Calcium and plasma membrane force-gated ion channels behind development

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Highlights

- High compression and tension forces are generated during organ development
- The plasma membrane at the interface between the cell wall and the cytoskeleton perceives and transmits forces
- Force gated channels allow the membrane to behave as a mechanical probe
- Fine tuning of force gated channels transduces mechanical cues into developmental Ca^{2+} signals

Abstract

During development, tissues are submitted to high variation of compression and tension forces. The roles of the cell wall, the cytoskeleton, the turgor pressure and the cell geometry during this process have received due attention. In contrast, apart from its role in the establishment of turgor pressure, the involvement of the plasma membrane as a transducer of mechanical forces during development has been under studied. Force gated (FG) or Mechanosensitive (MS) ion channels embedded in the bilayer represent “per se” archetypal mechanosensor able to directly and instantaneously transduce membrane forces into electrical and calcium signals. We discuss here how their fine-tuning, combined with their ability to detect micro-curvature and local membrane tension, allows FG channels to transduce mechanical cues into developmental signals.

Keywords

Mechanotransduction, mechanosensitive channel, force gated ion channel, stretch-activated channel, calcium, plasma-membrane

Abbreviations

MS: mechano-sensitive, FG: force gated, SAM: shoot apical meristem, DEK: Defective Kernel, RMA: Rapid Mechanically Activated

Introduction

When a seed germinates, imbibition causes a huge increase in volume, while the seed is constrained by the teguments and the embryo is delineated by the proto-epidermis [1]. At the same time, new mechanical fields of force develop within forming tissue. Hence, the formation of new organs by cell division at the meristem involves fields of constraints underpinned by the cytoskeleton orientation [2,3]. Cell elongation, which is a major determinant of plant growth, is controlled by the balance between osmotic pressure and cell extensibility [3,4]. Thus, the final architecture and size of a plant result from the perception and integration of chemical signals and physical cues. Whereas the mechanisms of hormonal control of plant development have been extensively studied [5,6], many molecular players involved in the perception and transduction of mechanical signals remain to be identified. Sensing of physical cues has been proposed to take place in the cell wall and cytoskeleton, where candidate proteins have been suggested to act as sensors [7,8].

Similar to integrins in animal cells, complexes linking the extracellular matrix of the cell wall to the cytoskeleton are likely involved in the perception of tensions within plant tissues. In addition, force gated ion channels embedded in the membrane also represent prime candidates to translate physical cues into chemical signals leading to biological responses. For example, channel opening could trigger an intracellular calcium increase leading to calcium dependent protein phosphorylation.

Lateral root emergence illustrates the importance of physical stress in plant development

Tissues are submitted to high compression and tension forces during the development of an organ. A striking example is the formation of lateral roots, which is initiated by a stereotype pattern of cell divisions in the pericycle cell layer, deep within root tissues [9,10]. Mechanical forces seem involved in the location of the first division initiating lateral root development, at the curved parts of the root. Indeed, the main root constantly reorients its directional growth to avoid obstacles in the soil while maintaining geotropism. This leads to successive curvatures, and 80% of the lateral roots are initiated at the convex side of root curvatures [11,12](Figure 1a). Tension in the pericycle, or surrounding tissues, seems thus the major determinant of the site of lateral root emergence. This mechanical cue likely precedes the formation of the auxin gradient triggering the initial cell division and initiates subsequent calcium signaling (Figure 1b) [12–14]. On its way to the surface, the newly formed lateral root needs to grow through three overlying cell layers: the endodermis, the cortex and the epidermis [6,10] (Figure 1c). Root emergence is driven by inner forces (turgor pressure) counterbalanced by resistance forces of the surrounding tissues. Interestingly, in reaction of the lateral root growth, the cortical tissues actively decrease their mechanical resistance by activating aquaporins [15]. This points out that cortical root cells are sensing compressive forces. After emergence, the lateral root needs to adapt its growth to the soil passive constraints due to its intrinsic physical properties, such as hardness and granulometry (Figure 1d red arrows). Even if the need of force sensing is well established for the lateral root formation, the mechanisms of the perception in the different tissues is still unknown, contrary to the more studied apical shoot meristem, which is easier to access. In this latter case, a

strong relationship between cytoskeleton organization and forces orientation has been observed [2,3,16].

