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Toward unveiling plant adaptation mechanisms to environmental stresses

Water transport, perception, and response in plants

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Abstract
Sufficient water availability in the environment is critical for plant survival. Perception of water by plants is necessary to balance water uptake and water loss and to control plant growth. Plant physiology and soil science research have contributed greatly to our understanding of how water moves through soil, is taken up by roots, and moves to leaves where it is lost to the atmosphere by transpiration. Water uptake from the soil is affected by soil texture itself and soil water content. Hydraulic resistances for water flow through soil can be a major limitation for plant water uptake. Changes in water supply and water loss affect water potential gradients inside plants. Likewise, growth creates water potential gradients. It is known that plants respond to changes in these gradients. Water flow and loss are controlled through stomata and regulation of hydraulic conductance via aquaporins. When water availability declines, water loss is limited through stomatal closure and by adjusting hydraulic conductance to maintain cell turgor. Plants also adapt to changes in water supply by growing their roots towards water and through refinements to their root system architecture. Mechanosensitive ion channels, aquaporins, proteins that sense the cell wall and cell membrane environment, and proteins that change conformation in response to osmotic or turgor changes could serve as putative sensors. Future research is required to better understand processes in the rhizosphere during soil drying and how plants respond to spatial differences in water availability. It remains to be investigated how changes in water availability and water loss affect different tissues and cells in plants and how these biophysical signals are translated into chemical signals that feed into signaling pathways like abscisic acid response or organ development.

Keywords Water perception · Drought stress · Plant water relations · Stomatal regulation · Aquaporins · Hydropatterning

Introduction

Water is essential for plants. It is used as a solvent for chemical reactions, to transport nutrients and metabolites, as a coolant, and to generate turgor pressure for growth. Early plants evolved from green algae in an aqueous environment (McCourt et al. 2004). However, when plants began to colonize the land, approximately 700 million years ago (Heckman et al. 2001), they needed to develop or repurpose mechanisms to detect water in their environment and balance water uptake with water loss to avoid dehydration. Plants developed a vascular system to transport water by bulk flow over long-distances through a transpiration driven cohesion–tension mechanism (Lucas et al. 2013). To reduce water loss from the shoot and leaves, plants developed a waxy cuticle (Edwards et al. 1982). The development of stomata that can be actively regulated helped plants to improve their uptake of CO_2 for photosynthesis and limit their water loss by transpiration (Jones 1998).

By the 1800's physiologists had already recognized some of the complex ways plants responded to variation in water availability. Charles Darwin and his son Sir Francis Darwin observed that plants respond to water in their environment. They studied how roots would grow towards water (Darwin and Darwin 1880) and Sir Francis Darwin published his observations on stomatal closing in response to water deficit or dry air (Darwin 1898). Since then, many other processes have been identified. Plant responses towards water can be divided into short-term and long-term responses. For example, root hydraulic conductance is reduced with a half time of approximately 5 min through the action of

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aquaporins, which are integral membrane proteins that serve as transmembrane water channels, when leaves are removed from the shoot (Vandeleur et al. 2014). Similarly, stomata close within 20 min in response to changes of vapor pressure deficit (VPD) (McAdam and Brodribb 2016; Mott and Peak 2010). In contrast, developmental acclimation to water availability in the environment is usually a long-term response. While root bending induced by water potential gradients, termed hydrotropism, is observed after just 1 h in *Arabidopsis thaliana* (Shkolnik et al. 2018), the formation of different root architectures can take days or even weeks (Rellán-Álvarez et al. 2015).

Roots take on different architectures depending on water availability in the rhizosphere (Lynch 2013; Trachsel et al. 2011). A recently discovered response is hydropatterning (Bao et al. 2014; Robbins and Dinneny 2018). Plants that show hydropatterning respond to spatial differences in moisture availability around their roots and initiate lateral roots preferentially towards the side of the root that is in contact with more moisture. Similar to hydropatterning, xerobranching describes the suppression of lateral root initiation when roots grow through an air gap or a very dry area in the soil (Orman-Ligeza et al. 2018). Xerobranching may well be a more extreme case of hydropatterning. It has also been shown that the root crown in maize plants and other grasses responds locally to soil drying by making fewer shoot-born roots (Sebastian et al. 2016).

Plants respond to changes in moisture in the rhizosphere and the atmosphere. Water in the environment flows along the soil–plant–atmosphere continuum, which means that water moves through the soil, is taken up into the plant via the roots, transported to the shoot via a cohesion–tension mechanism driven by transpiration, evaporates in the substomatal cavities, and is transpired back to the atmosphere (Caldwell et al. 1998; Steudle 2001). Water transport along this continuum is driven by gradients in water potential and controlled through changes in hydraulic conductance. Changes in water availability lead to shifts in hydraulic gradients and turgor pressure inside plants. Severe water deficit occurs when there is an imbalance between water loss by transpiration and water uptake from the soil and results in turgor loss in whole tissues and wilting. Plants have several mechanisms such as the regulation of stomatal aperture (Tardieu and Davies 1993), regulation of tissue hydraulic conductivities (Sade et al. 2015), osmoregulation (Morgan 1984), and developmental responses (Dietrich et al. 2017; Robbins and Dinneny 2018) to acclimate to their environment and balance water loss with water uptake.

Much research has been done to understand how water flows through plants and how plants respond to changes in water availability. However, it is still not known what physical properties of water are perceived by plants, what tissues or organs are involved in water sensing and what molecular machinery serves as water sensors. Here we present an overview on the biophysics of water movement in plants and how changes in water availability affect these. We combine this overview with a summary of plant responses to changes in water availability. Finally, we present putative molecular mechanisms involved in plant water sensing.

