Trends in Plant Science

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Review

How roots and shoots communicate through stressful times

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When plants face an environmental stress such as water deficit, soil salinity, high temperature, or shade, good communication between above- and belowground organs is necessary to coordinate growth and development. Various signals including hormones, peptides, proteins, hydraulic signals, and metabolites are transported mostly through the vasculature to distant tissues. How shoots and roots synchronize their response to stress using mobile signals is an emerging field of research. We summarize recent advances on mobile signals regulating shoot stomatal movement and root development in response to highly localized environmental cues. In addition, we highlight how the vascular system is not only a conduit but is also flexible in its development in response to abiotic stress.

Highlights

Limitations in water uptake in roots and sucrose supply from shoots under abiotic stress can be encoded into signals that regulate the growth and development of distant tissues.

Root-localized stress signals trigger changes in xylem hydraulics, mobile peptides, reactive oxygen species (ROS), and Ca^{2+}, which lead to remote effects and induce shoot stomatal closure.

The mobility of HY5 protein and its downstream targets via the phloem conveys shoot-sensed light and temperature information to affect both primary and lateral root growth.

Shoot-derived sucrose loading/unloading in the phloem is highly responsive to environmental changes, and triggers signaling pathways that regulate root development.

Developmental plasticity of the vasculature in response to abiotic stresses is of key importance for long-distance transport of substances to assist plant stress resilience.

Shoot–root communication: a long-distance relationship

Tissues in higher plants are highly specialized. The shoot captures solar energy by photosynthesis and carries out reproduction, whereas the root extracts water and minerals from the soil. The coordination of these specialized functions is critical for plants to thrive. The plant vascular system, comprising **xylem** and **phloem** (see Glossary), supports the plant body while also transporting many signaling molecules from shoots to roots and vice versa. Hormones are well-studied integrators of root and shoot development. Abscisic acid (ABA) [1], auxin [2], gibberellins [3], cytokinins (CKs) [4], and jasmonic acid and its relatives [5] are known to travel through the vasculature and to act in distant tissues (Figure 1, Key figure). More recently, several small peptides, proteins, and RNA molecules have been found to be mobile in xylem or phloem and to coordinate nutrient uptake and distal stress responses [6–10] (Figure 1).

Localized environmental stresses such as soil salinity or light signals require controlled long-distance transport of stress signals to elicit acclimation responses at the whole-plant level [11,12]. Understanding how mobile signals activate distal stress-responsive signaling pathways and how local and distant developmental pathways are reprogrammed is an important aspect of abiotic stress tolerance. The long-distance signaling that mediates the nutrient stress response has been recently reviewed [7]. In this review we focus on recent developments in how different mobile signals coordinate shoot stomatal movements and root development in response to salinity, water-related stresses, and light and temperature changes. Furthermore, we highlight the developmental plasticity of the plant vascular system which is the central transportation path that allows mobile signals to travel over long distances in times of stress.

Bottom-up approaches: stressed roots signal to shoots

Root-derived hydraulic signals mediate the plant shoot stress response

Water limitation has a profound impact on plant growth [13]. Water absorbed from the soil moves radially to the root xylem both via the **apoplastic pathway** and via cell-to-cell pathways through transcellular transport and the **symplastic pathway**. Subsequently, water is axially transported along the xylem towards shoots following a water potential gradient, and generally the lowest water potential is present in leaves [14,15]. The turgor pressure of leaf cells rapidly declines

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when roots experience water shortage, causing a drop in root local water potential, and such turgor changes can be propagated from roots to shoots as hydraulic signals [15]. Root turgor pressure changes were able to trigger local root ABA signaling near vascular bundles as well as shoot ABA accumulation to regulate stomatal closure [15], indicating that hydraulic signals are correlated with ABA signaling. However, rapid hydraulic signals are also observed in the ABA biosynthesis and signaling mutants *aba2* and *abi1-1*, respectively, indicating that these signals may be ABA-independent [15]. So far, it is unclear how root hydraulic signals are perceived by plants and are subsequently linked to ABA signaling, although putative sensing mechanisms have been postulated and reviewed [14].

Reduced water availability in root surroundings, caused by salt and osmotic stress, has been shown to reduce root hydraulic conductivity (Lp_r) – the ability of roots to transport water from soil across a water potential gradient to the shoot xylem [16–19]. Under water-limitation conditions, Lp_r in both rice (*Oryza sativum*) and arabidopsis (*Arabidopsis thaliana*) was shown to be positively associated with shoot dry weight, suggesting that an increase in Lp_r could improve plant performance [16,20]. Recently, the XYLEM NAC DOMAIN 1 (XND1) transcription factor was identified as a negative regulator of Lp_r in arabidopsis [16]. Loss of function of *XND1* increased shoot fresh weight and dry weight. Conversely, overexpression of *XND1* reduced shoot fresh weight and negatively regulated Lp_r and drought tolerance [16]. Aquaporins are classic water channels that gate radial water transport transcellularly in roots and therefore regulate Lp_r [21,22]. Silencing of PLASMA MEMBRANE INTRINSIC PROTEIN (PIP) aquaporins or the application of aquaporin blockers significantly reduced the Lp_r, whereas overexpression of PIP-type aquaporins resulted in an increase in Lp_r [16,21,23,24]. However, the reduced Lp_r under salt or osmotic stress was not always accompanied by consistent changes in the transcriptional level of aquaporins, suggesting that there are additional levels of regulation in aquaporin-mediated Lp_r changes, such as post-transcriptional regulation and membrane trafficking of aquaporins [25–29].

Lp_r reduction is also commonly found during the plant response to hypoxia and chilling stress. The Raf-like MAP kinase kinase kinase gene *HYDRAULIC CONDUCTIVITY OF ROOT 1* (*HCR1*) was identified to modulate Lp_r by a quantitative trait locus mapping approach [30]. HCR1 reduces Lp_r under K^+-replete and O_2-deficient (referred to as hypoxia) conditions via upregulation of the protein abundance of RELATED TO AP2.12, which is a key transcription factor mediating oxygen sensing [30]. Consistent with the positive connection between Lp_r and plant growth, less reduction of fresh weight and water content was observed in *hcr1* mutants than in wild-type (WT) plants when roots were exposed to hypoxia, but not under control conditions [30]. A chilling-tolerant variety of rice was shown to restore Lp_r and water uptake faster than sensitive plants when challenged by cold stress [31]. The increase in the Lp_r was attributed to increased expression of aquaporins during the recovery stage. Taken together, obstruction of root water uptake by abiotic stress can be encoded into hydraulic signals towards the shoots to elicit growth adaptations, and regulation of Lp_r, often associated with aquaporin modulation, is a plant response to several stress conditions.

