Mechanotransduction in the spotlight of mechano-sensitive channels

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Highlights

- Mechanosensitive channels convert instantaneously (ms range) membrane tension variations into ionic and electrical signals.

- The MS channels identified and partially characterized in plants belong to MSL, MCA, Piezo, OSCA and TPK families.

- Upon activation, MS channels mediate, Ca^{2+} signals, electrical signals or osmotic signals.

- Next challenge: mapping forces at the cellular scale in order understand under which conditions and at which locations MS channels activate “in cellulo”.

Abstract

The study of mechanosensitive channels (MS) in living organisms has progressed considerably over the past two decades. The understanding of their roles in mechanosensation and mechanotransduction was consecrated by the awarding the Nobel Prize in 2021 to A. Patapoutian for his discoveries on the role of MS channels in mechanoperception in humans. In this review, we first summarize the fundamental properties of MS channels and their mode of operation. Then in a second step, we provide an update on the knowledge on the families of MS channels identified in plants and the roles and functions that have been attributed to them.

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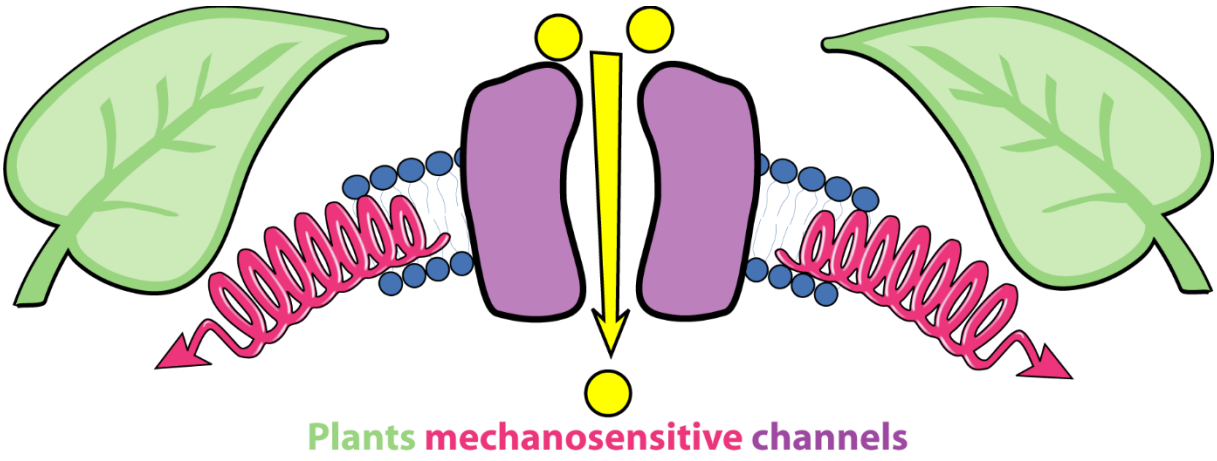
Abbreviations: CESA, cellulose-synthase; MS channel, mechanosensitive channel; MSL, MscS-Like; MCA, Mid1-Complementing Activity; OSCA, hyperosmolality-gated calcium-permeable channels; TPK, Two-Pore K^+channel; MscL , Mechanosensitive channel of Large conductance, MscS , Mechanosensitive channel of Small conductance; ENaC, epithelial sodium channels; MeT, mechano-electrical transduction; NOMPC, no mechanoreceptor potential C; OGs, oligogalacturonides



Graphical abstract

Plants are subjected to physical constraints either from their environment or due to tension and compression forces within their tissues. Mechanosensitive ion channels are prime candidates to sense these constraints and mediate plant adaptive responses. Here, after providing a brief overview of the fundamental properties of mechanosensitive ion channels, we review the main families of mechanosensitive channels identified in plants and discuss their functions.

Introduction

Terrestrial plants are subjected to physical constraints due to their environment. For example, aerial organs are exposed to mechanical stimulations delivered by the wind, rain impact, contact with insects and other animals, while underground organs have to deal with constraints associated to the soil such as stones or cavities explored by the root apex as well as sudden changes of osmolarity caused by rain infiltrating the soil. Even in absence of environmental mechanical solicitation, plants are constantly exposed to mechanical forces due to their high internal cell turgor pressure. At the cellular scale, hydrostatic pressure generated by the vacuole “pushes” the cytosol against the cell wall, this situation is thought to put the plasma membrane or some of its domains under tension [1]. At the tissue scale, it was shown in the shoot apical meristem and in the hypocotyl that the epidermis is under tension whilst inner tissues are under compression [2]–[5].

