An introduction to the mechanics of morphogenesis for plant biologists

Arezki Boudaoud

Laboratoire de Reproduction et Développement des Plantes, INRA, CNRS, ENS, Université de Lyon, 46 Allée d'Italie, 69364 Lyon Cedex 07, France

Plants are under tremendous mechanical forces generated by turgor pressure. How do these forces mediate growth and development? In order to answer this question, it is necessary to understand the mechanics of growth and morphogenesis. In this 'mathless' tutorial, the concepts of strain, mechanical stress and buckling are reviewed and illustrated with recent work on leaf shape, on leaf vasculature, and on organogenesis at the shoot apical meristem.

How can mechanics shape tissues?

Plants raise their aerial organs against gravity. In this endeavor, mechanical support is provided by cell walls and turgor pressure [1], while growth is believed to be driven by the yielding of cell walls to the tension induced by turgor [2,3]. Indeed, turgor can be as high as ten times the atmospheric pressure, generating tremendous forces in cell walls. How are these forces involved in growth and development? Although many of the molecular aspects of plant development are known in great detail, understanding how genes are translated into shape is still a challenge. Mechanical forces might be an important link in morphogenesis, as proposed by early physiologists [4] and fostered by Paul Green and coworkers [5–7]. How are these forces regulated at the cellular level? How is growth coordinated? Can these forces feedback on cellular behavior? Recent progress has renewed the interest in these issues concerning plant [8–10] and animal development [11,12]. For instance, applying mechanical forces on fruit fly embryos can ectopically induce the expression of a patterning gene [13]. In this context, it becomes necessary to understand mechanical concepts such as strain and stress, in order to assess the validity of mechanical approaches or to foster interdisciplinary research.

Strain – separating growth and elastic deformation

As will be discussed in more detail, mechanical stress describes forces in the tissue, whereas strain is about how shape changes [14–17]. For instance, when rising above ground, a plant stem mainly grows along its axis, whereas a leaf grows mostly in two directions expanding its lamina to a large area. This fundamental difference can be quantified by drawing a small circle on the epidermis and by monitoring its change in shape and/or size during plant growth ([18], Figure 1a). Strain is the measure of the deformation of this circle. Either the circle becomes an ellipse as on the stem, and the strain is anisotropic and the direction of anisotropy (or of maximal strain) is given by the long axis of the ellipse; or it remains a circle as approximately on a leaf, and the strain is then isotropic (discounting the direction of the leaf thickness, see Box 1 for strain in three dimensions).

Strain has no units as it measures the relative increase in length of all elements of the circle when it becomes an ellipse (see Box 1). Nevertheless, three numbers are sufficient to define strain in two dimensions: the maximal strain (corresponding to the major axis of the ellipse), the minimal strain (minor axis), and the direction of the maximal strain (an angle indicating the direction of the greater axis). For instance, on the stem in Figure 1a between panels i and ii (or between iii and iv), the radius of the circle has increased longitudinally by 50% and circumferentially by 10%: the value of maximal strain is 0.5, the value of the minimal strain is 0.1, while the direction of maximal strain is vertical. In principle, either of maximal or minimal strain can be positive or negative according to whether the ellipse axes are larger or smaller than the initial circle diameter.

Methods to measure strain include taking replicas of the growing organ [19], making inferences from genetic mosaics [20], visualizing cell plasma membranes [21], or image correlation techniques [22,23]. Although one might be tempted to consider the deformation of the circle as indicating growth, a careful analysis separates the observed strain into growth and elastic deformation [24], see Figure 1a, iii–vi. A similar separation can be observed when pulling on a plastic sheet by a large amount: the total change in length of the sheet is the sum of an irreversible part similar to growth (except that growth also implies synthesis of new materials), i.e. the length after releasing is greater than the initial length; and of an elastic part, i.e. the length of the sheet decreases when releasing. In either the plastic sheet or the epidermis, elastic strain can be visualized, in principle, by cutting out a small circular piece: this piece will deform to an ellipse, and the axes indicate the magnitude and anisotropy of the elastic strain (Figure 1a, from iii to v or from iv to vi).

Stress, stiffness and growth

Mechanical stress might seem more abstract as it is not as visible as strain. However, if we consider a cut piece of epidermis (Figure 1a, v and vi) we need to apply forces to restore the initial circular shape. This suggests that, before cutting, this piece was under mechanical forces exerted by

