent advances in the field of plant osmotic perception and early signaling in roots. We will also underline how systemic signaling can integrate local signals to modulate RSA.

Local perception and early signaling

Although being searched for many years, the exact nature of the signals that allow plants to perceive changes in water availability is not clearly defined yet. At the cellular level, mechanics e.g. cell wall/membrane tension, but also cell or subcellular volumes are directly impacted by changes in external osmolarity (Fig. 1A and B). Historically, comparison between different kingdoms has permitted the identification of some molecular players. Since osmotic perception is mandatory all along the plant life cycle, it is likely that many molecular mechanisms are actually superimposed in cells (Fig. 1C). New approaches, especially genetic screens, have recently allowed a striking expansion of knowledge on plant osmotic perception,

which is summarized and updated in the present paragraph.

Molecular mechanisms of perception

Histidine kinases (AtHK1)

Historically, the first osmosensing pathway has been uncovered in unicellular organisms. In *Saccharomyces cerevisiae*, perception is made by a two-component histidine kinase system, where recognition of the stimulus leads to kinase activation and phosphorylation of a histidine residue (Brewster and Gustin 1994). The Synthetic Lethal of N-end rule 1 (SLN1) changes its phosphorylation activity in response to osmotic signal and activates via several phosphorelays the High Osmolarity Glycerol (HOG1) MAP kinase (Ota and Varshavsky 1993; Maeda et al. 1995). In turn, HOG1 controls the expression of osmotic responsive genes including those involved in the biosynthesis of compatible osmolytes like glycerol.

Plants also show a conserved gene family of histidine kinases (HK) with members involved in hormonal signaling such as ethylene (Gamble et al. 2002) or cytokinins. The Arabidopsis genome contains 11 genes coding

for Histidine kinase like protein (Hutchison and Kieber 2002). In addition to its role in hormone signaling, Arabidopsis AtHK1 was shown to act as an osmosensor by complementing yeast *sln1* mutation (Urao et al. 1999) (Figs. 1C and 2). Localized to the plasma membrane, AtHK1 is a positive regulator of salt stress, drought and ABA signaling (Tran et al. 2007; Wohlbach et al. 2008). For instance, overexpression AtHK1 in plants increases the drought tolerance and results in the induction of genes involved in drought signaling including proline and sucrose biosynthesis (Tran et al. 2007). However, the role of AtHK1 as a main plant osmosensor has been questioned. Indeed, in several loss-of-function alleles of *athk1*, no hyperosmotic signaling-related phenotypes

such as ABA, or osmolyte accumulation were found (Kumar et al. 2013).

Mechanosensitive channels (MSL, OSCA1, Piezo, ...)

Due to its molecular anchors with the wall and the absence of folding, the plant plasma membrane of turgid cells is potentially under tension, especially during cell expansion and osmotic volume adjustment. Changes in membrane tension due to an osmotic challenge can therefore be perceived by cells through membrane mechanosensitive channels (Fig. 1C). The first mechanosensors involved in osmoregulation were molecularly identified from *Escherichia coli* spheroplasts (Martinac et al. 1987; Levina 1999). Several studies have solved the

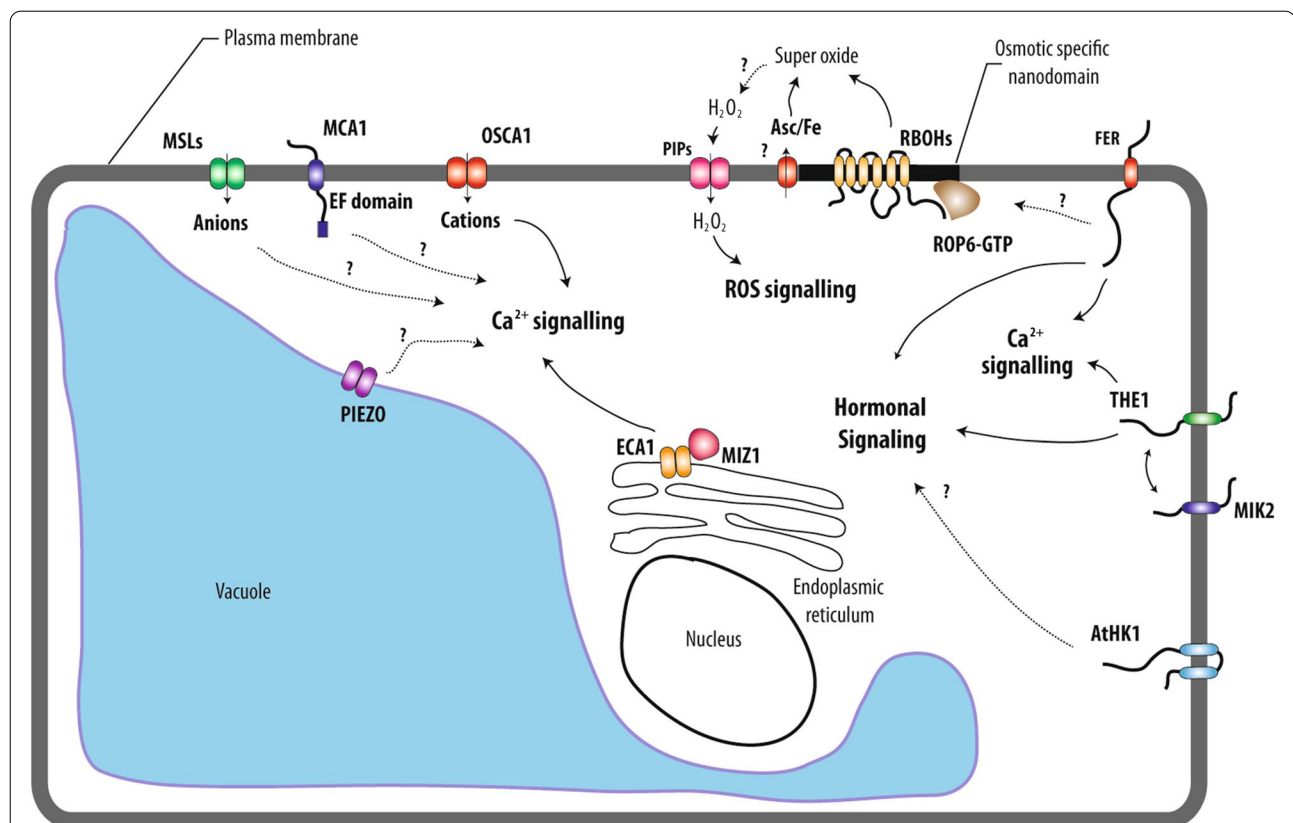


Fig. 2 Summary of currently known osmotic perception mechanisms in plants. Changes in membrane tension induced by osmolarity imbalance can be perceived by membrane mechanosensors such as OSCA1, MSLs, MCA1, PIEZO, ECA1/MIZ1. By transporting cations or anions, these sensors initiate cell calcium signaling by as yet unknown mechanisms. Receptor-like kinases belonging to the CrRLK family (e.g. FER, THE) perceive the cell wall status and their activation eventually leads to cell wall reinforcement. Whereas their exact role as osmotic sensors has yet to be established, these receptors definitely fine tune signaling of hormones such as ABA, auxin and jasmonate that are known to regulate plant development and physiological acclimation to osmotic stress. At the cell membrane, a partial integration of signals can be observed. For instance, LRR kinase MIK2, a receptor for phytochemicals that controls plant immunity, genetically interacts with THE, pointing to a link between osmotic and pathogen signaling. By similarity to the yeast system, the AtHK1 two component histidine kinase may also participate in osmotic signaling by modulating ABA signaling. In addition to hormones and calcium signaling, Reactive Oxygen Species (ROS) are also participating in early cell responses to osmotic stimuli. Cellular accumulation of ROS is dependent on NADPH oxidases (RBOHD and F) and iron reduction processes. Upon cell stimulation, ROP6 forms nanodomains together with the superoxide producing enzyme RBOHD/F. As a consequence, superoxide can be dismutated to hydrogen peroxide (H_2O_2) by apoplasmic SOD (Superoxide dismutase). H_2O_2 transport through the cell membrane is in turn facilitated by aquaporins

crystal structure of these low-conductance mechanosensors. They highlighted 3 common transmembrane helices that would serve as sensors of the membrane tension (Bass et al. 2002; Steinbacher et al. 2007; Lai et al. 2013). In addition, two recent cryomicroscopy studies have shown that *E. coli* MscS channels (MscS) association with lipids is an important determinant for the stabilization of the closed conformation and therefore plays a key role in channel sensitivity to tension (Flegler et al. 2021; Zhang et al. 2021b). The gating of *E. coli* MscS channels is conditioned by a pocket containing lipids. The anisotropic forces of the membrane created by tension could free this pocket of lipids or/and change the number of lipid acyl chains in it, causing a structural rearrangement and leading to pore opening (Pliotas et al. 2015; Flegler et al. 2021).

In plants, members of the MscS-like (MSL) gene family represent the closest homologs of bacterial MscS (Sukharev et al. 1994). MSLs are non-selective anion channels whose activity is regulated by voltage or mechanical stimulation of the membrane (Haswell 2007). Ten MSL have been described in Arabidopsis (Haswell 2007). In a landmark study, MSL9 and 10 were shown to control mechanosensitive activity of anion channels in the plasma membrane of root protoplasts (Haswell et al. 2008) (Fig. 2). Because neither the double *msl9/10* nor the quintuple *msl4/5/6/9/10* mutant showed alteration of their response under a variety of stimuli, e.g. osmotic, salt, mechanical or dehydration, the exact integrated function of these channels has remained enigmatic (Haswell et al. 2008). Whereas, MSL10 was demonstrated to be a true mechanosensitive channel after heterologous expression (Maksaev and Haswell 2012), its function has been recently uncovered using an elegant experimental strategy. By playing both with cell wall inhibitor that loose the cell wall and osmoticum to modulate cell turgor, Maksaev and co-authors show that MSL10 potentiate cell responses to swelling (Basu et al. 2020). Hypoosmotic shock induced several responses including cytoplasmic calcium increases, ROS accumulation and transcriptional regulation that are under the control of MSL10 (Basu et al. 2020). In addition, this channel determines the induction of programmed cell death (PCD) in response to a hypo-osmotic challenge. This response is dependent on the phosphorylation of MSL10 N-terminus (Veley et al. 2014; Basu et al. 2020; Basu and Haswell 2020). In a recent preprint, MSL10 was found to localize and function at ER-plasma membrane contact sites (EPCSs) (Codjoe et al. 2022). In plants, EPCSs regulate lipid homeostasis between compartment and cell integrity (Schapire et al. 2008; Ruiz-Lopez et al. 2021). Those results suggest an interesting connection between mechanosensitive channel and regulation of cell volumes.

MSLs are also important for regulation of organelle volume within cells. MSL2 and MSL3 that localize to plastid membranes, modulate their division, shape and size (Lee et al. 2019; Wilson et al. 2016). Because *msl2/3* plants develop a mass callus tissue at their shoot apical meristem, MSLs create a link between plastid osmoregulation and cell differentiation. MSLs were also associated with specific cell types like pollen tubes (Hamilton et al. 2015). MSL8 was shown to prevent cell bursting during pollen rehydration processes and membrane integrity during tip growth; highlighting again the role of MSLs during hypoosmotic choc. However, a recent preprint suggests that MSL8 effect on pollen tube hydration is not due to a simple tension-gated osmoregulator. MSL8 would rather regulate ions fluxes that are needed for cell wall modification during pollen hydration (Miller et al. 2022).

Other types of mechanosensitive channels have been identified in Arabidopsis. Mid1-Complementing Activity (MCA1) was cloned by complementing the lethal mutation of *mid1* yeast lacking the putative Ca^{2+} permeable stretch-activated channel component (Nakagawa et al. 2007 PNAS). MCA1 and its Arabidopsis paralog, MCA2, exhibited a Ca^{2+} permeable mechanosensitive channel activity in *Xenopus* (Furuichi et al. 2012 PSB). Interestingly, MCAs consist of single pass transmembrane proteins (Kamano et al. 2015). Their first 200 amino acids contain both the TM and the EF domains that are sufficient for channel activity under membrane stretching (Yoshimura et al. 2021). MCA loss of function mutants show root growth defects in media with high concentration of agar and a hypersensitivity to cold stress (Nakagawa et al. 2007; Mori et al. 2018) (Fig. 2). However, *mca1 mca2* showed no alteration in calcium influx after osmotic stimulation, questioning the role of the two channels in the osmosensing pathway (Stephan et al. 2016).

Members of the PIEZO gene family, from the Greek “*pîesi*” which means pressure, are plasma membrane localized cation channels involved in mechanosensory processes and necessary for light touch perception, compressive force proprioception, among other processes. Their discovery was recognized by the 2021’s Nobel prize award. Arabidopsis genome encode for unique PIEZO homolog. at the AtPIEZO channel was first identified as a regulator of virus spreading and of root cap mechanotransduction (Mousavi et al. 2021; Zhang et al. 2019b). However, AtPIEZO1 seems to also act in tip growing cells. The two homologues encoded by the moss *Physcomitrella patens* genome are localized in the tonoplast and control cell growth and cytoplasmic calcium oscillation (Radin et al. 2021). Analysis of loss and gain of function mutants showed that moss PIEZO act on the vacuole membrane through tubulation, internalization

or fission (Radin et al. 2021). AtPIEZO is also localized in the tonoplast and acts on vacuole morphology of pollen tube; showing that PIEZO function on tip growing cells is conserved among land plants (Radin et al. 2021). These observations shade light onto the role of the plant vacuole in mechanoperception and maybe osmosensing (Fig. 2).

In addition to searching in the plant genome for homologs of prokaryotic or eukaryotic mechanosensors, direct genetic screens have been realized to identify plant osmosensors. Calcium influx in the cytoplasm is probably one of the fastest cell responses to osmotic stimulation. Following a calcium imaging screen, the gene REDUCED HYPEROSMOLALITY-INDUCED $[Ca^{2+}]$ INCREASE 1/ (OSCA1.1) was therefore identified from an EMS mutagenized population. OSCA1.1 encodes for a hyperosmolality-gated calcium-permeable channel, which is responsible for calcium signaling, but also regulation of root growth, stomata closure and transpiration upon osmotic stimulation (Yuan et al. 2014) (Fig. 2). Interestingly, OSCA1 is not required for ABA- or H_2O_2 -induced calcium cellular influxes suggesting a strong specificity of the channel for osmotic signaling. Arabidopsis Calcium-permeable Stress-gated cation Channel 1 (AtCSC1/OSAC1.2), a close homolog of OSCA1, is also responsible for osmotic-dependent calcium influx when expressed in Chinese hamster ovary (CHO) cells (Hou et al. 2014).

Atomic structure and cryo-microscopy analyses have shown that OSCA1.2 is composed of 11 transmembrane helices forming homodimers. This channel has a cytosolic domain with RNA recognition motifs and 2 α -helices anchoring the protein in membrane lipids (Jojoa-Cruz et al. 2018; Liu et al. 2018). The two additive helices are cytosolic and might serve as a lateral sensor for tension within the inner plasma membrane leaflet (Maity et al. 2019). Except for the OSCA4.1 isoform belonging to clade 4, the mechanosensitive channel activity seems to be conserved among the OSCA gene family when expressed in HEK cells or in proteoliposomes (Murthy et al. 2018). However, the isoforms present distinct ion conductances and sensitivities to pressure (Murthy et al. 2018). Knowledge on the role of OSCAs in planta has recently been expanding. For instance, OSCA1.3 behaves as a Ca^{2+} permeable channel in yeast and contributes, with its close homologue OSCA1.7, to pattern-triggered immunity (PTI)-dependent stomatal closure (Thor et al. 2020). Thus, OSCA function in plants is not strictly restricted to mechano or osmoperception.

Cell wall sensing (CrRLKs, WAKs, ...)

Since the cell wall is way stiffer than the membrane, most of the tensile stress induced by turgor is borne by the wall. Recently, knowledge of biological processes

that perceive the cell wall status has rapidly expanded. A number of transmembrane receptor like kinases (RLKs) such as *Catharanthus roseus* RLK1-Like kinases (CrRLK), Wall Associated Kinases (WAK), Lectin Receptor-Kinase (LRK), Proline-rich Extensin-like Receptor Kinases (PERKs), and formins have been shown to interact with the cell wall (Wolf et al. 2012). Some of these are known to act as sensors of the cell wall status. Historically, the *THESEUS* (THE) CrRLK was isolated from a genetic screen for suppression of the short hypocotyl and ectopic lignin phenotype of the cell wall synthase mutant *cesa6^{prc1-1}* (Hématy et al. 2007). Indeed, the retarded growth induced by inhibition of cellulose synthesis is not the direct result of structural changes in the cell wall linked to reduce cellulose content. It rather involves active inhibition of growth through receptor kinases like THE (Hématy et al. 2007). In addition to its role as a wall integrity sensor, THE acts on lateral root initiation through perception of its ligand, RALF34 (Gonneau et al. 2018). THE1 signaling is also needed to control ABA accumulation after osmotic stress (Bacete et al. 2022) (Fig. 2). These results illustrate the intricacy between wall integrity sensors, the maintenance of cell mechanics and ABA signaling as a typical osmotic signaling marker.

