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# Widespread mechanosensing controls the structure behind the architecture in plants

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Mechanical forces play an instructing role for many aspects of animal cell biology, such as division, polarity and fate. Although the associated mechanoperception pathways still remain largely elusive in plants, physical cues have long been thought to guide development in parallel to biochemical factors. With the development of new imaging techniques, micromechanics tools and modeling approaches, the role of mechanical signals in plant development is now re-examined and fully integrated with modern cell biology. Using recent examples from the literature, I propose to use a multiscale perspective, from the whole plant down to the cell wall, to fully appreciate the diversity of developmental processes that depend on mechanical signals. Incidentally, this also illustrates how conceptually rich this field is.

## Addresses

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## Sensing mechanical cues from the environment

Mechanical cues from the environment play a major role in plant development. Although most labs work on roots in a rather stress-free environment, a petri dish containing an agar-based medium, the physical properties of the soil can have dramatic effects on root development in nature [1]. For instance, it is thought that plants decrease their growth in the early phase of a drought, not because of the lack of available water in the soil, but at least in part because the soil becomes stiffer as it dries out [2]. The plant stem is also subjected to mechanical stresses from the environment, whether it is aquatic (high viscosity currents) or aerial (wind). Plants usually adopt two different strategies: tolerance, that is maximizing resistance to stress, or avoidance, that is minimizing the forces experienced by the plant. A recent study on 28 species of

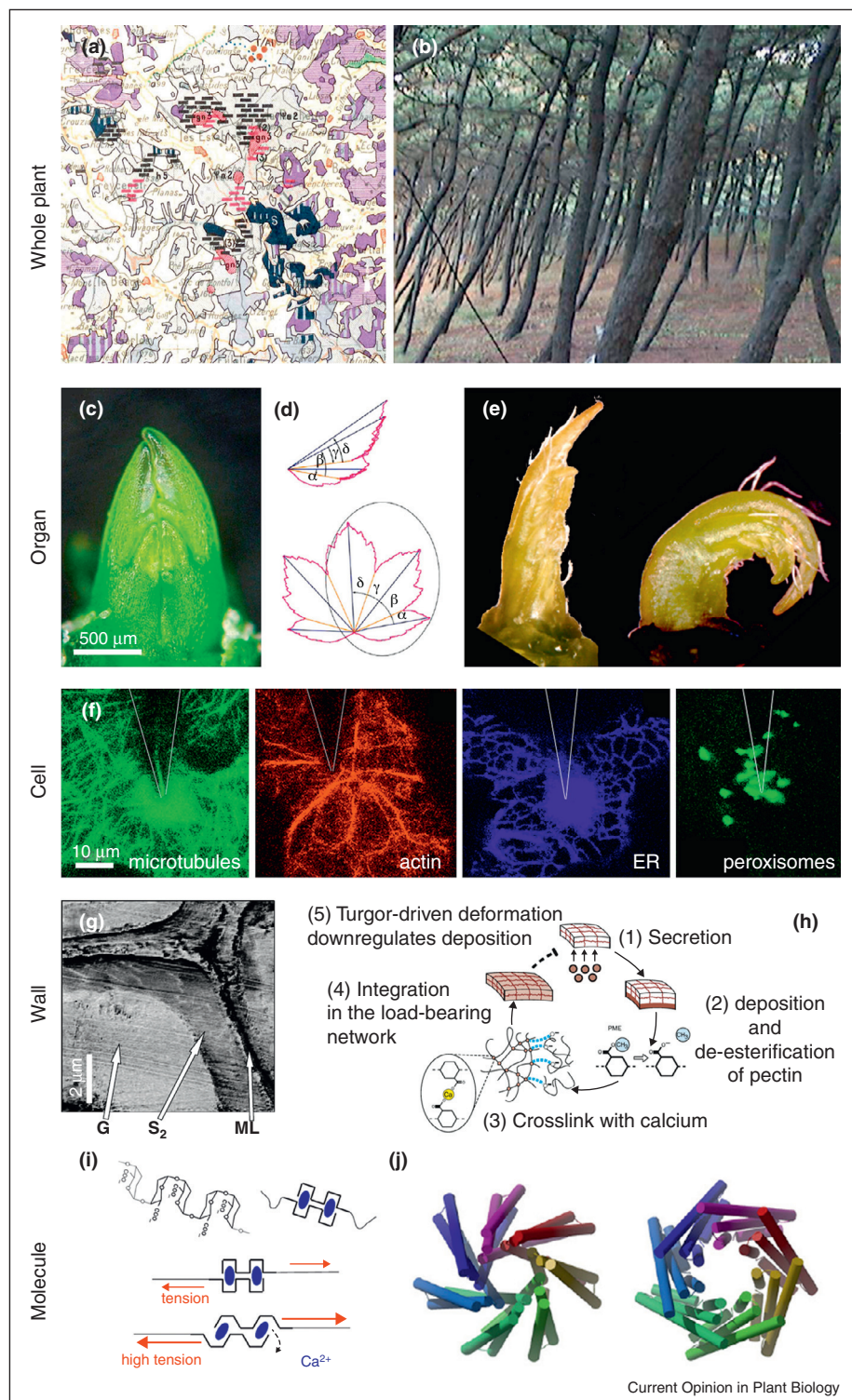
aquatic plants suggests that these strategies are mutually exclusive and thus, that there is an avoidance-tolerance trade-off [3]. Sensing mechanical cues may thus be an important factor channeling the evolution of plants. This also implies that the developmental program is largely constrained by the ability of plants to respond to mechanical cues.

