Hydraulic signals in long-distance signaling
Alexander Christmann, Erwin Grill and Jin Huang

Higher plants are sessile organisms that continuously adapt their metabolism and development in response to a changing environment. Control of water uptake and the maintenance of water status are key for the survival and optimal growth of plants. Environmental factors such as radiation, air temperature, rainfall, and humidity have a high impact on plant water relations. Hence, plants require a coordinated and timely response in above-ground and below-ground organs to cope with the changing need to take up and preserve water. In this review we will focus on changes in plant water availability and on how information on the water status is communicated to remote plant organs. We will summarize the current knowledge of long-distance signaling by hydraulic cues and of potential sensors required to convert a physical signal into a chemical messenger, namely the plant hormone abscisic acid (ABA).

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Homeostasis of water status
Plants are an integral component in the global movement of water from the soil to the atmosphere, which is referred to as the hydraulic soil–plant–air continuum [2]. Gradients of water vapor generate strong forces for water mobilization. At 20 °C, for example, a one per cent difference in water saturation between plant tissues and the air generates a water potential difference of ~1.35 MPa (~13.5 bar) which drives transpiration [3]. In essence, plants facilitate the translocation of water from the soil to the air through plant tissues along the water potential (Ψv) gradient, with lowest values of Ψv in the leaves (Box 1). If the gradient is inverted, water will take the opposite route [4,5], which is of relevance for water uptake via the shoot [6].

In terrestrial plants, transpiration gives rise to a need to balance water consumption and uptake. Plants have evolved sophisticated mechanisms to control water uptake, conductance, and release by long-term regulation of root and shoot development, by short-term adjustments of water potential, control of apoplastic and symplastic routes of water movement, and by control of gas exchange via stomata [7,8,9,10,11].

Water deficit represents a severe challenge for the maintenance of a proper plant water status. Drought stress induces ABA-dependent and ABA-independent reactions [12]. Stomatal closure is a rapid response to a reduced Ψv [1] as is initiation of osmotic adjustment [13]. ABA is the central endogenous messenger in this water deficit reaction, as it controls many of the physiological responses. ABA biosynthesis is strongly stimulated by water deficit [14,15]. ABA mediates stomatal closure [7,10,11] and enhances the biosynthesis of protective proteins and osmoles such as proline [16,17]. The plant hormone maintains root growth at low substrate water potentials [18] while, through closing stomata during drought, impairs shoot growth by inhibiting biomass accumulation [19]. Water uptake and distribution during drought is controlled by aquaporin activity [20,21]. Spatial and temporal modulations of aquaporin activity have a high impact on local tissue water status and foster nitrate acquisition by the root system [22] as well as lateral root emergence [23]. ABA increases aquaporin expression and this translates into increased hydraulic conductance [24,25]. However, ABA negatively affects aquaporin gating in shoots [26] involving changes in aquaporin phosphorylation status [27], pointing to a sophisticated adjustment at the whole plant level. The symplastic nature of the plant, where only guard cells are sympodially isolated, requires the orchestrated and timely response of the entire organism to changes in Ψv. Water deficit in leaves leads not only to a need to reduce transpiration but to a need for increased water delivery via the root system. However, under mild drought stress root hydraulic conductivity is at best maintained and declines under increasing stress conditions [28,29]. The root system has, however, the capacity to enhance water flux as observed in ABA-overproducing maize lines [25].

The limited adjustment of water delivery from roots to changing demands is also reflected in the phenomenon of ‘midday depression of transpiration’ [30] where under nondrought conditions trees temporarily reduce transpiration when the evaporative demand peaks around noon. In essence, the homeostatic control of the water status requires sophisticated and coordinated adjustments including responses to local challenges at remote sites.
Box 1 Differences in water potential $\psi_w$ define the direction of water flux where water flows to the medium with more negative $\psi_w$. $\psi_w$ is the sum of several potentials, the pressure potential $\psi_P$ (e.g., turgor pressure, water tension), osmotic potential $\psi_S$, and the gravitational contribution $\psi_G$:

$$\psi_w = \psi_P + \psi_S + \psi_G$$

$\psi_w$ decreases along the soil-plant-air continuum. Conductance of water in the plant and its leaf water release is restricted by a number of resistances along the water path such as symplastic water movement and its control by endodermal and bundle sheath cells, xylem-structure related resistances to flow, and stomatal aperture. During daytime, tension (negative pressure) frequently develop in water conducting xylem because of imbalance between water release and uptake. $\psi_P$ in vessels then becomes negative and causes a decrease in turgor in living neighboring cells. Turgor can only be maintained if $\psi_S$ compensates for this tension, that is, is sufficiently negative, which is accomplished by osmotic adjustment. Changes in $\psi_S$ of the substratum result in changes of the turgor pressure in mesophyll cells (see Box Figure 1).