On the way: more mobile signals in the regulation of stomatal closure

ABA was once considered to be a good candidate for the long-distance mobile hormone that travels from the roots to regulate stomatal closure. This assumption was supported by the fact that ABA accumulates in plant roots and xylem sap under water deficit [1]. However, local ABA biosynthesis also occurs in the shoot (Figure 1A) [1]. Elegant grafting experiments between WT plants and *aba2-1* (ABA-deficient) mutants showed that impaired ABA biosynthesis in roots did not affect stomatal closure in response to water deficit [15]. By contrast, grafts with impaired

Glossary

Apoplastic pathway: the intercellular pathway that transports water and solutes through cell walls or intracellular spaces.
Meta- and protoxylem: both differentiate from procambial cells and function together in transporting water and minerals towards shoots, but protoxylem differentiates earlier than metaxylem. Protoxylem has annular or spiral secondary cell walls, whereas the secondary cell walls of metaxylem are in a reticulate or pitted pattern.
Hydraulic redistribution: a passive mechanism by which water moves from moist to dry soils via plant roots.
Phloem: consists of sieve elements and companion cells. Sieve elements are living enucleated cells that allow translocation of water, photosynthates, hormones, and other mobile molecules. Companion cells are connected to sieve elements through specialized plasmodesmata and load/unload to/from sieve elements.
(Pro)cambial cells/(pro)cambium: undifferentiated cells/meristematic tissue that contains some procambial cells that differentiate into phloem and xylem, whereas others remain undifferentiated.
Secondary cell wall (SCW): a structure between the primary cell wall and the plasma membrane in some plant cells, which has multiple functions such as providing mechanical support and preventing water loss out of the xylem.
Symplastic pathway: the transport pathway that transports molecules between the cytoplasm and the vacuoles through plasmodesmata.
Xylem: consists of multiple cell types such as tracheary elements, xylem parenchyma cells, and xylem fibers; it provides mechanical support for plants and facilitates the transportation of water, minerals, metabolites, and peptides.
Xylem vessels: also known as tracheary elements, these are the conductive cells of xylem because all intracellular contents, including nucleus and cytoplasm, are cleared during maturation.

Key figure

Mobile signals mediate shoot-to-root and root-to-shoot communication in response to environmental cues