The impact of wind on plant morphology has been studied extensively. In particular, plants adapt their local growth to wind loads, e.g. by developing stiffer stems and by becoming shorter, in a process called thigmomorphogenesis (Figure 1a,b). While this could appear rather specific, this response actually has important consequences on essential aspects of the developmental program. For instance, while the maximum height of trees is thought to depend primarily on xylem embolism risk, which relates to tension in the water column and the diameter of tracheids [4], it also depends on the ability of the tree to resist wind [5]. The diameter of the trunk is also in part prescribed by a response to wind. In particular, it has been proposed that the diameter of the trunk is determined so as to maintain the bending stress, due to wind, constant along the whole length of the trunk [6]. Recently, this proposition has been elegantly extended to the whole branching architecture of the tree through mathematical modeling: the intrinsic ability of the tree to resist wind is in principle sufficient to reproduce realistic branching architecture [7]. Remarkably, the response of trees to wind could even explain Leonardo da Vinci's self similarity observation that “all the branches of a tree at every stage of its height when put together are equal in thickness to the trunk” [7].

Not surprisingly, mechanical loads from the environment also influence gene expression patterns and a long list of *TOUCH* genes is available [8], some of which have also been associated with jasmonate signaling [9]. Interestingly, it has been shown that plants can also become desensitized to these mechanical cues [10]. In particular, when bending young poplars once or twice a day for several days, the impact of bending on the expression of four *TOUCH* genes (*PtaZFP2*, *PtaTCH2*, *PtaTCH4*, and *PtaACS6*) decreased from day 2 onwards. The same desensitization was detected when measuring diameter growth after bending. The desensitization is itself reversible: it takes about a week to recover full sensitivity to bending in poplar [10]. Altogether, this illustrates how plants integrate mechanical cues from their environment to control their growth, and acclimate to the timing and magnitude of their mechanical environment.

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Figure 1



Mechanical cues affect plant development at every scale. **(a)** Plant population map: the summit of the isolated Mount Mezenc (center) in central France is characterized by the presence of *Juniperus nana* (pink), a dwarf plant adapted to high winds. From [48]. **(b)** Slanted Japanese black pine (*Pinus thunbergii*) trees caused by the winds along the coast of Japan. From Zhu *et al.* [50]. **(c)** Morphology of a pair of young leaves inside a maple tree bud (*Acer pseudoplatanus*): the growth of each leaf is limited by the presence of the opposite one. From [15]. **(d)** Sketch of a folded and unfolded leaf revealing how leaf folding in the bud can generate compound leaves. From [14]. **(e)** Ablation of one of the two young leaves leads to excess of growth and curvature of the remaining one. From [15]. **(f)** Microtubules depolymerization, actin filaments polymerization, endoplasmic reticulum (ER)

Building on these observations, and scaling down, it is natural to think that in addition to mechanical cues from the environment, tissues also respond to mechanical perturbations caused by their own growth. Several recent articles illustrate this idea.