Biophysics of water in the soil–plant–atmosphere continuum

Water cycles as liquid and water vapor through the soil–plant–atmosphere continuum. It is a polar molecule due to the difference in electronegativity between the oxygen and hydrogen atoms (Taiz and Zeiger 2010). This polarity makes water a good solvent for hydrophilic organic molecules and salts. Hence, water is ideally suited to transport nutrients and metabolites in plants. The polarity of water molecules allows them to form hydrogen bonds between each other resulting in a high capillary force and surface tension. Capillary force has important functions in both soil and plants. In soil, capillary action enables soil particles to retain water and allows movement of water from wet to dry areas. In plants, capillary action and surface tension help water to rise in the narrow xylem vessels up to the leaves. Due to the strong hydrogen bonds, water has also a high latent heat. Therefore, evaporation or transpiration of water causes significant cooling that helps plants to maintain their optimal temperature. As a fluid, water is also essentially incompressible which enables the formation of turgor pressure. Water vapor has a lower density than air and rises in the atmosphere. Finally, water is also involved as a reactant in many chemical reactions in plants, particularly in photosynthesis and respiration.

In the soil–plant–atmosphere continuum, water flow is driven by the water potential difference between the soil and the atmosphere (Fig. 1a) (Kramer and Boyer 1995). Water potential is the sum of pressure, osmotic, gravimetric, air pressure and matric potentials. Changes in soil water availability or atmospheric humidity, modulate the water potential gradient between soil and atmosphere. Accordingly, water potential gradients change inside plants as well. These changes can be buffered, to a certain degree, through regulation of hydraulic and stomatal conductance, which affect water flow rates through tissues, the xylem, and finally water loss by transpiration. On a plant tissue level, these water potentials are in equilibrium with the water potential of each cell. When plant water potentials decrease, water moves out of the cells and turgor pressure drops. This drop can be avoided to a certain degree by osmotic adjustment, which occurs through the accumulation of solutes. The water potential at which cells lose turgor and plants start to wilt is called the turgor loss point (Bartlett et al. 2014). Most likely this interplay between plant water potentials, turgor pressure

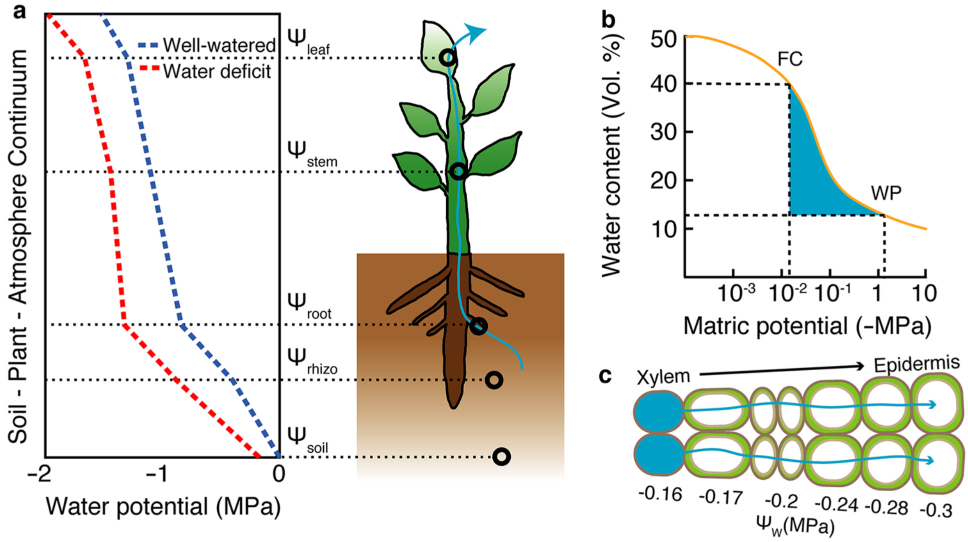

Fig. 1 Schematics of water relations in the soil–plant–atmosphere continuum. **a** Water potential gradients from soil to leaves (Ψ_{soil}, Ψ_{rhizo}, Ψ_{root}, Ψ_{stem}, Ψ_{leaf} are water potentials of soil, rhizosphere, root, stem, and leaf, respectively) for plants grown under well-watered (blue dashed line) or water deficit (red dashed line) conditions [modified after Tardieu et al. (2017)]. **b** Soil–water–retention curve showing the plant available water (blue area) in soils between field capacity (FC) and permanent wilting point (WP). **c** Radial water flow along growth induced water potential (Ψ_W) gradients in growing hypocotyls [based on research by Nonami and Boyer (1993)]

and osmotic potential change is perceived by plants and serves as a signal in biophysical and molecular responses.

The following sections will describe how water moves through soils and plants, how water availability changes water potential gradients and hydraulic conductance, how these influence cell water balance, and how plant growth generates water potential gradients inside plants.

Water in soils and the rhizosphere

Soil water retention and hydraulics depend on pore size distribution and organic content within those soils. Pore size distribution is mostly connected to soil texture. Soil texture is determined by the different proportions of sand, clay, silt and organic matter. Due to the grain sizes, sand has higher proportions of macro-pores (grain size: 0.05–2 mm), clay has higher proportions of intermediate pores (grain size: 0.002–0.05 mm), and silt higher proportions of micropores (grain size: < 0.002 mm) (Soil Science Division Staff 2017). Water drains more easily from larger pores compared to smaller pores due to lower capillary action, which leads to different soil water retention properties and soil hydraulic conductivity (Saxton and Rawls 2006; Tracy et al. 2015). Therefore, water deficit experiments may lead to different progressions in plant responses depending on the soil type that is used.

Plant available water is defined as the portion of water in the soil that is retained between field capacity, the amount of water free-draining soil can naturally hold, and the permanent wilting point, which is the maximum negative suction a plant can apply to extract water from the soil (Fig. 1b). Field capacity for most soils is around − 33 kPa soil matric potential, unless the soils contain a high proportion of sand (Richards and Weaver 1944), and the permanent wilting point is typically − 1.5 MPa soil matric potential (Richards and Weaver 1943). Soil matric potential approximately equals soil water potential, since ions are typically bound to the charged soil particles. It can be measured with a tensiometer. Depending on the soil texture, soils can hold different amounts of water between field capacity and permanent wilting point. Some plants also excrete mucilage into the rhizosphere which forms a film around soil particles and may improve soil water retention (Kroener et al. 2018; Walker et al. 2003). Interestingly, it was observed that water content was higher close to roots compared to the bulk soil in lupin and maize using neutron tomography (Moradi et al. 2011). Therefore, measurements of bulk soil water content may often not be an accurate representation of what plants actually experience around their roots.