Interestingly, THE also controls some salt-induced related phenotypes, like root skewing. This response also needs MALE DISCOVERER 1-INTERACTING RECEPTOR-LIKE KINASE 2 (MIK2). This LRR kinase was identified from a reverse genetic screen for impaired ectopic lignin deposition under treatment with isoxaben, an inhibitor of cellulose deposition (Van der Does et al. 2017). Allelic variation in *MIK2* has been associated with changes in rosette dry weight in response to mild salt (Julkowska et al. 2016) (Fig. 2). MIK2 binds to SERINE RICH ENDOGENOUS PEPTIDE12 (SCOOP12), a phyto cytokine that is secreted and regulates immunity in plants (Hou et al. 2021; Rhodes et al. 2021). These observations suggest an interaction between cell wall sensing pathways, including response to osmotic stimulation, and plant immune responses.

FERONIA (FER) is another CrRLK that participates in cell wall sensing. Loss-of-function studies have revealed that FER is involved in many processes such as cell elongation, root hair development, responses to hormones, nutrition and plant defense (Li et al. 2016). In addition, loss-of-function studies of FER have shown defects in responses to mechanical stimuli e.g. inability to penetrate hard layers of agar (Shih et al. 2014). FER has also a tight link to ABA signaling and loss of function plants show a resistant phenotype to osmotic stress and a hyper sensitivity to salt stress, although salt stress also results

in osmotic stress (Chen et al. 2016 PNAS) (Fig. 2). Feng and co-authors also highlighted the specific role of FER in response to salt stress (Feng et al. 2018). FER induces relatively late calcium influx in the cell that is needed to sustain cell wall reinforcement. It was proposed that FER would sense the impact of sodium ions on pectin filament organization, rather than directly sensing turgor or plasmolysis (Feng et al. 2018).

Molecular mechanisms of early signaling

Calcium

Calcium is a secondary messenger that allows the transmission of many biotic and abiotic stimuli and converts them into cellular signals. Intracellular calcium homeostasis is modulated by channels, pumps and transporters. The calcium signal is transmitted by calcium-binding proteins that subsequently feed into signaling cascades (Dodd et al. 2010; Kudla et al. 2010). Fluorescent Ca^{2+} probes have been actively used to identify quantitative characteristics like amplitude or frequency of calcium responses; revealing the concept of calcium signatures for specific signals (Monshausen 2012). According to this, a pure osmotic stimulus induces intracellular calcium signals that are different from those induced by stimuli like cold or salt, that are only partially composed of an osmotic component (Tracy et al. 2008; Huang et al. 2017a). In addition, Ca^{2+} varies also in space within the cell, with the nucleus and cytoplasm responding differently to osmotic stimulation probably through independent molecular mechanisms (Huang et al. 2017a; Luo et al. 2020). Whereas OSCA1 appears as a crucial actor of osmotically driven calcium influx, the exact role of other mechanosensitive channels like MSLs or MCAs remains debated (Yuan et al. 2014; Stephan et al. 2016). Interestingly, intracellular compartments also play critical roles in controlling calcium signaling in response to osmotic signals. The K^{+} exchange antiporters (KEAs), which perform plastid localized potassium antiport, are needed to maintain plastid ion homeostasis. In corresponding loss of function plants, plastids were swollen and had impaired calcium influx after osmotic stimulation (Stephan et al. 2016). Nevertheless, the link between plastid ion homeostasis and calcium signaling remains to be explored. In addition, calcium signal decoding processes in response to osmotic signals remain largely uncharacterized.

At the root tissue level, imaging approaches have identified calcium movements according to water potential gradient (Shkolnik et al. 2018). The calcium flux propagates along the phloem until it reaches the root elongation zone to control hydrotropic responses, i.e. directed root growth towards higher soil water potentials (Shkolnik et al. 2018). Both the osmotic stress-induced

calcium increase and hydrotropic response need functional ECA1, an endoplasmic reticulum Ca^{2+} pump, and MIZU-KUSSEI1 (MIZ1) (Fig. 2). The latter gene was originally identified from a forward genetic screen based on hydrotropic response (Kobayashi et al. 2007). These data suggest that calcium participates as a secondary messenger at the cellular level but also at distances allowing hydrotropism.

ROS

In addition to calcium, reactive oxygen species (ROS) accumulate minutes after cell stimulation (Leshem and Levine 2007; Martinière et al. 2019). Superoxide, hydrogen peroxide, but also other ROS are generated from both cellular metabolism and through specific generator systems. Indeed, ROS not only represent stress-induced damaging components, but also serve as genuine cell secondary messengers (Devireddy et al. 2021; Fichman and Mittler 2020). Upon an osmotic signal, ROS was linked to root hydrotropic responses. Indeed, inhibition of peroxidases and Respiratory Burst Oxidase Homolog family (RBOHs), which are classical ROS consumer and producer respectively, induce altered root curvature when plants are grown on plate containing a water potential gradient (Krieger et al. 2016; Jiménez-Nopala et al. 2018). In fact, it was found that ROS accumulation in the elongation zone participate to root gravitropic response, maybe through regulation of autophagy and amyloplast degradation (Nakayama et al. 2012; Krieger et al. 2016). This agravitropic phenotype leads to a stronger hydrotropic response. Then, ROS function in tuning root tropic responses by promoting gravitropism and therefore negatively regulating hydrotropism response. Strikingly, the RBOHD and F can only partially account for the osmotically-induced ROS production. Indeed, upon signal, the cytoplasmic reducing power is transferred to the apoplast, leading to ascorbate accumulation. Ascorbate is further used to reduce iron that reacts with di-oxygen to generate superoxide (Martinière et al. 2019). In cells, the ROS generated by RBOHs or the ascorbate/iron pair end up with different responses (Fig. 2). Whereas the two ROS generating pathways are needed for membrane internalization, RBOH-dependent ROS induces the internalization of specific cargo proteins such as the PIP2;1 aquaporin (Martinière et al. 2019). Interestingly, certain ROS species have the particularity of being able to travel through cell compartments. For instance, membrane transport of hydrogen peroxide (H_2O_2) is facilitated by certain aquaporins localized at the PM (PIP1–4) (Tian et al. 2016), PIP2;1 (Rodrigues et al. 2017) or the tonoplast e.g. TIP1;1 and TIP1;2 (Bienert et al. 2007) (Fig. 2). Therefore, H_2O_2 might itself regulate its own membrane permeability by acting on aquaporin cycling.

Recently, Rho of Plant6 (ROP6) was found to be necessary and sufficient to induce osmotically-induced ROS production (Smokvarska et al. 2020). Rho-GTPases (RAC/ROP) are involved in cell responses to various stimuli such as auxin, ABA or chitin elicitation (Feiguelman et al. 2018). ROPs are molecules that switch from an inactive to an active form by binding to GDP or GTP, respectively (Feiguelman et al. 2018). Models linking ROPs and NADPH oxidase have been described for root hair or pollen growth and immune response (Duan et al. 2010; Boisson-dernier et al. 2013). After osmotic stimulation, ROP6 is activated and recruited in PM domains of nanometric size, together with RBOHD and F (Fig. 2). Interestingly, the co-recruitment of RBOHDs within nanodomains seems to be specific for the osmotic signal. To convey auxin signaling, ROP6 has also to form nanodomains, which however are exempt of RBOHDs. As a result, no ROS accumulates in cells under auxin treatment (Platre et al. 2019; Smokvarska et al. 2020). These observations suggest that the ROP6 activation mechanism can itself control the specificity of the downstream response.

Osmotically-induced ROS are associated with numerous downstream cellular and physiological responses such as a decrease in root hydraulic conductivity or accumulation of compatible osmolytes like proline (Boursiac et al. 2008; Ben Rejeb et al. 2015). Detoxification mechanisms through specific enzymes like superoxide dismutases (SOD), ascorbate peroxidases (APX), catalases (CAT), glutathione peroxidases (GPX) and peroxiredoxins (PRX) (Mittler et al. 2004) are needed. For instance, AtGPX3/GPXL3 was linked to drought stress and ABA signaling. *Atgpx3/gpxl3* plants showed enhanced water losses under drought stress (Miao et al. 2006). In vitro phosphorylation assays showed that oxidized AtGPX3/GPXL3 acts on phosphatase activity of ABA INSENSITIVE2 (ABI2) (Miao et al. 2006). Consistently, AtGPX3/GPXL3 links ABA signaling, ROS and osmotic signaling. Because the AtGPX3/GPXL3 catalytic domain is facing the lumen of the secretory pathway, it remains muddled how AtGPX3/GPXL3 oxidation is mechanistically associated to ABI2 (Attacha et al. 2017).

Systemic signaling and developmental responses

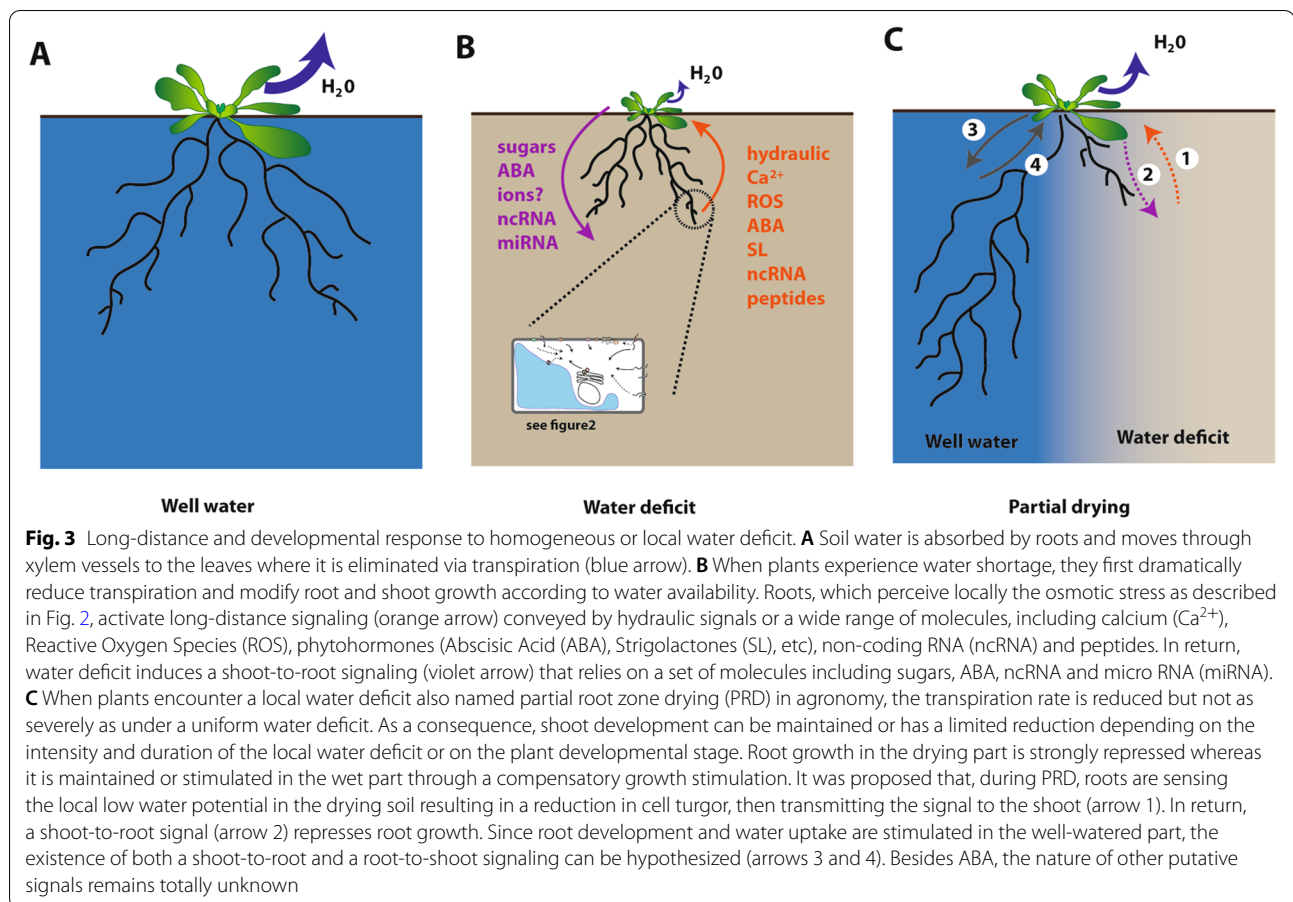
To cope with their complex and fluctuating environment, plants have to constantly sense the surrounding fluctuations and integrate all this local information into coordinated whole plant responses. This is accomplished through a complex systemic communication network involving a wide spectrum of physical, chemical and molecular components. The following section will explore the molecular bases of long distance osmotic signaling in plants from 3 types of signals, which are hydraulic, electric and chemical in nature. We will focus

on inter organ signaling and more specifically on the root to shoot and shoot to root signals. Long distance communication has long been proposed to use the mass flow of sap within the vascular system. Accordingly, many molecules have been identified as traveling from root to shoots through the xylem vessels or from shoots to roots through phloem (reviewed in Ham and Lucas 2017; Winter and Kragler 2018).

Molecular bases of long distance signaling

Hydraulic signal

Water absorbed by roots is axially transported along the xylem towards shoots down the plant water potential gradient. Leaf water potential, which is the lowest in the plant, induces a tension in the vessels. Thus, any physical damage or disturbance that breaks the integrity of the water column present in the xylem vessels can release this tension, thereby inducing a pressure change that will almost instantly be transmitted through the vasculature. This physical signaling named hydraulic signaling has been proposed several decades ago to be involved in the fast response to leaf wounding (Houwink 1935) (Fig. 3B). The pressure wave generated through this process may be involved in the propagation of chemicals from the wounded tissue or directly trigger mechanical systemic signals in sensitive tissues (Farmer et al. 2014; Evans and Morris 2017). However, wounding experiments suggest that the hydraulic signal is moving up to 10,000 times faster than the observed propagation of the Ca^{2+} in tissues, thereby challenging the idea of a chemical propagation (Evans and Morris 2017). Nevertheless, more recent work suggests that change in hydraulic pressure induced by wounding is abolished in *rbohD* (NADPH oxidase) and *glr3.3 glr3.6* (glutamate receptor-like protein) (Fichman and Mittler 2021). This suggests that hydraulic signal is not solely determined as a physical signal. In response to water deficit, the turgor pressure of leaf cells rapidly declines when roots experience water shortage. A drop in soil local water potential can also modify root turgor pressure and ultimately xylem tension. These changes can propagate from root to shoots as a so-called hydraulic signal (Christmann et al. 2007; Christmann et al. 2013). Alterations in root turgor pressure were also found to induce local accumulation and signaling of the well characterized water stress hormone Abscissic Acid (ABA) both in root and shoots (Christmann et al. 2007) indicating that hydraulic signaling may somehow be correlated to ABA signaling. However, a rapid response of stomata to water deficit was also observed in the ABA biosynthesis mutant (*aba2*) or signaling mutant (*abi1*) indicating an ABA independent signal (Christmann et al. 2013). In addition, grass stomata have subsidiary cells coupling osmotic and turgor adjustment to fasten



stomatal movements (Franks and Farquhar 2007; Raisig et al. 2017). The action of hydraulic signals transmitted through the plant vasculature to the stomata thereby represents a rapid signaling mechanism well correlated to plant architecture and anatomy. However, whether the putative hydraulic signal is translated locally into chemical signals like ABA or acts locally through as yet unknown leaf structures remains an experimental challenge and a matter of vivid debate (Evans and Morris 2017; Farmer et al. 2020).

Electrical signal

Electrical signals have initially been identified in the folding of leaflets and petiole movements of *Mimosa pudica* in response to mechanical and other physical stimuli. These movements are driven by a turgor-powered motor and the rapid signaling involved appears linked to propagation of electrical signals that are moving through the sieve tube (recently reviewed by Johns et al. 2021). Plants maintain a -200 mV electrical potential difference across their plasma membrane through the action of ion channels, pumps (including H^+ -ATPases) and transporters. Transient depolarization and repolarization events

with set amplitude, velocity and duration or variation of potential can convey key information about the strength and distance of the stimulus that triggered such electrical signals, within and between plant organs. These signals rely on fluxes of ions including K^+ , Cl^- , H^+ or Ca^{2+} , the latter being the most documented. Electrical signaling has been reported to be involved in the response to heat, cold, touch, salt, flooding, hypoxia, osmotic stress, and drought (reviewed by Wilkins et al. 2016; Kudla et al. 2018). To explain such wide range of responses, it was hypothesized that the Ca^{2+} -permeable channels controlling cell influx contain a stress-specific fingerprint that varies in amplitude, timing, and frequency and can be formed by the activation of different Ca^{2+} channels depending on the different stresses (Wang et al. 2019). In the case of drought, Ca^{2+} has been reported to move up in the transpiration stream and may couple Ca^{2+} supplied from the roots to stomatal response in the leaves (Han et al. 2003) (Fig. 3B). Storti et al. (2018) also measured Ca^{2+} waves propagation in response to osmotic stress in the non-vascular moss *Physcomitrella patens*. The lower propagation rate compared to the one measured in *Arabidopsis* confirms the cell-to-cell and vascular

dependent routes. Such mobile Ca^{2+} has recently been found to act through a plastid based receptor system in the guard cells that itself may further integrate these responses with other stimuli as observed during photoacclimation (Cutolo et al. 2019).