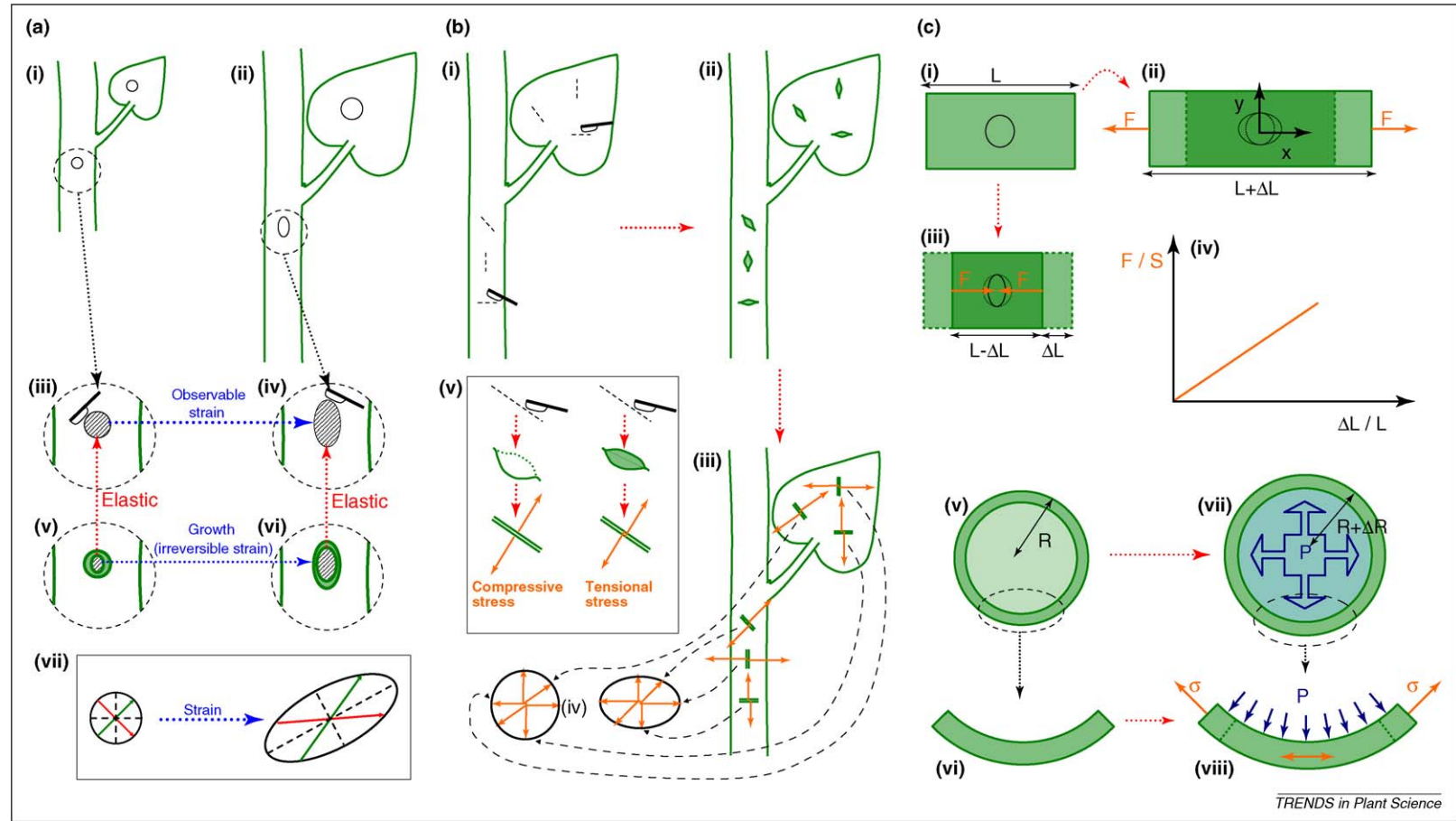*Corresponding author:* Boudaoud, A. (Arezki.Boudaoud@ens-lyon.fr).

Figure 1. Strain and stress, the concepts in schematics. **(a)** Strain as measure of deformation. Strain can be visualized by drawing a circle on a leaf or on a stem **(i)**. This circle changes into an ellipse as the plant grows **(ii)**. The geometry of the ellipse indicates the maximum strain (major axis), minimum strain (minor axis) and the direction of maximum strain (direction of major axis); these directions are marked by dashed lines in **(vii)**. Strain is roughly isotropic on the leaf while it is mainly axial on the stem **(i and ii)**. In principle, elastic strain can be isolated by cutting and peeling a piece of the epidermis with a razor blade (as magnified in iii and iv); elastic strain measures how this piece is deformed from a configuration with no external force (when disconnected from the remaining of the tissue) to the observed configuration. Strictly speaking, irreversible strain, or growth, measures the deformation of the force-free configuration, and only describes the addition of material to the growing body. Note that this drawing is only schematic and that the direction of maximal elastic strain can be transverse in mature stems [29]. **(b)** Stress as a measure of physical forces. Stress can be visualized by making cuts across the tissue (as indicated with the sketch of a razor blade in part i). The stress in the direction perpendicular to the cut is given by the magnitude of the force (orange arrows in iii–v) needed to bring together the lips of the cut; this means that before cutting, the same force was present in order to hold the tissue together. The stress is tensional if the cut opens, while it is compressive if the cuts closes or if one lip slides over the other lip **(v)**. By varying the direction of the cut at a given point, the force arrows draw an ellipse **(iv)**. This ellipse gives the maximal and minimal stress (major and minor axes of the ellipse) and the direction of maximal stress (direction of major axis). Here, stress is isotropic on the leaf and anisotropic on the stem. **(c)** Elasticity. A force of magnitude F (depicted by orange arrows in ii and iii) is needed to deform by a length ΔL a piece of material of length L and side area S **(i)**. If the force per unit surface F/S is plotted against the relative increase in length $\Delta L/L$, the curve only depends on the properties of the material **(iv)**. At small deformation, this curve is straight and its slope defines the elastic modulus E of the material. Bottom **(v–viii)**: the mechanics of isolated plant cells. Because an elastic spherical shell (drawn in cross section in v) is loaded by turgor pressure P, its radius increases from R to ΔR **(vii)**. A cut in the shell would open, indicating a tensional stress σ. The magnification of a piece of the shell **(vi–viii)** shows that this stress is needed to balance the (outward) turgor pressure.

Box 1. A simplified algebra of strain and stress

Strain and stress

Figures 1 a and b show that strain and stress (as long as it is tensional) can be represented using ellipses in two dimensions. The orientation of the major axis defines the main direction (with one angle), while the lengths of two axes yield the two magnitudes of the tensor. Strain has no units, and can be defined as the relative increase in length of one axis. If L is the initial diameter of the circle in Figure 1a, vii, and L' is the length of one axis of the resulting ellipse, then the corresponding strain can be defined as $(L' - L)/L$. Shear is a concept often used instead of the direction of maximal strain; it quantifies the change in angle between the colored arrows of Figure 1a, vii. In particular, the directions of minimal and maximal strain are shear-free, as the angle between the dashed lines does not change. Stress has units of force per area, like hydrostatic pressure: N/m^2 or, equivalently, Pascals (Pa, 1 Pa = 1 N/m^2). The magnitude of stress in one direction can be defined as the force per unit surface needed to bring together the lips of a cut perpendicular to that direction as in Figure 1b, iii and v. Technically, strain and stress are termed symmetric tensors [70]. In three dimensions, three orientations and three magnitudes are necessary to define them.