In soils, water movement can be described by the Buckingham–Darcy equation:

$$Q = -k_{soil} \times \Delta\Psi_m \quad (1)$$

where k_{soil} is the soil hydraulic conductivity and $\Delta\Psi_m$ the soil matric potential gradient. As described above, soil matric potential is a function of soil water content. Soil hydraulic conductivity is a function of both soil water content and soil matric potential and declines rapidly with decreasing soil water content limiting the flow rate of water to roots. Hydraulic conductivity depends on soil texture and may differ between bulk soil and rhizosphere. Measurements using X-ray computed tomography and modelling suggested that bulk soil may have higher hydraulic conductivities than the rhizosphere due to aggregation of soil particles by roots (Daly et al. 2015). These differences were stronger in clay compared to sand. It has also been shown that dry roots shrink in soil and air gaps develop between soil and roots (Carminati et al. 2009; Nobel and Cui 1992). This shrinkage leads to a significant decrease in hydraulic conductivity. Hence, it was suggested that soil hydraulic conductivity is a major limiting factor for water uptake by plant roots. Root hair formation is one mechanism of plants to alleviate this effect and improve hydraulic connection (Bao et al. 2014; Carminati et al. 2017).

The observations show that soils are a very heterogeneous environment (Brady and Weil 2008). Interesting observations are being made about soil hydraulics and how these change depending on soil texture and the rhizosphere. Often, research on root development or water deficit are made on agar medium or in hydroponic systems using osmotica like polyethylene glycol (Robbins and Dinneny 2016; van der Weele et al. 2000). These set-ups are more convenient due to the sterile environment, known nutrient content and ease of observation. However, this also takes away most features that soils have. For example, changes in hydraulic conductivity and the occurrence of air gaps cannot be replicated easily. This may limit the way new adaptive mechanisms of plants to changes in soil hydraulic properties can be discovered. At the same time, experiments in soils require a careful characterization to understand how the specific soil properties contribute to observations.

Water in plants

In plants, transpiration creates a water potential gradient from the roots to the leaves that drives water flow. Water flow through the plant is mainly dependent on hydraulic conductivity and the potential gradient and can be described by the Ohm's law analogue:

$$J_v = \frac{\Delta\Psi_{plant}}{R_{plant}} = \frac{\Psi_{soil} - \Psi_{root}}{R_{root}} + \frac{\Psi_{root} - \Psi_{stem}}{R_{stem}} + \frac{\Psi_{stem} - \Psi_{leaf}}{R_{leaf}} \tag{2}$$

where J_v is the flow rate that approximately equals transpiration, R_{plant} the hydraulic resistance along the whole plant which is the inverse of hydraulic conductivity $R = 1/L$, and $\Delta\Psi_{plant}$ the potential gradient driving flow (Van den Honert 1948). Similar to Ohm's law, hydraulic resistances (R_{root}, R_{stem}, R_{leaf}) and water potential gradients (Ψ_{soil}, Ψ_{root}, Ψ_{stem}, Ψ_{leaf}) between individual parts of the plant can be written in series. Therefore, water potential gradients of individual parts of the plants can be controlled through changes in hydraulic resistance in those parts.

The cohesion–tension theory is most widely accepted as being a likely explanation for how water moves from soil to leaves (Schenk et al. 2017; Steudle 2001). The theory postulates that water forms columns inside the capillary network of plants due to its high cohesive forces. Transpiration creates negative water potentials inside leaves and water moves through the xylem towards the sites of evaporation. This negative sap pressure that drives bulk flow through the plant can be measured using a pressure chamber (Scholander et al. 1965) and the pressure probe (Steudle 2001).

Root water uptake occurs through the apoplast and by cell-to-cell pathways (symplastic and transcellular) (Steudle and Peterson 1998). Water flow from soil to the xylem through the apoplast occurs mainly by bulk flow that can be described by Darcy's Law, similar to water flow through soils, where flow rate is a function of hydraulic conductivity and the pressure gradient driving flow. In the cell-to-cell pathway, water moves transcellular (across cell membranes) by diffusion and symplastically through plasmodesmata. Symplastic and transcellular water flow are important components of root water uptake, since hydrophobic barriers restrict apoplastic water movement in mature parts of roots. Hydrophobic barriers, such as the Casparian strips and suberin lamellae in the endodermis, have important functions in controlling nutrient and water uptake into the stele (Barberon 2017). It was found that increased suberin content in roots of Arabidopsis caused a decrease in day time transpiration (Baxter et al. 2009). Observation of increased suberin lamellae deposition in drought stressed grapevine roots indicate that this may be an important function for drought tolerance (Vandeleur et al. 2009). Fiscus and Kramer (1975) proposed a simple equation that describes both osmotic and pressure driven water flow through roots:

$$J_v = L_p \times [P_a - P_s + \sigma(\pi_a - \pi_s)] \tag{3}$$

where J_v is the volume flow rate, L_p the hydraulic conductivity, P_a and P_s the pressure potential of the apoplast and symplast, respectively, σ the reflection coefficient, and π_a and π_s the osmotic potentials of the apoplast and symplast, respectively. Water flow is dependent both on pressure and osmotic gradients and flow rate is controlled by hydraulic conductivity. Hydraulic conductivity is controlled through active gating of aquaporins. Therefore, aquaporins significantly influence hydraulic conductance for radial water flow through the root. This finding is supported through observations by Knipfer and Fricke (2010) who measured significant radial water transport through the cell-to-cell pathway in barley roots. A comparison in maize roots showed that axial hydraulic conductivity was significantly larger than radial hydraulic conductivity, except for the apical zone (Frensch and Steudle 1989). Therefore, radial water flow is limiting for root water uptake.