Many studies have been performed over the last twenty years to decipher how plants probe these mechanical forces. Research has been devoted to the identification of plant mechanosensors, their operating mechanism, and their functions at the cell and organ levels. Although the number of mechanosensors identified is limited, they are diverse in terms of structure, shape, mode of operation, and cellular location.

At the cell periphery, cortical microtubules are highly sensitive to mechanical stress [6]. Microtubules are organized in a network and form stiff rods of 25 nm diameter, which are difficult to bend [7]. Their orientation is governed by the forces occurring in tissues under tension, such as the epidermis. This was particularly highlighted in the shoot apical meristem where the microtubule orientation is parallel to the maximal predicted force [2]. This orientation is independent of biochemical factors, such as

hormones or calcium signals, but is intrinsically stress-dependent. Microtubules provide a rail to guide the cellulose-synthase (CESA) and thus determine the orientation of cellulose microfibrils that confer cell wall mechanical resistance [8]. Therefore, microtubules *per se* contribute to the adaptation of the cell wall to environmental constraints.

In the apoplast, the cell wall is subjected to external and internal mechanical solicitations. Constraints undergone by the components of the wall under mechanical stimulation are detected and activate signaling pathways. It was argued that a mechanical tension applied to the cell wall induces the release of oligogalacturonides (OGs) originating from the fragmentation of pectin [9], [10]. These OGs have been proposed to bind to receptors in the cell wall or at the plasma membrane contributing to the control of cell wall integrity [11].

Recent studies identified receptor-like kinases from *Catharanthus roseus* RLK1-like subfamily (CrRLK1) [12]. Among CrRLK1s, FERONIA (FER) is the best-described receptor involved in the perception of external mechanical signals. FER is a transmembrane protein, with a receptor domain facing the apoplast and a cytosolic protein kinase domain, controlling cell wall integrity. The *fer* mutant plants display alterations of the calcium signals elicited by mechanical or osmotic stimulations, such as a touch or a bending of the root [13] or salt stress [14]. FER protein would link the perception of wall constraints to calcium signaling.

At the plasma membrane, the lipid composition of the membrane affects its mechanical properties. For example, a positive correlation between the accumulation of Phosphatidylinositol-4,5-bisphosphate PI(4,5)P2 in the plasma-membrane and mechanical stresses in the boundary zones suggests that the PI(4,5)P2 distribution pattern could be linked with tissue mechanics and mechanical signal transduction [15]. Since the composition of the membrane is heterogeneous, its associated mechanical properties are non-homogeneously distributed. For example, some domains called membrane rafts are liquid-ordered domains more tightly packed than the surrounding non-raft phase of the membrane bilayer [16]. These rafts would provide platforms that facilitate specific interactions between proteins involved in a same signaling pathway [17] .

Then, it seems that the activity of a large variety of membrane proteins is tuned by the stiffness of the membrane. Among these diverse potential mechanosensors, MS channels are able to convert instantaneously a small variation of membrane tension into a biological signal. With these properties, MS channels represent the most efficient mechanosensors encountered in living organisms [18]–[21].

MS channels are force-gated channels

Mechanosensitive channels are pore-forming complexes of proteins inserted in the membrane. These multimeric complexes switch from a non-conducting (closed) to a conducting (open) state upon application of a mechanical force to the membrane. The precise mechanism of gating of MS channels is still incompletely understood. For mammalian MS channels, two gating paradigms have been classically proposed. One is called “force-from-lipids” and the other is called “force-from-filaments” (Fig. 1A) [22]. The force-from-lipids mechanism means that the force responsible for channel activation is transmitted only through the membrane without requiring external components. In contrast, the “force-from-filament” mechanism involves other cellular components than the membrane, linking the channel to the extracellular matrix or to the cytoskeleton. In the latter case, the force is transmitted through intra or extracellular filaments, which act as springs.

Initial studies performed on bacteria showed that their MS channels were gated according to the force-from-lipid mechanism [23]–[25]. Recent studies on eukaryotic cells show that the paradigm of force-from-lipid could be extended to mammalian MS channels, as exemplified by Piezo1 [26], [27] and to plants with OSCA1.2 [28], MCA2 [29] and MSLs [30] channels.