Linear elasticity

Let a force F be applied to a piece of elastic material in the x-direction as in Figure 1c, i–iii. Stress is then uniaxial: its main direction is x, its magnitude is 0 in the y-direction and F/S in the x-direction. Strain is unidirectional (in a more rigorous drawing, the material should also shrink in the y-direction) and has a magnitude $\Delta L/L$. If the material is elastic and if the strain is small enough, then stress is proportional to strain, $F/S = E\,\Delta L/L$, and the coefficient of proportionality E has units of force per area or pressure (N/m^2 = Pa).

Elastic equilibrium

One can use Newton's law on the balance of forces in a body at equilibrium to find the stress and strain fields everywhere in the material. This becomes the mathematical problem of solving partial differential equations and is beyond the scope of this review.

Inflated shells

Consider an elastic shell of radius R and thickness h, which is inflated by an internal pressure P to a radius $R + \Delta R$ (Figure 1c, v–viii). This roughly corresponds to inflating a rubber balloon (assuming that rubber remains linearly elastic). A cut in the balloon would open, indicating a tensional stress σ in the plane of the balloon. The balance of forces imposed requires the stress σ be proportional to the internal pressure P, $\sigma = 2PR/h$. In the case of the balloon (e.g. h = 1 mm, R = 5 cm, P = 0.1 bar = 10^4 N/m^2), the stress is of the order of 10^6 N/m^2, to be compared to an elastic modulus $E = 10^7$ N/m^2. In the case of a unicellular algae (e.g. h = 0.2 μm, R = 10 μm, P = 10 bar = 1 MPa =10^6 N/m^2), the stress reaches 10^8 N/m^2, compared to an elastic modulus of the order of $E = 10^9$ N/m^2. A measure of the elastic strain is the relative increase in radius $\Delta R/R$, Hooke's law indicates that (approximately) $\sigma = E\Delta R/R$, which in the two cases yields a relative increase of about 10%.

the surrounding tissue. Alternatively, these forces can be visualized by making straight cuts (Figure 1b, i), as was performed in the epidermis of sunflower (*Helianthus annuus*) [25] or of tomato (*Solanum lycopersicum*) [26]. The observation of the lips indicates the stress that is perpendicular to the direction of the cut: the lips open when the body is in tension, while they close or slide over each other when the body is in compression (Figure 1b, ii and v). The forces needed to bring the lips together may vary with the direction of the cut (Figure 1b, iii). These restoring forces are a manifestation of stress: the ends of the force arrows draw an ellipse (Figure 1b, iv). As for strain, three quantities are sufficient to define stress in two dimensions: the maximal stress (major axis of the ellipse), the minimal stress (minor axis of the ellipse), and the angle giving the direction of maximal stress. Maximal and minimal stress correspond to forces per unit surface of the cut, so that they have units of force per area (Newtons per square meters, N/m^2).

The relation between stress and strain depends on the material. In a purely viscous material, stress is proportional to the rate of change of strain (i.e. how quickly strain increases or decreases). Most solid materials are linearly elastic at small strain: stress is proportional to strain (this is termed as Hooke's law [1], Box 1 and Figure 1c, i–iv). The proportionality coefficient is called Young's modulus and has units of force per area; it stands for the stress needed to double the length of the body (if it remained linearly elastic). As an illustration, the Young's modulus of paper is around 10^9 N/m^2, i.e. a stress of 10^9 N/m^2 would be required to increase its length twofold, or more realistically a stress $\sigma = 1\% \times 10^9$ $N/m^2 = 10^7$ N/m^2 is needed to increase its length by 1%; if we consider a piece of paper of width 10 cm and thickness 0.1 mm (area of cross section $S = 10^{-5}$ m^2), this stress corresponds to a force $\sigma S = 10^2$ N; in other words, the weight of a mass 10 kg can

increase the length of the piece by 1% (on the earth surface, a mass of 1 kg is subject to a gravitational force of approximately 10 N). Examples of soft materials include gelatin or soft animal tissues with Young's moduli of about 10^4 N/m^2, while stiff materials are exemplified by metals with moduli $>10^{11}$ N/m^2. Plant tissues fall in between, with moduli in the range 10^6 to 10^{10} N/m^2 according to the age of the tissue (obviously lignified tissues are stiffer), although the composite structure of the tissue can make their elastic behavior more complex [1].

The process of cutting discussed above suppresses forces between different parts of the tissue and allows monitoring stress at the tissue level; however, cell walls remain under mechanical stress because of turgor pressure [27–29], so that removing all stress in cell walls requires the suppression of turgor as well. The role of turgor pressure by itself can be addressed by considering a unicellular green alga with a spherical wall (as in Figure 1c, v–viii), which can be roughly compared to an inflated rubber balloon. The stress in the cell wall is proportional to turgor and to the radius of the cell, and inversely proportional to the thickness of the wall (Box 1). If the material only supports a given stress before yielding or breaking, the thickness of the wall must increase with cell size [30]. Yielding, or elongation of the wall, would occur when tension exceeds the threshold stress, or equivalently when turgor exceeds a threshold in pressure. This is in part the rationale behind Lockhart's equation that describes growth of an isolated plant cell [9,24]. The control of the wall mechanical properties (stiffness and threshold stress) appears as a way to regulate growth.