It was shown that not all roots had the same conductance for water uptake in maize plants (Ahmed et al. 2018). Higher radial water flow was measured for crown roots compared to seminal roots. While axial hydraulic conductivity was similar for crown and seminal roots close to the root tip, distal parts of crown roots had much higher conductivity compared to seminal roots. In comparison to the fibrous root system of maize plants, estimations of hydraulic conductivities in lupin taproots by modelling suggested that lateral roots were the main points of water uptake in the root system and that hydraulic conductivities increased towards root tips (Zarebanadkouki et al. 2016). Modelling of xylem water potentials of roots in the same study suggested that water potentials would be less negative towards root tips (− 0.02 to − 0.035 MPa) and more negative towards the shoot (− 0.1 to − 0.2 MPa). Interestingly, modelling of water potentials in the apical growth zone of maize roots indicates that growth could induce much lower water potentials in this zone (Wiegers et al. 2009; Robbins and Dinneny 2018). This is supported by psychrometer measurements on maize roots that found water potentials below − 0.4 MPa close to the root apex (Westgate and Boyer 1985). Additional modelling approaches have been taken to understand hydraulics and water uptake of roots (Couvreur et al. 2018; Meunier et al. 2017).

Interestingly, roots are able to continue growth at low water potentials even when shoot growth is inhibited (Sharp et al. 1988). This is partly due to osmotic adjustment of the growing tissue to maintain turgor (Voetberg and Sharp 1991). Nonetheless, growing tissue showed lower turgor when grown in media with low water potentials. Therefore, it was suggested that changes in cell wall properties may compensate for lower turgor pressure and allow continued growth (Spollen and Sharp 1991). While root growth does respond to changes in root water uptake, water supply to growing tissues through the phloem may significantly contribute to growth as well (Wiegers et al. 2009; Boyer et al. 2010).

These findings point to the significant role of cell-to-cell water transport in roots controlled by aquaporins. Water flow rate or water potential changes may therefore be perceived by cell membranes along this pathway. Higher water uptake by root tips and certain root types suggest that not all parts of a root system are well connected with their environment and sensitivity for water perception may correlate with higher conductivity. Moreover, root growth responses to changes in water potential indicate that water perception may occur in those tissues.

Shoot water transport happens via bulk flow through the xylem. Therefore, the xylem allows high volume and low resistance water transport. It was shown that hydrogels localized to inter-vessel bordered pits in the xylem control hydraulic conductance and, hence, water potential gradients (Zwieniecki et al. 2001). According to this research, increases in potassium ions lead to deswelling of hydrogels leading to higher hydraulic conductance. It was hypothesized, that potassium ions could move into the xylem by recycling from the phloem in response to increasing transpiration. This could provide a passive control mechanism for xylem hydraulic conductance.

Growth induced water potential gradients were first observed in the hypocotyl of soybean seedlings (Molz and Boyer 1978; Nonami and Boyer 1993). In the elongating region, more negative water potentials were measured near the epidermis compared to the xylem (Fig. 1c). These gradients were absent in mature regions of the hypocotyl. It was proposed that these gradients are necessary to transport water from the xylem through the growing tissue. The water potential gradients were shown to be due to osmotic adjustment of cells in growing tissues (Westgate and Boyer 1985).

Interestingly, measurements seem to be very sensitive to the experimental setup. In the elongating hypocotyl of Ricinus seedlings no such water potential gradients were found, but significant gradients in turgor pressure were observed when measured with a pressure probe (Meshcheryakov et al. 1992). However, when elongating cells in the hypocotyl of soybean seedlings were measured using a pressure probe, growth induced water potential gradients were observed (Nonami and Boyer 1993). The authors suggested that transpiration induced water potential gradients in the xylem could mask the growth induced water potential gradients.

Similar to the hypocotyl, growth induced water potential gradients were observed in growing leaf and root tissues of maize (Westgate and Boyer 1984). Water potentials in mature tissue responded mainly to transpiration and became more negative from the roots to the leaves. In growing tissue, water potentials were influenced both by transpiration and growth. Subsequent research showed that the axial transpiration-induced water potential gradients were smaller than the radial growth-induced gradients (Tang and Boyer 2002). Water deficit caused the disappearance of growth induced gradients and leaf elongation ceased. Pressurization of the root system helped to re-establish the water potential gradients and leaf growth resumed (Tang and Boyer 2003). This cessation is contrary to root growth, which is maintained during some degree of water deficit. It was hypothesized that leaf growth may be more sensitive to water deficit compared to root growth due to a stronger effect of water deficit on leaf water potential compared to root water potential, which affect the growth induced water potential gradients (Westgate and Boyer 1985).

Growth induced water potential gradients and their sensitivity to changes in water supply are an interesting area for understanding how plant growth could respond to changes in water availability. Using modelling, it was demonstrated how these gradients could explain patterning of lateral roots

(Robbins and Dinneny 2018). More experimental work is needed to directly and reliably collect data on these gradients that could be used for modelling. Regulatory mechanisms like hydrogel swelling in xylem border pits which would be regulated by phloem recycling of potassium ions suggests that passive feedback systems could play a role in adaptation to changes in water availability (Zwieniecki et al. 2001). Aquaporins that function as dual water and ion channels could be involved in moving potassium ions from the phloem to the xylem to facilitate this regulation (Byrt et al. 2017).