ROS accumulation and calcium production are closely interconnected and enhance each other during abiotic stress. For instance, superoxide produced by RBOH D activates calcium channels, which activate the vacuolar calcium channel TWO PORE CHANNEL1 (TPC1). This releases Ca^{2+} into the cytosol which in turn enhances the activation of RBOH protein D (Evans et al. 2016). This calcium/ROS feedback loop is likely instrumental for propagation of the ROS and Ca^{2+} waves during salt stress and a proper acclimation response. However, until recently, it remained unknown how ROS are perceived by cells to trigger calcium waves. The Leucine-rich-repeated receptor kinase (HPCA1) was identified from a forward genetic screen for impaired ROS-induced Ca^{2+} waves (Wu et al. 2020). Via covalent modification of its extracellular cysteine residues, HPCA1 is autophosphorylated, activated calcium influx and is required for stomata closure after H_2O_2 treatment. In a preprint, HPCA1 appear to be also necessary for propagation of ROS/Ca waves in response to high light signal (Fichman and Mittler 2020). Drought and high temperatures both induce calcium and ROS waves across the plasma membrane, but no in-depth mechanistic analysis on long distance propagation has been performed yet. The many different origins of ROS and corresponding Ca^{2+} waves suggest sophisticated signaling mechanisms. Thus, integrative studies are still needed to sort between the common and specific ROS-calcium signaling pathways that contribute to the specificity of plant responses to different stress conditions.

Sugars and long distance signaling

Drought, high salinity or temperature dramatically modify the metabolic profiles of plants (Urano et al. 2010; Cramer et al. 2011). It has long been proposed that uncharged metabolites such as proline or glycine-betaine, accumulate to promote water retention in the plant tissues without interfering with normal metabolism (Verslues and Sharma 2010). They, in concert with other specialized/secondary metabolites, also act as free radical scavengers removing excess ROS and reestablishing a cellular redox balance (reviewed by Takahashi et al. 2020). Sucrose, glucose, and fructose also highly accumulate in roots upon exposure to drought suggesting they can replace other osmolytes as major compatible solutes (reviewed by Takahashi et al. 2020). More recently, sugars have emerged as key players during shoot to root communication in response to water stress (Fig. 3B). In Arabidopsis, phloem transport of sucrose is mainly achieved

through the activity of sugar transporters. Phloem loading of sucrose from photosynthetic leaf mesophyll cells is mediated first by the vasculature-localized sugar transporters SWEET11 and 12. They move sucrose from parenchyma cells into the apoplast where it is loaded into phloem companion cells by SUC2 (Chen et al. 2012). In the root, sucrose is unloaded either through an apoplastic pathway (via SUC/SWEET sugar transporters) or through a symplastic pathway (via the hydrostatic pressure) (Milne et al. 2018). Very recently Chen et al. (2022) showed that both SWEET11 and 12 are phosphorylated by drought or ABA activated SNF1-RELATED PROTEIN KINASE 2 (SnRK2) protein kinases, which enhance sucrose export to roots. This increased allocation is modulated by ABA signaling, promotes root development and increases foraging. The putative link between this sucrose dependent root growth stimulation and the SnRK1–target of rapamycin (TOR) energy signaling pathway remains to be elucidated. Indeed, sucrose accumulation may release the TOR1 dependent repression of transcription factors such as bZIP1, bZIP11 and bZIP53 or local auxin accumulation in primary root tip thereby promoting root growth (Hartmann et al. 2015; Weiste et al. 2017). Under drought stress, ABA activated SnRK2 can however phosphorylate TOR, thereby modulating the tradeoff between plant growth and drought response stress (Wang et al. 2018). A similar role for TOR can also be considered for primordia initiation through the regulation of WOX7, a sucrose dependent repressor of the cell cycle gene CYCD6 (Kong et al. 2016).

ABA also induces trehalose accumulation which in turns inhibits root growth (Wang et al. 2020). Finally, trehalose 6-phosphate (Tre6P) has also been demonstrated as a key regulator of source-sink relationships (Figuerola and Lunn 2016). In Arabidopsis, Tre6P is produced in the phloem and stomatal guard cells (Fichtner and Lunn 2021). Tre6P synthase (TPS), the enzyme that synthesizes Tre6P, plays a key role in the nexus between sucrose and Tre6P, operating in the phloem loading zone of leaves. Tre6P has a dual function as a signal molecule and homeostatic regulator of sucrose levels in plants in response to abiotic stresses such as drought. Most flowering plants contain barely detectable amounts of trehalose compared to sucrose. Despite the low amount of Tre6P, overexpression of TPS and TPP enzymes led to severe growth and developmental defects suggesting that changes in the level of Tre6P, the intermediate in the pathway, rather than in the level of trehalose itself, were responsible for the phenotypes. The concept that Tre6P functions primarily as a signal and regulator of sucrose levels in plants supports the existence of systemic signals for source-sink coordination (Fichtner et al. 2020; Fichtner and Lunn 2021). In growing sink organs, Tre6P would regulate the

utilization of sucrose for growth and the accumulation of storage reserves, in part via complex interactions with TOR (Figueroa and Lunn 2016).

Taken together, shoot-originated sucrose and its underlying signaling network involving ABA and other phytohormones, SnRK2, TOR and potentially Tre6P seems to be involved in the fine tuning of root development under drought. Yet, further exploration is needed to better characterize the complex interactions shaping these signaling networks.

Hormones

Several hormones have been identified both in xylem and phloem sap and have been proposed to play a key role in the coordination of systemic stress response (Fig. 3B). Among these, ABA has been identified for long as a master regulator of plant responses to drought-, salt-, osmotic-, and freezing-based water limitations. ABA mediates drought stress response and resistance by regulating stomatal closure and stress responsive gene expression (Cutler et al. 2010). The involvement of ABA in drought responses has been extensively documented (recently reviewed by Kuromori et al. 2022) and will not be detailed here. In response to drought stress, ABA accumulates in all plant tissues but its accumulation is dramatically enhanced in leaves and more specifically in the vasculature of leaves as most of the ABA biosynthesis genes are expressed in this tissue (Kuromori et al. 2018). In addition, several ABA transporters are predominantly expressed in vascular tissues. Thus, long distance transport of ABA can occur through both xylem (Davies and Zhang 1991; Schachtman and Goodger 2008; Jiang and Hartung 2008) and phloem (Zhong et al. 1996), with reports of both root and shoot derived pools during water stress (Hartung et al. 2002; Manzi et al. 2015). Although the vasculature and apoplastic areas are described as the typical routes for systemic signaling, it is not completely understood how ABA movement from tissue to tissue is regulated. Recent studies have suggested that signaling peptides could be involved in the ABA dependent long distance signaling (see below).

Strigolactones (SL) form the most recently discovered class of phytohormones. ABA and strigolactones share a carotenoid precursor, from which strigolactone synthesis proceeds through a partially known series of enzymes to produce bioactive strigolactones (reviewed by Waters et al. 2017). Strigolactones have been shown to modulate several aspects of root and shoot development and interactions with rhizosphere organisms (Al-Babili and Bouwmeester 2015; Lanfranco et al. 2018). They also are thought to be involved in nutritional and abiotic stresses (Mostofa et al. 2018). Several dicot plants with defective strigolactone synthesis or signaling are hypersensitive to

drought, salt and osmotic stress while exogenous application of SL reinforce drought tolerance in many species (Cardinale et al. 2018). In *Arabidopsis*, *Lotus japonicus* and tomato, SL positively control stomatal movements. Indeed, mutants in SL biosynthesis exhibited reduced stomatal closure (Ha et al. 2014; Liu et al. 2015; Visentin et al. 2016) whereas enhanced closure and drought tolerance was observed in plants treated with exogenous SL or over producing SL (Lv et al. 2018; Visentin et al. 2016; Zhang et al. 2018). Using grafting experiments in tomato, Visentin et al. (2016) confirmed that drought results in reduced SL accumulation in roots and over accumulation in shoots. Their experiments demonstrated that under-accumulation of SL in roots is responsible for its over accumulation in shoots. Thus, SL was identified as a long distance signal for drought dependent stomatal closure. SL acts on stomatal closure both in an ABA dependent and an ABA independent manner. The ABA-dependent pathway relies, at least in part, on ABA synthesis, transport and/or sensitivity. Accordingly, SL depletion decreases sensitivity to exogenous ABA in several species (Lv et al. 2018; Visentin et al. 2016). On the other hand, treatment with the synthetic SL analogue GR24 increases sensitivity to ABA in tomatoes (Visentin et al. 2016). Recently, Visentin et al. (2020) identified SL as a molecular component linking drought to miR156 accumulation and integrated miR156 in a model that links SL and ABA in tomato.

Also, it should be noted that the above-described model may be dependent on drought stress intensity and may be restricted to dicot plants. In rice, for instance, most SL biosynthetic mutants produce more ABA than the wild-type and thus are more resistant to drought (Haider et al. 2018). Finally, the local and systemic effects of drought-dependent under accumulation of SL in roots remain poorly documented.

Besides ABA and SL, several other hormones that have been identified in xylem and phloem sap (reviewed by Koenig and Hoffmann-Benning 2020) have been proposed to participate in plant adaptive responses to water deficit. For example, Brassinosteroids and Auxin are involved in the regulation of root and shoot growth under drought (reviewed by Gupta et al. 2020). Cytokinins were reported to mitigate water deficit growth limitation and stabilize yield (Hai et al. 2020). Finally, methyl jasmonate, that is well known for mediating long distance signaling in response to wounding or biotic stresses induces stomatal closure similar to ABA (Huang et al. 2017b). Jasmonoyl-isoleucine (JA-Ile) was also associated with osmotic signals, since it accumulates in cells under hypo-osmotic condition and conversely is reduced under hyperosmotic stress (Mielke et al. 2021, Science advances). The involvement of multiple hormonal

pathways in different plant tissues emphasizes the complexity of plant hormonal responses to drought (reviewed by Hai et al. (2020); Sirko et al. (2021) and Kuromori et al. (2022)) and their role in long distance signaling of water deficit most often remains to be established.

Nucleic acids

Nucleic acids, more specifically RNA species, are among the most well studied long distance signaling molecules. In their extensive recent review Gelaw and Sanan-Mishra (2021) collected a large panel of non coding RNA that are differentially expressed in response to drought suggesting a central role in signaling (Fig. 3B). Representatives of all types of RNA, such as mRNA, micro RNA (miRNA), small interfering RNA (siRNA), and other non-coding RNA (ncRNA) have been identified in the sap of many plant species including *Arabidopsis*, rice, barley, maize, pumpkin and many others (Kehr and Kragler 2018; Liu and Chen 2018; Guo et al. 2013; Westwood 2015). As systemic signals, mobile RNAs are regulatory elements by which plants respond to dynamic changes in the environment. Breakthroughs studies on the regulatory mechanisms of long-distance RNA transport have been made in recent years. For detailed reviews of RNA trafficking see the publications of Ham and Lucas (2017); Kehr and Kragler (2018); Liu and Chen (2018) or Zhang et al. (2021a, b). While the existence of mRNAs and ncRNAs in the vascular system hints at their mobility and possible role, identification alone does not conclusively prove movement or physiological function. By using homo (intra species) and hetero (inter species) grafting, many studies in model plants, crops and woody plants have provided evidence for mobile mRNAs (Notaguchi et al. 2015; Thieme et al. 2015; Liu et al. (2020) and lncRNA (Zhang et al. 2009; Zhang et al. 2021a, b). Similar results were also reported for miRNAs (Pagliarani et al. 2017; Tolstyko et al. 2019). Data suggest that environmental conditions, including water deficit, may affect transcript mobility, independent of changes in gene expression (Thieme et al. 2015; Zhang et al. 2016; Tolstyko et al. 2019). In line with these results, Zhang et al. (2016) demonstrated that the transmissibility of mobile mRNAs is related to tRNA-like structural elements (TLs). TLs can modulate mRNA transport and are necessary for mediation of mRNA movement across the grafting junction. Recent studies by Yang et al. (2019) have shown that RNAs can contain 5-methylcytosine (M5C) and that this methylation can regulate long distance mRNA transport. Other studies have identified additional selective mechanisms including specific sequence motifs. For instance, untranslated regions or cis acting elements at 5' end appear to influence transcript stability for transport, impact delivery to

distal tissues and translation level (Banerjee et al. 2009; Li et al. 2009). Using a long stem hetero grafting system, Xia et al. (2018) showed that the abundance and the structure of mRNAs were degraded during the trafficking, suggesting putative modulation to stress response. Furthermore, using an elegant triple hetero grafting approach with a potato and a *Nicotiana benthamiana* scions grafted onto a tomato root stock, it was shown that mRNA transferred from the scion to the stock can be transported back to the scion after being transported again to shoots in a “shoot-root-shoot” cycling process (Xia et al. 2018; Wang et al. 2021). Taken together, the wide range of molecules, transport regulation and processing steps point to an extremely complex regulation network of long distance signaling.

Proteins and peptides

Several proteomic studies have identified up to thousands of proteins and peptides both in the xylem and phloem sap (Rodriguez-Medina et al. 2011; Carella et al. 2016). Recent analyses have elucidated the molecular mechanisms involving the long distance regulatory protein Flowering Locus T (FT). This 20kDa protein is phloem mobile from leaves to shoot apical meristem where it acts as a florigen signal inducing flowering transition (Putterill and Varkonyi-Gasic 2016). Besides this well documented example very little is known about protein signaling functions. Nevertheless, mobile peptides form an important class of molecules possibly involved in long distance signaling in response to abiotic stress. Over 7000 small open reading frames (ORF) can be expressed in response to a wide range of environments in *Arabidopsis* suggesting a multitudes of functions (Hanada et al. 2007; Hanada et al. 2013; Ren et al. 2021) (Fig. 3B). A recent study has shown that the CLAVATA3/EMBRYO-SURROUNDING REGION- related25 (CLE25) peptide is a mobile, long-distance signaling molecule originating from roots and sensed in leaves where its perception induces ABA biosynthesis and stomatal closure (Takahashi et al. 2018). CLE25 was found to be produced in root vasculature and moves from root to shoots through the vascular system. In leaves, it is recognized by the BARELY ANY MERISTEM1 (BAM1) and BAM3 receptors that induce NINE-CIS-EPOXYCAROTENOID DIOXY- GENASE3 (NCED3) expression to enhance ABA accumulation in leaves. This, in turn, regulates stomatal aperture in response to dehydration stress thereby reducing water losses (Takahashi et al. 2018). Although the mechanisms involved in regulating CLE25 production, loading and unloading, and CLE25–BAM ABA production remain to be elucidated, these results identify the CLE25–BAM long-distance signaling system as a key component

of drought stress response. Interestingly, other CLE peptides (CLE 9/10) were found to be involved more locally in stomatal development and regulation (Qian et al. 2018). CLE9 has also a role in stomatal closure in response to drought in a ABA dependent manner (Zhang et al. 2018). While this peptide-dependent mechanism is definitely slower than hydraulic signaling, it may be an important component during mid-term and long-term dehydration stress responses. It may also be involved in the response to gradual soil drying as generally observed under natural conditions. One can also expect that the CLE-BAM long distance signaling mechanism plays a crucial role under heterogeneous water supply to the roots, when part of the root system experiences water deficit while other parts are well-watered. Interestingly, a similar mechanism has also been reported in response to nitrogen deficiency. Local root nitrate deficiency induces production of C-TERMINALLY ENCODED peptides (CEP) that are translocated to shoots where they are recognized by the CEP Receptor (CEPR). This in turn induces the local accumulation and transport to roots of the CEP DOWNSTREAM1 and 2 (CEPD1 and 2) polypeptides (Ohkubo et al. 2017). Thus, the CEP–CEPR–CEPD system mediates long-distance signaling from roots to shoots to roots in order to transmit the nitrogen deficit signal throughout the whole plant. Interestingly, a similar roots-to-shoots-to-roots signaling has also been documented during the control of nodule formation in the legume plant *Lotus Japonicus*. This systemic regulation that involves cytokinins connects nutritional status, development and hormonal signalization (reviewed by Okamoto et al. 2016; Ferguson et al. 2019). Similar mechanisms have not yet been reported in response to drought but several works identified CEPs which expression is induced by water deficit (Smith et al. 2020) suggesting they could also exist to adjust and coordinate development and water homeostasis.