Box Figure 1

A decrease in soil water potential translates to a decrease in steady-state levels of turgor pressure in mesophyll cells. Turgor was measured in rosette leaves of 4-week-old Arabidopsis plants (filled symbols) grown in soil. Soil water potential was lowered by adding sorbitol solutions adjusted to different water potentials. Single rosette leaves were fed with water on their adaxial sides and, as a consequence, turgor values increased (open symbols; modified from [1]).

Long-distance signaling

A number of different endogenous signals have been proposed for long-distance communication of water deficit of roots to leaves. These range from chemical [31], to hydraulic [32], and electric signals [33]. ABA was identified as a chemical being delivered in increased amounts to the shoot in the transpiration stream during drought [34]. Electrical signals emanate from water-stressed roots [33] or from roots after re-irrigation and have been suggested to be relayed independently of hydraulic signals [35]. Eloquent grafting experiments using ABA-deficient tomato questioned the importance of root-derived ABA for shoot responses [36] and the results were corroborated in Arabidopsis [1] showing the necessity of ABA biosynthesis in leaves but not in the root system for timely stomatal regulation. Plants revealed a rapid turgor decline of leaf cells in response to a root-evoked drop in $\psi_w$ [1]. The observed speed of propagation of the turgor response was faster than 2 cm/min. In a recent experiment which allowed more rapid equilibration between substrate and mannitol solution ($\psi_c = -0.8$ MPa) the signal relay was faster than 40 cm/min (A Christmann, unpublished), that means too fast to be explained by ABA movement from the root to the leaf.

The importance of leaf $\psi_w$ for the timely response to root-evoked water deficit was shown by external water application which relieved the leaf $\psi_w$ and attenuated ABA signaling in leaves [1]. The water-feeding still would have allowed long-distance signaling by a chemical or electrical signal from the root. In conclusion, the analysis identified a decoding of changes in $\psi_w$ not only in Arabidopsis but also in beech and maple, which are transmitted rapidly and over long distances as a hydraulic signal.

A root-derived hydraulic signal will result in local $\psi_w$ changes and, concomitantly, in turgor changes (see Box Figure 1), which can be compensated by solute adjustment ($\psi_c$). Owing to the barriers of water movement within the plant, local changes in $\psi_w$ evoked in roots by drying soil or leaves by transpiration will first generate an accentuated hydraulic signal in the root system outside the endodermis or in leaf tissue outside the bundle sheaths, respectively [1,37]. The changes in water potential will be relayed into the inner stele and increase the tension on the capillary water in the xylem vessels for rapid long-distance signaling. In addition, the $\psi_w$ changes will be perceived by parenchyma cells including those of the vasculature, which are sites of ABA biosynthesis [15], and throughout the symplastic system of the plant, where only guard cells are symplastically isolated [11**].

Thus, hydraulic signaling is not a one-way communication but relays gradients of water potentials throughout the plant [4]. Accordingly, a downward hydraulic signal was observed in soybean which rapidly propagated to the root in response to a reduction of leaf area by pruning (S Tyerman et al., unpublished). ABA is tightly connected to hydraulic signals because it is generated in response to the local $\psi_w$ decreases and it mediates adaptive physiological responses.

Decoding the hydraulic signal

How is the change in $\psi_w$ sensed within the plant? The hydraulic signal generated by water deficit causes first, a reduction of turgor and second, a moderate increase in solute concentrations because of water withdrawal from cells, and third, mechanical forces exerted at the cell wall and at the cell wall-plasma membrane interface. Pioneering
work uncovered the importance of turgor loss for triggering ABA biosynthesis [38] whereas lowering cellular osmotic potential without reducing turgor was not efficient [39] pointing to a turgor-dependent sensor. Though the molecular mechanism underlying the sensing of the hydraulic signal in plants is still not known, there are two general modes of decoding, either by sensing the osmotic environment or sensing changes in mechanical forces exerted by changes in $\Psi_w$.