In the force-from-lipids gating mechanism, the tension in the plan of the plasma membrane has been postulated as the main mechanism driving the opening of mechanosensitive channels. As illustrated in figure 1B, increasing the membrane tension activates the channels EcMscL and EcMscS from *E. coli* as well as AtMSL10 from Arabidopsis at different threshold values (activation tension respectively of ~10 mNm-1, ~5 mNm-1 and ~4 mNm-1; [31]–[33]. Then increasing the tension leads to the recruitment of additional channels, therefore enhancing the overall channel activity, up to a saturating tension value corresponding to the recruitment of a maximal number of channels (Fig. 1B). The Boltzmann law of activation followed by prokaryotic MscS and MscL channels, as well as mammalian Piezo channels was verified for the plant channels MSL10 and Oscas [28], [34].

An alternative way to modify the membrane tension is to induce its curvature. Because of the tension of the upper lipid leaflet and the compression of the lower leaflet, the local radius (approximatively 50 nm) but not the global curvature (cell scale, radius 0.5–5 mm) of the membrane triggers the opening of MS channels (Fig. 1A) [21], [35].

We have to keep in mind that the mechanosensitive properties are conferred to the complex by the association of the channel with its surrounding membrane lipids. Variation of the lateral tension [36] or the local curvature of the membrane [37] results in conformational changes and gating of the channel. For instance, in AtMSL1 three transmembrane domains of each subunit serve as a sensor paddle of membrane mechanical force leading to the opening of side portals of the channel [30]. Looking at PIEZOs, a large trimeric protein complex with a three-blade propeller architecture shapes the channel. Amphipathic helices constituting the blades are proposed to sense and/or induce membrane curvature then linking micro-deformation to channel gating [38]. Insights in the mechanism of other mechanically activated ion channel are provided in the review by Kefauver *et al.* [38]. The membrane also acts in a global manner via its overall stiffness. Xue *et al.* [39] showed that modifying the lipid composition of a bilayer changed the activation properties of EcMscS through a modification of the membrane elasticity. As a consequence, EcMscS activates at a lower tension threshold when inserted in a softer membrane than in a stiffer membrane (dotted line Fig. 1B) [32] . It should be noted that, although MS channels can be distinguished by their specific membrane tension-activity relationship, they all activate at tensions below the lytic tension that causes the rupture of the membrane around 15 to 25 mNm-1 [32], [40], [41].

Finally, the mechanism of activation by force-from-filaments was proposed for the mechano-electrical transduction (MeT) of the mechanosensory hair cells and the no mechanoreceptor potential C (NOMPC), a TRP channel expressed in ciliated mechanosensory organs of *D. melanogaster* [38] [42]. Other channels, such as the epithelial epithelial sodium channels (ENaC) proteins, have been implicated in mechanosensation, but whether their activation is direct or not needs to be clarified [38], [43]. The fact that channels known to be activated through filaments connected to cytoskeleton keep their mechanoactivation when reconstituted in lipid bilayers, lead the authors to consider that the "force-from-filaments" gating mechanism does not exclude a contribution of "force-from-lipids" [22], [42]. Although it has been shown in *Vicia faba* that the activity of MS channels is modulated by the state of the actin network, until now, no plant channel has been clearly shown to be activated by force-from-filaments [44].