Physiological and developmental response to soil water heterogeneity

Heterogeneity of water availability around plant roots is a widespread phenomenon, occurring both in natural and agricultural environments (Fig. 3C). At macro-scale, when rainfall or irrigation are limited, the upper soil layers typically dry faster as they are exposed to evaporation and water uptake by plant roots where their density is the highest. This results in an uneven vertical distribution of soil moisture with depth (Beff et al. 2013; Mohanty 2013; Zhang and Davies 1989). Water availability can also be horizontally heterogeneous, because of plant competition and local soil water retention (Ivanov et al. 2010). Due to the high heterogeneity in structure and composition of soil, water can also be heterogeneously distributed at

the local or micro scale. One of the most striking examples is the presence of macropores that locally induce an extreme water deficit (see extensive reviews by Beven and Germann 1982 and Jarvis 2007). Recent studies have identified the molecular mechanisms that allow roots to locally sense moisture gradients and direct their growth or formation of new lateral roots towards increased water availability. These local adaptations to water availability are referred to as hydrotropic response (Dietrich et al. 2017) and hydro-patterning (Bao et al. 2014; Orosa-Puente et al. 2018), respectively. Similarly, Orman-Ligeza et al. (2018) described a process called xerobanching which accounts for the repression of lateral root formation when a root grows through a large air-filled soil macropore. In all cases, root tip growth and root branching are positioned towards regions of higher water availability. While many mechanistic details are being uncovered from laboratory experiments, it will be fascinating and critical to understand how these growth and development adjustments mutually interact and operate during growth of roots in real, drying soils and how they allow optimizing soil foraging and water uptake at the whole plant level.

As an illustration, irrigation strategies have been introduced in agriculture to deliberately create a heterogeneous distribution of soil water, both spatially and temporally. One of these techniques called partial root zone drying (PRD), aims at locally irrigating a limited part of the root system while the other part of the root system faces water deficit (Dbara et al. 2016; Fu et al. 2017; Puértolas et al. 2015; Stoll et al. 2000). In agricultural production, PRD usually requires a regular permutation of watered and unwatered sides, to ensure the survival of the entire root system, thus forming a cycle of root drying and wetting. This technique was found to improve water use efficiency (WUE) compared to irrigation at field capacity in many greenhouse and field trials (Iqbal et al. 2020). For several crops, such as cotton (Du et al. 2008; Tang et al. 2005), tomato (Kirda et al. 2004; Zegbe et al. 2006), hot pepper (Kang et al. 2001; Shao et al. 2008), grape (De la Hera et al. 2007), and pear (Kang et al. 2002), PRD improved WUE without significant effect on yield compared to fully irrigated plants. However, studies in other crops showed more contrasted results. In maize for instance, some studies showed improved WUE with no reduction or even increase of grain yield (Fu et al. 2017; Kang et al. 2000; Sepaskhah and Khajehabdollahi 2005; Sepaskhah and Parand 2006) whereas another showed a lowered grain yield (Hakeem et al. 2016).

It is proposed that, during PRD, the drying roots sense the locally low water potential resulting in a reduction in cell turgor and thereby inducing a systemic partial stomatal closure and reduced leaf expansion. Concomitantly, roots in wet parts of the soil absorb large amounts of soil water to maintain elevated water content in shoots, consequently increasing water use efficiency (Kang and Zhang 2004; Christmann et al. 2013). Alteration of leaf growth and development and changes in metabolism can hinder the use of carbon, energy, and allocation of the plant's photoassimilates, which are then preferentially reallocated to roots enhancing root expansion in the irrigated part (Taiz and Zeiger 2006). Yet, the nature of the local and systemic signals involved in responses of the whole root system remains unknown. At the functional and molecular level, temporal PRD study in a riparian *Melaleuca* species showed the root hydraulic conductance and aquaporin abundance to be rapidly increased in the wet side (within 24 hours) after local dehydration of the root system (McLean et al. 2011), suggesting a systemic compensation and regulation of water uptake during PRD.

Several investigations have been carried out using a split-root system to mimic PRD and explore the local and systemic signaling governing PRD. ABA is the most studied non-hydraulic signal that may regulate and coordinate the underlying developmental and functional responses. Early studies have shown that tomatoes under root-zone water deficit had a lower stomatal conductance and greater root hydraulic conductivity due to overproduction of ABA (Thompson et al. 2007). However, Liu et al. (2008) noted that PRD plants had a lower stomatal conductance and similar photosynthesis compared to fully irrigated plants. Yet, the xylem sap ABA concentration of PRD plants was not higher than fully irrigated plants in the first day of PRD, making ABA questionable as the root to shoot signal in the early stage of PRD.

The different effects of water heterogeneity within the root zone have also been explored in pot experiments (Puértolas et al. 2013; Puértolas et al. 2015). In a set of experiments using beans (Puértolas et al. 2013) or potatoes (Puértolas et al. 2015) grown in soil columns that received different irrigation treatments to induce distinct vertical soil moisture gradients, it was observed that root ABA concentration and root water potential were homogeneous within the different root parts. On the contrary, horizontal heterogeneous soil moisture induced much higher ABA accumulation in the roots (Puértolas et al. 2015). These results and others on barley (Martin-Vertedor and Dodd 2011) challenge a direct correlation between local water deficit and ABA signaling. Many molecules including sugar, proline and other metabolites

(Abdallah et al. 2019; Iqbal et al. 2019; Raza et al. 2017) or proteins (Sadak et al. 2019; Sadak et al. 2020) were found to be produced and over accumulate under PRD irrigation conditions (Fig. 3C). However, there is no direct evidence yet to prove a possible role in systemic signaling. Furthermore, the role during PRD of other putative signals such as small RNA, microRNA, ncRNA and peptides has not been explored yet (Fig. 3C).

Conclusion and prospects

In recent years, much progress has been made in deciphering the mechanisms for sensing and signaling water deficit. The identification of several sensing molecules exemplify the central role of osmosensing in plant. But, how these molecules interconnect remains mostly unexplored. They might act in parallel pathway reflecting the diversity of osmotic signal that cells have to face. Alternatively, they could share some redundancy in the perception machinery or in triggering the downstream signaling. Unfortunately, our current knowledge remains too fragmented to assess the proper kinetic of events. Interestingly, most of the molecular actors described so far are localized to the plasma membrane, as it is suspected to be the ideal place for water sensing. Nevertheless, we realize that changes in cell volume or turgor could be perceived in subcellular compartments or structures deprived of membranes. For instance, liquid-liquid phase separation (LLPS) is a process where two liquids can be separated into non-miscible phases depending on concentration and which can be modulated by physico chemical alterations of the system (Cuevas-Velazquez and Dinneny 2018; Korkmazhan et al. 2021). LLPS can happen at many cell locations including contacts with a membrane but also in the cytoplasm or nucleoplasm, where it was originally discovered (Nucleolus, Cajal bodies, nuclear speckles). In animal cells, processing bodies (PBs) containing mRNA-decapping enzyme 1A (DCP1A) are examples of subcellular compartments that are deprived of membranes and rapidly phase separate under hyperosmotic stress while dissolving back upon isotonic rescue (Jalihal et al. 2020). These PBs sequester pre-mRNA cleavage factors from actively transcribing genome loci (Jalihal et al. 2020). This example provides a mechanical framework for gene regulation under hyperosmotic stimulation. Similarly, the apoptosis signal-regulating kinase 3 (ASK3) is inhibited by phase separation under hyperosmotic stress (Watanabe et al. 2021). In plants, phase separation can be associated to many processes like regulation of flowering time, temperature sensing, and auxin or SA signaling, (Fang et al. 2019; Powers et al. 2019; Zavaliev et al. 2020; Jung et al. 2020). Regarding water sensing, FLOE1, a prion like structured

protein, undergoes phase separation in vitro and during seed imbibition (Dorone et al. 2021). The biophysical state of FLOE1 modulates its biological activity in suppressing seed germination under unfavorable environments. Moreover, it was found that natural variation in the coding sequence of FLOE1 is associated with adaptive germination strategies in natural populations (Dorone et al. 2021). These findings on significance of LLPS in biology open new avenues to re-investigate the molecular mechanisms of plant osmotic sensing.

Like for osmotic perception, a large and ever increasing number of molecules have been proposed to act in local and long distance signaling of water availability. Strikingly enough, most of these signaling molecules and their corresponding receptors are likely to possess more functions than those that were originally assigned, revealing a complex array of interactions and interplays. Moreover, these molecular mechanisms have been identified in a limited number of model plants cultivated under highly controlled and often artificial growth conditions. In contrast, responses at the whole plant level have been mostly investigated in crops or understudied species. This is particularly striking for PRD where researches were conducted in crops/trees grown in a wide range of stresses (localization intensity, duration). Thus, it is difficult to integrate all available information to build a systemic signal network for plant response to heterogeneous water distribution. Furthermore, many of the signal molecules and mechanisms identified under homogeneous water deficit condition have not been or very partially investigated under heterogeneous water distribution.

Accordingly, little is known about the nature, the temporality and the function of sensing and local and systemic responses to heterogeneous water availability. We believe that studying rapid and long term responses to local water deficit in model species and under controlled conditions should lead to breakthroughs in the identification of the molecules and of their interactions that trigger plant acclimation responses. Identifying the main actors that trigger, prime or coordinate plant responses to water availability will provide a first step toward improving the efficiency and coordination of these responses. In the long term, these studies will allow identifying novel breeding targets to enhance crop tolerance to drought and develop new varieties that are well adapted to water saving irrigation strategies.

Abbreviations

ABA: Absciscic Acid; ABI: Absciscic Acid Insensitive; APX: Ascorbate Peroxidases; ASK3: Apoptosis Signal-regulating Kinase 3; At: *Arabidopsis thaliana*; BAM1: Barely Any Meristem 1; bZIP: Basic region, leucine Zipper; Ca^{2+} : Calcium; CAT: Catalases; CEP: C-terminally Encoded Peptides; CEPD: CEP Downstream; CHO: Chinese Hamster Ovary; Cl: Chloride; CLE25: CLAVATA3/

EMBRYO-SURROUNDING REGION- related25; CrRLK: *Catharanthus roseus* RLK1-Like kinases; CSC1: Calcium-permeable Stress-gated cation Channel 1; CYCD: Cyclin D; DCP1A: mRNA-Decapping enzyme 1A; EF domains: Helix-loop-helix structural domain; EMS: Ethyl Methane Sulfonate; ECA1: Endoplasmic reticulum Ca^{2+} pump; E PCs: ER-plasma membrane Contact Sites; FER: FERONIA; FLOE: "Sheet of floating ice"; FT: Flowering Locus T; GLR: Glutamate Receptor-like protein; GPX: Glutathione Peroxidases; H^+ : Hydrogen; H_2O_2 : Hydrogen peroxide; HEK: Human Embryonic Kidney; HK: Histidine Kinases; HOG1: High Osmolarity Glycerol 1; HPCA1: Hydrogen Peroxide sensor; K^+ : Potassium; KEAs: K^+ Exchange Antiporters; LLPS: Liquid-Liquid Phase Separation; lncRNA: Long non coding RNA; LRK: Lectin Receptor-Kinase; LRR: Leucine Repeat; M5C: 5-methylcytosine; MAP kinase: Mitogen-Activated Protein Kinases; MCA1: Mid1-Complementing Activity; MIK2: MALE DISCOVERER 1-INTERACTING RECEPTOR-LIKE KINASE 2; MIZ1: MIZU-KUSSEI1; mRNA: Messenger RNA; miRNA: Micro RNA; MscS: Mesenchymal stem cells; MSL: MscS-like; NADPH: Nicotinamide Adenine Dinucleotide Phosphate Hydrogen; NCD3: NINE-CIS-EPOXYCAROTENOID DIOXY- GENASE3; ncRNA: Non-coding RNA; ORF: Open Reading Frames; OSCA1: REDUCED HYPEROSMOLALITY-INDUCED [Ca^{2+}] INCREASE 1; PBs: Processing Bodies; PCD: Programmed Cell Death; PRD: Partial Root zone Drying; PERKs: Proline-rich Extensin-like Receptor Kinases; PIP: Plasma membrane Intrinsic Protein; PM: Plasma Membrane; PRX: Peroxiredoxins; PTI: Pattern-Triggered Immunity; RALF34: Rapid Alkalinization Factor; RBOHD and F: Respiratory Burst Oxidase Homolog D and F family; Rho: Ras-homologous family proteins; RLKs: Receptor Like Kinases; RNA: Ribonucleic acid; ROP6: Rho of Plant 6; ROS: Reactive Oxygen Species; RSA: Root System Architecture; SA: Salicylic Acid; SCOOP12: SERINE RICH ENDOGENOUS PEPTIDE12; siRNA: Small interfering RNA; SL: Strigolactone; SLN1: Synthetic Lethal of N-end rule 1; SnRK: SNF1-RELATED PROTEIN KINASE; SOD: Superoxide Dismutases; THE: THESEUS; TIP: Tonoplast Intrinsic Protein; TLs: tRNA-Like structural elements; TOR: Target Of Rapamycin; TPC1: Two Pore Channel 1; TPS: Tre6P Synthase; Tre6P: Trehalose 6 Phosphate; TM: Trans Membrane; WAK: Wall Associated Kinases; WOX: Wuschel-like homeobox; WUE: Water Use Efficiency.

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Authors' contributions

A.M and P.N conceived the overall organization of the manuscript. L.G, X.L. A.M and P.N. wrote the manuscript and designed the graphical arts. C.M. supervised and contributed to the final version of the manuscript. The author(s) read and approved the final manuscript.

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Declarations

Competing interests

C.M. is a member of the Editorial Board but was not involved in the journal's review of, or any decisions related to, this manuscript.

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References

- Abdallah MMS, El-Bassiouny HMS, AbouSeeda MA (2019) Potential role of kaolin or potassium sulfate as anti-transpirant on improving physiological, biochemical aspects and yield of wheat plants under different watering regimes. *Bull Natl Res Cent* 43(1):134. <https://doi.org/10.1186/s42269-019-0177-8>