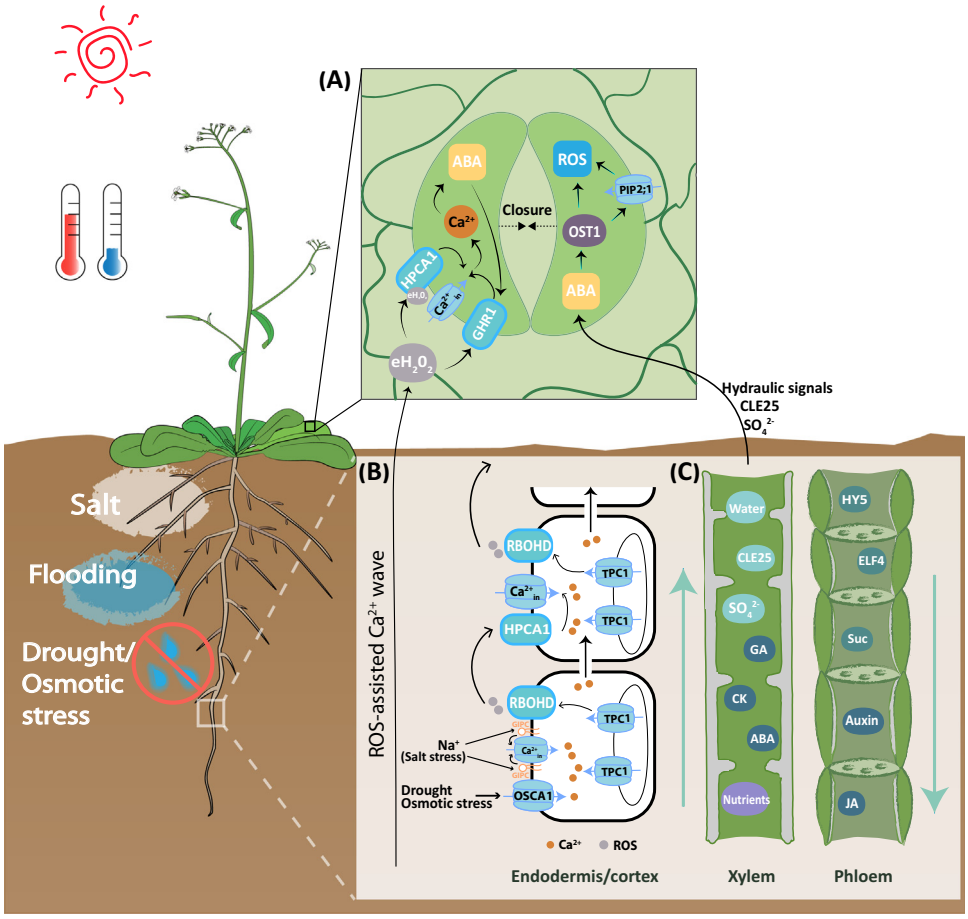

Figure 1. (A) Shoot stomatal closure in response to stress. Root-derived Ca^{2+}/ROS, hydraulics, sulfate (SO_4^{2-}), and CLE25 trigger ABA-mediated stomatal closure. Downstream of ABA, SnRK2.6/OST1 and GHR1 activate membrane-located anion channels leading to stomatal closure [108,109]. OST1 also promotes ROS accumulation in guard cells by phosphorylation of NADPH oxidases and the aquaporin PIP2;1 to activate anion channels to close stomata [110,111]. The root-derived ROS-assisted Ca^{2+} wave induces eH_2O_2 to activate HPCA1 and GHR1, and subsequently the cytosolic Ca^{2+} level is increased for ABA-mediated stomatal closure [39,40]. (B) A model for the transmission of ROS-assisted Ca^{2+} waves in endodermal and cortical cells. Osmotic and salt stresses in roots are sensed by their potential sensors MOCA1, encoding a glucuronosyltransferase for plant cell-surface GIPC sphingolipids, and OSCA1, respectively [36,37], which induce $[Ca^{2+}]_i$ increase through Ca^{2+}-permeable channels. Subsequently the vacuolar channel TPC1 is activated and induces RBOHD for apoplastic ROS production which is sensed by HPCA1 of neighboring cells [11,38,39]. HPCA1-induced $[Ca^{2+}]_i$ increase leads to the continuous symplastic progress of a Ca^{2+} wave. Root-derived Ca^{2+} and ROS are indicated by brown and gray dots, respectively. (C) Mobile signals in the root vasculature – xylem and phloem. The xylem transports nutrients, hormones, and water, as well as stress-evoked mobile signals such as SO_4^{2-}, CLE25, and hydraulic signals, towards shoots, whereas the phloem transports mobile proteins (e.g., HY5, ELF4), sucrose, and auxin [2,9,41,48,52,60]. Arrows indicate the induction of a process/product or the direction of signal movements. The cartoon of an arabidopsis (*Arabidopsis thaliana*) plant was adapted, with permission, from Figshare (B. Frédéric, 2018_Arabidopsis_growing_on_soil.eps;

(Figure legend continued at the bottom of the next page.)

ABA biosynthesis in shoots were unable to close their stomata [15], suggesting that shoot-derived ABA is necessary and sufficient for stomatal closure.

Recent studies have shown that shoot ABA mediates the shoot water-stress response via interacting with other root-derived mobile signals. Under water deficit, the root-derived small peptide CLAVATA3/EMBRYO SURROUNDING REGION-RELATED 25 (CLE25) moves from roots to shoots to regulate stomatal closure in an ABA-dependent manner (Figure 1A) [9]. When *cle25* mutant shoots were grafted onto WT roots (*cle25/WT*), drought stress still induced the expression of the ABA biosynthesis gene *NINE-CIS-EPOXYCAROTENOID DIOXYGENASE 3* (*NCED3*) in dehydrated leaves [9]. *WT/cle25* grafts were no longer able to induce *NCED3* in the shoots. CLE25 is perceived in leaves by two receptor-like kinases – BARELY ANY MERISTEM 1 and 3 (BAM1 and 3). Local loss of function of *BAM1* and *BAM3* in the shoot abolished the upregulation of *NCED3* in response to CLE25. Notably, a higher rate of water loss in the *cle25* mutants than in the WT plants was already observed within 1 h of dehydration stress, whereas ABA accumulation in leaves did not differ between WT plants and *cle25* mutants at that time [9]. These results imply that root-derived CLE25 may act together with other rapid signals, in addition to ABA, in regulating stomatal closure.

Both reactive oxygen species (ROS) and Ca^{2+} are stress-induced rapid signals that work closely together with the ABA pathway in guard cells to regulate stomatal closure [33]. Beyond their local action in stomatal closure, ROS and Ca^{2+} also act as long-distance signals. ROS waves mediated by *RESPIRATORY BURST OXIDASE HOMOLOG D* (*RBOHD*) have been identified as a long-distance signal that coordinates leaf-to-leaf communication and elicits acclimation responses under high light and heat stress [12,34,35]. Under light stress, the stomatal closure response in distant leaves was prevented either by blocking ROS accumulation or Ca^{2+} waves between local and distant leaves [12], suggesting ROS and Ca^{2+} waves work closely together to regulate the distal stomatal response.

Salt stress elicits transient cytosolic Ca^{2+} ($[Ca^{2+}]_i$) influx in roots, and this induces a subsequent wave of Ca^{2+} release that progresses from cell to cell within the root cortex and endodermis cell layers towards the shoot [11]. MONOCATION-INDUCED $[Ca^{2+}]_i$ INCREASES 1 (MOCA1) and REDUCED HYPEROSMOLALITY-INDUCED $[Ca^{2+}]_i$ INCREASE1 (OSCA1) are potential sensors of ionic and osmotic stress, respectively [36,37]. Both are required for $[Ca^{2+}]_i$ elevation in the roots in a stress-specific manner. The $[Ca^{2+}]_i$ -activated slow vacuolar (SV) channel TWO-PORE CHANNEL 1(TPC1) is required for the subsequent salt-evoked Ca^{2+} wave and downstream induction of stress-responsive genes in shoots [11]. Interestingly, Ca^{2+} wave propagation in response to salt was slowed down in ROS-defective *atrbohD* mutants, which is in line with a modeling analysis showing that the *TPC1*-mediated Ca^{2+} wave alone is insufficient to explain the velocity of Ca^{2+} wave transmission, whereas the model with ROS-triggered elements was quantitatively consistent with the observed Ca^{2+} wave [38]. Recently, HYDROGEN PEROXIDE-INDUCED Ca^{2+} INCREASES 1 (HPCA1), a membrane-localized leucine-rich repeat receptor-like kinase (LRR-RLK), has been identified as the sensor of extracellular ROS (eH_2O_2) [39].

https://figshare.com/articles/figure/2018_Arabidopsis_growing_on_soil/7159961). Abbreviations: ABA, abscisic acid; Ca^{2+}_{in}, Ca^{2+}-permeable channels; CK, cytokinins; CLE25, CLAVATA3/EMBRYO SURROUNDING REGION-RELATED 25; eH_2O_2, extracellular H_2O_2; ELF4, EARLY FLOWERING 4; GA, gibberellins; GHR1, GUARD CELL HYDROGEN PEROXIDE-RESISTANT 1; GIPC, glycosyl inositol phosphorylceramide; HPCA1, HYDROGEN-PEROXYDE-INDUCED Ca^{2+} INCREASES 1; HY5, ELONGATED HYPOCOTYL5; MOCA1, MONOCATION-INDUCED $[Ca^{2+}]_i$ INCREASES 1; JA, jasmonate; OSCA1, REDUCED HYPEROSMOLALITY, INDUCED CA^{2+} INCREASE 1; OST1, OPEN STOMATA1; PIP2;1, PLASMA MEMBRANE INTRINSIC PROTEIN 2;1; TPC1, TWO-PORE CHANNEL 1; RBOHD, RESPIRATORY BURST OXIDASE PROTEIN D; ROS, reactive oxygen species; Suc, sucrose.