Differential growth induces stress

Growth is most likely controlled by a cell-autonomous biochemical activity. An enhanced growth rate in a given cell would induce a mismatch with neighboring cells. A similar mismatch can occur at the tissue level. For
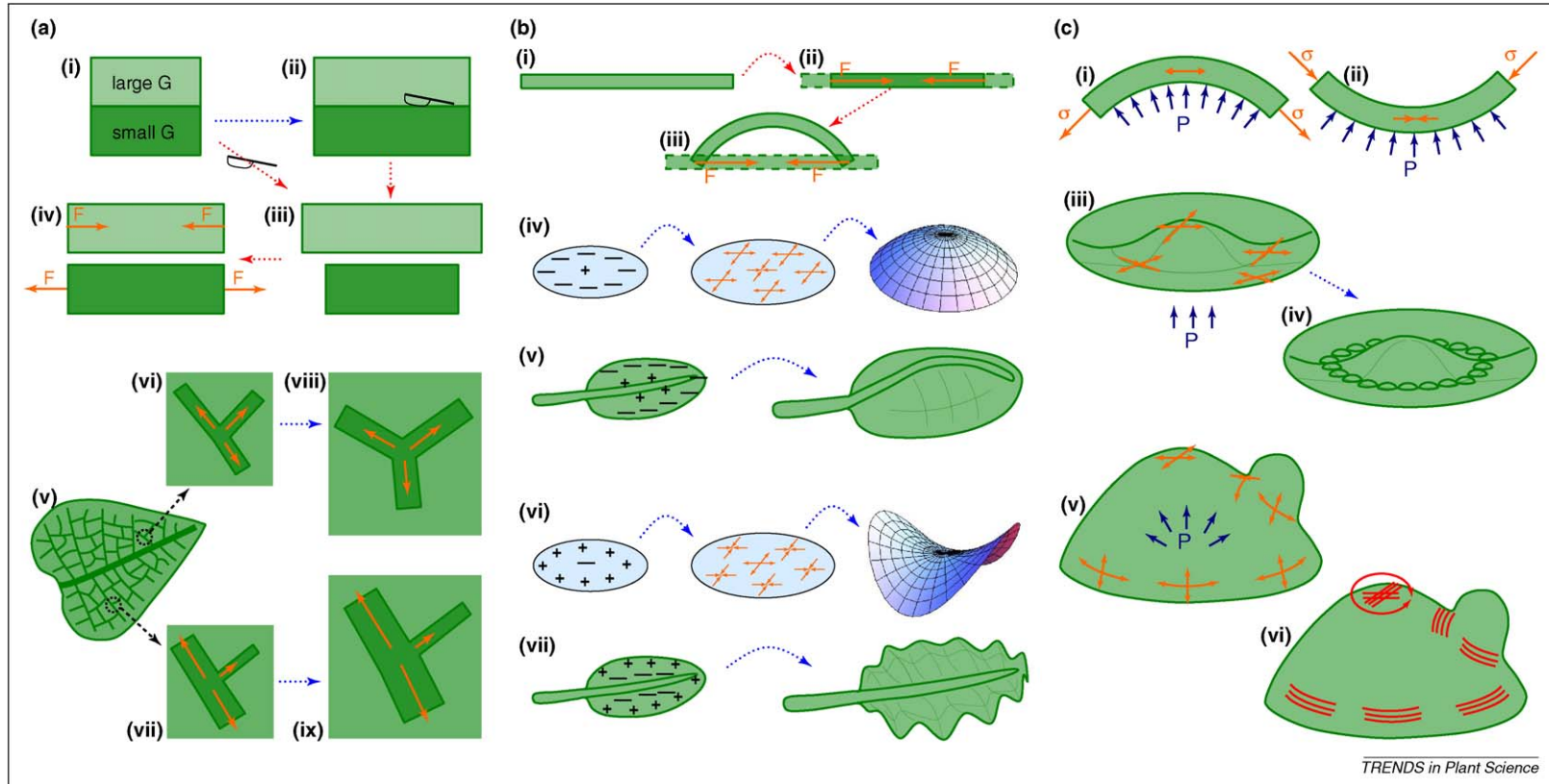
Figure 2. The mechanics of patterning. **(a)** Differential growth induces stress – the case of leaf vasculature. Consider a two-layered tissue growing in length, such that the upper layer has a larger growth rate (G) than the lower layer: if separated by cutting (as indicated with the sketch of a razor blade from i to **iii**), the upper layer grows to a larger length. After cutting, forces (orange arrows in **iv**) are needed to bring together the two tissues – a compressive force for the upper layer and a tensional force for the lower layer. More generally, slowly growing tissues are under a tensional stress exerted by the rapidly growing tissues. Bottom: illustration of leaf vasculature following Ref [43]. Within the hypothesis that veins are stiffer than the ground tissue, a vein grows more slowly so that it is under a tensional force (orange arrows in **vi–ix**) that is proportional to the vein thickness. As a consequence, junctions between veins behave differently according to their thickness: three veins of similar thickness **(vi)** end up making angles of 120° **(viii)**, while a thin vein **(vii)** merely pulls on the junction **(ix)**. **(b)** Buckling and leaf shape. Top (**i–iii**): when applying an axial compressive force (orange arrows) to a thin elastic rod, it first responds by shortening **(ii)**, as in Figure 1c, iii. When shortening exceeds a well-defined threshold **(iii)**, the rod bends upwards or downwards (with equal probability if the rod is perfect). This symmetry-breaking phenomenon is known as buckling. Middle (**iv** and **v**): a thin disk-shaped tissue **(iv)** has an enhanced growth in the center ('+' indicates more growth and '–' less growth). According to part **(a)** of this figure, the center is under compressive stress (orange arrows). When this compression is sufficient, buckling occurs, yielding a dome-shaped surface **(iv)**. The leaves of the *peapod* mutant of *Arabidopsis* [47] probably follow this mechanism **(v)**. Bottom (**vi** and **vii**): the disk-shaped tissue has enhanced growth at the periphery, inducing a compressive stress there **(vi)**. At large enough compression, buckling results in a saddle-like surface **(vi)**. The leaves of the *cincinnata* mutant of Antirrhinum [45] or the *jaw* mutant of *Arabidopsis* [46] seem to follow this mechanism **(vii)**. **(c)** Stress in the shoot apical meristem. Assuming the epidermis to be stiffer than internal tissues, a pressurized shell may be taken as a mechanical model: an elastic shell inflated by turgor pressure P. Top (**i** and **ii**): as in Figure 1c, vii, turgor generates a tensional stress (orange arrows) in the shell if it is curved outwards **(i)**, while a compressive stress is induced if the shell is curved inwards **(ii)**. Middle (**iii** and **iv**): the sunflower capitulum (sunflower inflorescence) has a region with inward curvature, resulting in a circumferential compressive stress **(iii)**. According to the hypothesis of Paul Green [44], this induces florets primordia by buckling. Bottom (**v** and **vi**): shoot apical meristems are generally dome-like, with protruding leaf or flower primordia (only one is pictured for simplification). Stress (orange arrows) is probably tensional – isotropic at the apex and anisotropic on the flanks – except in the crease between the apex and the primordium where it is compressive along the inwardly curved direction **(v)**. Microtubules (**vi**, in red, the curved arrow indicating a dynamic orientation) are observed to follow the direction of largest stress [60].