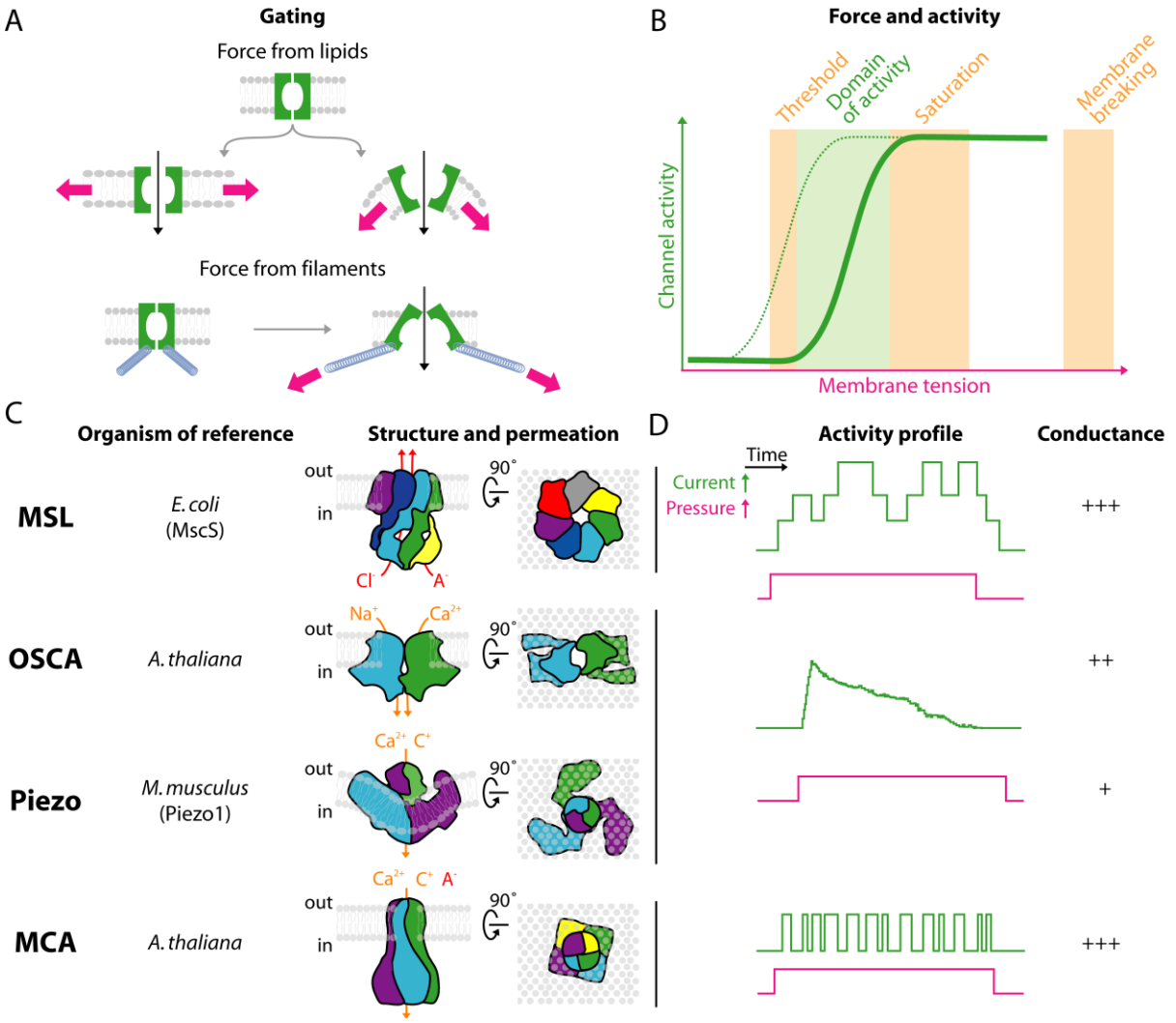


Figure 1: MS channels are pore-forming complexes of proteins embedded in the membrane gated by force applied onto the membrane. (A) Illustration of the two classically admitted modes of gating of MS channels; "force-from-lipids", "force-from-filaments" (adapted from P. Ridone et al. [22]). (B) The force-activity relationship of the MS channel follow a Boltzmann law. three domains of tension with boundaries specific for each channel are remarkable:(1) threshold activation of the channel (mNm-1) ~4 for AtMSL10 [31], ~5 for EcMscS [32], [33], ~10 for EcMscL [32], [33], (2) domain of activity ,(3) saturation ~8 for EcMscS [32], [33], ~14 for EcMscL [32], [33]. The lytic membrane tension is estimated within 15 to 25 [32], [40], [41]. (C) Structures of the complexes of proteins forming the four families of plant MS channels: MSL, OSCA, Piezo, MCA, for explanation see text in 2nd paragraph. (D) The activity profiles of the MS channels of the four families are characterized by a high conductance for MSLs and MCAs and lower conductance for OSCAs and Piezos with rapid activation kinetics followed by inactivation for the latter two. (MSL studied in protoplast [31], [34], Xenopus oocyte [100], HEK cell [65]; OSCA in HEK cell and liposome [28]; Piezo in HEK cell [77], [83]; MCA in lipid bilayer [29])

A diversity of channels for a diversity of functions

During the last years, new MS channels have been discovered and identified in plants. The study and understanding of their functions are still in their infancy. These channels belong to the five following families: MSL standing for Mechanosensitive channel of Small conductance Like, OSCA standing for hyperosmolality-gated calcium-permeable channels, MCA standing for Mid1-Complementing Activity, Piezo, a channel first identified from a mechanical screen of mouse neuroblastoma cell line and TPK

for Two-Pore K^+channel. TPKs proteins are localized at the vacuolar membrane and form K^+ selective channels [45]. Interestingly, the open probability of TPKs from *A. thaliana* (AtTPK1), barley (HvTPK1), and rice (OsTPKa), is modulated by the membrane tension [46]. However, unlike *bona fide* mechanosenstive channels, they also open in the absence of membrane tension. The trans-tonoplast osmotic gradient also changes the activity of TPKs from the three species. Then these channels were proposed to act as intracellular osmosensors [46]. TPKs present multiple regulations but no additional information has been provided concerning its mechanosenstive properties in the last decade [45]. Therefore, in this review, we will not discuss in more details this channels family.