Because *HPCA1* is broadly expressed throughout the plant, it may detect the ROS burst of neighboring cells produced by RBOHD, resulting in symplastic progress of Ca^{2+} waves in roots (Figure 1B) [11,38,39]. In guard cells, in response to eH_2O_2, HPCA1 triggers a $[Ca^{2+}]_i$ increase likely via the activation of Ca^{2+}-permeable channels in the plasma membrane, which leads to stomatal closure [39]. The LRR-RLK, GUARD CELL HYDROGEN PEROXIDE-RESISTANT 1 (GHR1), was identified to interact with Ca^{2+}-dependent kinase (CPK) 3 to activate anion channels leading to stomatal closure in response to eH_2O_2 (Figure 1A) [40]. Given that both HPCA1 and GHR1 are present in guard cells, an eH_2O_2-assisted Ca^{2+} wave could be directly perceived by shoot guard cells to regulate stomatal movement under abiotic stress.

In addition to ABA, hydraulic signals, and peptides, drought stress induces sulfate accumulation in the xylem sap of poplar plants and maize (*Zea mays*) [41,42] (Figure 1C). Sulfate application on detached leaves of arabidopsis led to stomatal closure, and sulfate promoted the expression of *NCED3* in leaves, and ABA accumulation was observed in guard cells [41–43]. It is possible that sulfate acts as a root-derived signal to regulate stomatal closure, although direct evidence in intact plants is still lacking.

Top-down organization: shoot to root signals

Mobile proteins transmit shoot-to-root light and temperature signals via phloem

Light limitation and extreme temperatures can be detrimental to plants, affecting growth, development, and circadian rhythms. To synchronize developmental activities at the whole-plant level it is crucial to transduce light and temperature information between shoots and roots. The arabidopsis ELONGATED HYPOCOTYL 5 (HY5) transcription factor is a key component downstream of the photoperception pathway that mediates photomorphogenesis [44]. Phytochrome B (phyB) acts as a sensor for both light and temperature to promote the gene expression and protein accumulation of HY5 [45–47]. The shoot-accumulated HY5–GFP protein was shown to translocate to the root to mediate light-promoted primary root elongation (Figure 2A) [48]. In response to light, shoot-derived HY5 activates *HY5* expression in roots and upregulates the nitrate (N) transporter *NRT2.1* to promote N uptake in roots [48]. HY5 also promotes sugar export in the shoots by promoting the expression of sugar transporter genes *SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTERS* (*SWEET*) *11* and *12*. HY5 therefore contributes to carbon and N metabolism and distribution in response to light cues [48,49].

During the shade-avoidance response, far-red (FR) light detected in the shoot induces HY5–YFP accumulation in lateral root primordia, which represses lateral root outgrowth by inhibiting the accumulation of the auxin transporters PIN-FORMED 3 (PIN3) and LIKE-AUXIN TRANSPORTER1 3 (LAX3) and by downregulating the auxin response factor ARF19 (Figure 2A) [50]. Notably, the direct application of FR light to roots did not reduce LR density, indicating that shoot-derived HY5 protein may play a role in lateral root inhibition [50]. In line with this, *HY5* expression driven by the *HY5* native or phloem companion cell-specific *SUCROSE-PROTON SYMPORTER 2* (*SUC2*) promoter suppressed lateral root growth in shade, which supports the idea that HY5 acts via the phloem [51]. More recent results have questioned the necessity of HY5 translocation in its regulation of root elongation [51]. HY5 fused to an N-terminal hemagglutinin (HA)–YFP–HA ('DOF') tag expressed in the shoots was undetectable in roots, but still rescued the short root phenotype of the *hy5* mutant. This suggests that an unknown target of HY5 might also travel from shoot to root to promote primary root growth, although it cannot be ruled out that an undetectable but sufficient amount of HY5 is in fact responsible.

Recently it was shown that EARLY FLOWERING 4 (ELF4), a key component of the circadian clock, is also shoot-to-root mobile [52]. ELF4 is involved in the regulation of the root clock by