Mechanosensors and osmosensors from bacteria, fungi and metazoans provide models for plant hydraulic sensors. Since in most cases the mode of action of the proposed sensors is unknown or has not been proven, we will use the term hydraulic sensor to cover sensors that putatively monitor changes in turgor, solute concentration or cell wall-plasma membrane associated tension. Beyond long-distance signaling of changes in water status, plants need to monitor and respond to changes in turgor or in tension in the cell wall whenever plant cells expand such as in meristems after cell division [40]. Tension in the cell wall of meristem cells is transferred to the plasma membrane resulting in local auxin accumulation [41]. During cell expansion, particularly in growing pollen tubes or root hairs, cell wall loosening and turgor-driven expansion needs to be carefully balanced by mechanosensory feedback loops [42]. Hence, hydraulic sensors might not be restricted in function to long-distance signaling.

An emerging paradigm for sensing solute concentrations is the *Escherichia coli* histidine kinase EnvZ [43]. Osmosensing of EnvZ deploys a change in protein conformation, with high osmolarity inducing a folded conformation that results in an increase in autophosphorylation. Similarly, the cytosolic DhlNik1 histidine kinase from the yeast *Debaryomyces Hansenii* monitors solute content by an osmolarity-dependent intramolecular interaction that controls kinase activity [44]. Living cells can be sensitive to 10 mM osmolite changes that cannot be explained by an intracellular osmosensor but rather via the perception of mechanical forces, presumably at the plasma membrane [45].

Several different sensors have evolved for sensing such mechanical forces (Figure 1). Among the turgor sensors are mechanosensitive channels such as MscS and MscL (Mechanosensitive channels of Small/Large conductance). When turgor increases under hypo-osmotic conditions, these perceive stretch forces acting on the plasma membrane to allow rapid release of solutes and water from the cell [46]. MscS but not MscL homologs have been found in all plant genomes examined to date. The Arabidopsis genome encodes ten MscS-related proteins, two of which, MSL2 and MSL3, seem to play a role in the osmoprotection of plastids similar to the role of MscS [46]. The physiological role of the other family members, of which MSLs 4, 5, 6, 9 and 10 are thought to encode chloride channels in root cells, remains to be determined [47].

When turgor decreases in a hyperosmotic environment, yeast activates the high osmolarity glycerol (HOG) MAPK pathway to induce synthesis of the osmolyte glycerol [48]. Two different membrane-localized sensor types control the HOG pathway, the histidine kinase Sln1p and the mucins Hkr1p/Msb2p together with their adaptor protein Sho1p. The extracellular domain of mucin is highly glycosylated and inserted into the cell wall which is compatible with a turgor sensor function; alternatively, changes in osmolarity could be sensed and

**Figure 1**

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<th>Hydraulic sensors in yeast</th>
<th>Plant sensor candidates</th>
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<td>probably turgor increase</td>
<td>increase in membrane tension or turgor increase</td>
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<td>turgor decrease</td>
<td>changes in cell wall tension</td>
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<td>probably turgor decrease</td>
<td>distortion of cell wall-plasma membrane contacts</td>
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Hydraulic sensors and sensor candidates. Sensors identified in yeast are shown and the respective parameter sensed is indicated. Candidate plant sensors are displayed with the parameter putatively sensed (see text for details).
transmitted to Sho1p [49]. No homolog of Hkr1p and Msh2p exists in plants. As regards Sln1p, however, the two-component-system-like AKH1 kinase is an Arabidopsis homolog that functionally complements Sln1p-deficient yeast suggesting an osmosensor [50] or turgor sensor [51] function. However, a recent study challenges the postulated role of AKH1 as a relevant sensor in the context of osmotic adjustment and ABA accumulation in response to low $\Psi_w$ [52*].

In addition to above-mentioned osmosensors and turgor sensors, yeast has other cell wall-associated stress sensors that are involved in the cell wall integrity (CWI) pathway. CWI sensors such as Wsc1p and Mid2p are implicated in sensing hypo-osmotic stress by virtue of their extracellular serine-rich and threonine-rich domain, which is thought to sense strain via a sprout-like structure owing to a high degree of O-mannosylation [53]. The mechanical behavior of Wsc1p is reminiscent of the mechanical features of ankyrin repeats [54] which have been implicated in gating of ion channels in animals in response to mechanosensation [55]. Ankyrin repeats are found in a number of plant proteins [56] including kinases and potassium channels that should be considered as candidates for proteins involved in hydraulic sensing.

