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Mechanical control of plant morphogenesis: concepts and progress

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Understanding how the genome encodes organismal shape is fundamental to biology. Extensive molecular genetic studies have uncovered genes regulating morphogenesis, that is, the generation of shape, however, such genes do not directly determine cell and tissue shape. Recent studies have started to elucidate how mechanical cues mediate the physical shaping of cells and tissues. In particular, the mechanical force generated during cell and tissue growth coordinates deformation at the tissue and organ scale. In this review, we summarize the recent progress of mechanical regulation of plant development. We focus our discussion on how patterns of mechanical stresses are formed, how mechanical cues are perceived, and how they guide cell and organ morphogenesis.

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Introduction

How the coordinated behavior of cells determines three-dimensional (3D) forms of organs and tissues is an outstanding question in biology. Whereas organ shapes are encoded by the genome, it is largely unknown how gene activities are translated into variations in cell growth and tissue deformation. Recent studies have associated gene activities to growth rate variations [1–3]. However, determining the precise chains of events that bridge genotype and phenotype remains an active area of research.

Mechanical force is a key component acting between gene activity and organ shape [4]. Plant cell growth reflects the balance between turgor pressure and cell wall extensibility [5]. Plant cells and tissues are pre-stressed structures with high turgor pressure, which is at a level two to ten times greater than atmospheric pressure [6]. Compared with stress at the cellular level, plant tissues as pre-stressed structures is a less well recognized concept. The fact that plant tissues are pre-stressed can be inferred from a classical experiment: the epidermis is peeled off a piece of stem, and the peeled epidermis contracts while the inner stem tissues elongate. The epidermis is thus under tension due to the pressure exerted from the inner tissues [7]. Because plant cells are glued together by cell walls and do not migrate, mechanical forces are efficient signals for cell-to-cell communication and tissue-scale growth coordination. Indeed, accumulating evidence shows that mechanical forces play fundamental roles in multiple aspects of plant development and plant–environment interaction [5,8,9].

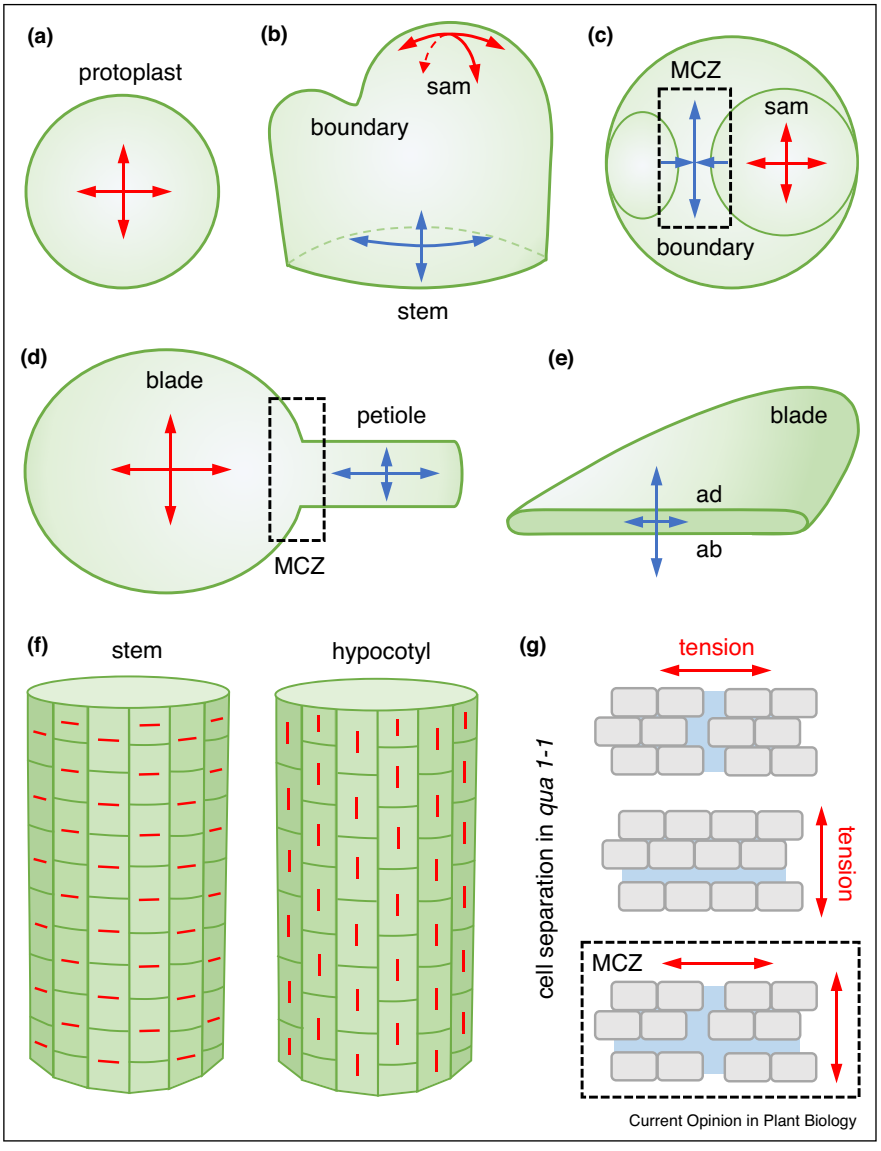
In addition to intrinsic growth, environmental cues, such as wind and raindrop loads, soil strength, and touch from herbivores and insects, are often associated with mechanical forces or perturbations. It has long been known that repetitive touch stimuli can lead to reduced growth and delayed flowering in plants, which is termed thigmomorphogenesis [10]. For instance, plants develop shorter stems in regions with high winds to reduce the forces experienced [11]. Soil strength affects the penetration of roots and shapes the root system architecture [12]. Compared with intrinsic stimuli, the effect of environmental stress on plant morphogenetic alterations can be slower and gradual. Wind triggered bending of branch and trunk takes years to result in 'flagged' trees with asymmetric crowns and a significantly lower drag to resist strong winds [13].