instance, consider a two-layered tissue such that the upper layer undergoes more growth than the lower layer (Figure 2a, i). If a cut is made so as to separate the two layers (Figure 2a, ii), the upper layer will swell while the lower layer will shrink (Figure 2a, iii) (note that these two deformations correspond to the elastic strain). In order to re-bond the two layers, forces are needed – compressive in the upper layer with large growth rate and tensional in the lower layer (Figure 2a, iv). This means that in the intact tissue, the regions with a larger growth rate are under compressive stress, and conversely, the regions with a smaller growth rate are under tensional stress. In short, differential growth induces stress.

Leaf vasculature

The concept of differential growth can be illustrated by recent proposals for mechanisms of morphogenesis in leaves. In many angiosperms, most veins are not free-ending but reconnect to neighboring veins, forming a reticulated network. The formation of veins is generally believed to be driven by the canalization of auxin flux [31–36]. However, canalization models generally yield tree-like vasculature and have some difficulty in reproducing the reticulated network of many angiosperms, see Refs [37,38]. This led to the proposal that the differentiation into vein cells could be triggered by mechanical stress [37], as implemented in Refs [39,40]. Indeed, a cut in a leaf epidermis tends to open, indicating a tensional stress there. As explained above, this suggests that the epidermis has a smaller growth rate than the mesophyll, which also implies a compressive stress in the mesophyll. This compressive stress would induce the differentiation into procambial cells along well-defined lines, similarly to the compression of a honeycomb-like material which induces flattening (failure) of cells along well-defined lines. This mechanism is known to generate loops in physical systems, as exemplified by the network of cracks at the surface of drying mud. However, although mechanical stress can influence the differentiation of mammalian cells [41], there is currently no such evidence for plant cells.

A second point regarding leaf vasculature concerns the geometry of junctions between veins. Both biochemical and mechanical vein differentiation mechanisms yield very narrow distributions of angles between veins (e.g. mostly 90 and 180° in the mechanical hypothesis), in contrast with measurements on mature leaves [42]. Therefore, it is necessary to account for the deformation of the vasculature network from a young to a mature leaf. Within the hypothesis that the growth rate of veins is smaller than that of the ground tissue, a tension is generated in the veins, so that the geometry of a junction changes as the leaf expands (see caption of Figure 2a, v–ix). This hypothesis was implemented in a two-dimensional cell-based computer model [43]. The results of this model reproduced the geometrical properties measured in Ref [42].

Rods, plates and buckling

We now consider more specifically thin bodies, either one-dimensional (rods) or two-dimensional (plates if flat and shells if curved). A stick, a sheet of paper, or a piece of a ping-pong ball have two modes of deformation: stretching/compression in which the body does not change curvature (e.g. the stick remains straight, Fig. 1c, ii and iii), and bending in which the body changes curvature (Figure 2b, iii). Stretching and bending stiffness coefficients can be defined to measure how easy it is to deform the body. The stretching stiffness is proportional to the elastic modulus of the material and to the thickness of the body. The bending stiffness is also proportional to the elastic modulus; less intuitively, the bending stiffness of a plate is proportional to the cube of its thickness, while that of a rod is proportional to the fourth power of its radius [1]. For instance, being 3.5 thinner than microtubules, actin filaments are $3.5^4 = 150$ times easier to bend, as reflected by the more curly aspect of actin fibers in cells. The different dependence of bending and stretching stiffness on radius also accounts for the fact that it is much easier to bend a rod than to either stretch it or compress it while keeping it straight. As a consequence, when a longitudinal force is applied to a rod (Figure 2b, i–iii) or a sheet, it remains straight as long as the force is below a well-defined threshold, but bends when the force is increased beyond this threshold. This is known as buckling, a symmetry-breaking phenomenon: the rod is initially up–down symmetric, while it is bent upward or downward after buckling. When the rod is free, only one bump appears. When the rod is bound to another body, many bumps may appear. The main feature of buckling is that a compressive stress induces a wavy shape, which led to the suggestion that buckling might be involved in various plant patterning mechanisms [8,44].