Although structural homologs of Wsc1p or Mid2p are missing, a CWI pathway also exists in plants, which is associated with turgor homeostasis during cell expansion and pathogen defense [42*]. CWI sensing is critical in germinated pollen. Entry of the male gametophyte into the female gametophyte triggers a turgor increase in the apical region of the pollen tube resulting in bursting of the tip [57]. Receptor-like kinases (RLKs) belonging to the Catharanthus roseus RLK1-like family [58] are involved in turgor control and have extracellular domains thought to mediate carbohydrate binding at cell wall [59*], compatible with a hydraulic sensor function. In addition to RLK1-like kinases, Arabidopsis has wall-associated protein kinases (WAKs) that bind pectins in the cell wall. These protein kinases also regulate cell expansion and responses to pathogen attack [60]. Interestingly, activation of WAK2 initiates a turgor increase via induction of vacuolar invertase [60] which links WAK activity to water status homeostasis. Potential plant CWI sensor candidates include the group of L-type lectin RLKs and the proline-rich extensin-like receptor kinases (PERKs). One RLK family member has been shown to bind the tripedal integrin-recognition motif Arg-Gly-Asp (RGD) [61]. PERKs are involved in Ca$^{2+}$ signaling and thus might translate mechanical stress at the cell wall into a Ca$^{2+}$ signal [62]. A role in Ca$^{2+}$ signaling in response to mechanical stimuli has been implicated for the putative plasma membrane calcium channel MCA1 [63]. Functional complementation of the CWI sensor Mid2-deficient yeast by MCA1 is in agreement with a function of MCA1 in sensing tension at the cell wall [63].

Mechanosensors are also involved in the perception of touch. In Caenorhabditis elegans, the MEC-4/MEC-10 sodium channel complex is part of an epithelial mechanosensory complex that is tethered to both the extracellular matrix and large-diameter microtubules [64*]. Touch-induced dislocation of the tethering points controls channel gating. Similarly, the dual-tether model has been proposed for integrin sensing in metazoans. Integrins are central components of plasma membrane-localized protein complexes with external domains binding to proteins of the extracellular matrix via the RGD motif while the cytoplasmic domains interact with the cytoskeleton recruiting additional adaptor proteins [65]. Integrin complexes are thought to signal distortions or changes in the rigidity of the extracellular matrix to the cytoskeleton and appear to function in mechanosensing of shear stress [66]. Neither homologs of MEC-4/MEC-10 nor integrins are found in plants. However, several structurally diverse integrin-like proteins are encoded by plant genomes. Some of these appear to stabilize cell wall-plasma membrane adhesion and could have an integrin-like role in plants [67*,68*].

Hydraulic signaling
Hydraulic signaling starts with the generation of a hydraulic signal, that is, changes in $\Psi_w$ induced by changes in water tension, turgor or osmotic potential. Local changes in $\Psi_w$ are quickly relayed throughout the plant because of the cohesion and tension properties of water. Such a hydraulic signal moves in rigid pipes with the speed of sound [69], in plants the information spread is less fast because of cellular resistances and volume changes that have a dampening effect. The perception of the hydraulic signal by yet unknown sensor(s) leads to conversion of the physical signal into the chemical ABA, which mediates the various adaptive responses. Sensor candidates such as MCA1 [63] and PERKs [62] indicate that cytoplasmic Ca$^{2+}$ transients could be an early response to hydraulic signals. It has long been known that calcium is involved in the early responses of plants to touch [70]. In addition, calcium transients are induced in Arabidopsis seedlings within seconds of osmotic treatments [71]. These observations have been substantiated by recent studies where cytoplasmic calcium transients occurred in response to mechanical perturbations [72] and make it likely that such an increase is an early event in hydraulic signaling. However, Ca$^{2+}$ transients are also involved in early ABA responses [7,73] therefore it is difficult to discern of Ca$^{2+}$-action upstream or downstream of ABA, or both. Ca$^{2+}$ transients may then activate NADPH oxidase RBOH C thereby generating a ROS signal [72]. Interestingly, ROS signals as well are also part of the ABA signaling pathway [10] and include stimulation of NADPH oxidase by the ABA-activated SnRK protein kinase OST1 [74]. Shared signal components between hydraulic and ABA action provide the possibility of signal integration and regulatory links. As an output of hydraulic signaling, endogenous levels of ABA increase (Figure 2) which is likely a result of
Hydraulic long-distance signaling