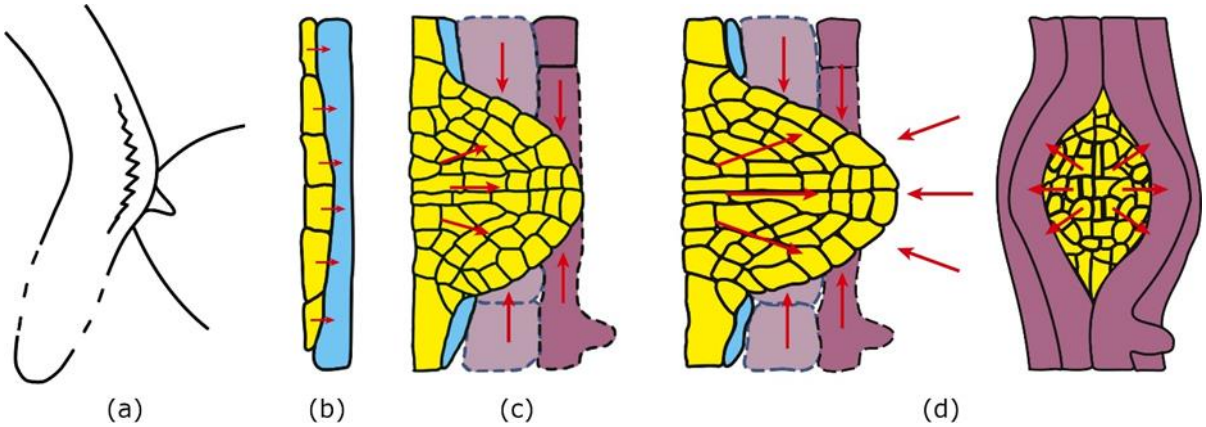


Figure 1: Example of mechanical stresses that tissue undergoes during the lateral root emergence in Arabidopsis thaliana. (a) Most of the lateral roots are initiated at the convex side of root curvatures, experiencing higher tension [11,12]. Root emergence is driven by inner forces (turgor pressure) (b) at early stage lateral root primordium cells (yellow) show a slight swelling, (c) on its way to the surface the newly formed lateral root needs to counterbalance the resistance forces of the three overlying cell layers; the endodermis, cortex and epidermis, (d) after emergence, the lateral root needs to adapt its growth in response to passive constraints of the soil substrate. Arrows represent inner and outer forces experience by the tissues. Red arrows represent forces applied to the system. Figure modified from [6].

Membrane perceives and transmits forces during development

The roles of the cell wall, the cytoskeleton, the turgor pressure and the cell geometry are now often considered in the modeling of organ development [1,17–20]. These actors are central to generate mechanical tension both at the tissue and cellular levels. In contrast, apart from its role in the establishment of turgor pressure, the involvement of the plasma membrane is generally not considered when addressing cell and tissue mechanical properties. The plasma membrane is a heterogeneous mixture of lipids and proteins constituting a fluid compartment allowing lateral movements. Nevertheless, it is also characterized by compartmentalization into domains in which the local composition, lateral organization, and/or dynamics differ from the average [21]. Due to its position at the interface between the cell wall and the cytoskeleton, the plasma membrane is well suited to perceive and transmit mechanical forces. The curvature of the plasma membrane varies greatly within a cell with extreme values at the cell corners and, as suggested by Zhang et al.[22], at the mouth of plasmodesmata (Figure 2a). At these locations, asymmetrical tension between the internal and external leaflets generates mechanical forces inside the membrane. Similarly, protein complexes that connect the cytoskeleton to the cell wall are necessarily anchored in the plasma membrane. Hence, any strain of these complexes, for example by changes of turgor pressure, will translate into tension in the membrane at the vicinity of the anchor sites (Figure 2b). This is likely to occur for example at the constriction zones in lob shaped leaf pavement cells [20]. In the context of cell elongation, acidification and polymer modification lead to cell wall loosening, which allows turgor pressure to generate tensions into the plasma membrane (Figure 2c). Based on these local variations in membrane tension, membrane-localized mechanical sensors may allow a cell to dynamically probe its own shape.