In leaves, water moves from the xylem to the substomatal cavities (Zwieniecki et al. 2007). It appears that the strength of hydraulic connections in leaves depend on plant species. In gymnosperms, a weak hydraulic connection was found between the xylem and epidermis, creating distinct water pools. In angiosperms, bundle sheath extensions functioned as hydraulic bridges or the whole leaf was hydraulically well connected. These different hydraulic gradients may cause water potential gradients and help with improved hydropassive regulation of stomatal conductance (Buckley et al. 2011). It was observed that aquaporins have a significant role in the regulation of symplastic water flow through the bundle sheath (Sade et al. 2014). By gating water flow through the bundle sheath, they could provide a hydraulic feed-forward signal for stomatal regulation. Past the bundle sheath, modelling suggested that most water may flow through the apoplast in leaves, which is likely to be contrary to the more symplastic radial water movement in roots (Buckley 2015).

Stomata are the terminal gatekeepers for plant water relations and have a significant regulatory role for CO_2 uptake and transpiration. Transpiration is driven by the vapor pressure deficit (VPD) between the atmosphere and substomatal cavities. Water potential of the atmosphere depends mainly on relative humidity and to some extent on temperature; 30–80% relative humidity (rH) equates to a water potential range of − 150 to − 30 MPa. Plants respond to VPD, which is a function of temperature and relative humidity differences between the atmosphere and substomatal cavities, rather than absolute measures of humidity (Grantz 1990).

Experiments on isolated epidermis showed that stomata are more sensitive to changes in humidity on the inside of the epidermis than on the outside (Shope et al. 2008). Also, McAdam and Brodribb (2016) showed that stomata respond to changes in leaf turgor through the action of abscisic acid (ABA). In grasses, stomata have subsidiary cells that help with fast stomatal movements through coupled osmotic and turgor adjustment (Franks and Farquhar 2007; Raissig et al. 2017).

Both hydraulic and stomatal control play significant roles in leaf gas exchange. Therefore, water perception mechanisms may be localized to structures like the bundle sheath and guard cells. Responses to changes in turgor indicate that turgor status may be translated into chemical signals like ABA in leaves. Further research is needed to localize leaf structures that perceive turgor changes and how these lead to the translation into chemical signals. Furthermore, it remains to be explored if alternative mechanisms to ABA have a significant regulatory role for stomatal conductance.

Plant responses to changes in water availability

Plants can easily balance their water uptake against water loss when soils are at field capacity and VPD is low. Under these conditions, only small gradients in water potential that drive water flow from the soil to the atmosphere develop inside plants. When plant water potential is low, cells can maintain high turgor pressure and stay fully hydrated.

However, when soil water content drops, hydraulic resistance for water flow through the soil increases and soil matric potential decreases. This change causes steeper water potential gradients inside the plant, i.e. plant water potential becomes more negative, which drives water flow through the plant. Similarly, higher VPD causes an increase in transpiration rates and steeper water potential gradients in the plant.

Plants respond in different ways to water deficit. They can make developmental decisions like redirecting root growth to increase their water uptake or producing fewer stomata to decrease water loss. Alternatively, they can respond more quickly through regulatory mechanisms like stomatal closure, osmotic adjustment or control of tissue hydraulic conductivity.

Water deficit is often perceived on a systemic level when soil water availability decreases and stress responses are initiated in all parts of the plant (Chaves et al. 2003). However, it has been demonstrated that plants can also respond to local differences in water availability (Robbins and Dinneny 2018). To date, systemic effects of water deficit have received significantly more attention than responses to local differences in water availability.

Systemic effects of water deficit

Stomatal regulation is one of the most studied plant responses to water deficit (Darwin 1898; Jones 1998). Plants can close their stomata to reduce water loss by transpiration and therefore decrease flow rate, which leads to a reduction in the water potential gradients inside the plants. However, this closure leads also to a reduction in photosynthesis since CO_2 uptake is reduced as well. Therefore, reducing water loss while maintaining CO_2 uptake is a significant dilemma for plants.

Stomata respond both to changes in soil water availability and changes in atmospheric humidity (Tardieu and Simonneau 1998). Some plants exhibit strict control over stomatal movements to maintain a more steady leaf water potential (isohydric) while other plants have a less conservative control with leaf water potentials decreasing more dramatically during water deficit (anisohydric). These relationships between leaf water potential and stomatal conductance indicate that changes in leaf water potential may serve as a direct or indirect signal to inform plants about water availability in their environment.

Stomata were found to be sensitive to the plant hormone ABA (Jones and Mansfield 1972). Briefly, ABA causes increases in cytosolic calcium (Ca^{2+}) in guard cells (Fig. 2a) (Munemasa et al. 2015). Calcium signaling triggers the release of anions (A^-) leading to membrane depolarization. Membrane depolarization activates outward-rectifying K^+ channels and causes turgor loss leading to stomatal closure. ABA is a very important stress signaling compound, which is why it's method of action has been a major focus in abiotic stress research. Early research suggested that ABA was produced in the roots and transported to the shoot where it closed stomata during water deficit (Zhang et al. 1987). However, Holbrook et al. (2002) showed that ABA biosynthesis and stomatal closure were even induced by water deficit if roots could not synthesize ABA. Experiments by Christmann et al. (2007) suggest that a long-distance hydraulic signal from the roots may induce ABA biosynthesis in the shoots. Likewise, McAdam and Brodribb (2016) demonstrated that external pressure induced changes in leaf cell turgor can trigger ABA biosynthesis required for stomatal closure. Their work demonstrates that hydraulic signaling is an important component to induce stress responses in the shoot. It remains, however, unknown how these hydraulic signals are perceived. The CLAVATA3/EMBRYO-SURROUNDING REGION-RELATED 25 (CLE25) peptide has been reported as long-distance signal from the roots to the shoot (Takahashi et al. 2018). While these would be slower than hydraulic signals, they may be an important mechanism during gradual soil drying which would be most common under natural conditions. Interestingly, other CLE peptides were found to be involved more locally in stomatal development and regulation. It was discovered that CLE9 has a role in stomatal closure in response to drought mediated by ABA (Zhang et al. 2018). In addition, CLE9/10 peptides negatively regulate stomatal development by destabilizing SPCH (Qian et al. 2018). Another root to shoot long-distance signal that regulates stomatal closure could be sulfate (Batool et al. 2018; Kataoka et al. 2004).