Leaves: to be or not to be flat

In general, mature leaves are flat, or can be flattened without tearing. However, mutations in snapdragon (*Antirrhinium majus*) [45] and *Arabidopsis* (*Arabidopsis thaliana*) [46,47] yield leaves that cannot be flattened, instead these leaves have either crinkled margins or are dome-like. In the *cincinnata* mutant of snapdragon [45], and *jaw* mutant of *Arabidopsis* [46], proliferation is enhanced at the margins, while in the *peapod* mutant of *Arabidopsis* [47], proliferation is enhanced in the lamina (see Figure 2b, v and vii). If the final size of cells is unaffected, more proliferation results in more growth. As enhanced growth generates compressive stress, buckling is expected: in the center of the lamina for *peapod* (Figure 2b, iv and v) and close to the margins for *cincinnata* and *jaw* (Figure 2b, vi and vii). Ruffles or a dome-like shape would be a manifestation of buckling. Indeed, physical experiments mimicking differential growth [48–50] show ruffle-like or dome-like shapes. It turns out that the leaf shape could depend on its thickness. In other words, differential growth does not fully prescribe shapes, so that both elasticity and geometry are required to predict actual shapes [48,51–53]. In this way, the combination of differential growth and buckling might generate complex shapes.

How do new organs emerge?

A step further is to investigate whether organogenesis can be triggered by mechanical stress, as pioneered by Paul Green [44]. Guided by the shape of the sunflower capitulum, he proposed that primordia appear through a buck-

ling instability; using the hypothesis that the L1 epidermal layer supports most of internal pressure because cells have much thicker walls, the mechanical structure can be represented as an inflated elastic shell. The geometry of the shell surface at a given point can be characterized by looking at the lines sitting on the surface and running through this point. If the epidermis is dome-like (all these lines are curved inwards) then it is in tension, as for an inflated balloon (Figure 2c, i). If the epidermis is saddle-like (some lines are curved inwards and others curve outwards) then there is a direction in which it is compressed (Figure 2c, ii). This compression would lead to buckling and to the appearance of bumps (Figure 2c, iii and iv) arranged in phyllotactic patterns [44,54]. Indeed, a cut across the capitulum opens, if made at the dome-like center; whereas the cut closes, if made radial in the saddle-like periphery where primordia appear [25]. However, analysis of auxin transport shows that primordia are specified before being morphologically apparent [55]. More strikingly, most shoot apical meristems are only dome-like; such as in tomato where cuts through the epidermis remain open, suggesting a tensional stress only [26]. Therefore, the mechanical buckling theory does not seem sufficient to explain organogenesis.

Yet, ectopic leaves can be induced by applying external compressive forces to a meristem [5]. Additionally, cell walls can be mechanically manipulated with expansin [56,57] or pectin methyl-esterase [58]. As both types of proteins induce cell wall loosening [59], a bump would be expected at the application or induction region if the epidermis is in tension there. Surprisingly, this biochemical manipulation can trigger the development of a whole organ [56–58]. This suggests that the modification of the stress pattern can induce the formation of a new organ.

As shape is mainly dictated by cell walls, this induction might involve a mechanism related to wall synthesis. Knowing that the deposition of cellulose microfibrils tend to follow the orientation of cortical microtubules [18,59], what is the correlation between stress and microtubules? Using the same strong hypothesis that internal layers are negligible, the meristem may be modeled as a pressurized shell [60]. Stress is found to be isotropic at the dome apex matching the dynamic orientation of microtubules (the orientation changes with time), while it is strongly anisotropic in the crease between a primordium and the apex, and on the flanks of the meristem; the direction of largest stress always matches the direction of microtubules (Figure 2c, v and vi). The subsequent deposition of cellulose microfibrils around the basis of the primordium might generate a reinforcing hoop that stabilizes growth in the direction perpendicular to the hoop [60,61], activating a first step in primordium development.

Similarly, the emergence of lateral roots can be induced by mechanical bending. A very early event in this process is the re-orientation of the auxin efflux facilitators PIN1 (PIN-FORMED 1), leading to auxin accumulation at the site of induction [62]. This suggests that auxin transport is sensitive to mechanical stimulation, and that stress might lead to the initiation of primordia through auxin accumulation.

These observations point towards a role for mechanical stress in positional information. By acting on the cytoskeleton or on PIN1 polarization, stress would provide cells with a readout of geometry.

From mechanosensing to development

If stress were to play the role of a signal in differentiation and development, it would need to be sensed and transduced. Actually, plants are known to be responsive to mechanical stimuli, through the so-called thigmo responses [63], which might be mediated by mechanosensitive ion channels in the plasma membrane [63,64]. However, this raises the question of how the stimulus exerted on walls is transmitted to the plasma membrane [63,65]. Moreover, how can a fluid membrane sustain stress over a long period of time during the developmental responses discussed above? Finally, it is difficult to imagine a mechanism involving such channels and providing a directional cue to microtubules, which led to the proposal that cellulose microfibrils themselves mediate mechanosensing [66]. A second issue concerns the perceived stimulus. Careful studies on stem bending [67,68] showed that the thigmo response – measured by the slowing of the stem elongation or by the level of expression of a primary transcription factor – was strongly correlated with strain integrated over the bent tissues involved in the response, and not with stress at the tissue level. The study of microtubule orientation in roots led to proposing maximal growth as a directional cue [69] whereas recent work on the shoot apical meristem found stress to better match microtubule orientation [60]. In fact, stress can only be measured indirectly through the elongation of a flexible device (as with cuts). Cellulose microfibrils [66] might provide such a device; they are synthesized free of mechanical forces, but they are progressively stretched by the wall stress while they are incorporated in the wall. Clarification of these issues requires a deeper understanding of the molecular mechanisms along with the mechanical stress patterns in plant tissues.

Coming back to development and patterning, differential growth can generate mechanical stress. In turn, the inhomogeneity of mechanical stress across tissues could orient growth. A distinctive property of mechanical signals is that they travel at the speed of sound, much faster than any morphogen. Thus, mechanical stress patterns could also efficiently provide positional information. Acting along with biochemical signals, they would provide more robustness to developmental processes.