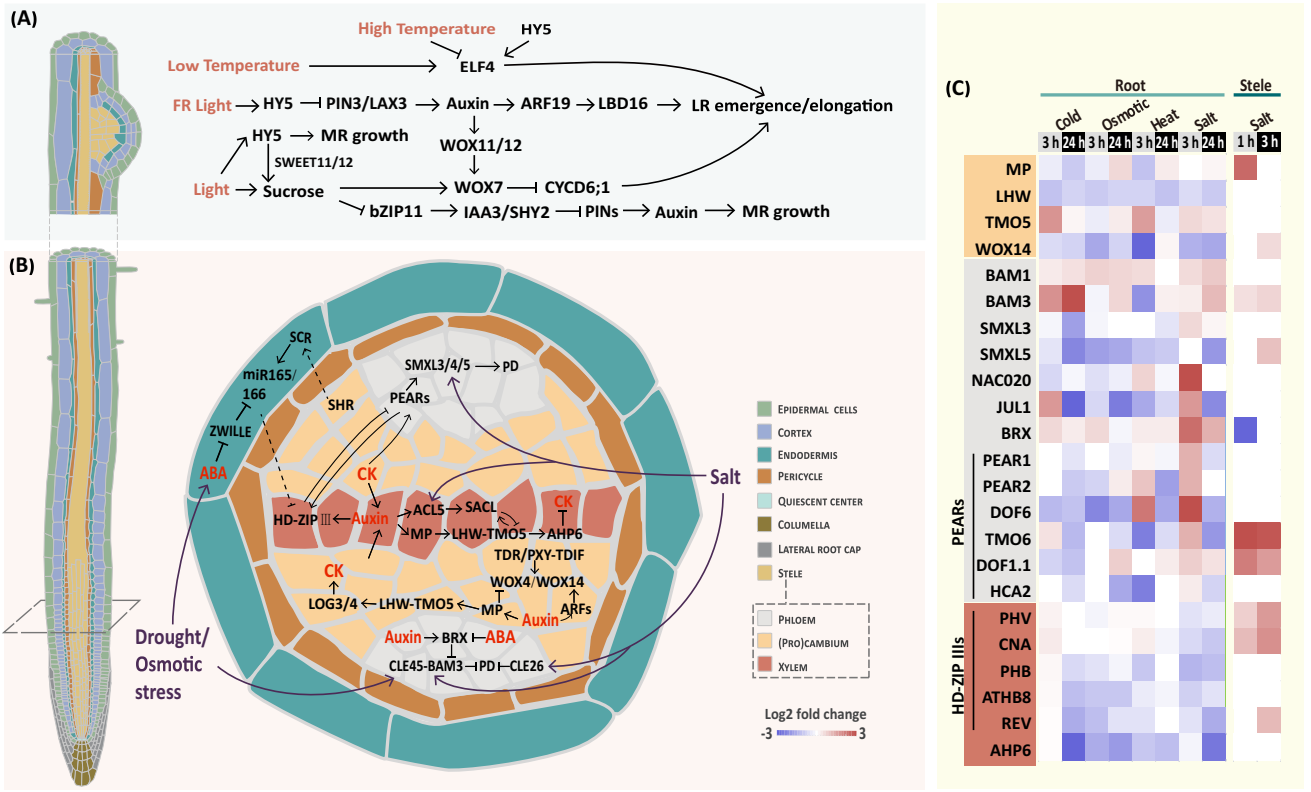

Figure 2. Shoot-derived stress signals and hormones integrate with local signals coordinating root developmental plasticity. (A) Shoot-derived signals shape root-system architecture in response to light and temperature. Shoot-detected light signals mediate both primary root growth and lateral root (LR) growth through HY5 and sucrose [48,50,60]. Light-induced primary root elongation requires HY5. Far-red (FR) light-induced HY5 represses LR development by inhibiting the auxin transport and downstream auxin response factor, ARF19, which is upstream of the LR key regulator LBD16 [48,50,112]. Temperature changes regulate lateral root development via ELF4, acting downstream of HY5 [52]. Photosynthate sucrose transports to roots and influences root growth. Light-induced HY5 regulates shoot-to-root sucrose export via binding to the promoters of the sugar transporter genes *SWEET11/12*. Sugar promotes WOX7, acting downstream of WOX11/12, to suppress *CYCD6;1* expression and inhibit LR emergence [65]. Sucrose represses the expression of *bZIP11* which is required to activate the negative regulator IAA3/SHY2 for MR growth [64]. (B) Molecular mechanism of vasculature development and the involvement of abiotic stress signaling. Abiotic stress signaling effects on basal hormonal regulation pathways (see Box 1 in the main text) have profound effects on root vasculature development. During xylem development, drought-induced endodermal ABA signaling promotes miR165/166 and subsequently represses HD-ZIP IIIs [68,69]. Salt affects the auxin–CK feedback loop to regulate xylem development via ACL5 (see Box 1 in the main text) [74,105]. In phloem, several key pathways/regulators have been shown to be induced by drought, salt, and ABA signaling, including BRX, CLE peptide–BAM signaling, and the PEARs–SMXL3/4/5 module [81–85]. (C) Expression patterns of key genes regulating vasculature development upon several environmental stimuli. The heatmap shows the relative expression (log_2 fold change) of root vasculature development regulators in response to diverse abiotic stresses in the root at 3 h and 24 h, and salt stress in the root stele tissue at 1 h and 3 h. Expression data were extracted from published datasets and analyzed by GEO2R (https://www.ncbi.nlm.nih.gov/geo/geo2r) [113–115]. The cartoon of cross- and longitudinal sections of arabidopsis (*Arabidopsis thaliana*) roots was adapted, with permission, from Figshare (B. Peret, Primary and lateral root.ai; B. Frédéric, Arabidopsis_root_tissues_FB.ai; https://figshare.com/collections/Root_illustrations/3701038). Arrows indicate induction or promotion of a process or product; T bars indicate inhibition of a process or molecule; dashed arrows indicate intercellular movement. Abbreviations: ABA, abscisic acid; ACL5, ACAULIS 5; BAM3, BARELY ANY MERISTEM 3; AHP6, ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEIN 6; ARF19, AUXIN RESPONSE FACTOR 19; ATHB8, homeobox protein 8; BAM1/3, BARELY ANY MERISTEM 1/3; BRX, BREVIS RADIX; bZIP11, BASIC LEUCINE-ZIPPER 11; CLE26/45, CLAVATA3/EMBRYO SURROUNDING REGION-RELATED 26/45; CK, cytokinins; CNA, CORONA; CYCD6;1, cyclin D 6;1; DOF6, DOF TRANSCRIPTION FACTOR 6; ELF4, EARLY FLOWERING 4; FR light, far-red light; HCA2, HIGH CAMBIAL ACTIVITY 2; HD-ZIP III, class III HOMEODOMAIN LEUCINE ZIPPER; HY5, ELONGATED HYPOCOTYL 5; IAA3/SHY2, INDOLE-3-ACETIC ACID INDUCIBLE 3/SHORT HYPOCOTYL 2; JUL1, JULGI1; NAC020, NAC DOMAIN-CONTAINING PROTEIN 20; PD, phloem development; LBD16, LATERAL ORGAN BOUNDARIES-DOMAIN 16; LHW–TMO5, LONESOME HIGHWAY–TARGET OF MONOPTEROS 5; LOG3/4, LONELY GUY 3/4; LR, lateral root; LRD3, LATERAL ROOT DEVELOPMENT 3; MP, MONOPTEROS; miR165/166, microRNA 165/166; MR, main root; PEARs, PHLOEM EARLY DOFs; PHB, PHABULOSA; PHV, PHAVOLUTA; PIN3/LAX3, PIN-FORMED 3/LIKE AUX1 3; REV, REVOLUTA; SACL, SUPPRESSOR OF ACAULIS51-LIKE; SCR, SCARECROW; SHR, SHORT ROOT; SMXL 3/4/5, SUPPRESSOR OF MAX2-LIKE 3/4/5. SWEET11/12, SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTERS 11/12; TDR/PXY–TDIF, TDIF RECEPTOR/PHLOEM INTERCALATED WITH XYLEM–TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY FACTOR; TMO6, TARGET OF MONOPTEROS 6; WOX, WUSCHEL RELATED HOMEOBOX.