While ABA is an important hormonal signal for stomatal regulation, not all plants are sensitive to ABA (McAdam and Brodribb 2012) and even ABA biosynthesis mutants in Arabidopsis can still show stomatal closure in response to changes in VPD (Assmann et al. 2000). In contrast, Bauer

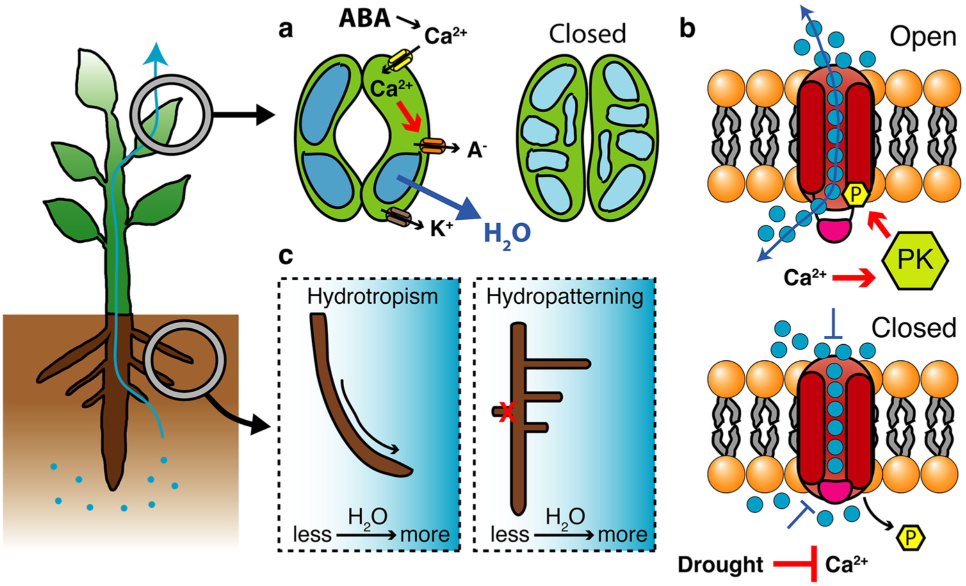

Fig. 2 Plant responses to changes in water availability. **a** ABA induced stomatal closure. ABA induces cytosolic calcium (Ca^{2+}) increases. This activates anion channels (A^-) causing membrane depolarization and potassium (K^+) efflux. Ion efflux promotes water efflux causing turgor loss and, hence, stomatal closure. **b** Aquaporin gating might be controlled through calcium induced phosphorylation by a protein kinase (PK). Water deficit may inhibit mechanosensitive calcium channels causing dephosphorylation (phosphoryl group is shown as yellow hexagon with the letter P) of aquaporins leading to closure through a conformational change of loop D (pink shape). Water molecules are symbolized by blue circles. **c** Spatial differences in water availability lead to hydrotropism, root growth towards areas of higher moisture, and hydropatterning, moisture dependent lateral root patterning

et al. (2013) claimed that stomata require the ability to synthesize ABA in the guard cells themselves, in order to respond to changes in atmospheric VPD. This controversy shows that further research is needed to investigate whether there are several parallel mechanisms for stomatal regulation and how ABA biosynthesis is induced by hydraulic signals.

Aquaporins, which are water permeable integral membrane channels, can adjust plant water status by regulation of tissue hydraulic conductivity (Chaumont and Tyerman 2014). For example, aquaporins have significant roles in controlling root and shoot hydraulic conductivity (Javot et al. 2003; Postaire et al. 2010; Steudle 2000). Through this control, they can adjust water potential gradients inside the plant. While it is known that aquaporin gene expression (Alexandersson et al. 2010) and activity, regulated by phosphorylation (Maurel et al. 1995; Tornroth-Horsefield et al. 2006), is affected by water availability, it is not clearly known how aquaporins perceive these changes. It was proposed by Johansson et al. (1998) that mechanosensitive calcium channels could respond to changes in water potential and regulate calcium signaling that would activate phosphorylation of aquaporins by a protein kinase (Fig. 2b). Interestingly it has been shown that the AtPIP2;1 aquaporin in guard cells can be phosphorylated by the OST1 protein kinase involved in stomatal regulation and facilitate water and hydrogen peroxide transport (Grondin et al. 2015; Rodrigues et al. 2017). Therefore, aquaporins may also be involved in stomatal control directly. Also, Byrt et al. (2017) observed that the AtPIP2;1 aquaporin functions as a non-selective cation channel. Therefore, this aquaporin could be involved in rapid turgor regulation as observed in guard cells. Apart from water, some aquaporins facilitate the transport of CO_2 (Zhao et al. 2017). This dual transport creates a connection between water transport and photosynthesis. However, CO_2 transport may be through a different part of the pore than water transport.

Aquaporins may also be involved in stomatal regulation through a hydraulic feed-forward control mechanism of stomata by bundle sheath hydraulic conductivity (Sade et al. 2014; Shatil-Cohen et al. 2011). It was found that bundle sheath hydraulic conductivity is a bottleneck for water flow in leaves and could be controlled by aquaporins which are sensitive to ABA. This would send a hydraulic signal to stomata inducing closure. This mechanism could increase guard cell sensitivity to water deficit stress beyond purely direct ABA induced stomatal closure. It was demonstrated that this hydraulic regulation could even induce stomatal closure when guard cells themselves were insensitive to ABA (Pantin et al. 2013). Hence, a strong hydraulic component must be involved in stomatal regulation.