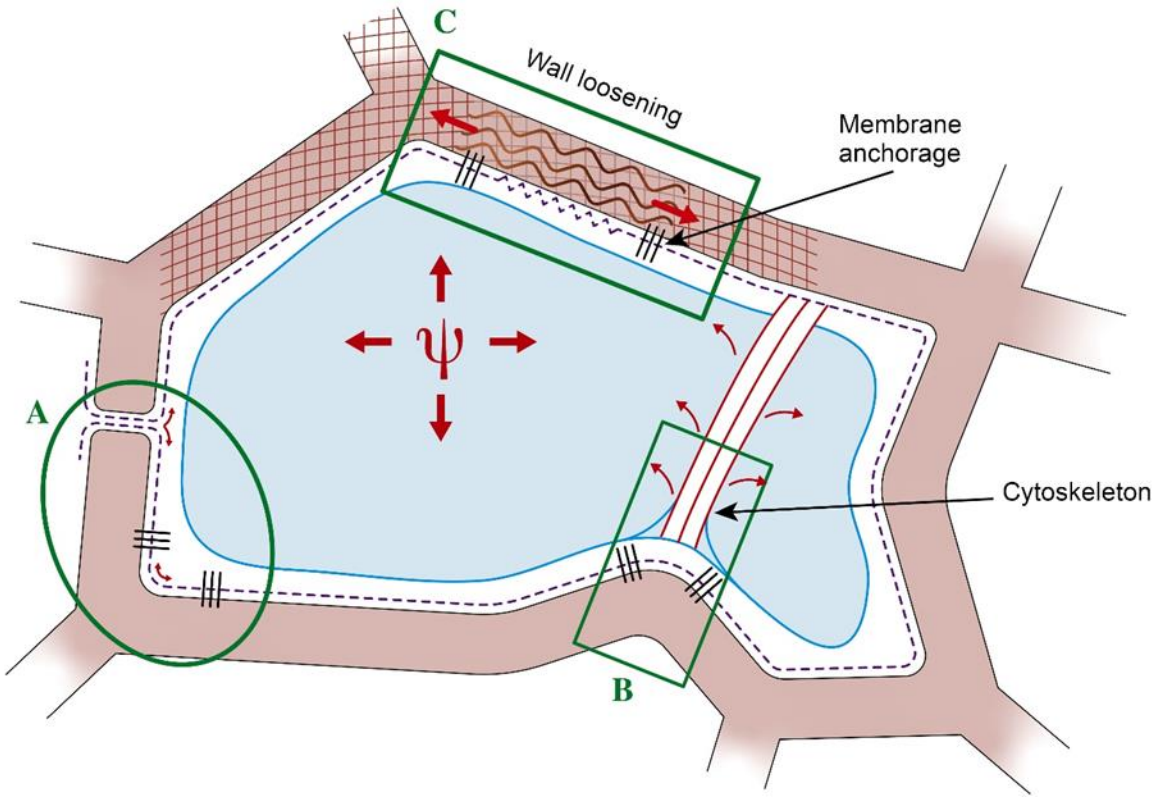


Figure 2: Local domains of mechanical tension generated within the plasma membrane. The high turgor pressure Ψ generated in the vacuole induces an increase in the membrane tension (a) at point where plasma membrane is under strong curvature at the edge of the cell or at the mouth of plasmodesmata (b) at the vicinity of the anchor sites that likely to occur at the constriction zones in lob shaped leaf pavement cells (c) at domains of cell wall loosening which generate an expansion of the plasma membrane area. Red arrows represent forces applied to the system.