modulating the expression of core clock genes such as *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*), *LATE ELONGATED HYPOCOTYL* (*LHY*) and *PSEUDO-RESPONSE REGULATOR* (*PRR*) *7* and *9*. Movement of ELF4 through the vasculature allows the shoot clock to coordinate the rhythm of the root clock. Interestingly, the translocation of ELF4 was temperature-dependent. Cool temperatures promoted ELF4 movement, whereas warm temperatures suppressed ELF4 movement. As a result, the root clock ran slower at cool temperatures because the repression on *PRR9* was enhanced by mobile ELF4 [52]. Moreover, the *ELF4* loss-of-function mutant showed reduced lateral root density (Figure 2A), suggesting a role of *ELF4* during root development in response to temperature changes [52]. In summary, the movement of HY5 and ELF4, together with their local expression patterns, mediates root growth in response to diverse light and temperature conditions.

Sugar signals regulate root growth via phloem loading and unloading

Roots rely on shoot-derived sucrose as an energy supply for growth. Environmental stresses tighten the sucrose budget owing to impaired photosynthesis and sugar accumulation in the shoot (reviewed in [53]). The sucrose allocation towards roots under abiotic stress may change accordingly. In arabidopsis, sucrose transport in phloem is mainly achieved through the regulation of sugar transporters. Sucrose loading from photosynthetic leaf mesophyll cells into the phloem is mediated first by the vasculature-localized sugar transporters SWEET11 and 12 [49]. SWEET11 and 12 channel sucrose from phloem parenchyma cells into the apoplast. Apoplastic sucrose is then transported into phloem companion cells by SUC2 [49,54,55]. In the root, sucrose is unloaded through an apoplastic pathway (via SUC/SWEET sugar transporters) or through a symplastic pathway (via bulk flow and changes in hydrostatic pressure) [56].

As mentioned earlier, HY5 promotes *SWEET11* and *SWEET12* expression to enhance phloem sucrose loading in the light [48]. In potato (*Solanum tuberosum*), another mobile transcription factor, StSP6A, interacts with StSWEET11 in stolons [57]. Binding of StSP6A to SWEET11 is thought to reduce the pumping of sucrose into the apoplast, thereby increasing the transport of sucrose via the symplastic pathway. It has been proposed that this directs the flow of sucrose into the developing tuber [57]. The transcripts of *SUC2*, *SWEET11*, and *SWEET12* are elevated in arabidopsis leaves in response to water deficit [58]. *AtSUC1*, highly expressed in the root, is thought to mediate sugar unloading and is downregulated in response to osmotic stress [59]. Two ABA-induced transcription factors, ABA INSENSITIVE 5 (ABI5) and ABA-RESPONSIVE ELEMENT BINDING PROTEIN 3 (AREB3), were shown to bind to the *AtSUC1* promoter in yeast one-hybrid analyses, and ABI5 was able to inhibit the expression of *SUC1* [116]. This suggests that the inhibition of *SUC1* expression under drought and salt stress may be achieved through ABA signaling. These studies have shown that the regulation of sucrose transport from shoots to roots is responsive to environmental changes, and transcriptional regulation of sugar transporters is probably important for surviving stress.

Disturbed carbon translocation from shoot to root under abiotic stress subsequently may affect root growth. Cotyledon-derived sucrose promotes primary root growth in response to light because sucrose supply rescued darkness-inhibited root elongation (Figure 2A) [60]. Both longer light exposure of shoots and bigger shoot size further promote root elongation, and this may be due to enhanced sucrose production via photosynthesis [60]. Enhanced carbon export from shoots to roots under water deficit via upregulation of sugar transporters may support deeper rooting, instead of horizontal expansion, that allows the root to reach water supplies in deeper soil layers [58].

Altered root growth due to sugar limitation may be mediated by the SNF1-RELATED PROTEIN KINASE 1 (SnRK1)–target of rapamycin (TOR) energy signaling pathway and its interaction with

ABA or auxin signaling, which are essential for mediating root system architecture changes in response to abiotic stress [61,62]. For example, downstream of SnRK1, the expression of the C/S1 BASIC LEUCINE ZIPPER (bZIP) transcription factors *bZIP1* and *bZIP53* is induced by salt stress in arabidopsis roots [63]. Both are required for primary carbohydrate metabolic reprogramming, and salt-induced *bZIP53* expression is dependent on ABA signaling. Similarly, *bZIP11* is activated by SnRK1 low-energy signaling and directly activates *INDOLE-3-ACETIC ACID INDUCIBLE 3/SHORT HYPOCOTYL 2* (*IAA3/SHY2*) transcription in the root [64]. This leads to decreased auxin transport to the root tips and a restriction of primary root growth (Figure 2A).

In lateral roots, WUSCHEL RELATED HOMEOBOX 7 (WOX7) suppresses lateral root initiation in a sucrose-dependent manner through repression of the cell-cycle gene *CYCD6;1* (Figure 2A) [65]. In parallel with LATERAL ORGAN BOUNDARIES-DOMAIN 16 (LBD16), WOX7 acts downstream of WOX11/12 regulating root primordia initiation in an auxin-dependent manner [66]. Taken together, shoot-originated sucrose and its underlying signaling networks via SnRK1 signaling could be involved in the crosstalk with major hormonal pathway, which in turn influences root development in response to environmental cues.