MSLs: The Arabidopsis genome encodes 10 members of the MSL family. Phylogenetic analysis of the AtMSL family shows that they fall into two clades. A clade includes AtMSL4-10 that are localized on the plasma membrane or on the endoplasmic reticulum (ER). All the members of this clade belong to eukaryotic organisms: plants, fungi, and green algae. AtMSL1-3, which form the second clade, are more closely related to *E. coli* EcMscS. This clade includes channels from both prokaryotes and eukaryotes [47]. AtMSL1 has been localized in the mitochondria inner membrane, while AtMSL2 and AtMSL3 are in the chloroplast inner membrane, in agreement with the prokaryotic origin of these organelles [47]. Homologs of *Ec*MscS are found in bacteria [48] [49] [50] [51], fungi [52], and plants [53] [54], but they have not been identified in animals. The recent resolution of the AtMSL1 structure, obtained by cryoelectron-microscopy, indicates that the plant channel, as the bacterial one, associates in a homo-heptameric complex to form the transmembrane pore (Fig. 1C). On the other hand, the 3D structure identified an additional transmembrane domain in plants compared with the *E. coli* channel. Four transmembrane helices, named TM(-1), TM1–TM3, are assigned to the transmembrane domain. TM3 is the pore-forming helix. The surrounding helices, TM(-1) TM1-TM2, form the sensor paddle that may respond to the membrane tension [30]. Comparison of closed and open states structures in combination with functional analyses led Deng *et al.* to propose that while membrane tension increase, the curved transmembrane domain of MSL1 flattens and expands inducing channel opening [55]. On the cytoplasmic side, the seven-sided portal and vestibular portal define the pathway for ion permeation [30]. A recent study on FLYCATCHER1 (FLYC1/DmMSL10), the AtMSL10 homolog in the carnivorous plant Venus flytrap, identified conformation-specific intramolecular interactions within the protein involved in channel deactivation [56].

Functions: All investigations about the ion channel function of MSLs assign them either to osmoregulation or to signaling, including calcium signaling (Fig. 2). The *Atmsl2Atmsl3* double mutants present several plastid structural defects. At the plant scale, dwarfing and leaf variegation are observed [57]. These developmental phenotypes are interpreted as a consequence of plastid osmotic dysregulation [54], [58]. The studies of genetic and physical interactions between the mitochondrial channel, AtMSL1, and the chloroplastic channels, AtMSL2 and AtMSL3, led the authors to hypothesize the existence of common osmotic stress signaling pathways in mitochondria and chloroplasts [57]. The plasma-membrane localized AtMSL8 was shown to tune the optimal osmotic potential required for pollen germination and prevent lysis of the pollen tube. This function is proposed to be achieved (at least partially) by the release of osmolytes through the channel when it is activated by membrane tension [59]. The combination of cell wall softening with an increase in cell turgor in Arabidopsis seedlings induces a burst of [Ca^{2+}], ROS accumulation, an increase of the transcript levels of mechano-inducible genes, and cell death. These responses are reduced in *msl10* null mutants and enhanced in MSL10 gain-of-function lines. This indicates that the plasma-membrane localized channel AtMSL10 functions as a cell swelling sensor [60]. The functions of AtMSL1, AtMSL2, *AtMSL*3, *AtMSL*8, and *AtMSL*10 are reminiscent of the role of “osmotic safety valve” of the bacterial MscS channel [61], [62]. At*MSL*10, which is the most extensively studied member of the family, is also involved in cell signaling.