### Sensing mechanical cues in organs

Tissue folding is at the heart of most developmental processes. On the basis of data from *Cardamine* and *Arabidopsis* mainly, the formation of compound leaf involves processes homologous to those described in the shoot apical meristem, at the site where the tissue folds. In particular polar auxin transport and the regulation of *CUC* gene expression are thought to play key roles [11,12]. An alternative, and non exclusive, scenario has been proposed for compound leaves of most trees: the final shape of leaves would be determined by the way they are folded when grown inside a bud. More specifically, the walls of the bud provide a mechanical barrier that would restrict the growth of the young leaf, which would then fold so as to fill the bud space completely (Figure 1c). At the onset of spring, the bud opens, the young leaf unfolds and, because of the folding profile, the flat leaf then exhibits lobes and necks. Remarkably, when unfolding manually the young leaf at the bud stage, its geometrical features are similar to the fully grown leaf (Figure 1d). In this scenario, the final leaf shape would thus depend on how the leaf was folded and how growth was arrested. In other words, the design of compound leaves would not be related to a specific physiological function, but would be a consequence of its packing inside the bud [13\*,14]. This hypothesis has been further consolidated by microsurgical experiments [15] (Figure 1e). Even though this rule cannot apply to all compound leaves, it illustrates how mechanical cues may control plant shapes at a more local level. Incidentally, this finding is also a nice way to correlate leaf shapes to paleoclimates, as the presence of compound leaves imprints in fossils is classically associated with temperate climates and as bud dormancy represents an adaptation to the cold season.

Beyond the case of the compound leaf, plants have a more general ability to sense their own growth, a phenomenon called proprioception. For instance, the expression level of the *PtaZFP2* gene can be linearly correlated to the bending angle of a poplar stem thus suggesting that the plant may use the expression of at least this gene as a readout of its own shape [16]. The contribution of proprioception has recently been investigated in the context

of shoot gravitropism. When an *Arabidopsis* plant is positioned horizontally in the dark, the stem bends upwards so as to become vertical again. However, using a modeling approach, the perception of gravity is not sufficient to explain the observed stem response. In particular, a mechanism purely based on gravisensing leads to oscillations of the stem as it bends upwards. Adding a proprioception component, that is the perception of local curvatures, to the model prevents the stem from overshooting back and forth and provides a stable and much more realistic outcome [17\*\*]. While the molecular machinery behind proprioception remains unknown, recent progress in cell imaging and modeling may help us understand how the effectors of the cell respond to mechanical cues.

### Sensing mechanical cues from adjacent cells

Many effectors of the cell are affected by mechanical cues (e.g. [18], Figure 1f). Cortical microtubules have been shown to orient along the local direction of maximal mechanical stress, thus providing one putative mechanism for proprioception at the cellular level [19–21]. While the microtubule response to stress has obvious morphogenetic consequences, via its effect on cellulose deposition and growth anisotropy, it also has more unexpected consequences. In particular, using a modeling and quantitative imaging approach, it was proposed that, as cells orient their microtubules to resist local stresses, their growth rate diverges from that of their neighbors. In other words, sensing mechanical stress promotes growth heterogeneity. This also implies that growth heterogeneity is both a cause and a consequence of mechanical stress. As growth homogenization is not favored, this may help the tissue to increase growth rates more easily, and therefore potentiate organogenesis [22\*\*]. While this needs to be confirmed in other contexts, the link between mechanical forces and growth heterogeneity is particularly attractive as mechanical forces may also affect the local heterogeneity of other processes, such as gene expression, the stochasticity of which is often overlooked.