Sensing of this tension may be required to adjust the area of the plasma membrane during cell elongation (Figure 3). Calcium channels activated by membrane tension would be perfect candidates to couple cell wall loosening to increase in membrane area according to the scenario described figure 3 in which tension generated in the membrane would locally trigger the opening of FG calcium channels allowing calcium influx known to stimulate exocytosis [23,24]. The massive exocytosis would then release the membrane tension, closing the channels and thus terminating the calcium signaling, in an homeostatic loop (Figure 3). Similarly, a scenario involving FG channel calcium flux and microtubule stabilization, might be proposed for the lob shaping of a pavement cell (Fig. 2b). Organization and dynamics of microtubules is regulated by regulatory proteins, GTP and calcium [25]. We could imagine a feedback or amplifying loop mechanism in which microtubule destabilization, via a release of membrane tension, activate FG Ca channel, which in tune by a local calcium flux regulate (microtubule stabilization) or amplify (microtubule destabilization) the process.

To substantiate these hypotheses, it will be necessary to develop tools to measure local physical tensions at the subcellular level.

Plasma membrane force gated channels convert mechanical signal into biological signal

Force gated (FG) or mechanosensitive ion channels are integral membrane proteins that form aqueous ion pores across the lipid bilayer. In the absence of membrane tension, the pore is closed. When