In this review, we focus on basic concepts and recent progress in mechanical control of plant morphogenesis at the cellular level and at tissue and organ levels.

The source and pattern of intrinsic mechanical forces

Cells experience intrinsic stress, which is the force per unit area, from turgor pressure, tissue shape, and differential growth. When there is differential growth, slowly growing cells are stretched by fast-growing neighboring cells and fast-growing cells are also stretched by slowly growing neighbors [4,5]. Mechanical stress patterns can be calculated (Figure 1). Recently, the *quasimodo* (*qua*) mutant with cell–cell adhesion defects has been used to

Figure 1



Mechanical stress patterns at the cell and organ levels. Isotropic and anisotropic stress patterns are indicated by red and blue arrows, respectively, in **(a)–(e)**. Mechanical conflict zone (MCZ) is indicated by a black box with dashed line in (c) and (d). (a) In spherical cells like protoplasts, stresses are uniform in all directions (isotropic). (b) Side-view of a shoot apex. Dome shape (SAM) displays isotropic stress pattern. In a cylindrical cell or organ (stem), the circumferential stress is twice as much as the longitudinal stress. (c) Top-view of the shoot apex in (b). An MCZ is generated in the boundary region, which is due to tissue folding between SAM and organ primordium. (d) In the horizontal plane of a cotyledon blade, the stress pattern is close to isotropic, which generates an MCZ with an anisotropic stress pattern in the petiole. (e) In the transverse plane of a cotyledon or leaf blade, the stress along the adaxial–abaxial (ad–ab) axis is larger than the horizontal stress. **(f)** The stress pattern in the epidermis of a cylindrical organ bearing either shape-derived stress (left, representing the case in Arabidopsis stem) or growth-derived stress (right, representing the case in Arabidopsis hypocotyl). Only the maximal tensile stress direction of each cell is shown as a red bar. Note that the maximal stress in hypocotyl epidermis is not in the circumferential direction as in stem, which is likely due to the fact that fast and unidirectional growth of inner tissues can generate a longitudinal tension on the outer wall of the epidermis [14•]. **(g)** Tissue-wide stress patterns can be reflected by the cell separation patterns (crack in blue) in *qua1-1* mutants. Crack directions are usually perpendicular to the directions of maximal tensile stress (red arrows in top and middle panels). In the MCZ, cracks can form in multiple directions (bottom panel). (b) and (c) are adapted from Ref. [16]; (g) is adapted from Ref. [14•].

directly reflect organ-scale tensile stress patterns. In *qua* mutants, the epidermis cracks form perpendicular to the main direction of stress [14•] (Figure 1g).