The polar localization of the PIN1 auxin efflux carrier has also been related to the mechanical status of the cell. In particular, when the mechanical stress pattern is artificially modified, PIN1 relocates to the predicted most tensed membranes [23,24\*]. While this provides a possible mechanism triggering PIN1 polarity, it does not exclude other non mechanical-based scenarios. In other words, mechanical stress may provide an additional instructing signal to

**(Figure 1 Legend Continued)** accumulation and peroxisomes clustering 5–10 min after prolonged indentation with a microneedle on the surface of a cotyledon epidermis. Adapted from [18]. **(g)** Atomic force microscopy-based analysis of cell wall stiffness in oak tension wood. The elasticity map reveals layers of increased stiffness (lighter shades). ML: middle lamella, G, S2: wall layers. From [49]. **(h)** Relation between wall synthesis and mechanical deformation. An hypothetical negative feedback loop couples the chemistry and the mechanics of pollen tube walls, matching relevant experimental evidence. From [46\*]. **(i)** Pectate distortion under tension. The acidic groups of pectate are amenable to bind calcium and form cross-links. Model: tension in the wall leads to distortion of pectate structure and calcium release. From [45]. **(j)** Conformational change, and gate opening, of the *E. coli* mechanosensitive channel of small conductance (MscS) before (left) and after (right) application of membrane tension. From [29\*].

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add robustness to the direction of auxin fluxes, and associated organogenesis, in the meristem.

Organogenesis in the root also involves mechanical cues. Lateral roots can be initiated by bending roots [25]. Furthermore, as it is initiated in the pericycle, the emerging lateral root has to make its way through several cell layers. Recently it has been shown that auxin modulates the mechanical properties of the tissue to facilitate this process. This is notably mediated by the regulated expression of the water channel PIP2;1 aquaporin by auxin [26]. Modifying the mechanical properties of the tissues overlaying the emerging lateral root also hindered organogenesis. Interestingly, the impact of the mechanical properties of the overlaying tissue could be uncoupled from the tissue topology, when using mutants with altered division plane orientations [27]. How mechanical signals may in turn channel or pattern lateral root initiation remains to be explored.

#### Bottom line: the mechanics of cell walls

Mechanical signals are classically thought to be transduced by stretch-activated channels and by wall sensors (Figure 1i,j, [28\*,29\*,30,31\*,32]). As the initial mechanical stimulus likely emanates from the cell wall, investigating the contribution of mechanical signals in morphogenesis requires a precise assessment of the mechanical status of the cell wall. An array of methods has been developed in the past years (for a review, see [33,34], Figure 1g): relatively large (ca. 1  $\mu\text{m}$  deep) indentation on plasmolyzed tissues revealed the presence of softer cell walls in inner tissues, preceding organ outgrowth at the shoot apex [35\*\*], large indentation on turgid cells provided quantified values for turgor pressure [36\*], small indentation (ca. 100 nm deep) revealed the stiffness of outer walls in living meristematic cells [37\*], osmotic treatment coupled with high resolution quantification of the resulting cell deformations revealed patterns of stiffness in tissues and suggested that cells at the tip of the shoot meristem are strain-stiffened [38\*\*]. These methods are also used to investigate the interplay between hormones and mechanics. For instance, the softening of walls by auxin-induced pectin demethylesterification was measured at presumptive organ initiation sites in the shoot apical meristem [39]. Interestingly, plasmolysis of liverwort thalli can induce cell dedifferentiation [40], suggesting that the mechanical status of the cell can also hinder or trigger developmental programs, a question that could be revisited in liverwort with the methods listed above.

In fact a large range of mechanical properties can be found in plant cells. A recent review points that elastic moduli range from 0.3 MPa in parenchyma to 30 GPa in certain palms [41], reflecting the diversity of cell wall textures and composition. The development of super resolution techniques is a key prospect for the future of this field of research. For instance, the organization of crystalline

cellulose has been studied in poplar wood using synchrotron radiation microdiffraction and revealed that tension wood, which increases mechanical resistance of the stem, is associated with increased lattice spacing of cellulose [42].