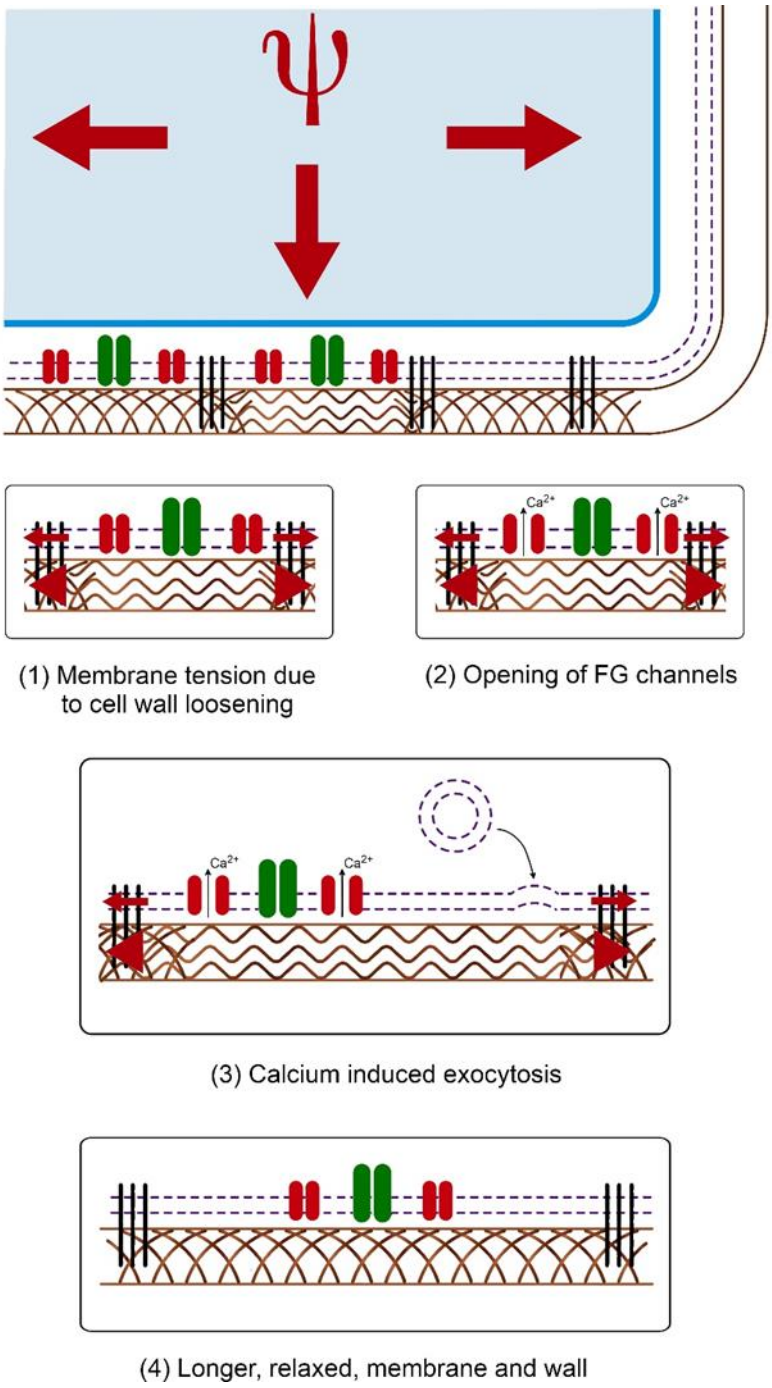


Figure 3: FG calcium channels activated by membrane tension represent the right candidates to couple cell wall loosening to increase in membrane area according to the following scenario: (1) cell wall loosening under turgor pressure would generate tension in the membrane, (2) membrane tension would locally trigger the opening of tension responsive channels (in red), (3) channel opening would allow calcium influx at the vicinity of the plasma membrane, which is known to stimulate exocytosis, (4) massive exocytosis would allow the release membrane tension, the closure of the channels, the termination of calcium signaling and an increase in the membrane area, in an homeostatic loop. Red arrows or triangles represent forces applied to the system. FG calcium channels are represented in red, a non FG channel is represented in green.

tension is applied to the membrane, conformational changes lead to pore opening (activation) allowing ions to flow through the membrane, generating electrical currents. When membrane tension is released, FG channels close according to a process called deactivation. Some channels spontaneously

close even though the tension is sustained according to a process called inactivation. The closed state that is reached upon inactivation does not allow immediate reopening, leading to a refractory period. The channels progressively recover from the inactivated status to a closed status allowing the channel to open again in response to membrane tension [26] (Figure 4). Inactivation allows accommodation to the stimulus.