References

1 Niklas, K.J. (1992) *Plant Biomechanics: An Engineering Approach to Plant Form and Function*, The University of Chicago Press
2 Schopfer, P. (2006) Biomechanics of plant growth. *Am. J. Bot.* 93, 1415–1425
3 Zonia, L. and Munnik, T. (2007) Life under pressure: hydrostatic pressure in cell growth and function. *Trends Plant Sci.* 12, 90–97

4 Peters, W.S. and Tomos, A.D. (1996) The history of tissue tension. *Ann. Bot.* 77, 657–665

5 Green, P. (1999) Expression of pattern in plants: combining molecular and calculus-based biophysical paradigms. *Am. J. Bot.* 86, 1059

6 Lynch, T.M. and Lintilhac, P.M. (1997) Mechanical signals in plant development: a new method for single cell studies. *Dev. Biol.* 181, 246–256

7 Hejnowicz, Z. (2000) Mechanical stress patterns in plant cell walls and their morphogenetical importance. In *Pattern Formation in Biology, Vision and Dynamics* (Carbone, A. *et al.*, eds), pp. 240–251, World Scientific

8 Dumais, J. (2007) Can mechanics control pattern formation in plants? *Curr. Opin. Plant Biol.* 10, 58–62

9 Geitmann, A. and Ortega, J.K.E. (2009) Mechanics and modeling of plant cell growth. *Trends Plant Sci.* 14, 467–478

10 Hamant, O. and Traas, J. (2010) The mechanics behind plant development. *New Phytol.* 185, 369–385

11 Shraiman, B. (2005) Mechanical feedback as a possible regulator of tissue growth. *Proc. Natl. Acad. Sci. U. S. A.* 102, 3318–3323

12 Lecuit, T. and Lenne, P-F. (2007) Cell surface mechanics and the control of cell shape, tissue patterns and morphogenesis. *Nat. Rev. Mol. Cell. Biol.* 8, 633–644

13 Farge, E. (2003) Mechanical induction of twist in the Drosophila foregut/stomodeal primordium. *Curr. Biol.* 13, 1365–1377

14 Erickson, R. (1976) Modeling of plant growth. *Annu. Rev. Plant Physiol.* 27, 407–434

15 Silk, W.K. (1984) Quantitative descriptions of development. *Annu. Rev. Plant Physiol.* 35, 479–518

16 Hejnowicz, Z. and Romberger, J. (1984) Growth tensor of plant organs. *J. Theor. Biol.* 110, 93–114

17 Moulia, B. and Fournier, M. (2009) The power and control of gravitropic movements in plants: a biomechanical and systems biology view. *J. Exp. Bot.* 60, 461–486

18 Baskin, T.I. (2005) Anisotropic expansion of the plant cell wall. *Annu. Rev. Cell Dev. Biol.* 21, 203–222

19 Kwiatkowska, D. and Dumais, J. (2003) Growth and morphogenesis at the vegetative shoot apex of *Anagallis arvensis* L. *J. Exp. Bot.* 54, 1585–1595

20 Rolland-Lagan, A-G. *et al.* (2005) A computational method for inferring growth parameters and shape changes during development based on clonal analysis. *J. Theor. Biol.* 232, 157–177

21 de Reuille, P.B. *et al.* (2005) A protocol to analyse cellular dynamics during plant development. *Plant J.* 44, 1045–1053

22 Supatto, W. *et al.* (2005) In vivo modulation of morphogenetic movements in Drosophila embryos with femtosecond laser pulses. *Proc. Natl. Acad. Sci. U. S. A.* 102, 1047–1052

23 Schmundt, D. *et al.* (1998) Quantitative analysis of the local rates of growth of dicot leaves at a high temporal and spatial resolution, using image sequence analysis. *Plant J.* 16, 505–514

24 Proseus, T. *et al.* (1999) Separating growth from elastic deformation during cell enlargement. *Plant Physiol.* 119, 775–784

25 Dumais, J. and Steele, C. (2000) New evidence for the role of mechanical forces in the shoot apical meristem. *J. Plant Growth Regul.* 19, 7–18

26 Reinhardt, D. *et al.* (2005) Microsurgical and laser ablation analysis of leaf positioning and dorsoventral patterning in tomato. *Development* 132, 15–26

27 Hejnowicz, Z. (1997) Graviresponses in herbs and trees: A major role for the redistribution of tissue and growth stresses. *Planta* 203, S136–S146

28 Peters, W. and Tomos, A. (2000) The mechanic state of "Inner tissue" in the growing zone of sunflower hypocotyls and the regulation of its growth rate following excision. *Plant Physiol.* 123, 605–612

29 Hejnowicz, Z. and Sievers, A. (1996) Tissue stresses and their graviresponsive changes in stems of *Reynoutria japonica* Houtt. *J. Plant Physiol.* 149, 91–101

30 Boudaoud, A. (2003) Growth of walled cells: from shells to vesicles. *Phys. Rev. Lett.* 91, 018104

31 Sachs, T. (1981) The control of the differentiation of patterned tissues. *Adv. Bot. Res.* 9, 151–262

32 Mitchison, G. (1980) A model for vein formation in higher plants. *P. Roy. Soc. Lond. B Bio.* 207, 79–109

33 Scheres, B. and Xu, J. (2006) Polar auxin transport and patterning: grow with the flow. *Genes Dev.* 20, 922–926

34 Berleth, T. *et al.* (2007) Towards the systems biology of auxin-transport-mediated patterning. *Trends Plant Sci.* 12, 151–159

35 Sawchuk, M.G. *et al.* (2007) Time-lapse imaging of Arabidopsis leaf development shows dynamic patterns of procambium formation. *New Phytol.* 176, 560–571