The ballistic strategies of plant dissemination indirectly illustrate the putative complexity of cell wall mechanics. In liverworts, a hygroscopic cell wall from the elater that is attached to the spores expands and contracts in function of humidity, thus promoting dispersion. In dead seed capsules from the ice plant (*Delosperma nakurense*), mechanical energy is stored in dry capsules and upon hydration of a swellable cellulose layer in so-called keel cells, this energy is released and promotes seed dispersal through an elaborated origami-like reversible unfolding [43]. Similarly, the catapult of fern sporangia reveals the mechanical polarity of cell walls: in this system, spores are embedded in a capsule surrounded by an annulus consisting of 12–13 cells with thick walls except for the outer wall that is much thinner. As the annulus dries out, water tension builds up in the annulus cells, and the capsule slowly opens because of the mechanical heterogeneity of cell walls: the catapult is armed. Water tension then reaches a threshold beyond which cavitation occurs, that is bubbles form, in annulus cells. This leads to immediate (10 ms) inflation of annulus cells, valve unfolding and spore dispersal [44\*]. These examples illustrate how the plant uses the mechanical properties of cell walls to achieve specific functions. This may very well include mechanosensing too, as a specific wall texture and composition may influence the way mechanical signals are propagated and transduced to the cell.

#### Sensing mechanical cues inside the cell wall

How do cell walls respond to mechanical cues in living cells? As discussed above, there is experimental evidence suggesting that walls stiffen after bending and that cellulose microfibrils are oriented so as to resist maximal mechanical stress direction via cortical microtubules guidance. To go beyond these global findings, one needs to dig into the internal dynamics, and mechanics, of the structural elements inside the cell wall. A few pioneering studies have started to tackle this question. For instance, tension seems to modulate pectate function in the cell wall. This hypothesis relies on elegant experiments in which giant *Chara corallina* internode cell walls are subjected to an imposed turgor pressure with a pressure probe and deformation is measured, while modifying pectate chemistry. Based on these quantifications, it was proposed that tension distorts the structure of pectate. This would then weaken the cross-links with calcium and increase the mechanical deformation of walls [45]. Incidentally, this suggests that pectate acts as tension sensor (Figure 1i).

Recent modeling approaches also tend to bridge the gap between the molecular dynamics of cell walls and their

mechanical properties. Based on several experimental observations, including the fact that fast growing pollen tubes tend to have thicker walls, the increased deposition of new material in the cell wall was proposed to stimulate the turnover of cross-links between wall elements, thus increasing wall extensibility. In turn, wall and membrane tension due to turgor pressure would lead to calcium entry inside the cytoplasm via stretch-activated channels. This would result in the downregulation of actin polymerization, and as a consequence, reduced delivery of material into the wall by secretory vesicles in pollen tubes apices. Although this negative feedback loop might be specific of tip-growing cells, this model is consistent with experimental observations, and most notably, the observed growth oscillations in fast growing pollen tubes (Figure 1h, [46\*\*]).

What could be the situation by default, that is when the cells are not responding to stress? As we still lack a true mechanoperception mutant, this remains an open question. Nonetheless, a recent study offers some partial clues. In the *csi1* mutant, cellulose synthase trajectories are largely uncoupled from cortical microtubules. Therefore, when mechanical stress impacts the behavior of microtubules, this in principle does not affect the orientation of cellulose deposition. While this mutant has not yet been used to link cellulose orientation to signals from the environment, analyzing the texture of its cell wall in a control situation is already quite informative. In the *csi1* mutant, and contrary to the wild type, cellulose microfibrils are tilted in the hypocotyl epidermis. This provides a speculative scenario in which cell wall would display helical cellulose microfibrils in the absence of mechanical cues; sensing mechanical stress, the maximal direction of which is circumferential in stems, would lead to transverse cortical microtubules, and would enforce the cellulose deposition in transverse hoops in the wild type. Interestingly, the presence of tilted microfibrils in *csi1* also leads to a right-hand stem torsion, and as a result, a novel bimodal phyllotactic pattern [47\*].

Altogether these recent examples illustrate how mechanical signals contribute to most (if not all) aspects of plant development. This actually makes sense from an evolutionary perspective as plants ancestors were also subjected to mechanical stress. One might even say that mechanics was a critical factor for the very first cell, as the consensus among bacteria, fungi, algae and plants to build a wall primarily addresses a response to a mechanical cue: surviving in a hypo-osmotic environment. One important avenue for future research in plant signaling is to understand the molecular mechanisms through which plant cells respond to mechanical cues. Several candidates are available [28\*,29\*,30,31\*,32] and there is no doubt that the corresponding mechanotransduction pathways will be characterized soon, opening the way for further integration and interdisciplinary research in the plant signaling field.

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