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Can mechanics control pattern formation in plants?

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Development of the plant body entails many pattern forming events at scales ranging from the cellular level to the whole plant. Recent evidence suggests that mechanical forces play a role in establishing some of these patterns. The development of cellular configurations in glandular trichomes and the rippling of leaf surfaces are discussed in depth to illustrate how intricate patterns can emerge from simple and well-established molecular and cellular processes. The ability of plants to sense and transduce mechanical signals suggests that complex interactions between mechanics and chemistry are possible during plant development. The inclusion of mechanics alongside traditional molecular controls offers a more comprehensive view of developmental processes.

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Introduction

In the context of today's biology, mechanical forces are rarely held as great regulators of developmental processes. Undoubtedly, mechanics cannot provide the exquisite specificity demonstrated in numerous chemically controlled processes. However, Nature has no vested interest in chemistry and one must remain mindful of the fact that mechanics might have come to occupy a central place in the control of some biological processes. One clear example is plant growth, where the interplay of turgor pressure and wall mechanics determines, to a large extent, the direction and rate of cell expansion [1,2]. This review addresses an old idea – that mechanical forces can create patterns in plants.

Mechanical explanations for plant development were entertained by many German scientists [3,4] but the idea was developed to its fullest extent by D'Arcy Thompson [5]. Recent advances in the field have sparked renewed interest in the role of mechanics in development. Of the

many distinct ways that mechanics can create patterns, I discuss examples involving surface tension and buckling under compressive loads, focusing more explicitly on the necessary interactions that must exist between mechanics and chemistry to regulate development.

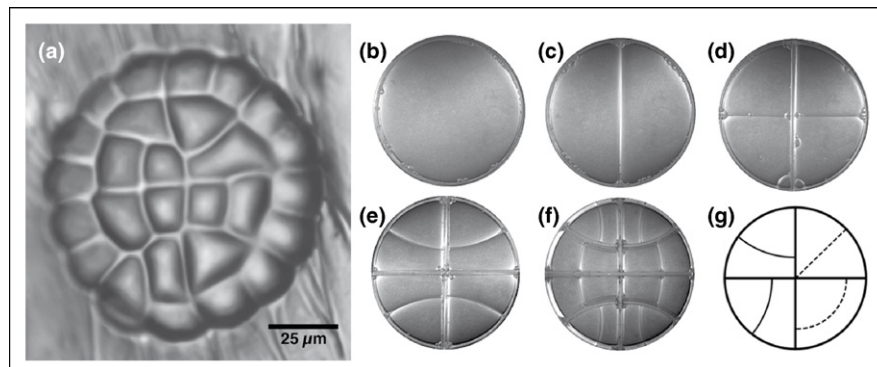
Cell patterning by surface tension

The plant body is characterized by a variety of cellular configurations, which often reflect specific functional needs at the tissue or organ level. A striking example is the formation of stomatal complexes from a series of well-orchestrated cell divisions. Other cellular patterns have been likened to the equilibrium geometry of soap bubbles [5]. Recent work suggests that the similarities go beyond the simple analogy.

Hayashi and Carthew [6] showed a close parallel between the configuration of cone cells within the *Drosophila* ommatidium and that of soap bubbles. The governing principle that shapes soap bubbles is the minimization of surface energy. Soap films are under tension and thus seek to reduce their surface area. One important contributor to the surface energy in cone cells is the adhesion protein N-cadherin. When N-cadherins are normally expressed within the four cone cells, these cells show greater affinity for each other than for the surrounding pigment cells. The resulting cell pattern is one that maximizes the cell-to-cell contact between cone cells and minimizes the contact with pigment cells. If N-cadherin expression is disrupted within one or more cone cells, the equilibrium geometry is shifted to the geometry predicted by the change in surface energy [6]. To my knowledge, the paper by Hayashi and Carthew provides the first direct connection between molecular components of the cell surface and the configuration of a group of cells; but as I shall show, the most spectacular example of cell patterning by mechanical forces was described in plants over a century ago [4].

Figure 1a shows the cellular pattern characteristic of the glandular trichomes present on the adaxial leaf surface of the Venus flytrap (*Dionaea muscipula*). The trichomes are made of a single cell layer atop a short stalk. The cell pattern is definitely intricate but offers, upon inspection, a few suggestive symmetries. We owe to D'Arcy Thompson the first detailed explanation for the development of this pattern. His argument is based on Errera's rule of cell division, which stipulates that new cell walls behave like soap films [7]. A consequence is that new walls take the configuration of least possible area subject to some constraints. Some of these constraints are that daughter cells are of nearly equal sizes and that new walls meet older

Figure 1



Cell patterning by tensional forces in glandular trichomes. **(a)** Fully developed glandular trichome from the adaxial leaf face of the Venus flytrap. **(b–f)** Sequential subdivision of a circular dish with soap bubbles. New walls are assumed to become rigid after formation, and then to serve as a fixed template for the next division. **(g)** Possible wall positions for the third round of cell division. The dashed lines indicate divisions that are not observed whereas the solid lines represent two possible geometries for soap bubbles, both of which are observed in Nature.