In terms of shape-derived stress, cells and tissues can be modeled as vessels with pressure inside. In a spherical cell (like a protoplast), stresses are equal in all directions, that

is, isotropic [15] (Figure 1a). A cylindrical shaped cell or organ (like a stem) bears anisotropic stress, in which the epidermal tension in the circumferential direction is always twice that in the longitudinal direction [15,16] (Figure 1b). The stress pattern in a dome shape (like the shoot apical meristem, SAM) is isotropic at the dome center [16] (Figure 1b,c). For a planar structure (like a leaf blade), the stress patterns along the horizontal and transverse directions are separable. The stress pattern along the horizontal blade plane is associated with the direction of growth and can be isotropic or anisotropic [14•,17] (Figure 1d). In contrast, the dominant stress of the transverse blade section aligns along the adaxial–abaxial (also termed dorsoventral) direction [18] (Figure 1e). The growth-derived stress may override shape-derived stress. For fast elongating Arabidopsis hypocotyls, the inner tissues pull the slow-growing epidermis longitudinally and generate a growth-derived tensile stress on the epidermis [14•,19,20] (Figure 1f).

Complex shapes and growth patterns induce mechanical conflicts at the level of organs, such as at the boundary between the SAM and an organ primordium [21•] (Figure 1c), and at the junction between an isotopically expanding cotyledon blade and an anisotropically expanding petiole [14•] (Figure 1d). Notably, such mechanical conflict zones (MCZs) usually generate enhanced stress, which can affect cell division patterns and gene expression [14•,21•,22] (Figure 1g).

Sensing mechanical cues at the cellular and organ scales

A mechanical load is initially sustained by cell walls, and cells are likely to perceive cell wall mechanics through interacting with the plasma membrane and associated proteins [23] (Figure 2). One of the early responses of plant cells to mechanical stimuli is a rapid influx of Ca^{2+}, and several Ca^{2+} mechanosensitive channels and their transmembrane interactors have been identified as potential sensors of mechanical stress [24,25]. *Arabidopsis* root bending causes a rapid increase of cytosolic Ca^{2+} and extracellular alkalinization, which is impaired in mutants of receptor-like kinase FERONIA (FER) [26]. FER is also required for the upregulation of multiple touch-responsive genes and the maintenance of cell wall integrity (CWI) [27–29]. A plausible mechanism is that plasma membrane-localized FER may respond to cell wall tension through interacting with wall-localized proteins. Consistently, FER interacts with LRXs, which are wall-localized extensin proteins, to transduce cell wall signals in the wall-membrane interface and to trigger cell expansion [30••,31] (Figure 2). It is also found that the extracellular domain of FER directly interacts with pectin *in vitro* [29]. DEFECTIVE KERNEL 1 (DEK1), a transmembrane protein required for epidermal identity, also links the perception of mechanical cues to CWI maintenance in *Arabidopsis* [32••]. DEK1 translates the membrane tension into an influx of Ca^{2+} via Rapid Mechanically Activated (RMA) channels, which promotes cleavage of the cytoplasmic CALPAIN domain of DEK1 protein [32••,33]. The CALPAIN domain, as the active form of DEK1, further triggers the modification of wall composition and thickening to resist tension [24,34]. Thus, this mechanism provides a feedback loop to reinforce the CWI and cell–cell adhesion (Figure 2). For a comprehensive understanding of CWI pathways in response to stress, two recent reviews are available [35,36].

Mechanical stress is directional in nature. Plant cells may sense the direction of stress through molecular structures whose organizational dynamics *per se* imply directional information (like cytoskeleton). Several lines of evidence support microtubules as a potential sensor of stress direction [37••]. Cortical microtubules (CMTs) are known to align along the predicted maximal tensile stress directions *in vivo* [16,19,38,39]. Moreover, CMTs quickly respond to local changes of stress and reorient their alignment [16,40,41]. *In silico* studies revealed that microtubules spontaneously localize in the cortical region of a cell and align along the main axis of the cell geometry without external force [42•]. The microtubule network is very sensitive to and reorients along the direction of external force [42•]. *In vitro* gliding assays, using either anchored microtubules on a stretchable substrate [43], or an optical tweezer [44], suggested that microtubules are able to withstand tension, while being destabilized by compression.