Tuning the communication channels: root vasculature developmental plasticity in response to stress

As discussed earlier, during abiotic stress the translocation of various mobile signals, energy carriers, and water relies on the vascular system, and vasculature architecture changes in response to stressful environments are therefore vital for its transportation function. Root vasculature specification and patterning events occur early during embryogenesis. Subsequent post-embryonic development and maintenance of root vasculature is a complex process that occurs in the root apical meristem (Box 1; reviewed in [67]). Root vascular architecture is highly flexible in response to environmental stresses. Additional root **protoxylem** strands and cell files are induced in arabidopsis under water deficit [68,69]. In trees, additional **xylem vessels** were found to avoid cavitation and thus ensure water supply under drought stress, and an increased number of **metaxylem** vessels enhanced water uptake and use in soybean under water deficiency [70,72]. In accordance with these observations, root xylem conduit diameters were shown to correlate positively with Lp_r and root **hydraulic redistribution** [73]. This may also explain the enhanced Lp_r and drought resistance of the arabidopsis *xnd1* mutants because a larger xylem area and an increased number of xylem vessels were observed in *xnd1* mutants [16]. In response to salinity, mutants of *ACAULIS5* (*ACL5*) – encoding a putative spermine synthase required for xylem specification – exhibit higher salt accumulation and hypersensitivity to salt stress compared with WT plants [74], which is likely caused by excessive Na^+ loading via the root xylem owing to extra xylem vessels in the mutants [75,76].

So far, little is known about whether and how the xylem is regulated by xylem-delivered signals such as hydraulic signals, although ABA signaling has been shown to be involved. In response to water deficit, endodermal ABA signaling promotes the expression of *miR165a/166b* that are involved in xylem specification, whereas the expression of their repressor, *ZWILLE/ARGONAUTE 10*, is suppressed (Box 1 and Figure 2B) [68,69]. ABA treatment also inhibits the expression of the HD-ZIP III-type transcription factor *PHABULOSA* (*PHB*) both at protein and mRNA levels, leading to the formation of extra protoxylem [68,69]. In addition, the formation of **secondary cell wall (SCW)**, which influences the cell-wall water permeability of the xylem, is also an important aspect of xylem development. SCW deposition has been shown to be tightly regulated by transcriptional regulatory networks in both arabidopsis and poplus (*Populus tremula* × *tremuloides*), which involves VASCULAR-RELATED NAC DOMAIN 7 (VND7) – a key factor responsible for xylem differentiation – and ETHYLENE RESPONSE FACTOR 139 as well as its downstream targets such as LBD15 and MYB86 [69,77,78]. *VND7* expression is induced by ABA and salt stress [69,77], whereas *LBD15* and *MYB86* are responsive to salt and drought stress [78]. Collectively,

Box 1. Mobile hormones shaping vasculature development

Vasculature development is coordinated by different hormonal pathways (Figure 2B). Auxin and cytokinin (CK) signaling play central roles in regulating vasculature development, and are also the two main mobile hormones transported via the vascular system. During embryo development, cotyledon-derived auxin is transported to the embryonic root to form a feedback loop with CK that maintains vasculature development (reviewed in [67]). The auxin response transcription factor MONOPTEROS/AUXIN RESPONSE FACTOR 5 (MP/ARF5) regulates the downstream basic helix-loop-helix (bHLH) transcription factors TARGET OF MONOPTEROSs (TMOs) including TMO3, TMO5, and TMO6 to control the early cell division events of the provascular cells [67]. TMO5 dimerizes with LONESOME HIGHWAY (LHW) to activate the expression of CK biosynthesis genes *LOG3* and *LOG4* which regulate periclinal cell divisions in (pro)cambium for secondary growth to produce new vasculature tissues [102].

ABA affects xylem specification through the SHORTROOT (SHR)–microRNA (miR) 165/166–class III HOMEODOMAIN LEUCINE ZIPPER (HD-ZIP III) pathway [68,69,103]. The endodermal SHR:SCR complex upregulates the expression of *miR165* and *miR166*. miR165 and miR166 subsequently move towards central of stele to restrict *HD-ZIP III* transcription. This system determines both *de novo* xylem formation and the cell identities of metaxylem and protoxylem [103]. In post-embryonic development, the auxin–CK feedback loop also plays a central role in xylem specification and maintenance. Protoxylem specification is dependent on the expression of the CK signaling repressor ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEIN 6 (AHP6), which is positively regulated by the auxin-TMO5-LHW cascade, whereas auxin transport from procambial cells to xylem cells is facilitated by auxin transporter PIN proteins in a CK-dependent manner [104]. On the other hand, auxin also triggers the expression of thermospermine synthase ACAULIS5 (ACL5) which promotes the formation of transcription module SAC51-LIKE (SACL)-LHW to limit LHW-TMO5 activity and prevent excessive cell proliferation [105]. In procambium, the key regulators of cell proliferation, WOX4 and WOX14, are induced by ARFs (MP, ARF7, and ARF19) in an auxin-dependent manner, and they are also targeted by ligand–receptor TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY FACTOR (TDIF)-TDIF RECEPTOR/PHLOEM INTERCALATED WITH XYLEM (TDR/PXY) signaling via the TOM6-WOX14-LBD4 network to control vascular proliferation [106,107]. Interestingly, CK-dependent PHLOEM EALRLY DOF (PEAR) proteins including TMO6 are antagonized by auxin-induced HD-ZIPIIIs to regulate cambium growth during xylem and phloem formation [83].

Abiotic stress signaling pathways that are induced by drought, salinity, and ABA have shown an effect on the auxin–CK-regulated vascular developmental pathways [68,69,74,84]. Transcriptome data mining of publicly available gene expression datasets reveals that various abiotic stresses can interfere with the expression of key regulators of vasculature development (Figure 2C), suggesting an impact of stress signaling on auxin–CK signaling to shape a functional vascular system to withstand various stress conditions.

ABA signaling and the transcriptional regulatory networks mediating xylem formation and SCW deposition shape xylem structure in response to environmental changes, allowing xylem conduits to fulfill their function in transporting water and minerals from roots to shoots (Figure 2B).