AtMSL10 is expressed in aerial organs and its activity is amplified by oscillatory stimulation at frequencies corresponding to wind-driven oscillations of plant stems and leaves. For these reasons, At*MSL*10 was proposed to represent a molecular component allowing the perception of oscillatory mechanical stimulations by plants [34]. At*MSL*10 was also proposed to be involved in long-distance electrical signaling induced by wounding.–AtMSL10 is expressed in plant vascular bundles. After wounding of a leaf, this channel is required for the generation and propagation of a full-amplitude electrical signal to distal leaves, as well as for the adequate kinetics of the systemic Ca^{2+} wave [63]. In the same line, FLYC1/DmMSL1 is highly expressed in mechanosensory cells within the trigger hair of Venus flytrap. As its AtMSL10 homologue in Arabidopsis, FLYC1/DmMSL1 exhibits a mechanosensitive channel activity. It is postulated to be involved in mechanical to electrical signal transduction leading to the closure of the trap [64] [65]. This role of At*MSL*s linking mechano-sensing with electric signaling is in line with the former squeeze cell and hydraulic dispersal hypotheses proposed by Farmer and Malone [66], [67].

It should also be mentioned that in parallel with the functions described above, *At*MSL10 possess a function that is independent of its channel activity. This independent function could be attributed to a domain of its cytosolic N-terminus. The expression of this domain is sufficient to induce cell death on its own [58]. A three-step model was proposed, in which tension-induced conformational changes in the C-terminus are transmitted to the N-terminus, leading to its dephosphorylation and the induction of adaptive responses [68].

MCAs: in Arabidopsis genome, AtMCA1 and AtMCA2 are encoded by two paralogous genes. The members of MCA channel family are found exclusively in land plants [69], [70]. MCA proteins localize on the plasma membrane, they present a single transmembrane helix and assemble in homotetramers to form the ion permeable pore of the channel. Recently, they were shown to be genuinely mechanosensitive, gated by force-from-lipids, and Ca^{2+} permeable although weakly selective (Fig. 1C and D) [29].

Functions: In Arabidopsis AtMCA1 and AtMCA2 have different but overlapping expression patterns [71]. The inhibition of the hypocotyl growth of Arabidopsis induced by hypergravity is reduced in *Atmca1* and *Atmca2*-null mutant and is enhanced in AtMCA1 and AtMCA*2*-overexpressing lines [72]. AtMCA1 is required for root penetration in a hard agar medium and for the perception of hyperosmotic stress (Fig. 2) [73]. In rice, OsMCA1, the sole homolog of Arabidopsis MCAs, has been reported to be involved in the regulation of hypo-osmotic shock-induced Ca^{2+} influx and to modulate the generation of reactive oxygen species [74]. This rice channel plays a role in establishing plant architecture [75], [76]. In addition, a maize homolog has been reported to coordinate organ growth and tissue patterning. MCA could thus be involved in the sensing of forces generated at the tissue level and controlling organ development.

Piezos: The founding member of this family was identified in mammals. Piezo genes are conserved among eukaryotes in plants and animals but are absent in fungi and prokaryotes [77]. Vertebrate as well as plant genomes encode up to three Piezo channels [78]. With a uniquely large size (>2000 amino acids) compared to other channels, the mouse MmPiezo1 protein contains at least 26 transmembrane helices [79] [80]. The mouse Piezo assembles in a homotrimeric three-bladed structure forming a central ion-conducting pore module (Fig. 1C). With distal blades and the central pore, the MmPiezo1 channel could have a lever-like mechanotransduction mechanism converting mechanical forces into a cation influx [81]. Whereas mammalian Piezos are plasma membrane channels, the only member characterized so far in plants, AtPiezo, localizes on the vacuolar membrane [78].

Functions: AtPiezo is involved in the immune response to the cucumber mosaic virus and to the turnip mosaic virus (Fig. 2). It is involved in the closure of the plasmodesmata, limiting in consequence the entry into the plant of the infectious agent [82]. Moussavi *et al.* [83] showed, that AtPiezo1 is expressed in the columella and lateral root cap cells of the root tip and that it is required to (i) maintain the root ability to penetrate hard substrates, and (ii) participates in calcium signaling induced by mechanical stimulation [83], [84]. In the moss *Physcomitrium patens*, *Pppiezo1* and *2* are involved in the regulation of vacuole shape in apical caulonemal cells [78], raising the question of the role of the vacuole in mechanosensing.