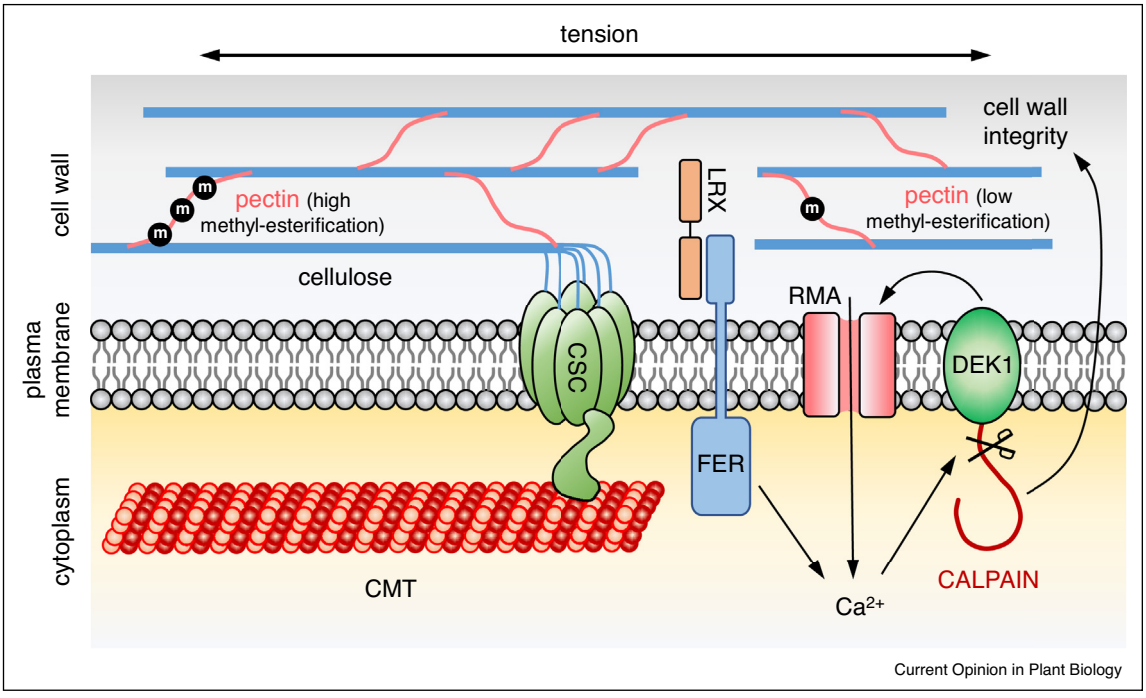
CMTs form a cell wall–membrane–microtubule continuum in plant cells, making it possible that the cell wall may contribute to and affect the CMT response to stress [37••] (Figure 2). Plant cell walls are composed of cellulose microfibrils embedded in a polysaccharide matrix of hemicellulose and pectin. Cell wall components and modifications, especially the methyl-esterification status of pectin, were found to affect the mechanical properties of the cell wall as well as the growth of cells and organs [45,46]. Moreover, cellulose microfibrils are movable under tension [47,48]. Heterogeneity and dynamics of the cell way may influence mechanical cues and microtubule patterns, adding another layer of regulation.

Mechanics as instructive signals during plant development

Cell growth and division pattern

CMTs align along the maximal tensile direction and direct the deposition of cellulose microfibrils that resist tension. Consequently, the cell growth direction is orthogonal to the maximal tensile direction where the wall restriction is weaker [37••]. If the stress is further strengthened by orthogonal growth, this chain of events generates a positive feedback loop, resulting in directional cell growth and organ deformation. When the cell