36 Rolland-Lagan, A-G. and Prusinkiewicz, P. (2005) Reviewing models of auxin canalization in the context of leaf vein pattern formation in Arabidopsis. *Plant J.* 44, 854–865

37 Couder, Y. *et al.* (2002) The leaf venation as formed in a tensorial field. *Eur. Phys. J. B* 28, 135–138

38 Feugier, F.G. and Iwasa, Y. (2006) How canalization can make loops: A new model of reticulated leaf vascular pattern formation. *J. Theor. Biol.* 243, 235–244

39 Laguna, M.F. *et al.* (2008) The role of elastic stresses on leaf venation morphogenesis. *PLoS Comput. Biol.* 4, e1000055

40 Corson, F. *et al.* (2010) A model for hierarchical patterns under mechanical stresses. *Philos. Mag.* 90, 357–373

41 Brown, A.E.X. and Discher, D.E. (2009) Conformational changes and signaling in cell and matrix physics. *Curr. Biol.* 19, R781–R789

42 Bohn, S. *et al.* (2002) Constitutive property of the local organization of leaf venation networks. *Phys. Rev. E* 65, 061914

43 Corson, F. *et al.* (2009) In silico leaf venation networks: growth and reorganization driven by mechanical forces. *J. Theor. Biol.* 259, 440–448

44 Green, P. *et al.* (1996) Phyllotactic patterns: A biophysical mechanism for their origin. *Ann. Bot.* 77, 515–527

45 Nath, U. *et al.* (2003) Genetic control of surface curvature. *Science* 299, 1404–1407

46 Palatnik, J. *et al.* (2003) Control of leaf morphogenesis by microRNAs. *Nature* 425, 257–263

47 White, D.W.R. (2006) PEAPOD regulates lamina size and curvature in Arabidopsis. *Proc. Natl. Acad. Sci. U. S. A.* 103, 13238–13243

48 Sharon, E. *et al.* (2002) Buckling cascades in free sheets. *Nature* 419, 579

49 Mora, T. and Boudaoud, A. (2006) Buckling of swelling gels. *Eur. Phys. J. E Soft Matter* 20, 119–124

50 Klein, Y. *et al.* (2007) Shaping of elastic sheets by prescription of non-Euclidean metrics. *Science* 315, 1116–1120

51 Audoly, B. and Boudaoud, A. (2003) Self-similar structures near boundaries in strained systems. *Phys. Rev. Lett.* 91, 086105

52 Dervaux, J. and Ben Amar, M. (2008) Morphogenesis of growing soft tissues. *Phys. Rev. Lett.* 101, 068101

53 Efrati, E. *et al.* (2009) Buckling transition and boundary layer in non-Euclidean plates. *Phys. Rev. E Stat. Nonlin. Soft Matter Phys.* 80, 016602

54 Shipman, P. and Newell, A. (2005) Polygonal planforms and phyllotaxis on plants. *J. Theor. Biol.* 236, 154–197

55 Kuhlemeier, C. (2007) Phyllotaxis. *Trends Plant Sci.* 12, 143–150

56 Fleming, A. *et al.* (1997) Induction of leaf primordia by the cell wall protein expansin. *Science* 276, 1415–1418

57 Pien, S. *et al.* (2001) Local expression of expansin induces the entire process of leaf development and modifies leaf shape. *Proc. Natl. Acad. Sci. U. S. A.* 98, 11812–11817

58 Peaucelle, A. *et al.* (2008) Arabidopsis phyllotaxis is controlled by the methyl-esterification status of cell-wall pectins. *Curr. Biol.* 18, 1943–1948

59 Szymanski, D.B. and Cosgrove, D.J. (2009) Dynamic coordination of cytoskeletal and cell wall systems during plant cell morphogenesis. *Curr. Biol.* 19, R800–R811

60 Hamant, O. *et al.* (2008) Developmental patterning by mechanical signals in Arabidopsis. *Science* 322, 1650–1655

61 Corson, F. *et al.* (2009) Turning a plant tissue into a living cell froth through isotropic growth. *Proc. Natl. Acad. Sci. U. S. A.* 106, 8453–8458

62 Ditengou, F.A. *et al.* (2008) Mechanical induction of lateral root initiation in Arabidopsis thaliana. *Proc. Natl. Acad. Sci. U. S. A.* 105, 18818–18823

63 Jaffe, M. *et al.* (2002) Thigmo responses in plants and fungi. *Am. J. Bot.* 89, 375–382

64 Haswell, E.S. *et al.* (2008) Two MscS homologs provide mechanosensitive channel activities in the Arabidopsis root. *Curr. Biol.* 18, 730–734

65 Zhou, J. *et al.* (2007) Responses of chrysanthemum cells to mechanical stimulation require intact microtubules and plasma membrane-cell wall adhesion. *J. Plant Growth Regul.* 26, 55–68

66 Williamson, R. (1990) Alignment of cortical microtubules by anisotropic wall stresses. *Aust. J. Plant Physiol.* 17, 601–613

67 Coutand, C. and Moulia, B. (2000) Biomechanical study of the effect of a controlled bending on tomato stem elongation: local strain sensing and spatial integration of the signal. *J. Exp. Bot.* 51, 1825–1842

68 Coutand, C. *et al.* (2009) Strain mechanosensing quantitatively controls diameter growth and PtaZFP2 gene expression in poplar. *Plant Physiol.* 151, 223–232

69 Fischer, K. and Schopfer, P. (1997) Interaction of auxin, light, and mechanical stress in orienting microtubules in relation to tropic curvature in the epidermis of maize coleoptiles. *Protoplasma* 196, 108–116

70 Edwards, C.H. and Penney, D.E. (1994) *Calculus with analytical geometry*, Prentice Hall

Plant Science Conferences in 2010

Plant Growth Regulation Society of America (PGRSA) 37th Annual Conference
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