OSCAs: OSCA1 was identified in a genetic screen for Arabidopsis mutants with altered calcium response to osmotic stress [85]. OSCAs are conserved across eukaryotes, including fungi, animals (TMEM63 homologous channels), and plants [28], [86]. The Arabidopsis genome encodes 15 members of the OSCA family distributed in four clades. Murty *et al.* [28] have functionally characterized at least one representative member of each clade. They found that, except for AtOSCA4.1, the representative of clade 4, they behave as MS channels that differ in their specific thresholds of activation and in the extent and kinetics of their inactivation (Fig. 1D). Cryo-electron microscopy studies have recently revealed the structures of OSCAs [87]. AtOSCA1.2 contains 11 transmembrane helices and forms homodimeric channels. Liu et al [88] proposed that the linker between two unique long transmembrane helices forms an anchor in the lipid bilayer that may be essential to confer mechanosensitivity and for the role of the channel in osmosensing.

Functions: In the seminal study by Yuan *et al.* [85] the authors showed that AtOSCA1.1 mediates osmotic signaling in guard cells and roots cells, and is involved in the control of water transpiration and root growth in response to osmotic stress (Fig. 2). AtOSCA1.3 channel although not still shown as mechanosensitive, is also involved in the control of stomata aperture: its activation, through flg22-induced BIK1-mediated phosphorylation of the channel N terminus, is critical for plant stomatal immunity [89].

Studies performed with ZmOSCA2.4 indicate that this maize homolog could enhance drought tolerance in transgenic Arabidopsis [90]. Overexpression of rice OsOSCA1.4 in Arabidopsis *osca1* mutant complemented osmotic Ca^{2+} signaling, root growth, and stomatal movement in response to hyperosmolality and salt stress [91]. In the same line, genome analysis of OSCA genes in Mung bean (*Vigna radiata*) identified candidates to confer abiotic stress tolerance to the plant [92].

All these studies on Arabidopsis and crop plants indicate that OSCAs are involved in drought tolerance and are required for signaling in response to hyperosmotic shock. This raises the question of how a hyperosmotic shock could generate membrane tension? During plasmolysis, the cell shrinks and the membrane separates from the cell wall but stays tethered to it in few points inducing inward curvature. One hypothesis is that this situation increases the tension on the plasma membrane compared to isosmotic conditions and that curved zones might also undergo local tension. Another hypothesis is that the increased membrane fluidity produced by sterol synthesis in salt stress condition will lower the activation threshold of the channel [93]. More generally, there is a need to pursue studies on all OSCA members to understand their role, as they may represent key players in plant resistance to drought and to pathogen infection.