- Al-Babili S, Bouwmeester HJ (2015) Strigolactones, a novel carotenoid-derived plant hormone. *Annu Rev Plant Biol* 66:161–186. <https://doi.org/10.1146/annurev-arplant-043014-114759>
- Attacha S, Solbach D, Bela K, Moseler A, Wagner S, Schwarzländer M, Aller I, Müller SJ, Meyer AJ (2017) Glutathione peroxidase-like enzymes cover five distinct cell compartments and membrane surfaces in *Arabidopsis thaliana*: subcellular localization of GPXs in *Arabidopsis*. *Plant Cell Environ* 40(8):1281–1295. <https://doi.org/10.1111/pce.12919>
- Bacete L, Schulz J, Engelsdorf T, Bartosova Z, Vaahtera L, Yan G, Gerhold JM, Tichá T, Øvstebø C, Gigli-Bisceglia N, Johannessen-Starheim S, Marguerit J, Kollist H, Dehoux T, McAdam SAM, Hamann T (2022) THESEUS1 modulates cell wall stiffness and abscisic acid production in *Arabidopsis thaliana*. *Proc Natl Acad Sci U S A* 119(1):e2119258119. <https://doi.org/10.1073/pnas.2119258119>
- Banerjee AK, Lin T, Hannapel DJ (2009) Untranslated regions of a mobile transcript mediate RNA metabolism. *Plant Physiol* 151(4):1831–1843. <https://doi.org/10.1104/pp.109.144428>
- Bao Y, Aggarwal P, Robbins NE, Sturrock CJ, Thompson MC, Tan HQ, Tham C, Duan L, Rodriguez PL, Vernoux T, Mooney SJ, Bennett MJ, Dinneny JR (2014) Plant roots use a patterning mechanism to position lateral root branches toward available water. *Proc Natl Acad Sci* 111(25):9319–9324. <https://doi.org/10.1073/pnas.1400966111>
- Bass RB, Strop P, Barclay M, Rees DC (2002) Crystal structure of *Escherichia coli* MscS, a voltage-modulated and mechanosensitive channel. *Science* 298(5598):1582–1587. <https://doi.org/10.1126/science.1077945>
- Basu D, Haswell ES (2020) The mechanosensitive Ion Channel MSL10 potentiates responses to cell swelling in *Arabidopsis* seedlings. *Curr Biol* 30(14):2716–2728.e6. <https://doi.org/10.1016/j.cub.2020.05.015>
- Basu D, Shoots JM, Haswell ES (2020) Interactions between the N- and C-termini of the mechanosensitive ion channel at MSL10 are consistent with a three-step mechanism for activation. *J Exp Bot* 71(14):4020–4032. <https://doi.org/10.1093/jxb/eraa192>
- Beff L, Günther T, Vandoorne B, Couvreur V, Javaux M (2013) Three-dimensional monitoring of soil water content in a maize field using electrical resistivity tomography. *Hydrol Earth Syst Sci* 17(2):595–609. <https://doi.org/10.5194/hess-17-595-2013>
- Ben Rejeb K, Lefebvre-De Vos D, Le Disquet I, Leprince A, Bordenave M, Maldiney R, Jdey A, Abdely C, Savouré A (2015) Hydrogen peroxide produced by NADPH oxidases increases proline accumulation during salt or mannitol stress in *arabidopsis thaliana*. *New Phytol* 208(4):1138–1148. <https://doi.org/10.1111/nph.13550>
- Beven K, Germann P (1982) Macropores and water flow in soils. *Water Resour Res* 18(5):1311–1325. <https://doi.org/10.1029/WR018i005p01311>
- Bienert GP, Möller ALB, Kristiansen KA, Schulz A, Möller IM, Schjoerring JK, Jahn TP (2007) Specific Aquaporins facilitate the diffusion of hydrogen peroxide across membranes. *J Biol Chem* 282(2):1183–1192. <https://doi.org/10.1074/jbc.M603761200>
- Boisson-Dernier A, Lituiev DS, Nestorova A, Franck CM, Thirugnanarajah S, Grossniklaus U (2013) ANXUR receptor-like kinases coordinate cell wall integrity with growth at the pollen tube tip via NADPH oxidases. *PLoS Biol* 11(11):e1001719. <https://doi.org/10.1371/journal.pbio.1001719>
- Boursiac Y, Boudet J, Postaire O, Luu D-T, Tournaire-Roux C, Maurel C (2008) Stimulus-induced downregulation of root water transport involves reactive oxygen species-activated cell signalling and plasma membrane intrinsic protein internalization: Aquaporins and reactive oxygen species. *Plant J* 56(2):207–218. <https://doi.org/10.1111/j.1365-313X.2008.03594.x>
- Brewster JL, Gustin MC (1994) Positioning of cell growth and division after osmotic stress requires a map kinase pathway. *Yeast* 10(4):425–439. <https://doi.org/10.1002/yea.320100402>
- Cardinale F, Korwin Krukowski P, Schubert A, Visentin I (2018) Strigolactones: mediators of osmotic stress responses with a potential for agrochemical manipulation of crop resilience. *J Exp Bot* 69(9):2291–2303. <https://doi.org/10.1093/jxb/erx494>
- Carella P, Wilson DC, Kempthorne CJ, Cameron RK (2016) Vascular sap proteomics: providing insight into long-distance signaling during stress. *Front Plant Sci* 7:651. <https://doi.org/10.3389/fpls.2016.00651>
- Chen J, Yu F, Liu Y, Du C, Li X, Zhu S, Wang X, Lan W, Rodriguez PL, Liu X, Li D, Chen L, Luan S (2016) FERONIA interacts with ABI2-type phosphatases to facilitate signaling cross-talk between abscisic acid and RALF peptide in *Arabidopsis*. *Proc Natl Acad Sci U S A* 113(37). <https://doi.org/10.1073/pnas.1608449113>
- Chen L-Q, Qu X-Q, Hou B-H, Sosso D, Osorio S, Fernie AR, Frommer WB (2012) Sucrose efflux mediated by SWEET proteins as a key step for phloem transport. *Science* 335(6065):207–211. <https://doi.org/10.1126/science.1213351>
- Chen Q, Hu T, Li X, Song C-P, Zhu J-K, Chen L, Zhao Y (2022) Phosphorylation of SWEET sucrose transporters regulates plant root:shoot ratio under drought. *Nat Plants* 8(1):68–77. <https://doi.org/10.1038/s41477-021-01040-7>
- Christmann A, Grill E, Huang J (2013) Hydraulic signals in long-distance signaling. *Curr Opin Plant Biol* 16(3):293–300. <https://doi.org/10.1016/j.pbi.2013.02.011>
- Christmann A, Weiler EW, Steudle E, Grill E (2007) A hydraulic signal in root-to-shoot signalling of water shortage. *Plant J* 52(1):167–174. <https://doi.org/10.1111/j.1365-313X.2007.03234.x>
- Codjoe JM, Richardson RA, Haswell ES (2022) Unbiased proteomic and forward genetic screens reveal that mechanosensitive ion channel MSL10 functions at ER-plasma membrane contact sites in *Arabidopsis thaliana*. *bioRxiv*. <https://doi.org/10.1101/2022.05.23.493056>
- Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. *BMC Plant Biol* 11:163. <https://doi.org/10.1186/1471-2229-11-163>
- Cuevas-Velazquez CL, Dinneny JR (2018) Organization out of disorder: liquid-liquid phase separation in plants. *Curr Opin Plant Biol* 45:68–74. <https://doi.org/10.1016/j.pbi.2018.05.005>
- Cutler SR, Rodriguez PL, Finkelstein RR, Abrams SR (2010) Abscisic acid: emergence of a core signaling network. *Annu Rev Plant Biol* 61(1):651–679. <https://doi.org/10.1146/annurev-arplant-042809-112122>
- Cutolo E, Parvin N, Ruge H, Pirayesh N, Roustan V, Weckwerth W, Teige M, Grieco M, Larosa V, Vothknecht UC (2019) The high light response in *Arabidopsis* requires the calcium sensor protein CAS, a target of STN7- and STN8-mediated phosphorylation. *Front Plant Sci* 10:974. <https://doi.org/10.3389/fpls.2019.00974>
- Davies WJ, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. *Annu Rev Plant Physiol Plant Mol Biol* 42(1):55–76. <https://doi.org/10.1146/annurev.pp.42.060191.000415>
- Dbara S, Haworth M, Emiliani G, Ben Mimoun M, Gómez-Cadenas A, Centritto M (2016) Partial root-zone drying of olive (*Olea europaea* var. ‘Chetoui’) induces reduced yield under field conditions. *PLoS One* 11(6):e0157089. <https://doi.org/10.1371/journal.pone.0157089>
- De la Hera ML, Romero P, Gómez-Plaza E, Martínez A (2007) Is partial root-zone drying an effective irrigation technique to improve water use efficiency and fruit quality in field-grown wine grapes under semiarid conditions? *Agric Water Manag* 87(3):261–274. <https://doi.org/10.1016/j.agwat.2006.08.001>
- Devireddy AR, Zandalinas SI, Fichman Y, Mittler R (2021) Integration of reactive oxygen species and hormone signaling during abiotic stress. *Plant J* 105(2):459–476. <https://doi.org/10.1111/tpj.15010>
- Dietrich D, Pang L, Kobayashi A, Fozard JA, Boudolf V, Bhosale R, Antoni R, Nguyen T, Hiratsuka S, Fujii N, Miyazawa Y, Bae T-W, Wells DM, Owen MR, Band LR, Dyson RJ, Jensen OE, King JR, Tracy SR, Sturrock CJ, Mooney SJ, Roberts JA, Bhalerao RP, Dinneny JR, Rodriguez PL, Nagatani A, Hosokawa Y, Baskin TI, Pridmore TP, De Veylder L, Takahashi H, Bennett MJ (2017) Root hydrotropism is controlled via a cortex-specific growth mechanism. *Nat Plants* 3(6):17057. <https://doi.org/10.1038/nplants.2017.57>
- Dodd AN, Kudla J, Sanders D (2010) The language of calcium signaling. *Annu Rev Plant Biol* 61(1):593–620. <https://doi.org/10.1146/annurev-arplant-070109-104628>
- Dorone Y, Boeynaems S, Flores E, Jin B, Hateley S, Bossi F, Lazarus E, Pennington JG, Michiels E, De Decker M, Vints K, Baatsen P, Bassel GW, Otegui MS, Holehouse AS, Exposito-Alonso M, Sukenik S, Gitler AD, Rhee SY (2021) A prion-like protein regulator of seed germination undergoes hydration-dependent phase separation. *Cell* 184(16):4284–4298.e27. <https://doi.org/10.1016/j.cell.2021.06.009>
- Du T, Kang S, Zhang J, Li F (2008) Water use and yield responses of cotton to alternate partial root-zone drip irrigation in the arid area of north-West China. *Irrig Sci* 26(2):147–159. <https://doi.org/10.1007/s00271-007-0081-0>

- Duan Q, Kita D, Li C, Cheung AY, Wu H-M (2010) FERONIA receptor-like kinase regulates RHO GTPase signaling of root hair development. *Proc Natl Acad Sci U S A* 107(41):17821–17826. <https://doi.org/10.1073/pnas.1005366107>
- Evans MJ, Choi W-G, Gilroy S, Morris RJ (2016) A ROS-assisted calcium wave dependent on the AtRBOHD NADPH oxidase and TPC1 Cation Channel propagates the systemic response to salt stress. *Plant Physiol* 171(3):1771–1784. <https://doi.org/10.1104/pp.16.00215>
- Evans MJ, Morris RJ (2017) Chemical agents transported by xylem mass flow propagate variation potentials. *Plant J* 91(6):1029–1037. <https://doi.org/10.1111/tpj.13624>
- Fang X, Wang L, Ishikawa R, Li Y, Fiedler M, Liu F, Calder G, Rowan B, Weigel D, Li P, Dean C (2019) Arabidopsis FLL2 promotes liquid–liquid phase separation of polyadenylation complexes. *Nature* 569(7755):265–269. <https://doi.org/10.1038/s41586-019-1165-8>
- Farmer EE, Gao Y-Q, Lenzoni G, Wolfender J-L, Wu Q (2020) Wound- and mechanostimulated electrical signals control hormone responses. *New Phytol* 227(4):1037–1050. <https://doi.org/10.1111/nph.16646>
- Farmer EE, Gasperini D, Acosta IF (2014) The squeeze cell hypothesis for the activation of jasmonate synthesis in response to wounding. *New Phytol* 204(2):282–288. <https://doi.org/10.1111/nph.12897>
- Feiguelman G, Fu Y, Yalovsky S (2018) ROP GTPases structure-function and signaling pathways. *Plant Physiol* 176(1):57–79. <https://doi.org/10.1104/pp.17.01415>
- Feng W, Kita D, Peaucelle A, Cartwright HN, Doan V, Duan Q, Liu M-C, Maman J, Steinhorst L, Schmitz-Thom I, Vron R, Kudla J, Wu H-M, Cheung AY, Dinneny JR (2018) The FERONIA receptor kinase maintains cell-wall integrity during salt stress through Ca^{2+} signaling. *Curr Biol* 28(5):666–675.e5. <https://doi.org/10.1016/j.cub.2018.01.023>
- Ferguson BJ, Mens C, Hastwell AH, Zhang M, Su H, Jones CH, Chu X, Gresshoff PM (2019) Legume nodulation: the host controls the party. *Plant Cell Environ* 42(1):41–51. <https://doi.org/10.1111/pce.13348>
- Fichman Y, Mittler R (2021) Integration of electric, calcium, reactive oxygen species and hydraulic signals during rapid systemic signaling in plants. *Plant J* 107(1):7–20. <https://doi.org/10.1111/tpj.15360>
- Fichtner F, Lunn JE (2021) The role of Trehalose 6-phosphate (Tre6P) in plant metabolism and development. *Annu Rev Plant Biol* 72:737–760. <https://doi.org/10.1146/annurev-arplant-050718-095929>
- Fichtner F, Olas JJ, Feil R, Watanabe M, Krause U, Hoefgen R, Stitt M, Lunn JE (2020) Functional features of TREHALOSE-6-PHOSPHATE SYNTHASE1, an essential enzyme in Arabidopsis. *Plant Cell* 32(6):1949–1972. <https://doi.org/10.1105/tpc.19.00837>
- Figuerola CM, Lunn JE (2016) A tale of two sugars: Trehalose 6-phosphate and sucrose. *Plant Physiol* 172(1):7–27. <https://doi.org/10.1104/pp.16.00417>
- Flegler VJ, Rasmussen A, Borbil K, Boten L, Chen H-A, Deinlein H, Halang J, Hellmanzik K, Löffler J, Schmidt V, Makbul C, Kraft C, Hedrich R, Rasmussen T, Böttcher B (2021) Mechanosensitive channel gating by delipidation. *Proc Natl Acad Sci U S A* 118(33):e2107095118. <https://doi.org/10.1073/pnas.2107095118>
- Franks PJ, Farquhar GD (2007) The mechanical diversity of stomata and its significance in gas-exchange control. *Plant Physiol* 143(1):78–87. <https://doi.org/10.1104/pp.106.089367>
- Fu F, Li F, Kang S (2017) Alternate partial root-zone drip irrigation improves water- and nitrogen- use efficiencies of sweet-waxy maize with nitrogen fertigation. *Sci Rep* 7(1):17256. <https://doi.org/10.1038/s41598-017-17560-2>
- Furuichi T, Iida H, Sokabe M, Tatsumi H (2012) Expression of Arabidopsis MCA1 enhanced mechanosensitive channel activity in the *Xenopus laevis* oocyte plasma membrane. *Plant Signal Behav* 7(8):1022–1026. <https://doi.org/10.4161/psb.20783>
- Gamble RL, Qu X, Schaller GE (2002) Mutational analysis of the ethylene receptor ETR1. Role of the histidine kinase domain in dominant ethylene insensitivity. *Plant Physiol* 128(4):1428–1438. <https://doi.org/10.1104/pp.010777>
- Gelaw TA, Sanan-Mishra N (2021) Non-coding RNAs in response to drought stress. *Int J Mol Sci* 22(22):12519. <https://doi.org/10.3390/ijms222212519>
- Gonneau M, Desprez T, Martin M, Doblas VG, Bacete L, Miart F, Sormani R, Hématy K, Renou J, Landrein B, Murphy E, Van De Cotte B, Vernhettes S, De Smet I, Höfte H (2018) Receptor kinase THESEUS1 is a rapid alkalinization factor 34 receptor in Arabidopsis. *Curr Biol* 28(15):2452–2458.e4. <https://doi.org/10.1016/j.cub.2018.05.075>
- Guo S, Zhang J, Sun H, Salse J, Lucas WJ, Zhang H, Zheng Y, Mao L, Ren Y, Wang Z, Min J, Guo X, Murat F, Ham B-K, Zhang Z, Gao S, Huang M, Xu Y, Zhong S, Bombarely A, Mueller LA, Zhao H, He H, Zhang Y, Zhang Z, Huang S, Tan T, Pang E, Lin K, Hu Q, Kuang H, Ni P, Wang B, Liu J, Kou Q, Hou W, Zou X, Jiang J, Gong G, Klee K, Schoof H, Huang Y, Hu X, Dong S, Liang D, Wang J, Wu K, Xia Y, Zhao X, Zheng Z, Xing M, Liang X, Huang B, Lv T, Wang J, Yin Y, Yi H, Li R, Wu M, Levi A, Zhang X, Giovannoni JJ, Wang J, Li Y, Fei Z, Xu Y (2013) The draft genome of watermelon (*Citrullus lanatus*) and resequencing of 20 diverse accessions. *Nat Genet* 45(1):51–58. <https://doi.org/10.1038/ng.2470>
- Gupta A, Rico-Medina A, Cano-Delgado AI (2020) The physiology of plant responses to drought. *Science* 368(6488):266–269. <https://doi.org/10.1126/science.aaz7614>
- Ha CV, Leyva-Gonzalez MA, Osakabe Y, Tran UT, Nishiyama R, Watanabe Y, Tanaka M, Seki M, Yamaguchi S, Dong NV, Yamaguchi-Shinozaki K, Shinozaki K, Herrera-Estrella L, Tran L-S (2014) Positive regulatory role of strigolactone in plant responses to drought and salt stress. *Proc Natl Acad Sci* 111(2):851–856. <https://doi.org/10.1073/pnas.1322135111>
- Hai NN, Chuong NN, Tu NHC, Kisiala A, Hoang XLT, Thao NP (2020) Role and regulation of cytokinins in plant response to drought stress. *Plants* (Basel) 9(4):E422. <https://doi.org/10.3390/plants9040422>
- Haider I, Andreo-Jimenez B, Bruno M, Bimbo A, Flokova K, Abuauuf H, Ntui VO, Guo X, Charnikova T, Al-Babili S, Bouwmeester HJ, Ruyter-Spira C (2018) The interaction of strigolactones with abscisic acid during the drought response in rice. *J Exp Bot* 69(9):2403–2414. <https://doi.org/10.1093/jxb/ery089>
- Hakeem A, Liu Y, Xie L, Samiullah HJ, Ata-UI-Karim S, Rehmani MIA, Rehmani MIA (2016) Comparative effects of alternate partial root-zone drying and conventional deficit irrigation on growth and yield of field grown maize (*Zea mays* L.) hybrid. *J Environ Agric Sci* 6:23–31
- Ham B-K, Lucas WJ (2017) Phloem-Mobile RNAs as systemic signaling agents. *Annu Rev Plant Biol* 68(1):173–195. <https://doi.org/10.1146/annurev-arplant-042916-041139>
- Hamilton ES, Jensen GS, Maksaev G, Katims A, Sherp AM, Haswell ES (2015) Mechanosensitive channel MSL8 regulates osmotic forces during pollen hydration and germination. *Science* 350(6259):438–441. <https://doi.org/10.1126/science.aac6014>
- Han S, Tang R, Anderson LK, Woerner TE, Pei Z-M (2003) A cell surface receptor mediates extracellular Ca^{2+} sensing in guard cells. *Nature* 425(6954):196–200. <https://doi.org/10.1038/nature01932>
- Hanada K, Higuchi-Takeuchi M, Okamoto M, Yoshizumi T, Shimizu M, Nakamimami K, Nishi R, Ohashi C, Iida K, Tanaka M, Horii Y, Kawashima M, Matsui K, Toyoda T, Shinozaki K, Seki M, Matsui M (2013) Small open reading frames associated with morphogenesis are hidden in plant genomes. *Proc Natl Acad Sci U S A* 110(6):2395–2400. <https://doi.org/10.1073/pnas.1213958110>
- Hanada K, Zhang X, Borevitz JO, Li W-H, Shiu S-H (2007) A large number of novel coding small open reading frames in the intergenic regions of the Arabidopsis thaliana genome are transcribed and/or under purifying selection. *Genome Res* 17(5):632–640. <https://doi.org/10.1101/gr.5836207>
- Hartmann L, Pedrotti L, Weiste C, Fekete A, Schierstaedt J, Gottler J, Kempa S, Kriskche M, Dietrich K, Mueller MJ, Vicente-Carabajosa J, Hanson J, Droge-Laser W (2015) Crosstalk between two bZIP signaling pathways orchestrates salt-induced metabolic reprogramming in Arabidopsis roots. *Plant Cell* 27(8):2244–2260. <https://doi.org/10.1105/tpc.15.00163>
- Hartung W, Sauter A, Hose E (2002) Abscisic acid in the xylem: where does it come from, where does it go to? *J Exp Bot* 53(366):27–32. <https://doi.org/10.1093/jexbot/53.366.27>
- Haswell ES (2007) MscS-Like proteins in plants. In: Current topics in membranes. Academic Press 58:329–359. [https://doi.org/10.1016/S1063-5823\(06\)58013-5](https://doi.org/10.1016/S1063-5823(06)58013-5)
- Haswell ES, Peyronnet R, Barbier-Brygoo H, Meyerowitz EM, Frachisse J-M (2008) Two MscS homologs provide mechanosensitive channel activities in the Arabidopsis root. *Curr Biol* 18(10):730–734. <https://doi.org/10.1016/j.cub.2008.04.039>
- Hématy K, Sado P-E, Van Tuinen A, Rochange S, Desnos T, Balzergue S, Pelletier S, Renou J-P, Höfte H (2007) A receptor-like kinase mediates the