walls at 90° . Errera's rule leads to a characteristic sequence of divisions (Figure 1b–f). An initial circular cell is first divided along one of its diameters (Figure 1c) and then at right angle from the first plane of division (Figure 1d). These two rounds of division lead to the four nearly equivalent quadrants seen in Figure 1a. The third round of the cell division is the most revealing for the simple reason that there are more than one division plane that would seem plausible. Perhaps the most natural inclination would be to divide the cell along the bisecting radial line, as in the previous two rounds of division (Figure 1g, upper right quadrant). Alternatively, the cell could divide periclinally (Figure 1g, lower right quadrant). The observed division is altogether different and culminates in the formation of asymmetric daughter cells that preserve none of the symmetries of the system (Figure 1e). Of the three alternatives listed above, the curved wall observed in trichomes has the least surface area and thus conforms to Errera's rule.

The ability of the mechanical argument to predict several rounds of cell division provides strong support for it. However, plant cells are not soap bubbles. We must therefore determine what structure could play the role of surface tension in dividing cells. In plant cells, transvacuolar strands and the phragmosome help to determine the plane of division. Severing experiments using laser microsurgery have demonstrated that these structures are maintained under tension by the cytoskeletal elements associated with them [8–10]. As a result of this tension, the strands that radiate from the pre-mitotic nucleus come to occupy the plane of least area. Green and Poethig [11] emphasized the striking fact that the complex cellular pattern arises from the application of the same set of rules at every cell division. Complexity emerges because the context in which these rules are applied, here the cell geometry, keeps evolving.

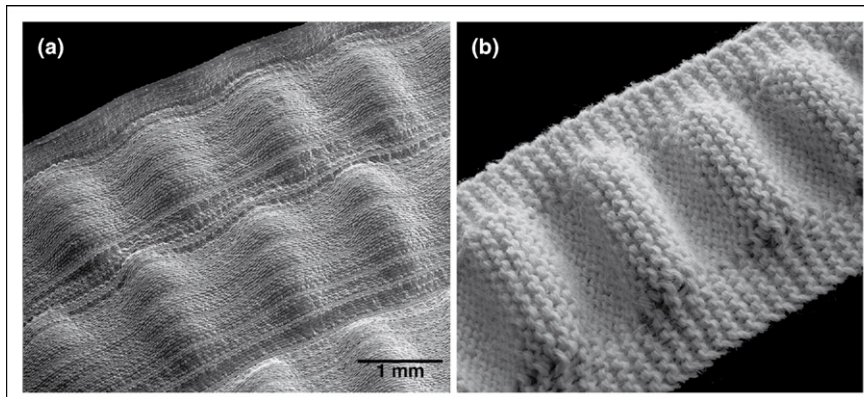
Patterns akin to the one just described were first studied by Berthold, who reported them from various algal species. Errera's rule was also verified in fern protonemata, where the apical cells switch from a transverse division plane to a longitudinal plane precisely when the latter becomes the plane of least area [12,13]. No doubt there are numerous exceptions to the rules just described. No developmental mechanism, whether chemical or mechanical, is universal. A notable exception to Errera's rule is the development of stomatal complexes [14]. Interestingly, although Errera's rule does not apply to the development of stomata, it has been suggested that alternative mechanical principles, such as local stress fields around the guard mother cells, might explain the characteristic division pattern of these clusters of cells [15].

Tissue patterning by buckling

Buckling arises when a slender object or sheet is spatially constrained. The rippling of a grass blade offers an exquisite example of patterning by buckling (Figure 2a). Here, a sheet of material, the leaf lamina, is confined by veins that run along the length of the leaf. If the elongation of the lamina exceeds that of the veins, the lamina is forced to buckle out of the plane. A similar pattern can be created in a knitted band whose central region has twice the number of stitches as the two flanking regions ([16]; Figure 2b).

Although buckling of the leaf surface is not a major developmental event, it offers an example of how the mechanical interactions of cells can lead to patterning at the tissue level. The knitted band example indicates that the conditions necessary for buckling to occur could be as simple as defining an extended domain over which surface expansion exceeds that of neighboring regions. The *cinnamata* (*cin*) mutation of *Antirrhinum* provides a beau-

Figure 2



Tissue patterning by mechanical buckling. (a) Rippling pattern of a grass blade. (b) Paul Green's tri-partite knitted band, showing rippling of the central region.

tiful illustration of this principle [17]. Mutation of the gene turns the normally flat leaves into crinkly surfaces with buckled margins. The buckled leaf arises because the mitotic arrest of the marginal regions of the leaf is delayed compared to that of the central region. Therefore, the leaf has extra margin. The function of the *CIN* gene might be to increase the sensitivity of marginal cells to mitotic arrest signals, so that expansion is uniform across the leaf surface. A similar control of leaf development is present in *Arabidopsis* [18]. This observation is important because there are many ways in which leaf development could be disrupted to yield a ruffled surface. If distantly related plants are shown to share the same regulatory pathways, we can be more confident that these recent studies have uncovered a fundamental aspect of leaf development.