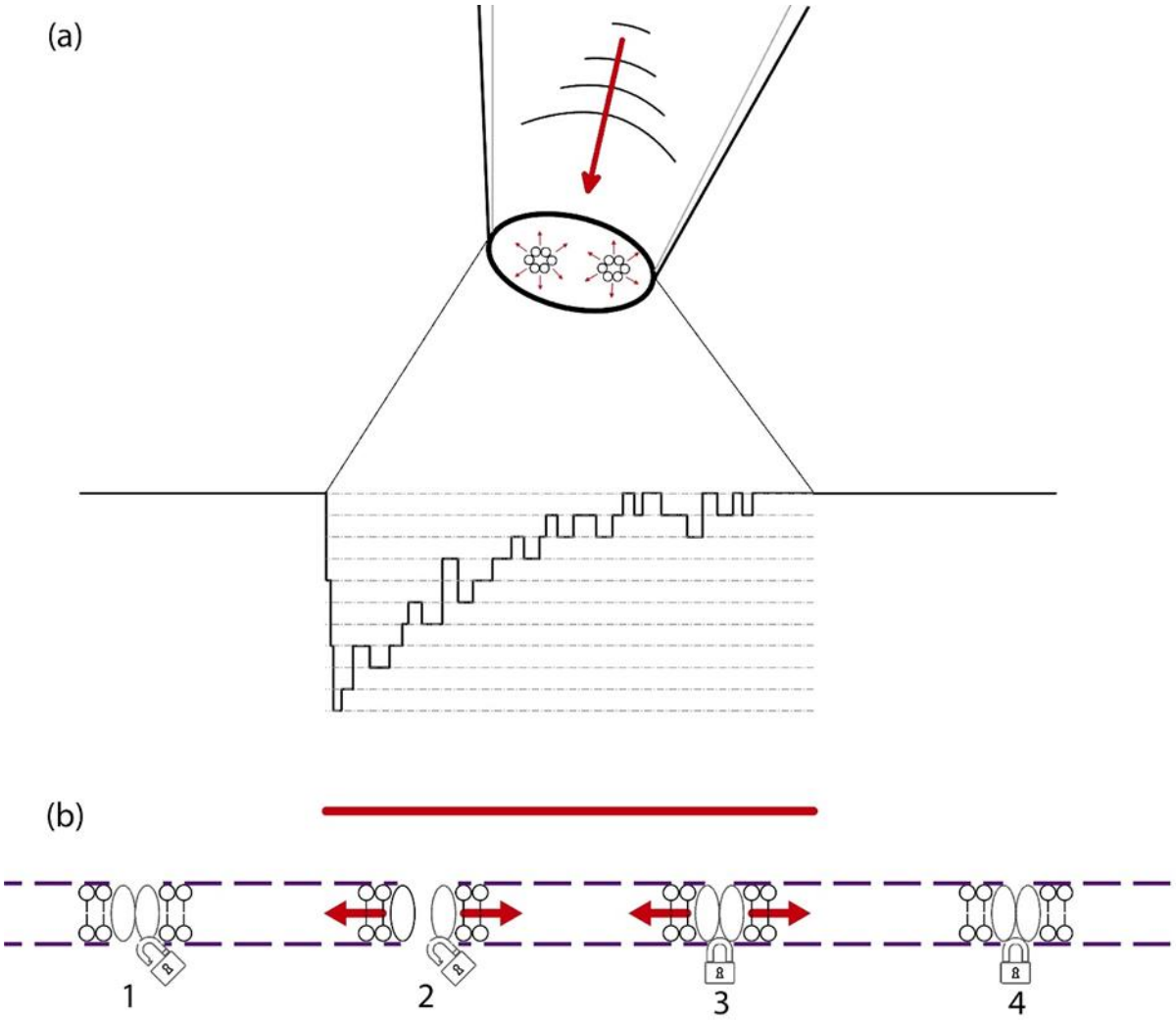


Figure 4: FG channels transducer of membrane tension. (a) Pressure applied in the patch pipette (big arrow) induces an increase of the tension in the membrane patch (small arrows) activating FG channels. Activation of a population of FG channels by the pressure pulse (red line) is visualized by a sudden rise of current (activation) followed by a decay of current (inactivation). (b) Cartoon illustrating conformational changes of FG channel: (1) in resting condition the channel is closed, tension applied to the membrane lead to (2) channel opening (activation) allowing ions to flow through the membrane, (3) spontaneously closing, even though the tension is sustained, according to a process called inactivation (padlock symbol) generating a decrease of ion flux, (4) after release of membrane tension the closed state reached upon inactivation does not allow immediate reopening, leading to a refractory period.

FG channels represent “per se” archetypal mechanosensor able to directly and instantaneously transduce a force into an electrical and ion signal. For some classes of FG channels, biophysical models that address the energetic interactions at the membrane-protein interface have been proposed [27,28]. In these different models, a tension applied to the membrane reorient the channel in the lipid bilayer, thus the responsiveness of an FG channel depends on highly dynamic interactions of channel