Figure 2



Perception of mechanical tensile stress occurs in a cell wall–membrane–microtubule continuum in plant cells. The cell wall is primarily composed of cellulose and wall matrixes including pectin polysaccharides. Cellulose organization and methyl-esterification (m) modifications of pectin both generate wall heterogeneity, which may influence the transduction of stress in the interface between cell wall and plasma membrane. Cellulose is synthesized by cellulose synthase complex (CSC). CSC is localized in the plasma membrane and moves along the trajectories of cortical microtubules (CMTs). Thus, the influence on CMT organization and dynamics can in turn affect the wall mechanics and further mechanical perception. Mechanical information is also sensed by transmembrane proteins and their partners. FER may sense the mechanical cues from the cell wall through the interaction with wall localized Leucine-rich repeat extensins (LRXs) and trigger an influx of Ca^{2+}. DEK1 may sense the mechanical cues and trigger an influx of Ca^{2+} through the RMA channel. Increased cytosolic Ca^{2+} promotes the autolytic activation of DEK1 through cleavage of the CALPAIN domain. The CALPAIN domain leads to modification of pectin and wall thickness through the cell wall integrity (CWI) pathways.

volume reaches a threshold, a cell may divide, and a new wall is established. Analyses of SAM cells suggest that cell division is orientated along the maximal tensile direction [21•], not always along the shortest possible geometric path [49]. This is most obvious in the boundary cells between SAM and an organ primordium [21•]. The mechanical-based rule is consistent with the observation that cells often divide parallel to the microtubule interphase array [50,51]. In addition to stress, cell geometry may also affect CMT patterns [52].

Microtubule network reorientation in response to stress direction changes requires severing by the katanin protein complex [40,53]. In *katanin* mutants, CMTs are less dynamic and cell growth becomes isotropic [40,41]. In contrast, SPIRAL2 (SPR2) prevents microtubule severing at crossovers, and *spr2* mutants display promoted microtubule severing and are hypersensitive to mechanical stress [41,54].

Cell wall integrity is required for coordinating tissue-wide mechanics with individual cell growth. As one of the key mechano-sensors, DEK1 maintains the cell wall integrity by regulating polysaccharide composition and wall thickness, which ensures mechanical stability during cell growth and division [34,55]. In Arabidopsis and moss *dek1* mutants, CMTs are disorganized and the correct cell wall positioning is severely affected during cell division [56,57]. FER is necessary to maintain cell wall integrity during salt stress, preventing the arrest of cell expansion and burst. It appears that FER can sense salinity-induced wall mechanical alterations through directly interacting with pectin [29]. FER also mediates pectin de-esterification and thus regulates the mechanical properties of the cell walls [58].

Anisotropic cell growth is essential in rapidly elongating organs. In dark-grown *Arabidopsis* hypocotyls, cell growth undergoes a transition from symmetry (isotropy) to asymmetry (anisotropy). Breaking growth symmetry depends on a pectin-based elastic asymmetry and wall mechanics [59]. Microtubule re-orientation along the maximal tensile stress directions also consolidates the growth axis [19,59]. In this process, both cellulose

deposition and pectin modifications contribute to anisotropy [46].

Cell geometry

Pavement cells on leaf epidermis provide an example of mechanical regulation of complex cell geometry [60,61]. In *Arabidopsis* and many other species, pavement cells exhibit a jigsaw puzzle-like shape with lobes and necks that interlock with neighboring cells. Computational simulations suggest that multiple levels of mechanical regulation contribute to pavement cell morphogenesis. Turgor-driven mechanical stress is sufficient to induce alternating locations of mechanical heterogeneity along anticlinal walls. Notably, stress hotspots can generate compressive stresses, which cause wall buckling [62,63••]. Alternatively, it was proposed that different elastic properties along and across the anticlinal walls generate a wave-like pattern under tension [64•]. Atomic force microscopy (AFM) measurement in the anticlinal walls of lobes and necks uncovered the heterogeneity of wall indentation compliance, which is associated with differences in pectin composition [64•]. Whether stretching of heterogeneous anticlinal walls is the initial cause of waviness remains a matter of debate [65,66].