Christmann, Grill and Huang 297

Figure 2

Hydraulic signaling: conversion of a long-distance signal from remote plant organs to a local biochemical signal. A hydraulic signal (decrease in $\Psi_w$) is transferred throughout the plant in the xylem and causes water flux down the gradient in $\Psi_w$, which is out of the parenchyma cells of, for example, shoot vasculature as shown here. Water loss leads to a strong decrease in turgor pressure $\Psi_p$ and a less pronounced decrease in osmotic potential $\Psi_s$ in parenchyma cells. An unidentified sensor responds by initiating a signaling cascade which comprises calcium transients and formation of reactive oxygen species (ROS) and targets ABA biosynthesis enzymes. ABA synthesized in parenchyma cells is exported to bundle sheath cells and beyond to trigger adaptive responses.

an enhanced biosynthesis [14,15] and may involve inhibition of ABA degradation [75] and liberation of ABA from its conjugate, ABA glucose ester [76] but only to a limited extent due to a small pool size of the conjugate. The parenchyma cells of the vasculature are the primary sites of ABA biosynthesis [15] from which ABA is exported probably with the help of the ABC-transporter AtABC25 [77]. ABA action in response to a hydraulic signal from the roots started to spread from this tissue to finally accumulate in guard cells [78]. It is likely, that the primary sites of ABA biosynthesis are also primary sites of hydraulic perception though every cell needs to control its water potential (Figure 2).

Conclusions and perspectives

How plants sense hydraulic signals and convert it into ABA is a key topic in understanding plant water status homeostasis. The nature of the sensor as well as the early steps in the signal relay after perception is still a big enigma. To elucidate this conundrum, screens for plant mutants affected in hydraulic signaling are indispensable. To this end, a search for Arabidopsis with altered activation of ABA biosynthesis genes in response to osmotic stress is a promising strategy. No hydraulic signaling elements have been reported in such screens so far [79]. By using the pAtH-B6::LUC reporter line [78], however, some novel mutants have been identified that have lesions upstream of ABA action (A Christmann et al., unpublished). In recent years, a number of promising candidates for osmosensors and turgor sensors from plants have been identified, but their roles as sensors have yet to be demonstrated. Considering that more than $30 \times 10^12$ tons of water are transpired by plants on our planet every year [80] and that this movement of water is controlled by hydraulic signals, it is important that we embark upon the elucidation of the molecular mechanisms that convert a physical water potential signal into the phytohormone ABA.

Competing interest statement

The authors declare that they have no competing interests.

Acknowledgements

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


Uptake of water in deep soil layers and hydraulic redistribution are important processes in many forests, savannas and shrublands. This study on different tree species in a semi-arid woodland demonstrates extensive and continuous hydraulic redistribution, involving every tree and most of the roots. The study highlights changes in water flow direction with alternating water potential gradients.


The cactus Opuntia microdasys grows in an arid environment and uses fog as an important source of water by means of an efficient fog collection system. While the study concentrates on the unique structural features of the cactus to monitor and calculate the movement of water on the spines, it is a nice example of how water with a high $\psi_w$ is internalized in above-ground organs flowing towards plant tissues with a low $\psi_c$.


The hypothesis is tested in Arabidopsis that plants under water deficit suffer from carbon shortage. Analyses of gene expression, enzyme activities, metabolism, carbon balance and growth are combined to demonstrate that carbon metabolism is maintained even under a sustained soil water deficit. Availability of carbon under such conditions rather increases and contributes to a promotion of root growth and osmotic adjustment.


ABA biosynthesis has been shown to occur in parenchyma cells of the vasculature (see Endo et al., 2008) yet it was not clear whether guard cells as well are capable of synthesizing the plant hormone. This paper now demonstrates that guard cell-autonomous ABA synthesis is required for and is sufficient for stomatal closure in response to low humidity. Guard cell-autonomous ABA synthesis allows the plant to readily respond to changing environmental conditions to maintain water status homeostasis.