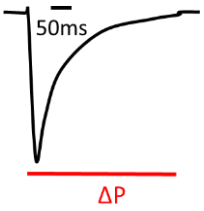
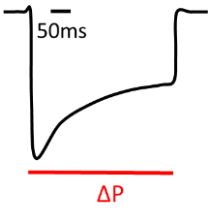
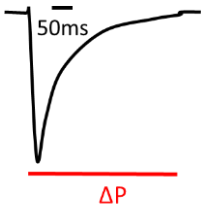
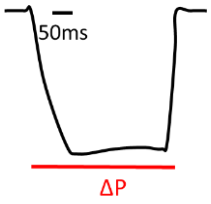
protein with the lipid bilayer. Thus one should consider that it is the complex membrane-channel that intrinsically represent the mechanosensor. Force gated channels were first molecularly and functionally identified in plant cells 15 years ago [29,30]. At the molecular level, plasma membrane localized or predicted FG channels identified in plants belong to the MSL, MCA, Osca and Piezo families [27,31–33]. FG channels are finely characterized by their electrophysiological properties [33,34]. Permeation and gating properties have been assessed for members of the MSL [29,35,36], and Osca [37,38] families, as well as for RMA current, a mechanosensitive channel activity requiring the DEK1 protein (Table 1) [39]. DEK1 combines a soluble intracellular domain homologous to the calcium dependent protease calpain and a transmembrane domain constituted by 32 membrane spanning alpha helices [40,41].

- MSL8, 9 and 10 are anion and cation permeable with a preference for anions. These channels of large unitary conductance with relatively slow activation kinetics display no inactivation. They represent good candidate to mediated sustained depolarization and ion fluxes upon mild tension. These channels could be involved in cell turgor regulation as pointed out for MSL8 in pollen grain [42].
- Osca channels are permeant for cations including calcium. The 15 members of the OSCA multigenic family display a wide diversity in unitary conductance, sensitivity to tension, and kinetics of inactivation [37,38]. Some members like OSCA1.1, OSCA1.2, OSCA3.1, present a strong inactivation while OSCA2.3 shows almost no inactivation (TABLE 1) [38]. This combination of conductances, thresholds of activation and inactivation kinetics opens plethora of possibilities to generate a calcium signature by OSCA channels in response to a variety of membrane tension changes.
- RMA (Rapid Mechanically Activated) is a rapidly activated calcium permeable channel activity. As OSCA1.1 and OSCA1.2, it displays inactivation upon continuous stimulation. Although, RMA activity requires the membrane domain of the DEK1 protein [39], the molecular identity of the pore forming unit of this conductance is not yet formally established. The electrophysiological properties of some members of the OSCA family and of Piezo in animal cells display striking resemblance with RMA [43]. Some OSCA or Arabidopsis Piezo could form a functional complex with DEK1 to generate the RMA conductance.

FG calcium channels, such as OSCA and Piezo, are prime candidates to convert mechanical signals into biological signals. Calcium is an intracellular secondary messenger. Cytosolic calcium is maintained at low concentration (typically 100nM), while extracellular calcium concentration is in the mM range [44,45]. Due to this strong electrochemical gradient, the opening of calcium permeable plasma membrane channels immediately leads to a massive increase in cytosolic calcium concentration. Many protein activities are regulated by calcium including kinases and phosphatases allowing the conversion of the calcium signal into a developmental output [46]. MSL could also be involved in calcium signaling by modulating the opening of non-mechanosensitive (but voltage dependent) calcium channels through a local change of the membrane voltage.

FG channels allow a fine-tuning of the transduction of mechanical forces. For example, rapid inactivation enables the channels to transduce stress variation (at the onset) but not sustained membrane tension [47]. For some FG channels, the gating is dependent only of the force generated by the phospholipids membrane bilayer (Force from Lipids) [48] depending of the composition and the thickness of the membrane and also of the membrane curvature [49]. For other channels, the gating is also modulated by the stiffness of the cytoskeleton [50].

Table 1: Biophysical properties of main FG channel candidates in plant. Kinetics of the current refers to the macroscopic current elicited, on a population of channels, by a sub-saturating pulse of pressure (see Figure 4). Activation τ refers to activation time constant for the macroscopic current elicited by a sub-saturating pulse of pressure. Inactivation τ refers to inactivation time constant of the macroscopic current under a sustained sub-saturating pulse of pressure. Conductance refers to the single channel conductance. Functions refers to putative functions; *Ca sign.*:Calcium signaling, elect. Sign.: electrical signaling or to identified functions; develop.: plant development, osmoregul., osmoregulation.