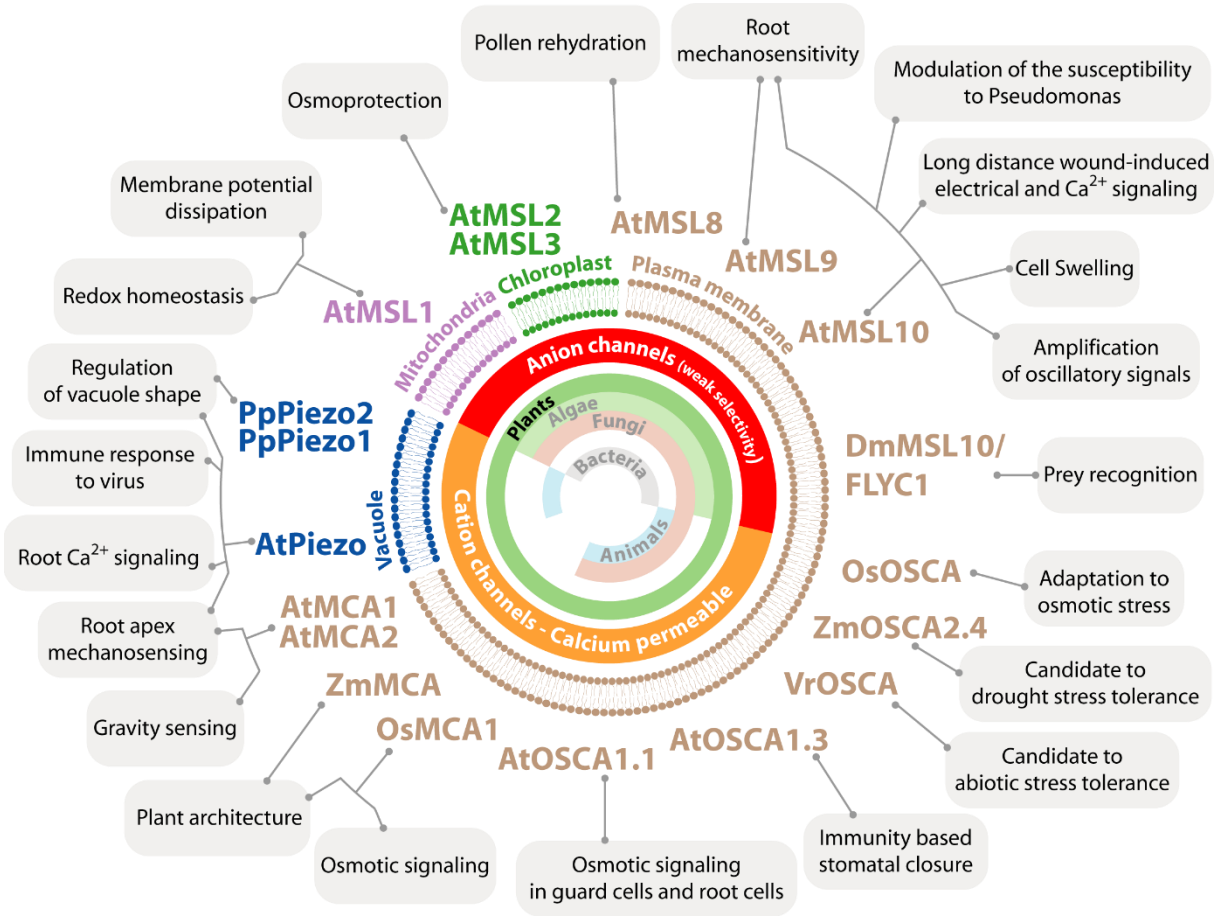


Figure 2: Phylogenetic distribution, membrane localization and functions of MSL, OSCA, MCA and Piezo channels. MSLs: Redox homeostasis and Membrane potential dissipation [101], Osmoprotection [102] [54], [103], Pollen rehydration [59], Root mechanosensitivity [31], Modulation of the susceptibility to Pseudomonas [58] [104], Long distance wound-induced electrical and Ca^{2+} signaling [63],Cell swelling [60], Amplification of oscillatory signals [34], Prey recognition [65] [64]; OSCAs: Adaptation to osmotic stress [91], Candidate to drought stress tolerance [90], Candidate to abiotic stress tolerance [92], Immunity based stomatal closure [89], Osmotic signaling in guard cells and root cells [85]; MCAs: Gravity sensing [72], Osmotic signaling [74], Plant architecture [75], [76], [105], Penetration of the root [73] [71]; Piezos: Root apex mechanosensing [83]and root Ca^{2+} signaling [83], [84], Immune response to virus [82], Regulation of vacuole shape [78]

Conclusion and prospects

Most of the studies addressing mechanical perception in plants are devoted to the cell wall and the cytoskeleton. It becomes more and more obvious that it is indispensable to take also into account the role played by the plasma and organelle membranes in mechano-transduction. Mechano-sensitive channels embedded in the membrane are essential players for this property, thanks to their ability to convert instantaneously a force into an ion or electrical signal. The presence of MS channels in plant cell organelles, such as the vacuole, indicates that their role as mechanosensors is not limited to the plasma membrane. In this view, the identification and characterization of MS channels that equip the vacuole and nucleus membrane/envelop represents one of the next challenges.

The characteristics of MS channels, described with the patch-clamp technique, are determined in the absence of a cell wall. To connect these data to the activity of the channel in its cellular environment, there is a need to map membrane tension at the cellular scale. The recent development of

mechanosensitive probes, such as Flip-TR based on changes in fluorescence lifetime upon membrane tension, enables the investigation of stress patterns at the micro- and nano metris scales at the membrane level [94]. Microviscosity probes, based on rigidochromic fluorescent molecular rotors, targeting specific compartments of the cell were also designed recently [95]. Thus quantifying tension in different membranes will allow specifying where and under which conditions MS channels operate.

As proposed for AtMSL10, MS channels could play a major role in long-distance electrical signaling, especially in the coupling between hydraulic and electrical signals. Pressure pulses can propagate over a long distance [96], [97]. It was recently shown that bending a poplar stem elicits a propagated electrical signal [98]. Considering the intrinsic property of MS channels to convert the mechanic signal into an electric signal, the role of the MS channel in long-distance pressure-electrical signaling is a promising avenue to explore [99].

Declaration of competing interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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● In this review, describing recent progress made on the understanding on the membrane and cell biophysics, the authors discuss the role of the membrane as a mechanosensor. They propose new prospect based on a cellular approach in order to explain how membrane detect and transduce external mechanical forces into intracellular signals.

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