In periclinal walls, higher tensile stress is predicted in the neck regions. Consistently, both CMT alignment and cellulose microfibrils correlate with the stress pattern and display higher accumulation and anisotropy in the necks [53,63••,67]. Such feedback strengthens the wall waviness. Cellulase treatment affects the interdigital intensity of pavement cells, but not the generation of wall waviness [62,68]. Furthermore, pectin de-esterification is enriched in periclinal walls of neck regions, adding another level of feedback augmenting mechanical heterogeneity [63••]. Together, this shows that a multistep mechano-chemical process underlies wavy pavement cell morphogenesis.

Cell and organ polarity

Lateral organ formation and patterning are regulated by mechanical cues in multiple steps. Organ primordia initiate from auxin maxima in the SAM periphery. Membrane-associated PIN1 efflux carrier profoundly contributes to auxin transport and auxin maxima formation. In the SAM epidermis, auxin maxima result from auxin transport up the gradient, that is, auxin flux toward neighboring cells with higher auxin concentration. How can a cell sense the auxin concentration of its neighbors and compare with its own? Mechanical signals provide a plausible scenario, in which a cell senses mechanical stress influenced by auxin from neighboring cells [23]. Mechanical stress stabilizes PIN1 localization to the plasma membrane, and auxin promotes cell expansion so that cells with higher auxin levels lead to higher mechanical stress with neighbors. Consistently, PIN1 localization correlates with a local mechanical stress pattern and is responsive to stress reorientation [69]. Alternatively, an auxin flux-based model, where the subcellular membrane accumulation of PIN1 is stabilized by local auxin flux, may also explain auxin maxima formation, as shown by *in silico* analysis [70,71]. The auxin maxima result in cell wall loosening, at least partially, through pectin de-methylesterification and other wall remodeling, as well as isotropic microtubule arrays, which all enable organ initiation [72–75].

The boundary region separates the SAM and an organ primordium. The homeobox gene *SHOOT MERISTEMLESS* (*STM*), and NAC transcription factor-encoding gene *CUP-SHAPED COTYLEDON3* (*CUC3*), are strongly expressed in the boundary region. The expression of *STM* and *CUC3* is promoted by mechanical stress derived from tissue folding [22,76]. A more detailed molecular mechanism, however, is so far unknown.

After initiation, the leaf primordium assumes and maintains a flattened structure, which is under mechanical control. The adaxial domain (facing the SAM) exhibits transient high methylesterification of cell wall pectins, which affects wall mechanics [45]. In addition, *WOX* genes are expressed at the leaf margins of the middle domain (between adaxial and abaxial domains), and promote cell division and growth. Computational modeling showed that the combination of organ-level wall mechanical heterogeneity and increased leaf margin growth can switch primordium growth from radial symmetry to asymmetry [77,78]. The breaking of growth symmetry is achieved by asymmetric pectin de-methylesterification and wall mechanics in adaxial and abaxial sides in *Arabidopsis* leaf primordia [45]. Subsequently, the above-mentioned microtubule-mediated mechanical feedback mechanism further amplifies the initial asymmetry to generate highly anisotropic blade growth [18].

Planar organs like leaves exhibit a tissue-wide cell polarity field, which may guide pavement cell morphogenesis and stomata differentiation [79,80]. Mechanical forces likely coordinate cell and tissue-wide polarity and affect polarized protein localization subcellularly. Membrane-associated stomatal proteins like BASL and its interaction partner BRXL2 are localized in the proximal end of epidermal cells, which predicts the orientations for both asymmetric cell division and leaf growth along the proximal-distal axis [79,80]. The polar localization of BRXL2 appears to be regulated by tissue-wide mechanical cues. BRXL2 localization is responsive to local stress changes and reorients in line with maximal tensile stress, in which process CMTs are not required [80].

Future directions

As an emerging field, there are many challenges in the research of mechanical regulation. On the one hand, the nature and tissue specificity of mechano-sensors needs to

be clarified. On the other hand, how mechanical force can regulate gene expression in the nuclei via signal transduction remains elusive. Measurements of mechanical parameters, including mechanical stress, turgor pressure, and wall mechanical properties, remain obstacles in the field. Cell walls are highly heterogeneous, and cell wall components need to be better understood [75,81]. A recent study showed that time-dependent wall extension (i.e. loosening or creep), is not coupled with the indentation compliance measured by AFM [82•], reminding us to rethink our understanding of wall mechanics.

Conflict of interest statement

Nothing declared.

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