FG channel	OSCA 1.1, OSCA1.2, OSCA1.8, OSCA3.1	OSCA 2.3	RMA	MSL8, MSL9, MSL10
Kinetics of the FG current				
Activation τ (ms)	~ 5 to 10	~ 20	~ 1	> 1000
Inactivation τ (ms)	~ 20 to 70 ms	> 100	~ 100	no
Permeability	Cations (Na+, Ca++)	Cations (Na+, Ca++)	Cations (Ca++, Ba++)	anion>cation (Cl-> Na+)
Conductance (Ps)	~ 25 to 200	n.d.	~ 10	~ 60 to 140
Functions : *putative* or identified	*Ca sign*.	*Ca sign*.	*Ca sign*. develop.	*elect. Sign.* osmoregul.
References	[37,38]	[38]	[39]	[29,36,42,43]

Accessing force gated channels and calcium signal in plant development

Only few studies have provided hints about the involvement of FG channels and related calcium signals in development so far.

The Defective Kernel 1 (DEK1) protein is required for both embryonic and post-embryonic development in angiosperms [40,41]. Plants with reduced DEK1 activity show major developmental defects, notably in epidermal differentiation and adhesion. Tran et al. [39] have shown that DEK1 protein is associated with a mechanically-activated Ca^{2+} current (called RMA for Rapid Mechanically Activated) in planta, providing strong evidence for a critical role of mechanical stress perception in plant development. It is noteworthy that expression of the calpain moiety of DEK1 partially restore the developmental defects of dek1 mutants. It will be important in the future to clarify the relationships between the 2 domains. For example, calcium transport by RMA may activate calpain protease activity and eventually induce self-cleavage to release calpain.

Li and coworkers [51] have provided new clues about the role of calcium signals, and potentially the role of MS channels in the shoot apical meristem (SAM) development. They showed that mechanical stimulation of the SAM causes transient changes in cytoplasmic calcium ion concentration (Ca^{2+}) and

that transient Ca^{2+} response is required for downstream changes in PIN-FORMED 1 (PIN1) polarity. It is worth to differentiate the static stress supposed to permanently strain the wall and therefore the plasma membrane adjacent to the wall from transient mechanical stresses which likely deform the membrane during a short time. The static stress, likely involved in the development, was proposed to orient interphase microtubules and PIN1 polarity [51,52] while transient stress will rapidly elicit a calcium signal through direct activation of FG channels via membrane deformation [28,51]. The spontaneous Ca^{2+} oscillations with a fairly regular frequency observed in the SAM by Li et al. [51] might be initiated at cellular scale by local membrane mechanical variation. This might be an important signaling process for PIN1 protein dynamic polarized movement during growth.

Conclusions-perspectives

To get an integrated view of development it is essential to consider the role of membranes as transducers of mechanical signals. The plasma membrane is the most obvious one to take into account, but we also have to consider the vacuolar membrane which occupy a large area within the cell and which also has been shown to be equipped with FG channels belonging to the TPK family [53] . As it has already been done for the cell wall and the cytoskeleton, modelling tensions (or stresses) and strains within membranes will serve to integrate FG channel and their mechanical fine-tuning into development.

Accessing membrane tension for mapping fields of force at cellular and supra-cellular scale will likely be possible in the next future using nano-reporters of mechanical forces. These reporters which are mostly trans-genetically expressed, transduce a force variation into a fluorescence variation but are not yet suitable for probing membrane tension. Recently, the discovery of the chemical fluorescent reporter [54], allowing to measure force within membrane, has provided a promising new tool.

Finally, the combined use of force membrane reporters and calcium reporters, together with a complete characterization of force-gated ion channels, will provide new actors to integrate membranes as mechano-transducers into developmental model system.

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