- response of Arabidopsis cells to the inhibition of cellulose synthesis. *Curr Biol* 17(11):922–931. <https://doi.org/10.1016/j.cub.2007.05.018>
- Hou C, Tian W, Kleist T, He K, Garcia V, Bai F, Hao Y, Luan S, Li L (2014) DUF221 proteins are a family of osmosensitive calcium-permeable cation channels conserved across eukaryotes. *Cell Res* 24(5):632–635. <https://doi.org/10.1038/cr.2014.14>
- Hou S, Liu D, Huang S, Luo D, Liu Z, Xiang Q, Wang P, Mu R, Han Z, Chen S, Chai J, Shan L, He P (2021) The Arabidopsis MK2 receptor elicits immunity by sensing a conserved signature from phytochemicals and microbes. *Nat Commun* 12(1):5494. <https://doi.org/10.1038/s41467-021-25580-w>
- Houwink AL (1935) The conduction of excitation in *Mimosa pudica*. *Recl Trav Bot Neerl* 32:51–91
- Huang F, Luo J, Ning T, Cao W, Jin X, Zhao H, Wang Y, Han S (2017a) Cytosolic and nucleosolic calcium signaling in response to osmotic and salt stresses are independent of each other in roots of Arabidopsis seedlings. *Front Plant Sci* 8:1648. <https://doi.org/10.3389/fpls.2017.01648>
- Huang H, Liu B, Liu L, Song S (2017b) Jasmonate action in plant growth and development. *J Exp Bot* 68(6):1349–1359. <https://doi.org/10.1093/jxb/erw495>
- Hutchison CE, Kieber JJ (2002) Cytokinin Signaling in Arabidopsis. *The Plant Cell* 14(S1):S47–S59. <https://doi.org/10.1105/tpc.010444>
- Iqbal N, Hussain S, Raza MA, Yang C-Q, Safdar ME, Brestic M, Aziz A, Hayyat MS, Asghar MA, Wang XC, Zhang J, Yang W, Liu J (2019) Drought tolerance of soybean (*Glycine max* L. Merr.) by improved photosynthetic characteristics and an efficient antioxidant enzyme activities under a Split-root system. *Front Physiol* 10:786. <https://doi.org/10.3389/fphys.2019.00786>
- Iqbal R, Raza MAS, Toleikienė M, Ayaz M, Hashemi F, Habib-ur-Rahman M, Zaheer MS, Ahmad S, Riaz U, Ali M, Aslam MU, Haider I (2020) Partial root-zone drying (PRD), its effects and agricultural significance: a review. *Bull Natl Res Centre* 44(1):159. <https://doi.org/10.1186/s42269-020-00413-w>
- Ivanov VY, Faticchi S, Jenerette GD, Espeleta JF, Troch PA, Huxman TE (2010) Hysteresis of soil moisture spatial heterogeneity and the “homogenizing” effect of vegetation: SOIL MOISTURE SPATIAL HETEROGENEITY. *Water Resour Res* 46(9). <https://doi.org/10.1029/2009WR008611>
- Jalil AP, Pitchaiya S, Xiao L, Bawa P, Jiang X, Bedi K, Parolia A, Cieslik M, Ljungman M, Chinnaiyan AM, Walter NG (2020) Multivalent proteins rapidly and reversibly phase-separate upon osmotic cell volume change. *Mol Cell* 79(6):978–990.e5. <https://doi.org/10.1016/j.molcel.2020.08.004>
- Jarvis NJ (2007) A review of non-equilibrium water flow and solute transport in soil macropores: principles, controlling factors and consequences for water quality. *Eur J Soil Sci* 58(3):523–546. <https://doi.org/10.1111/j.1365-2389.2007.00915.x>
- Jiang F, Hartung W (2008) Long-distance signalling of abscisic acid (ABA): the factors regulating the intensity of the ABA signal. *J Exp Bot* 59(1):37–43. <https://doi.org/10.1093/jxb/ern127>
- Jiménez-Nopala G, Salgado-Escobar AE, Cevallos-Porta D, Cárdenas L, Sepúlveda-Jiménez G, Cassab G, Porta H (2018) Autophagy mediates hydrotropic response in Arabidopsis thaliana roots. *Plant Sci* 272:1–13. <https://doi.org/10.1016/j.plantsci.2018.03.026>
- Johns S, Hagihara T, Toyota M, Gilroy S (2021) The fast and the furious: rapid long-range signaling in plants. *Plant Physiol* 185(3):694–706. <https://doi.org/10.1093/plphys/kiaa098>
- Jojoa-Cruz S, Saotome K, Murthy SE, Tsui CCA, Sansom MS, Patapoutian A, Ward AB (2018) Cryo-EM structure of the mechanically activated ion channel OSCA1.2. *eLife* 7:e41845. <https://doi.org/10.7554/eLife.41845>
- Julkowska MM, Klei K, Fokkens L, Haring MA, Schranz ME, Testerink C (2016) Natural variation in rosette size under salt stress conditions corresponds to developmental differences between Arabidopsis accessions and allelic variation in the *LRR-KISS* gene. *EXBOTJ* 67(8):2127–2138. <https://doi.org/10.1093/jxb/erw015>
- Jung J-H, Barbosa AD, Hutin S, Kumita JR, Gao M, Derwort D, Silva CS, Lai X, Pierre E, Geng F, Kim S-B, Baek S, Zubieta C, Jaeger KE, Wigge PA (2020) A prion-like domain in ELF3 functions as a thermosensor in Arabidopsis. *Nature* 585(7824):256–260. <https://doi.org/10.1038/s41586-020-2644-7>
- Kamano S, Kume S, Iida K, Lei K-J, Nakano M, Nakayama Y, Iida H (2015) Transmembrane topologies of Ca²⁺-permeable mechanosensitive channels MCA1 and MCA2 in *Arabidopsis thaliana*. *J Biol Chem* 290(52):30901–30909. <https://doi.org/10.1074/jbc.M115.692574>
- Kang S, Hu X, Goodwin I, Jerie P (2002) Soil water distribution, water use, and yield response to partial root zone drying under a shallow groundwater table condition in a pear orchard. *Sci Hortic* 92(3):277–291. [https://doi.org/10.1016/S0304-4238\(01\)00300-4](https://doi.org/10.1016/S0304-4238(01)00300-4)
- Kang S, Liang Z, Pan Y, Shi P, Zhang J (2000) Alternate furrow irrigation for maize production in an arid area. *Agric Water Manag* 45(3):267–274. [https://doi.org/10.1016/S0378-3774\(00\)00072-X](https://doi.org/10.1016/S0378-3774(00)00072-X)
- Kang S, Zhang J (2004) Controlled alternate partial root-zone irrigation: its physiological consequences and impact on water use efficiency. *J Exp Bot* 55(407):2437–2446. <https://doi.org/10.1093/jxb/erh249>
- Kang S, Zhang L, Hu X, Li Z, Jerie P (2001) An improved water use efficiency for hot pepper grown under controlled alternate drip irrigation on partial roots. *Sci Hortic* 89(4):257–267. [https://doi.org/10.1016/S0304-4238\(00\)00245-4](https://doi.org/10.1016/S0304-4238(00)00245-4)
- Kehr J, Kragler F (2018) Long distance RNA movement. *New Phytol* 218(1):29–40. <https://doi.org/10.1111/nph.15025>
- Kirda C, Cetin M, Dasgan Y, Topcu S, Kaman H, Ekici B, Derici MR, Ozguven AI (2004) Yield response of greenhouse grown tomato to partial root drying and conventional deficit irrigation. *Agric Water Manag* 69(3):191–201. <https://doi.org/10.1016/j.agwat.2004.04.008>
- Kobayashi A, Takahashi A, Kakimoto Y, Miyazawa Y, Fujii N, Higashitani A, Takahashi H (2007) A gene essential for hydrotropism in roots. *Proc Natl Acad Sci U S A* 104(11):4724–4729. <https://doi.org/10.1073/pnas.0609929104>
- Koenig AM, Hoffmann-Benning S (2020) The interplay of phloem-mobile signals in plant development and stress response. *Biosci Rep* 40(10):BSR20193329. <https://doi.org/10.1042/BSR20193329>
- Kong D, Hao Y, Cui H (2016) The WUSCHEL related homeobox protein WOX7 regulates the sugar response of lateral root development in Arabidopsis thaliana. *Mol Plant* 9(2):261–270. <https://doi.org/10.1016/j.molp.2015.11.006>
- Korkmazhan E, Tompa P, Dunn AR (2021) The role of ordered cooperative assembly in biomolecular condensates. *Nat Rev Mol Cell Biol* 22(10):647–648. <https://doi.org/10.1038/s41580-021-00408-z>
- Krieger G, Shkolnik D, Miller G, Fromm H (2016) Reactive oxygen species tune root tropic responses. *Plant Physiol* 172(2):1209–1220. <https://doi.org/10.1104/pp.16.00660>
- Kudla J, Batistich O, Hashimoto K (2010) Calcium signals: the lead currency of plant information processing. *Plant Cell* 22(3):541–563. <https://doi.org/10.1105/tpc.109.072686>
- Kudla J, Becker D, Grill E, Hedrich R, Hippler M, Kummer U, Parniske M, Romeis T, Schumacher K (2018) Advances and current challenges in calcium signaling. *New Phytol* 218(2):414–431. <https://doi.org/10.1111/nph.14966>
- Kumar MN, Jane W-N, Verslues PE (2013) Role of the putative Osmosensor Arabidopsis histidine Kinase1 in dehydration avoidance and low-water-potential response. *Plant Physiol* 161(2):942–953. <https://doi.org/10.1104/pp.112.209791>
- Kuromori T, Fujita M, Takahashi F, Yamaguchi-Shinozaki K, Shinozaki K (2022) Inter-tissue and inter-organ signaling in drought stress response and phenotyping of drought tolerance. *Plant J* 109(2):342–358. <https://doi.org/10.1111/tpj.15619>
- Kuromori T, Seo M, Shinozaki K (2018) ABA transport and plant water stress responses. *Trends Plant Sci* 23(6):513–522. <https://doi.org/10.1016/j.tplants.2018.04.001>
- Lai JY, Poon YS, Kaiser JT, Rees DC (2013) Open and shut: crystal structures of the dodecylmaltoside solubilized mechanosensitive channel of small conductance from *Escherichia coli* and *Helicobacter pylori* at 4.4 Å and 4.1 Å resolutions: low resolution crystal structures of MscS. *Protein Sci* 22(4):502–509. <https://doi.org/10.1002/pro.2222>
- Lanfranco L, Fiorilli V, Venice F, Bonfante P (2018) Strigolactones cross the kingdoms: plants, fungi, and bacteria in the arbuscular mycorrhizal symbiosis. *J Exp Bot* 69(9):2175–2188. <https://doi.org/10.1093/jxb/erx432>
- Lee JS, Wilson ME, Richardson RA, Haswell ES (2019) Genetic and physical interactions between the organellar mechanosensitive ion channel homologs MSL 1, MSL 2, and MSL 3 reveal a role for inter-organellar communication in plant development. *Plant Direct* 3(3). <https://doi.org/10.1002/pld3.124>
- Leshem Y, Levine A (2007) Intracellular ROS: what does it do there? *Plant Signal Behav* 2(3):155–156. <https://doi.org/10.4161/psb.2.3.3685>
- Levina N (1999) Protection of *Escherichia coli* cells against extreme turgor by activation of MscS and MscL mechanosensitive channels: identification