As mentioned earlier, a functional phloem is crucial for the translocation of shoot-derived chemical molecules and proteins to roots to support developmental activities and stress responses. Phloem formation defects cause overaccumulation of starch in shoots and impaired auxin transport, which may account for the altered root system architecture phenotypes commonly found in mutants of phloem development modulators [79,80]. SUPPRESSOR OF MAX2-LIKE 3, 4, and 5 (SMXL3, 4, and 5) proteins are redundantly required for early phloem development in the root [81] (Figure 2B). Interestingly, *SMXL4* (also known as *ATHSPR*) expression is induced by salt and ABA in both shoots and roots [82]. The *smxl4* mutants displayed compromised tolerance to both salt and drought stress, and are hypersensitive to salt-mediated reduction of primary root growth [82]. SMXL3 is a putative direct target of PHLOEM EARLY DOF2 (PEAR2), which is antagonized by HD-ZIP IIIs in regulating the cell division of **procambial cells** [83]. HD-ZIP IIIs are inhibited by endodermal ABA under drought stress [68,69], suggesting that the PEAR2–SMXL3 module may also participate in stress responses (Figure 2B).

Beyond SMXLs, other key players regulating phloem formation were also reported to be involved in stress signaling pathways. The plasma membrane-localized protein BREVIS RADIX (BRX), which is required for protophloem sieve element (PSE) development, interacts with auxin, brassinosteroid (BR), and ABA signaling pathways [84,85]. *brx1* mutants display discontinued

root phloem formation and ABA-hypersensitivity in regulating primary root growth [84]. Counteracted by BRX signaling, the CLE45 peptide, that is perceived by the BAM3 receptor, inhibits the differentiation of protophloem [86,87]. CLE45 was shown to be perceived by RECEPTOR LIKE PROTEIN KINASE 2 to regulate PSE identity by maintaining a plastic zone in the root meristem zone where the cell identities of PSE and PSE-adjacent companion cells are interchangeable, which is important for the formation of a functional phloem [88]. Interestingly, CLE45 signaling is locally antagonized by protophloem-specific BR perception to allow protophloem differentiation, which may trigger an unidentified phloem-derived mobile signal to rescue the dwarfism and patterning defects in *bri1*;*brl1*;*brl3* triple mutants [89]. CLE26 also represses protophloem development as well as primary root growth [90,91]. Many of the CLE peptides including CLE45 and CLE26 were shown to be responsive to environmental stimuli [91,92]. In addition, the *bam1;bam3* double mutant exhibits hypersensitivity to both dehydration and salt stresses [9]. These findings indicate that the CLE-BAM peptide–receptor pathways in roots may be regulated by environmental changes as well. Other phloem developmental genes such as *JAV1-ASSOCIATED UBIQUITIN LIGASE 1* (*JULIG1 or JUL1*) *and NAC DOMAIN-CONTAINING PROTEIN 20* (*NAC020*) were also found to be responsive to salt or other environmental stimuli (Figure 2C; reviewed in [93]). Taken together, our knowledge on phloem developmental plasticity is very limited. However, the stress-responsive expression of several key developmental genes could provide hints to further understand the molecular mechanisms underlying signaling in the phloem developmental response to abiotic stress (Figure 2).

Concluding remarks and future perspectives

Recent studies have highlighted diverse mobile signals that are transported between shoots and roots, orchestrating stress responses. These studies have greatly advanced our knowledge of coordination of shoot–root responses to abiotic stress and have also opened interesting fields for future research (see Outstanding questions). Balancing investments in growth and development with stress acclimation is of great importance under abiotic stress, and mobile signals play a crucial role in the fine-tuned synchronization of responses at the whole-plant level. Stomatal movements are described here as an example of how root-derived signals can activate signaling pathways and responses in the shoot. Newly identified regulators in these pathways provide strong support that hydraulic signals, CLE peptides, ROS, and Ca^{2+} are relevant signals regulating stomatal closure [9,15,38]. In the other direction, sucrose produced in the shoot and the mobile proteins HY5 and ELF4 affect the growth and development of the root system [48,50,52,60].

Numerous molecules including proteins and RNAs have been identified in vascular saps beyond those discussed here [94–96]. Vascular sap sampling and high-throughput functional characterization of mobile molecules in the saps will be critical steps to advance our understanding of long-distance signaling under abiotic stress. The development of 'omic' technology has permitted us to investigate plant transcriptome, proteome, and metabolome responses and identify mobile factors between shoots and roots in response to environmental changes [6,94,96,97]. Furthermore, as a connection bridging shoots and roots, a functional plant vascular system is essential for communication between different tissues. (Pro)cambial cells go through a complex process to become vascular conductive cells or other cell types that assist transport occurring in vasculature. However, our knowledge about this well-organized process remains limited. Recently, the emergence of single-cell sequencing technology enables the identification of cells at intermediate differentiation states and facilitates exploration of the ontogeny of different vasculature cell types [98–101], which will help us to understand the developmental plasticity of these vascular transport vessels. Intriguingly, many regulatory pathways or key growth regulators in the vascular system have now been shown to control growth plasticity and were demonstrated to be responsive to environmental challenges (Figure 2C) [67,93]. Further investigations of how these key regulators and pathways

Outstanding questions

Under water deficit stress, stomatal closure causes reduced sucrose synthesis, whereas carbon export to roots is enhanced. What are the molecular mechanisms underlying plant sucrose budget management?

How does sucrose translocation convey stress-specific information to adjust root growth, and how is SnRK1-TOR signaling activated in this process?

How does the root sense the shoot-experienced light changes delivered by HY5 and the temperature changes delivered by ELF4?

How does the endodermis/cortex-transmitted Ca^{2+} wave initiated in roots under salt stress progress to shoots to affect responses there?

Whether and how does mobile signal transmission play a role in reshaping vasculature morphology under stress conditions?

How is the movement of mobile signals affected by stress-shaped vasculature?

How are root hydraulic signals sensed by the shoot?

How do salt and drought stress affect phloem *de novo* formation, morphology, and cell identity?

coordinate growth and stress response will improve our knowledge on the interorgan communications that benefit plants as a whole. Therefore, the molecular mechanisms underlying morphological and physiological adaptations in the vasculature in response to abiotic stress represent an interesting field for future research.

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Declaration of interests

The authors declare no conflicts of interest.

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