Developmental acclimation was observed for plants in response to water deficit. Changes in stomatal density and shape allow plants to grow in certain environments. It has been observed in multiple species that plant water status influenced stomata density and guard cell size (Hamanishi et al. 2012; Lake and Woodward 2008; Xu and Zhou 2008). Inhibition of stomatal development by ABA accumulation during water deficit was proposed to be responsible for the link between plant water status and stomatal density (Tanaka et al. 2013). Interestingly, changes in stomatal density were also found to be controlled through humidity induced changes in DNA methylation in *SPEECHLESS* and *FAMA*, two genes involved in stomatal development (Tricker et al. 2012). These changes were even able to be transmitted across multiple generations (Tricker et al. 2013). Measurements of transpiration and nitrogen uptake in Arabidopsis lines with higher and lower stomatal densities revealed that water uptake and transpiration scaled with stomatal density (Hepworth et al. 2015). Interestingly, nitrogen uptake was not limited by lower water uptake in this experiment, but increased with higher transpiration and higher stomatal density.

Leaf expansion was found to be limited by hydraulic effects during water deficit (Pantin et al. 2011). Low leaf turgor pressure during the day correlated with reduced expansion. In roots, ABA accumulation has a positive effect on growth of the primary root at low water potentials, i.e. water deficit (Sharp et al. 2004). However, when plants are well watered, ABA inhibits root growth. These contrasting responses show that ABA can have a different effect depending on the water status of the plant. Likewise, ABA responses vary in different parts of the root. While primary root growth is induced by ABA under water deficit, lateral root growth is inhibited (Xing et al. 2016). Likewise, lateral roots were more affected by salt stress than primary roots, since salt stress induced high levels of ABA signaling that were specific to lateral roots (Duan et al. 2013). Interestingly, research by McAdam et al. (2016) indicated that root growth was promoted by ABA derived from the shoot and not the root itself. This idea suggests that perception of changes in water availability is done by the shoot. In Arabidopsis, it was shown that ABA applied to the shoot was transported to the root, but not vice versa, using a FRET-based ABA reporter (Waadt et al. 2014). The authors concluded that low transpiration in their experimental setup prevented ABA transport from the root to the shoot. However, the same experiment was not tested under transpiring conditions. In this regard, transpiration may be a prerequisite for root to shoot ABA signaling. Different plant responses to ABA depending in plant hydration status and tissue type demonstrate that ABA is not a simple switch for stress responses. Moreover, research is required to understand in which tissues physical signals are translated into chemical signals like ABA and whether ABA acts more locally or actually moves to different parts of a plant to coordinate stress responses.

Local effects of water deficit

Water deficit has mainly been studied in a whole plant context by looking at systemic effects. However significant local differences in water availability can occur in soils due to large air-filled pores or different soil textures. These local effects may not necessarily induce whole plant stress responses but may be perceived locally in the roots growing in these areas.

Already Charles Darwin and Sir Francis Darwin (1880) observed that roots of plants would grow towards water, a phenomenon that was called hydrotropism (Fig. 2c). Using pea seedlings lacking gravi—and phototropic responses, it was proposed that the root cap is required for the directional perception of water during hydrotropism (Jaffe et al. 1985). However, further research suggested that hydrotropic root bending is mediated by root cortex specific ABA signaling in the elongation zone and that the root cap is not required for those responses (Dietrich et al. 2017).

While hydrotropism affects root growth direction, it was observed by Babé et al. (2012) that a transient water deficit inhibited lateral root initiation in barley and maize within the root region that experienced the stress. It was demonstrated by Bao et al. (2014) that this phenomenon was not related to hydrotropism, but a separate response where lateral roots are preferentially patterned towards the direction of higher water availability (Fig. 2c). The newly discovered response was termed hydropatterning. Hydropatterning was not affected in mutants for ABA perception, biosynthesis and signaling pathways. A biophysical model was constructed which suggests that growth induced water potential gradients inside the root differentiation and elongation zone are required for hydropatterning (Robbins and Dinneny 2018). While it is not known how these water potential gradients could be perceived, it was found that SUMOylation of the auxin response factor ARF7 on the air side of lateral roots causes the inhibition of lateral root initiation (Orosa-Puente et al. 2018). According to Orman-Ligeza et al. (2018), transient water deficit induced lateral root inhibition is triggered by the PYR/PYL/RCAR-dependent ABA signaling pathway. They termed this phenomenon xerobranching and suggested that it may be a more extreme manifestation of hydropatterning. While in their experiments *pyr*/*pyl* mutants in Arabidopsis did not show any response to exogenous ABA application compared to wild-type plants that showed inhibition of lateral root growth, it remains unknown whether these mutants would also not respond to a transient water deficit. Alternative signaling pathways may be involved.

While many observations of systemic plant responses to water deficit are reported in the literature, local sensing or adaptation to changes in water availability are still rare. Reports on particular cell types that would sense changes in water availability are still few. ABA has a significant role in signaling of water deficit, but it is not clear how particular locations of ABA biosynthesis contribute to specific plant responses. It seems likely that several mechanisms and signaling cascades contribute to plant water deficit responses.

Putative water sensing mechanisms in plants

From physiological observations, it is known that plants are very sensitive to changes in water potential both on a systemic as well as a local level. Water itself is not limiting to chemical reactions in plants. Therefore, water availability cannot be sensed via reaction rates. However, water serves as a transport medium for nutrients and metabolites. Hence, limitations of certain components in chemical reactions may serve as an indirect signal for water availability or water flux rates through plants. A benefit of hydraulic signals themselves would be that they propagate very fast (at the speed of sound!). In particular, observations by Christmann et al. (2007) and Vandeleur et al. (2014) on hydraulic root to shoot or shoot to root signaling suggests that hydraulic signals may be very important and that these are transformed into chemical signals in the specific target tissue.