- of genes required for MscS activity. *EMBO J* 18(7):1730–1737. <https://doi.org/10.1093/emboj/18.7.1730>
- Li C, Wu H-M, Cheung AY (2016) FERONIA and her pals: functions and mechanisms. *Plant Physiol* 171(4):2379–2392. <https://doi.org/10.1104/pp.16.00667>
- Li C, Zhang K, Zeng X, Jackson S, Zhou Y, Hong Y (2009) A cis element within flowering locus T mRNA determines its mobility and facilitates trafficking of heterologous viral RNA. *J Virol* 83(8):3540–3548. <https://doi.org/10.1128/JVI.02346-08>
- Liu F, Song R, Zhang X, Shahnazari A, Andersen MN, Plauborg F, Jacobsen S-E, Jensen CR (2008) Measurement and modelling of ABA signalling in potato (*Solanum tuberosum* L.) during partial root-zone drying. *Environ Exp Bot* 63(1):385–391. <https://doi.org/10.1016/j.envexpbot.2007.11.015>
- Liu J, He H, Vitali M, Visentin I, Charnikova T, Haider I, Schubert A, Ruyter-Spira C, Bouwmeester HJ, Lovisolo C, Cardinale F (2015) Osmotic stress represses strigolactone biosynthesis in *Lotus japonicus* roots: exploring the interaction between strigolactones and ABA under abiotic stress. *Planta* 241(6):1435–1451. <https://doi.org/10.1007/s00425-015-2266-8>
- Liu L, Chen X (2018) Inter-cellular and systemic trafficking of RNAs in plants. *Nat Plants* 4(11):869–878. <https://doi.org/10.1038/s41477-018-0288-5>
- Liu W, Xiang C, Li X, Wang T, Lu X, Liu Z, Gao L, Zhang W (2020) Identification of long-distance transmissible mRNA between Scion and rootstock in cucurbit seedling heterografts. *IJMS* 21(15):5253. <https://doi.org/10.3390/ijms21155253>
- Liu X, Wang J, Sun L (2018) Structure of the hyperosmolality-gated calcium-permeable channel OSCA1.2. *Nat Commun* 9(1):5060. <https://doi.org/10.1038/s41467-018-07564-5>
- Luo J, Chen L, Huang F, Gao P, Zhao H, Wang Y, Han S (2020) Intraorganellar calcium imaging in Arabidopsis seedling roots using the GCaMP variants GCaMP6m and R-CEPIA1er. *J Plant Physiol* 246–247:153127. <https://doi.org/10.1016/j.jplph.2020.153127>
- Lv S, Zhang Y, Li C, Liu Z, Yang N, Pan L, Wu J, Wang J, Yang J, Lv Y, Zhang Y, Jiang W, She X, Wang G (2018) Strigolactone-triggered stomatal closure requires hydrogen peroxide synthesis and nitric oxide production in an abscisic acid-independent manner. *New Phytol* 217(1):290–304. <https://doi.org/10.1111/nph.14813>
- Maeda T, Takekawa M, Saito H (1995) Activation of yeast PBS2 MAPKK by MAPKKs or by binding of an SH3-containing Osmosensor. *Science* 269(5223):554–558. <https://doi.org/10.1126/science.7624781>
- Maity K, Heumann JM, McGrath AP, Kopcho NJ, Hsu P-K, Lee C-W, Mapes JH, Garza D, Krishnan S, Morgan GP, Hendargo KJ, Klose T, Rees SD, Medrano-Soto A, Saier MH, Piñeros M, Komives EA, Schroeder JI, Chang G, Stowell MHB (2019) Cryo-EM structure of OSCA1.2 from *Oryza sativa* elucidates the mechanical basis of potential membrane hyperosmolality gating. *Proc Natl Acad Sci U S A* 116(28):14309–14318. <https://doi.org/10.1073/pnas.1900774116>
- Maksaeve G, Haswell ES (2012) MscS-Like10 is a stretch-activated ion channel from *Arabidopsis thaliana* with a preference for anions. *Proc Natl Acad Sci U S A* 109(46):19015–19020. <https://doi.org/10.1073/pnas.1213931109>
- Manzi M, Lado J, Rodrigo MJ, Zacarias L, Arbona V, Gomez-Cadenas A (2015) Root ABA accumulation in long-term water-stressed plants is sustained by hormone transport from aerial organs. *Plant Cell Physiol* 56(12):2457–2466. <https://doi.org/10.1093/pcp/pcv161>
- Martinac B, Buechner M, Delcour AH, Adler J, Kung C (1987) Pressure-sensitive ion channel in *Escherichia coli*. *Proc Natl Acad Sci U S A* 84(8):2297–2301. <https://doi.org/10.1073/pnas.84.8.2297>
- Martinière A, Fiche JB, Smokvarská M, Mari S, Alcon C, Dumont X, Hematy K, Jaillais Y, Nollmann M, Maurel C (2019) Osmotic stress activates two reactive oxygen species pathways with distinct effects on protein Nanodomains and diffusion. *Plant Physiol* 179(4):1581–1593. <https://doi.org/10.1104/pp.18.01065>
- Martin-Vertedor AI, Dodd IC (2011) Root-to-shoot signalling when soil moisture is heterogeneous: increasing the proportion of root biomass in drying soil inhibits leaf growth and increases leaf abscisic acid concentration: root distribution and non-hydraulic signalling. *Plant Cell Environ* 34(7):1164–1175. <https://doi.org/10.1111/j.1365-3040.2011.02315.x>
- McLean EH, Ludwig M, Grierson PF (2011) Root hydraulic conductance and aquaporin abundance respond rapidly to partial root-zone drying events in a riparian *Melaleuca* species. *New Phytol* 192(3):664–675. <https://doi.org/10.1111/j.1469-8137.2011.03834.x>
- Miao Y, Lv D, Wang P, Wang X-C, Chen J, Miao C, Song C-P (2006) An Arabidopsis glutathione peroxidase functions as both a redox transducer and a scavenger in abscisic acid and drought stress responses. *Plant Cell* 18(10):2749–2766. <https://doi.org/10.1105/tpc.106.044230>
- Mielke S, Zimmer M, Meena MK, Dreos R, Stellmach H, Hause B, Voiniciuc C, Gasperini D (2021) Jasmonate biosynthesis arising from altered cell walls is prompted by turgor-driven mechanical compression. *Sci Adv* 7(7):eabf0356. <https://doi.org/10.1126/sciadv.abf0356>
- Miller K, Strychalski W, Nickaen M, Carlsson A, Haswell ES (2022) In vitro experiments and kinetic models of Arabidopsis pollen hydration mechanics show that MSL8 is not a simple tension-gated osmoregulator. *Curr Biol* 32(13):2921–2934
- Milne RJ, Grof CP, Patrick JW (2018) Mechanisms of phloem unloading: shaped by cellular pathways, their conductances and sink function. *Curr Opin Plant Biol* 43:8–15. <https://doi.org/10.1016/j.pbi.2017.11.003>
- Mittler R, Vanderauwera S, Gollery M, Van Breusegem F (2004) Reactive oxygen gene network of plants. *Trends Plant Sci* 9(10):490–498. <https://doi.org/10.1016/j.tplants.2004.08.009>
- Mohanty BP (2013) Soil hydraulic property estimation using remote sensing: a review. *Vadose Zone J* 12(4):1–9. <https://doi.org/10.2136/vzj2013.06.0100>
- Monshausen GB (2012) Visualizing Ca²⁺ signatures in plants. *Curr Opin Plant Biol* 15(6):677–682. <https://doi.org/10.1016/j.pbi.2012.09.014>
- Mori K, Renhu N, Naito M, Nakamura A, Shiba H, Yamamoto T, Suzuki T, Iida H, Miura K (2018) Ca²⁺—permeable mechanosensitive channels MCA1 and MCA2 mediate cold-induced cytosolic Ca²⁺ increase and cold tolerance in *Arabidopsis*. *Sci Rep* 8(1):550. <https://doi.org/10.1038/s41598-017-17483-y>
- Mostafa MG, Li W, Nguyen KH, Fujita M, Tran L-SP (2018) Strigolactones in plant adaptation to abiotic stresses: an emerging avenue of plant research. *Plant Cell Environ* 41(10):2227–2243. <https://doi.org/10.1111/pce.13364>
- Mousavi SAR, Dubin AE, Zeng W-Z, Coombs AM, Do K, Ghadir DA, Keenan WT, Ge C, Zhao Y, Patapoutian A (2021) PIEZO ion channel is required for root mechanotransduction in *Arabidopsis thaliana*. *Proc Natl Acad Sci U S A* 118(20):e2102188118. <https://doi.org/10.1073/pnas.2102188118>
- Murthy SE, Dubin AE, Whitwam T, Jojoa-Cruz S, Cahalan SM, Mousavi SAR, Ward AB, Patapoutian A (2018) OSCA/TMEM63 are an evolutionarily conserved family of mechanically activated ion channels. *eLife* 7:e41844. <https://doi.org/10.7554/eLife.41844>
- Nakagawa Y, Katagiri T, Shinozaki K, Qi Z, Tatsumi H, Furuichi T, Kishigami A, Sokabe M, Kojima I, Sato S, Kato T, Tabata S, Iida K, Terashima A, Nakano M, Ikeda M, Yamanaka T, Iida H (2007) Arabidopsis plasma membrane protein crucial for Ca²⁺ influx and touch sensing in roots. *Proc Natl Acad Sci U S A* 104(9):3639–3644. <https://doi.org/10.1073/pnas.0607703104>
- Nakayama M, Kaneko Y, Miyazawa Y, Fujii N, Higashitani N, Wada S, Ishida H, Yoshimoto K, Shirasu K, Yamada K, Nishimura M, Takahashi H (2012) A possible involvement of autophagy in amyloplast degradation in columella cells during hydrotropic response of *Arabidopsis* roots. *Planta* 236:999–1012. <https://doi.org/10.1007/s00425-012-1655-5>
- Notaguchi M, Higashiyama T, Suzuki T (2015) Identification of mRNAs that move over long distances using an RNA-Seq analysis of *Arabidopsis*/Nicotiana benthamiana heterografts. *Plant Cell Physiol* 56(2):311–321. <https://doi.org/10.1093/pcp/pcu210>
- Ohkubo Y, Tanaka M, Tabata R, Ogawa-Ohnishi M, Matsubayashi Y (2017) Shoot-to-root mobile polypeptides involved in systemic regulation of nitrogen acquisition. *Nat Plants* 3:17029. <https://doi.org/10.1038/nplants.2017.29>
- Okamoto S, Tabata R, Matsubayashi Y (2016) Long-distance peptide signalling essential for nutrient homeostasis in plants. *Curr Opin Plant Biol* 34:35–40. <https://doi.org/10.1016/j.pbi.2016.07.009>
- Orman-Ligeza B, Morris EC, Parizot B, Lavigne T, Babé A, Ligeza A, Klein S, Sturrock C, Xuan W, Novák O, Ljung K, Fernandez MA, Rodriguez PL, Dodd IC, De Smet I, Chaumont F, Batoko H, Périlleux C, Lynch JP, Bennett MJ, Beeckman T, Draye X (2018) The Xerobanching response represses lateral root formation when roots are not in contact with water. *Curr Biol* 28(19):3165–3173.e5. <https://doi.org/10.1016/j.cub.2018.07.074>
- Orosa-Puente B, Leftley N, von Wangenheim D, Banda J, Srivastava AK, Hill K, Truskina J, Bhosale R, Morris E, Srivastava M, Kumpers B, Goh T, Fukaki H, Vermeer JEM, Vernoux T, Dinneny JR, French AP, Bishopp A, Sadanandom A, Bennett MJ (2018) Root branching toward water involves

- posttranslational modification of transcription factor ARF7. *Science* 362(6421):1407–1410. <https://doi.org/10.1126/science.aau3956>
- Ota IM, Varshavsky A (1993) A yeast protein similar to bacterial two-component regulators. *Science* 262(5133):566–569. <https://doi.org/10.1126/science.8211183>
- Pagliarini C, Vitali M, Ferrero M, Vitulo N, Incarboni M, Lovisolo C, Valle G, Schubert A (2017) The accumulation of miRNAs differentially modulated by drought stress is affected by grafting in grapevine. *Plant Physiol* 173(4):2180–2195. <https://doi.org/10.1104/pp.16.01119>
- Platre MP, Bayle V, Armengot L, Bareille J, Marquès-Bueno M d M, Creff A, Maneta-Peyret L, Fiche J-B, Nollmann M, Miège C, Moreau P, Martinière A, Jaillais Y (2019) Developmental control of plant rho GTPase nano-organization by the lipid phosphatidylserine. *Science* 364(6435):57–62. <https://doi.org/10.1126/science.aav9959>
- Pliotas C, Dahl ACE, Rasmussen T, Mahendran KR, Smith TK, Marius P, Gault J, Banda T, Rasmussen A, Miller S, Robinson CV, Bayley H, Sansom MSP, Booth IR, Naismith JH (2015) The role of lipids in mechanosensation. *Nat Struct Mol Biol* 22(12):991–998. <https://doi.org/10.1038/nsmb.3120>
- Powers SK, Holehouse AS, Korasick DA, Schreiber KH, Clark NM, Jing H, Emenecker R, Han S, Tycksen E, Hwang I, Sozzani R, Jez JM, Pappu RV, Strader LC (2019) Nucleo-cytoplasmic partitioning of ARF proteins controls auxin responses in *Arabidopsis thaliana*. *Mol Cell* 76(1):177–190.e5. <https://doi.org/10.1016/j.molcel.2019.06.044>
- Puértolas J, Alcobendas R, Alarcón JJ, Dodd IC (2013) Long-distance abscisic acid signalling under different vertical soil moisture gradients depends on bulk root water potential and average soil water content in the root zone. *Plant Cell Environ* 36(8):1465–1475. <https://doi.org/10.1111/pce.12076>
- Puértolas J, Conesa MR, Ballester C, Dodd IC (2015) Local root abscisic acid (ABA) accumulation depends on the spatial distribution of soil moisture in potato: implications for ABA signalling under heterogeneous soil drying. *J Exp Bot* 66(8):2325–2334. <https://doi.org/10.1093/jxb/eru501>
- Putterill J, Varkonyi-Gasic E (2016) FT and florigen long-distance flowering control in plants. *Curr Opin Plant Biol* 33:77–82. <https://doi.org/10.1016/j.pbi.2016.06.008>
- Qian P, Song W, Yokoo T, Minobe A, Wang G, Ishida T, Sawa S, Chai J, Kakimoto T (2018) The CLE9/10 secretory peptide regulates stomatal and vascular development through distinct receptors. *Nat Plants* 4(12):1071–1081. <https://doi.org/10.1038/s41477-018-0317-4>
- Radin I, Richardson RA, Coomey JH, Weiner ER, Bascom CS, Li T, Bezanilla M, Haswell ES (2021) Plant PIEZO homologs modulate vacuole morphology during tip growth. *Science* 373(6554):586–590. <https://doi.org/10.1126/science.abe6310>
- Raissig MT, Matos JL, Anleu Gil MX, Kornfeld A, Bettadapur A, Abrash E, Allison HR, Badgley G, Vogel JP, Berry JA, Bergmann DC (2017) Mobile MUTE specifies subsidiary cells to build physiologically improved grass stomata. *Science* 355(6330):1215–1218. <https://doi.org/10.1126/science.aal3254>
- Raza MAS, Ahmad S, Saleem MF, Khan IH, Iqbal R, Zaheer MS, Haider I, Ali M (2017) Physiological and biochemical assisted screening of wheat varieties under partial rhizosphere drying. *Plant Physiol Biochem* 116:150–166. <https://doi.org/10.1016/j.plaphy.2017.05.007>
- Ren Y, Song Y, Zhang L, Guo D, He J, Wang L, Song S, Xu W, Zhang C, Lers A, Ma C, Wang S (2021) Coding of non-coding RNA: insights into the regulatory functions of Pri-MicroRNA-encoded peptides in plants. *Front Plant Sci* 12:641351. <https://doi.org/10.3389/fpls.2021.641351>
- Rhodes J, Yang H, Moussy S, Boutrot F, Santiago J, Zipfel C (2021) Perception of a divergent family of phytocytokines by the *Arabidopsis* receptor kinase M1K2. *Nat Commun* 12(1):705. <https://doi.org/10.1038/s41467-021-20932-y>
- Rodríguez O, Reshetnyak G, Grondin A, Saijo Y, Leonhardt N, Maurel C, Verdoucq L (2017) Aquaporins facilitate hydrogen peroxide entry into guard cells to mediate ABA- and pathogen-triggered stomatal closure. *Proc Natl Acad Sci U S A* 114(34):9200–9205. <https://doi.org/10.1073/pnas.1704754114>
- Rodríguez-Medina C, Atkins CA, Mann AJ, Jordan ME, Smith PM (2011) Macromolecular composition of phloem exudate from white lupin (*Lupinus albus* L.). *BMC Plant Biol* 11:36. <https://doi.org/10.1186/1471-2229-11-36>
- Ruiz-Lopez N, Pérez-Sánchez J, Del Valle AE, Haslam RP, Vanneste S, Catalá R, Perea-Resca C, Damme DV, García-Hernández S, Albert A, Vallarino J, Lin J, Friml J, Macho AP, Salinas J, Rosado A, Napier JA, Amorim-Silva V, Botella MA (2021) Synaptotagmins at the endoplasmic reticulum-plasma membrane contact sites maintain diacylglycerol homeostasis during abiotic stress. *The Plant Cell* 33(7):2431–2453. <https://doi.org/10.1093/plcell/koab122>
- Sadak MS, El-Bassiouny HMS, Dawood MG (2019) Role of trehalose on antioxidant defense system and some osmolytes of quinoa plants under water deficit. *Bull Natl Res Centre* 43(1):5. <https://doi.org/10.1186/s42269-018-0039-9>
- Sadak MS, Abdalla AM, Abd Elhamid EM, Ezzi MI (2020) Role of melatonin in improving growth, yield quantity and quality of *Moringa oleifera* L. plant under drought stress. *Bull Natl Res Cent* 44(1):18. <https://doi.org/10.1186/s42269-020-0275-7>
- Schachtman DP, Goodger JQD (2008) Chemical root to shoot signaling under drought. *Trends Plant Sci* 13(6):281–287. <https://doi.org/10.1016/j.tplan.2008.04.003>
- Schapiro AL, Voigt B, Jasik J, Rosado A, Lopez-Cobollo R, Menzel D, Salinas J, Mancuso S, Valpuesta V, Baluska F, Botella MA (2008) Arabidopsis synaptotagmin 1 is required for the maintenance of plasma membrane integrity and cell viability. *The Plant Cell* 20(12):3374–88. <https://doi.org/10.1105/tpc.108.063859>
- Sepaskhah AR, Khajehabdollahi MH (2005) Alternate furrow irrigation with different irrigation intervals for maize (*Zea mays* L.). *Plant Prod Sci* 8(5):592–600. <https://doi.org/10.1626/pps.8.592>
- Sepaskhah AR, Parand A-R (2006) Effects of alternate furrow irrigation with supplemental every-furrow irrigation at different growth stages on the yield of maize (*Zea mays* L.). *Plant Prod Sci* 9(4):415–421. <https://doi.org/10.1626/pps.9.415>
- Shao G-C, Zhang Z-Y, Liu N, Yu S-E, Xing W-G (2008) Comparative effects of deficit irrigation (DI) and partial rootzone drying (PRD) on soil water distribution, water use, growth and yield in greenhouse grown hot pepper. *Sci Hortic* 119(1):11–16. <https://doi.org/10.1016/j.scienta.2008.07.001>
- Shih H-W, Miller ND, Dai C, Spalding EP, Monshausen GB (2014) The receptor-like kinase FERONIA is required for mechanical signal transduction in *Arabidopsis* seedlings. *Curr Biol* 24(16):1887–1892. <https://doi.org/10.1016/j.cub.2014.06.064>
- Shkolnik D, Nuriel R, Bonza MC, Costa A, Fromm H (2018) MIZ1 regulates ECA1 to generate a slow, long-distance phloem-transmitted Ca^{2+} signal essential for root water tracking in *Arabidopsis*. *Proc Natl Acad Sci U S A* 115(31):8031–8036. <https://doi.org/10.1073/pnas.1804130115>
- Sirko A, Wawrzynska A, Brzywczy J, Sienko M (2021) Control of ABA signaling and crosstalk with other hormones by the selective degradation of pathway components. *Int J Mol Sci* 22(9):4638. <https://doi.org/10.3390/ijms22094638>
- Smith S, Zhu S, Joos L, Roberts I, Nikonov N, Vu LD, Stes E, Cho H, Larrieu A, Xuan W, Goodall B, Cotte B v d, Waite JM, Rigal A, Harborough SR, Persiau G, Vanneste S, Kirschner GK, Vandermarliere E, Martens L, Stahl Y, Audenaert D, Friml J, Felix G, Simon R, Bennett MJ, Bishopp A, Jaeger GD, Ljung K, Kepinski S, Robert S, Nemhauser J, Hwang I, Gevaert K, Beeckman T, Smet ID (2020) The CEP5 peptide promotes abiotic stress tolerance, as revealed by quantitative proteomics, and attenuates the AUX/IAA equilibrium in *Arabidopsis*. *Mol Cell Proteomics* 19(8):1248–1262. <https://doi.org/10.1074/mcp.RA119.001826>
- Smokvarská M, Francis C, Platre MP, Fiche J-B, Alcon C, Dumont X, Nacry P, Bayle V, Nollmann M, Maurel C, Jaillais Y, Martinière A (2020) A plasma membrane Nanodomain ensures signal specificity during osmotic signaling in plants. *Curr Biol* 30(23):4654–4664.e4. <https://doi.org/10.1016/j.cub.2020.09.013>
- Steinbacher S, Bass R, Strop P, Rees DC (2007) Structures of the prokaryotic mechanosensitive channels MscL and MscS. In: *Current topics in membranes*. Academic Press, pp 1–24. [https://doi.org/10.1016/S1063-5823\(06\)58001-9](https://doi.org/10.1016/S1063-5823(06)58001-9)
- Stephan AB, Kunz H-H, Yang E, Schroeder JI (2016) Rapid hyperosmotic-induced Ca^{2+} responses in *Arabidopsis thaliana* exhibit sensory potentiation and involvement of plastidial KEA transporters. *Proc Natl Acad Sci U S A* 113(35). <https://doi.org/10.1073/pnas.1519555113>
- Stoll M, Loveys B, Dry P (2000) Hormonal changes induced by partial rootzone drying of irrigated grapevine. *J Exp Bot* 51(350):1627–1634. <https://doi.org/10.1093/jexbot/51.350.1627>