ABA affects plant metabolism and water transfer via multiple mechanisms at cell, organ and whole plant levels. These mechanisms may translate into contradictory effects on leaf growth. This review provides elements to avoid confusions of effects and proposes three main effects of ABA on growth with the relative weight of each of these effects changing under different environmental scenarios.


It is well known that aquaporins control hydraulic conductance of plant organs. The authors here present an example where a sophisticated spatial and temporal regulation of aquaporin activity is required to facilitate lateral root emergence in Arabidopsis. The respective pattern is provided by a pattern of auxin distribution which translates into progressive exclusion of expressed aquaporin PIT2:1 from tissue overlaying the lateral root primordium. Thereby, water transport into this tissue is repressed to facilitate root emergence.


This paper provides us with a stimulating new view on the role of bundle sheath cells (BSCs) in plant water homeostasis during drought. The group demonstrates that aquaporin activity-mediated water permeability of BSCs is adjusted in response to drought stress and to ABA supplied via the transpiration stream.


The authors investigated changes in the Arabidopsis thaliana phosphoproteome within a period of 5–30 min following ABA treatment using a sophisticated experimental design for precise quantification of phosphopeptides. Among the 50 different phosphopeptides, which changed their...
phosphorylation state, were 4 aquaporins. Aquaporin phosphorylation status decreased in response to ABA.


This review provides an excellent overview of how cell wall biochemistry is altered during cell expansion and which sensor candidates likely probe mechanical deformations or changes in cell wall structure or in cell wall composition.


The bacterial EnvZ/OmpR system has long been implicated in osmosensing as part of a two-component signal transduction system with EnvZ being the site of autophosphorylation and OmpR the acceptor site for phosphotransfer. This study unravels how EnvZ senses, and exhibits a graded response to increasing osmotic stress. It is demonstrated that contrary to the current view the cytoplasmic domain of EnvZ is capable of osmosensing in vivo.


This comprehensive review covers the bacterial mechanosensitive channels MscS, MscL and their homologs in eukaryotes and summarizes how these channels may interpret membrane tension sensing cellular viability in the presence of hyposmotic stress. According to variation in structure and expression patterns among bacterial MscS-like channels and distinct cellular localizations of eukaryotic homologs, it is suggested that during evolution some MscS homologs may have acquired new functions.


Arabidopsis Histidine Kinase 1 (AHK1) has been proposed to act as a plant osmosensor because it can complement the osmosensitivity of yeast mutants lacking the turgor sensor SLN1. The careful study demonstrates that neither proline nor ABA accumulation is reduced in ahk1 mutants at low osm, rather than being a prominent osmosensor required for low osm, tolerance, AHK1 is suggested to play a role in controlling stomatal density and transcription of stress responsive genes.


This review introduces a plant receptor-like kinase group, the CrRLKs, which has been implicated in cell wall integrity sensing and summarizes the recent progress in making such a function more and more plausible. The authors highlights how six of these kinases are involved in the sophisticated male-female gametophytic dialogue during pollen tube reception. A comparison of the domain organization in the 17 Arabidopsis CrRLKs reveals the presence of putative carbohydrate-binding domains in most of these CrRLKs. It is suggested that hitherto uncharacterized
CrRLKs could sense cell wall alterations triggered by diverse environmental or developmental cues.


64. Árnadóttir J, Chalife M: Eukaryotic mechanosensitive channels. • Annu Rev Biophys 2010, 39:111-137. This review provides an excellent overview on mechanosensitive channel candidates with the majority found in metazoans so far. It highlights structure and function of the C. elegans MEC-4/MEC-10 channel as the first eukaryotic channel to be confirmed as a transducer of mechanical signals. The review emphasizes the importance of interactions between certain mechanosensory channels and extracellular and/or intracellular proteins for channel gating.


68. Knepper C, Savory EA, Day B: Arabidopsis NDR1 is an integrin-like protein with a role in fluid loss and plasma membrane-cell wall adhesion. Plant Physiol 2011, 156:286-300. Homology modeling of the structure of NDR1, a plasma membrane-localized protein implicated in pathogen defence, revealed similarities to animal integrins. NDR1 is shown to self-assemble reminiscent of integrin complexes and demonstrated to be involved in plasma membrane-cell wall adhesion. This implicates that the protein could serve an integrin-like function in Arabidopsis.