Mechanosensitive (MS) ion channels could act in target tissues to translate hydraulic cues into chemical signals (Christmann et al. 2013; Hamilton et al. 2015). For example, tension in membranes of turgid cells triggers a conformational change that opens the channel (Fig. 3a). In plants, five different families of MS ion channels have been identified: mid1-complementing activity (MCA), mechanosensitive channels of small conductance-like (MSL), OSCA, TMEM63, and two-pore potassium (TPK) families. Recently, it was demonstrated that the OSCA/TMEM63 family of ion channel proteins could be activated by pressure and indentation stimuli (Murthy et al. 2018). It was observed by Nakagawa et al. (2007) that the Ca^{2+}-permeable, stretch-activated channel MCA1 was required in Arabidopsis for penetration of hard agar medium. Tension and compression of tissues surrounding lateral roots meristems were observed to influence organ initiation (Vermeer et al. 2014). This is in line with observations that aquaporin expression in and around lateral root primordia is coordinated in a certain way that is important for proper lateral root emergence (Péret et al. 2012; Reinhardt et al. 2016). Aquaporins themselves have been suggested to be pressure gated channels (Leitao et al. 2014; Ozu et al. 2013; Ye et al. 2004). They could function not only in limiting water loss during dehydration or accelerating water uptake during rehydration, but also have a role in water deficit signal transmission through hydraulic feed-forward signaling for stomatal closure (Sade et al. 2014) or through ROS signal transmission (Grondin et al. 2015; Rodrigues et al. 2017). Plasmodesmata were

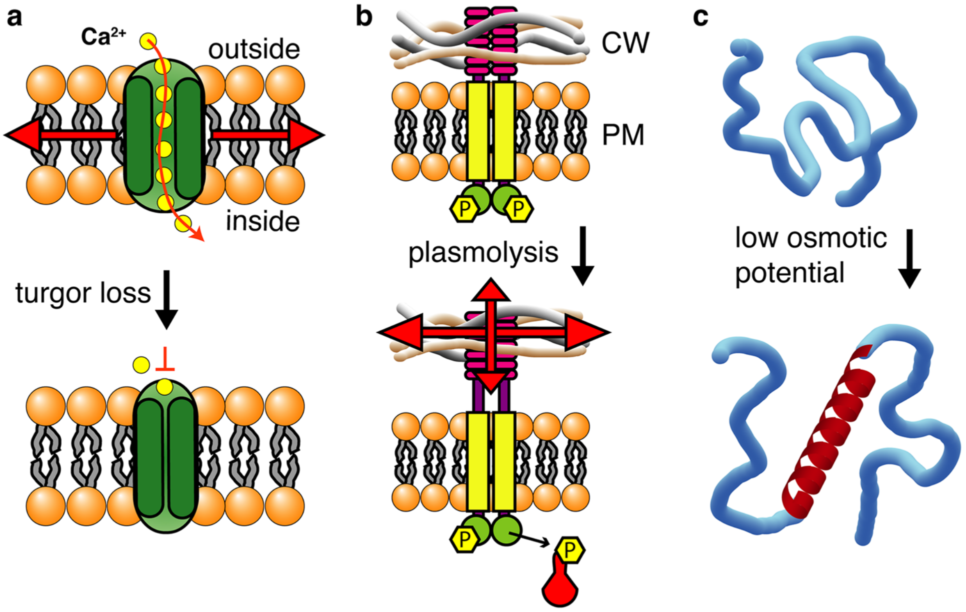

Fig. 3 Putative sensors for changes in water availability in plants. **a** Mechanosensitive ion channels are activated by tension (red arrows) in the cell membrane [for example calcium (Ca^{2+}, molecules symbolized as yellow circles) channels]. Reduced turgor causes loss of tension and closure of the channel. **b** Receptor-like kinases have extracellular domains that could sense the separation of the plasma membrane (PM) from the cell wall (CW) during plasmolysis. Phosphoryl groups (yellow hexagon with the letter P) are transferred to target proteins (red shape) during phosphorylation. **c** Intrinsically disordered domains (blue shape) in proteins could take on ordered structures like alpha helix domains (red shape) in response to changes in the osmotic potential and, therefore, acquire new functions

found to be important in the transmission of developmental signals specifically in lateral root patterning (Benitez-Alfonso et al. 2013; Zambryski and Crawford 2000). It was observed that plasmodesmata were directly gated by pressure gradients which could inhibit signal transmission (Oparka and Prior 1992). Cell volume sensing has been investigated for the mammalian TRPV4 ion channel (Toft-Bertelsen et al. 2018). The authors suggest that the channel is involved in volume sensing but not regulation. FERONIA, a receptor-like kinase, was found to be necessary to sense defects in the cell wall upon damage by salinity in Arabidopsis (Feng et al. 2018). Sensors like these could also be involved in sensing abiotic stress like water deficit that affect cell wall hydration and strain. For example, receptor-like kinases could potentially detect the separation of the plasma membrane from the cell wall during plasmolysis (Fig. 3b). Proteins with intrinsically disordered domains are a focus of recent research (Cuevas-Velazquez and Dinneny 2018). For example, Cuevas-Velazquez et al. (2016) showed that late embryogenesis abundant (LEA) proteins could take on ordered structures in response to water deficit (Fig. 3c). In this way water availability sensing could be performed by many other proteins with intrinsically disordered domains.

This overview shows that many different putative water sensing mechanisms are known in plants, but it is not clear under which conditions they are relevant. In particular, MS ion channels represent a large group of proteins that could have roles in perception of changes in turgor or water potential. Future research needs to connect sensing and signaling of those sensors to specific conditions where water availability changes.

Conclusions and future perspectives

Our review of the literature shows that changes in water potential gradients and turgor pressure occur as a result of changes in water availability or VPD both on a systemic, as well as local level, in plants. Plant responses to changes in water availability have been connected to changes in turgor or water potential gradients. It remains an open question how these biophysical cues are perceived and transformed into chemical signals. Knowing the precise locations where these changes occur will help to connect them to specific sensory mechanisms. To date, it is still challenging to measure changes in turgor or osmotic potentials at cellular resolution and deep within tissues. Computational modelling offers a huge opportunity to fill these gaps. Also, the knowledge of how external changes in the environment affect plant water relations will help to design specific experiments to study systemic or local effects of water deficit in plants. An important consideration for future experiments will also be to use physiologically relevant conditions and test how laboratory observations translate into soil or field grown plants.

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