- Storti M, Costa A, Golin S, Zottini M, Morosinotto T, Alboresi A (2018) Systemic calcium wave propagation in *Physcomitrella patens*. *Plant Cell Physiol* 59(7):1377–1384. <https://doi.org/10.1093/pcp/pcy104>
- Sukharev SI, Martinac B, Blount P, Kung C (1994) Functional reconstitution as an assay for biochemical isolation of channel proteins: application to the molecular identification of a bacterial mechanosensitive channel. *Methods* 6(1):51–59. <https://doi.org/10.1006/meth.1994.1007>
- Taiz L, Zeiger E (2006) *Plant physiology and development*, 6th edn
- Takahashi F, Kuromori T, Urano K, Yamaguchi-Shinozaki K, Shinozaki K (2020) Drought stress responses and resistance in plants: from cellular responses to long-distance intercellular communication. *Front Plant Sci* 11:556972. <https://doi.org/10.3389/fpls.2020.556972>
- Takahashi F, Suzuki T, Osakabe Y, Betsuyaku S, Kondo Y, Dohmae N, Fukuda H, Yamaguchi-Shinozaki K, Shinozaki K (2018) A small peptide modulates stomatal control via abscisic acid in long-distance signalling. *Nature* 556(7700):235–238. <https://doi.org/10.1038/s41586-018-0009-2>
- Tang L-S, Li Y, Zhang J (2005) Physiological and yield responses of cotton under partial rootzone irrigation. *Field Crop Res* 94(2):214–223. <https://doi.org/10.1016/j.fcr.2005.01.005>
- Thieme CJ, Rojas-Triana M, Stecyk E, Schudoma C, Zhang W, Yang L, Minambres M, Walther D, Schulze WX, Paz-Ares J, Scheible W-R, Kragler F (2015) Endogenous Arabidopsis messenger RNAs transported to distant tissues. *Nat Plants* 1(4):15025. <https://doi.org/10.1038/nplants.2015.25>
- Thompson AJ, Andrews J, Mulholland BJ, McKee JMT, Hilton HW, Horridge JS, Farquhar GD, Smeeton RC, Smillie IRA, Black CR, Taylor IB (2007) Overproduction of abscisic acid in tomato increases transpiration efficiency and root hydraulic conductivity and influences leaf expansion. *Plant Physiol* 143(4):1905–1917. <https://doi.org/10.1104/pp.106.093559>
- Thor K, Jiang S, Michard E, George J, Scherzer S, Huang S, Dindas J, Derbyshire P, Leitão N, DeFalco TA, Köster P, Hunter K, Kimura S, Gronnier J, Stransfeld L, Kadota Y, Bücherl CA, Charpentier M, Wrzaczek M, MacLean D, Oldroyd GED, Menke FLH, Roelfsema MRG, Hedrich R, Feijó J, Zipfel C (2020) The calcium-permeable channel OSCA1.3 regulates plant stomatal immunity. *Nature* 585(7826):569–573. <https://doi.org/10.1038/s41586-020-2702-1>
- Tian S, Wang X, Li P, Wang H, Ji H, Xie J, Qiu Q, Shen D, Dong H (2016) Plant aquaporin AtPIP1;4 links Apoptotic H₂O₂ induction to disease immunity pathways. *Plant Physiol* 171(3):1635–1650. <https://doi.org/10.1104/pp.15.01237>
- Tolstyk E, Lezzhov A, Solov'yev A (2019) Identification of miRNA precursors in the phloem of *Cucurbita maxima*. *PeerJ* 7:e8269. <https://doi.org/10.7717/peerj.8269>
- Tracy FE, Gilliam M, Dodd AN, Webb AAR, Tester M (2008) NaCl-induced changes in cytosolic free Ca²⁺ in *Arabidopsis thaliana* are heterogeneous and modified by external ionic composition. *Plant Cell Environ* 31(8):1063–1073. <https://doi.org/10.1111/j.1365-3040.2008.01817.x>
- Tran L-S, Urao T, Qin F, Maruyama K, Kakimoto T, Shinozaki K, Yamaguchi-Shinozaki K (2007) Functional analysis of AHK1/ATHK1 and cytokinin receptor histidine kinases in response to abscisic acid, drought, and salt stress in *Arabidopsis*. *Proc Natl Acad Sci U S A* 104(51):20623–20628. <https://doi.org/10.1073/pnas.0706547105>
- Urano K, Kurihara Y, Seki M, Shinozaki K (2010) "Omics" analyses of regulatory networks in plant abiotic stress responses. *Curr Opin Plant Biol* 13(2):132–138. <https://doi.org/10.1016/j.pbi.2009.12.006>
- Urao T, Yakubov B, Satoh R, Yamaguchi-Shinozaki K, Seki M, Hirayama T, Shinozaki K (1999) A transmembrane hybrid-type histidine kinase in *Arabidopsis* functions as an Osmosensor. *Plant Cell* 11(9):1743–1754. <https://doi.org/10.1105/tpc.11.9.1743>
- Van der Does D, Boutrot F, Engelsdorf T, Rhodes J, McKenna JF, Vernhettes S, Koevoets I, Tintor N, Veerabagu M, Miedes E, Segonzac C, Roux M, Breda AS, Hardtke CS, Molina A, Rep M, Testerink C, Mouille G, Höfte H, Hamann T, Zipfel C (2017) The *Arabidopsis* leucine-rich repeat receptor kinase MIK2/LRR-KISS connects cell wall integrity sensing, root growth and response to abiotic and biotic stresses. *PLoS Genet* 13(6):e1006832. <https://doi.org/10.1371/journal.pgen.1006832>
- Veley KM, Maksaev G, Frick EM, January E, Kloepper SC, Haswell ES (2014) *Arabidopsis* MSL10 has a regulated cell death signaling activity that is separable from its mechanosensitive Ion Channel activity. *Plant Cell* 26(7):3115–3131. <https://doi.org/10.1105/tpc.114.128082>
- Verslues PE, Sharma S (2010) Proline metabolism and its implications for plant-environment interaction. *Arabidopsis Book* 8:e0140. <https://doi.org/10.1199/tab.0140>
- Visentin I, Pagliarani C, Deva E, Caracci A, Tureckova V, Novak O, Lovisolo C, Schubert A, Cardinale F (2020) A novel strigolactone-miR156 module controls stomatal behaviour during drought recovery. *Plant Cell Environ* 43(7):1613–1624. <https://doi.org/10.1111/pce.13758>
- Visentin I, Vitali M, Ferrero M, Zhang Y, Ruyter-Spira C, Novák O, Strnad M, Lovisolo C, Schubert A, Cardinale F (2016) Low levels of strigolactones in roots as a component of the systemic signal of drought stress in tomato. *New Phytol* 212(4):954–963. <https://doi.org/10.1111/nph.14190>
- Wang C, Teng Y, Zhu S, Zhang L, Liu X (2019) NaCl and cold-induced stress activate difference Ca²⁺-permeable channels in *Arabidopsis thaliana*. *Plant Growth Regul* 87:217–225
- Wang P, Zhao Y, Li Z, Hsu C-C, Liu X, Fu L, Hou Y-J, Du Y, Xie S, Zhang C, Gao J, Cao M, Huang X, Zhu Y, Tang W, Wang X, Tao WA, Xiong Y, Zhu J-K (2018) Reciprocal regulation of the TOR kinase and ABA receptor balances plant growth and stress response. *Mol Cell* 69(1):100–112.e6. <https://doi.org/10.1016/j.molcel.2017.12.002>
- Wang T, Li X, Zhang X, Wang Q, Liu W, Lu X, Gao S, Liu Z, Liu M, Gao L, Zhang W (2021) RNA motifs and modification involve in RNA long-distance transport in plants. *Front Cell Dev Biol* 9:651278. <https://doi.org/10.3389/fcell.2021.651278>
- Wang W, Chen Q, Xu S, Liu W-C, Zhu X, Song C-P (2020) Trehalose-6-phosphate phosphatase E modulates ABA-controlled root growth and stomatal movement in *Arabidopsis*. *J Integr Plant Biol* 62(10):1518–1534. <https://doi.org/10.1111/jipb.12925>
- Watanabe K, Morishita K, Zhou X, Shiizaki S, Uchiyama Y, Koike M, Naguro I, Ichijo H (2021) Cells recognize osmotic stress through liquid-liquid phase separation lubricated with poly(ADP-ribose). *Nat Commun* 12(1):1353. <https://doi.org/10.1038/s41467-021-21614-5>
- Waters MT, Gutjahr C, Bennett T, Nelson DC (2017) Strigolactone signaling and evolution. *Annu Rev Plant Biol* 68:291–322. <https://doi.org/10.1146/annurev-arplant-042916-040925>
- Weiste C, Pedrotti L, Selvanayagam J, Muralidhara P, Fröschel C, Novák O, Ljung K, Hanson J, Dröge-Laser W (2017) The *Arabidopsis* bZIP1 transcription factor links low-energy signalling to auxin-mediated control of primary root growth. *PLoS Genet* 13(2):e1006607. <https://doi.org/10.1371/journal.pgen.1006607>
- Westwood JH (2015) RNA transport: delivering the message. *Nat Plants* 1(4):15038. <https://doi.org/10.1038/nplants.2015.38>
- Wilkins KA, Matthus E, Swarbrick SM, Davies JM (2016) Calcium-mediated abiotic stress signaling in roots. *Front Plant Sci* 7:1296. <https://doi.org/10.3389/fpls.2016.01296>
- Wilson ME, Mixdorf M, Berg RH, Haswell ES (2016) Plastid osmotic stress influences cell differentiation at the plant shoot apex. *Development*:dev136234. <https://doi.org/10.1242/dev.136234>
- Winter N, Kragler F (2018) Conceptual and methodological considerations on mRNA and proteins as intercellular and long-distance signals. *Plant Cell Physiol* 59(9):1700–1713. <https://doi.org/10.1093/pcp/pcy140>
- Wohlbach DJ, Quirino BF, Sussman MR (2008) Analysis of the *Arabidopsis* histidine kinase ATHK1 reveals a connection between vegetative osmotic stress sensing and seed maturation. *Plant Cell* 20(4):1101–1117. <https://doi.org/10.1105/tpc.107.055871>
- Wolf S, Hématy K, Höfte H (2012) Growth control and cell wall signaling in plants. *Annu Rev Plant Biol* 63(1):381–407. <https://doi.org/10.1146/annurev-arplant-042811-105449>
- Wu F, Chi Y, Jiang Z, Xu Y, Xie L, Huang F, Wan D, Ni J, Yuan F, Wu X, Zhang Y, Wang L, Ye R, Byeon B, Wang W, Zhang S, Sima M, Chen S, Zhu M, Pei J, Johnson DM, Zhu S, Cao X, Pei C, Zai Z, Liu Y, Liu T, Swift GB, Zhang W, Yu M, Hu Z, Siedow JN, Chen X, Pei ZM (2020) Hydrogen peroxide sensor HPCA1 is an LRR receptor kinase in *Arabidopsis*. *Nature* 578(7796):577–581. <https://doi.org/10.1038/s41586-020-2032-3>
- Xia C, Zheng Y, Huang J, Zhou X, Li R, Zha M, Wang S, Huang Z, Lan H, Turgeon R, Fei Z, Zhang C (2018) Elucidation of the mechanisms of long-distance mRNA movement in a *Nicotiana benthamiana*/tomato heterograft system. *Plant Physiol* 177(2):745–758. <https://doi.org/10.1104/pp.17.01836>
- Yang L, Perrera V, Saplaoura E, Apelt F, Bahin M, Kramdi A, Olas J, Mueller-Roeber B, Sokolowska E, Zhang W, Li R, Pitzalis N, Heinlein M, Zhang S, Genovesio A, Colot V, Kragler F (2019) m5C methylation guides

- systemic transport of messenger RNA over graft junctions in plants. *Curr Biol* 29(15):2465–2476.e5. <https://doi.org/10.1016/j.cub.2019.06.042>
- Yoshimura K, Iida K, Iida H (2021) MCAs in *Arabidopsis* are Ca^{2+} -permeable mechanosensitive channels inherently sensitive to membrane tension. *Nat Commun* 12(1):6074. <https://doi.org/10.1038/s41467-021-26363-z>
- Yuan F, Yang H, Xue Y, Kong D, Ye R, Li C, Zhang J, Theprungsirikul L, Shrift T, Krichilsky B, Johnson DM, Swift GB, He Y, Siedow JN, Pei Z-M (2014) OSCA1 mediates osmotic-stress-evoked Ca^{2+} increases vital for osmosensing in *Arabidopsis*. *Nature* 514(7522):367–371. <https://doi.org/10.1038/nature13593>
- Zavaliev R, Mohan R, Chen T, Dong X (2020) Formation of NPR1 condensates promotes cell survival during the plant immune response. *Cell* 182(5):1093–1108.e18. <https://doi.org/10.1016/j.cell.2020.07.016>
- Zegbe JA, Behboudian MH, Clothier BE (2006) Responses of ‘Petopride’ processing tomato to partial rootzone drying at different phenological stages. *Irrig Sci* 24(3):203–210. <https://doi.org/10.1007/s00271-005-0018-4>
- Zhang G, Kong G, Li Y (2021a) Long-distance communication through systemic macromolecular signaling mediates stress defense responses in plants. *Physiol Plant* 173(4):1926–1934. <https://doi.org/10.1111/ppl.13535>
- Zhang J, Davies WJ (1989) Absciscic acid produced in dehydrating roots may enable the plant to measure the water status of the soil. *Plant Cell Environ* 12(1):73–81. <https://doi.org/10.1111/j.1365-3040.1989.tb01918.x>
- Zhang L, Shi X, Zhang Y, Wang J, Yang J, Ishida T, Jiang W, Han X, Kang J, Wang X, Pan L, Lv S, Cao B, Zhang Y, Wu J, Han H, Hu Z, Cui L, Sawa S, He J, Wang G (2019a) CLE9 peptide-induced stomatal closure is mediated by abscisic acid, hydrogen peroxide, and nitric oxide in *Arabidopsis thaliana*. *Plant Cell Environ* 42(3):1033–1044. <https://doi.org/10.1111/pce.13475>
- Zhang S, Sun L, Kragler F (2009) The phloem-delivered RNA pool contains small noncoding RNAs and interferes with translation. *Plant Physiol* 150(1):378–387. <https://doi.org/10.1104/pp.108.134767>
- Zhang Y, Daday C, Gu R-X, Cox CD, Martinac B, de Groot BL, Walz T (2021b) Visualization of the mechanosensitive ion channel MscS under membrane tension. *Nature* 590(7846):509–514. <https://doi.org/10.1038/s41586-021-03196-w>
- Zhang Y, Lv S, Wang G (2018) Strigolactones are common regulators in induction of stomatal closure in plants. *Plant Signal Behav* 13(3):e1444322. <https://doi.org/10.1080/15592324.2018.1444322>
- Zhang Z, Tong X, Liu S-Y, Chai L-X, Zhu F-F, Zhang X-P, Zou J-Z, Wang X-B (2019b) Genetic analysis of a Piezo-like protein suppressing systemic movement of plant viruses in *Arabidopsis thaliana*. *Sci Rep* 9(1):3187. <https://doi.org/10.1038/s41598-019-39436-3>
- Zhang Z, Zheng Y, Ham B-K, Chen J, Yoshida A, Kochian LV, Fei Z, Lucas WJ (2016) Vascular-mediated signalling involved in early phosphate stress response in plants. *Nat Plants* 2:16033. <https://doi.org/10.1038/nplants.2016.33>
- Zhong W, Hartung W, Komor E, Schobert C (1996) Phloem transport of abscisic acid in *Ricinus communis* L. seedlings. *Plant Cell Environ* 19(4):471–477. <https://doi.org/10.1111/j.1365-3040.1996.tb00339.x>

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