The *cin* mutation provides a mechanism through which buckling could be developmentally controlled. The frequent appearance of superfluous rippling patterns in plant structures is perhaps evidence that expansion of plant surfaces without buckling represents a significant challenge. If so, plant development would require tight controls over the spatial distribution of growth, which might be provided in part by the *CIN* gene.

Buckling, however, need not be deleterious. It is, in fact, possible that buckling has been co-opted to create patterns during development. One of the most intriguing suggestions is that mechanical buckling determines the position of lateral organs at the shoot apical meristem. Several models have been proposed [19,20,21]. The gist of the argument is that differential growth of the meristem surface would lead to a buckling pattern akin to the pattern illustrated in Figure 2a. On this surface, the ridges and creases would experience different patterns of tension and compression, which could serve as a signal for differentiation into separate primordia.

Mechanical models for leaf initiation all share one basic requirement: the region where the pattern first emerges must be under compression. This clear prediction has motivated several experiments to determine whether the forces that act in the meristem are compatible with buckling. In the sunflower capitulum, a striking overlap between the zone of organogenesis and a narrow strip of circumferential compression was observed even as the meristem underwent dramatic geometrical changes [22]. Furthermore, in sunflower capitula, applied compressive stresses alter the pattern of floret initiation [23]. These observations support an involvement of mechanics in patterning at the shoot apical meristem. Earlier experiments in other species produced mixed results, however, with two separate groups concluding that the shoot apical meristem of *Euphorbia lathyris* is strictly under tension [24,25]. This result stands as a challenge to a mechanical interpretation of primordium initiation and must be addressed if mechanics is to remain a viable explanation. A more likely explanation for primordium induction involves the production of auxin and its transport by influx and efflux carriers. Data on this mechanism, accumulated over the past decade, have culminated in a series of very compelling models [26–28].

Beyond geometrical patterns — mechanotransduction

Surface tension and buckling illustrate how mechanics can break symmetry to create new geometrical patterns. On the other hand, many plant patterns, if first expressed at the mechanical level, would have to be transduced into biochemical signals so that further development is possible. Therefore, mechanics can be intimately involved in developmental processes only to the extent that plants possess some form of mechanotransduction.

The role of mechanotransduction in the regulation of animal development has recently received a growing

amount of attention [29]. As a result, processes as fundamental as the determination of left–right asymmetry have been shown to have a mechanical component [30]. The range of thigmoresponses observed in plants provides ample evidence that plants are also capable of mechanotransduction [31]. Several mechanisms have been proposed for the transduction of forces at the molecular level [32*]. One possible mechanism is the mediation of mechanical forces by stretch-activated ion channels located within the plasma membrane. The presence of tension in the membrane is thought to increase the probability of these channels to be opened. Another alternative for mechanotransduction is a tension-induced conformational change in an enzyme, which would expose or shield an active site [32*].

The mechanically induced changes can lead to the expression of specific genes and thus differentiation. Much work remains to be done to connect these molecular transduction mechanisms with processes that operate at the cell or tissue level; but given the pervasive role played by turgor pressure in plant growth and development, the potential for mechano–chemical interactions is great.

Conclusions

The cellular organization of glandular trichomes and the buckling of leaf surfaces provide two examples of pattern formation in plants being driven by mechanical forces. Other examples abound. Although mechanics lacks the specificity of molecular reactions, the examples given above show that mechanics can explain surprisingly subtle pattern-forming events in ways that are compatible with our current understanding of cellular and developmental biology. The demonstration that plants can transduce mechanical signals expands greatly the scope of developmental events in which mechanics could play a role. It would seem odd that Life, having made use of chemistry with such proficiency, would have only tinkered with mechanics. In all probability, the involvement of mechanics in plant development is greater than commonly acknowledged. The evidence is there for those who care to look for it!

Acknowledgements

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Congratulations to the winners of the poster prizes at the 3rd Tri-national Arabidopsis meeting, supported by *Current Opinion in Plant Biology*

A jury of the conference committee awarded prizes for the best poster in each of four sessions:

Metabolic networks

Ralf Stracke, Hirofumi Ishihara, Gunnar Huetp, Aiko Barsch and Bern Weisshaar
Differential regulation of closely related R2R3-MYB transcription factors controls flavonol accumulation in different parts of the *Arabidopsis thaliana* seedling.

Functional genomics

Andrea Ditzer, Simeon Kotchoni, Christine Kuhns, Hans-Hubert Kirch and Dorothea Bartels
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Development

Rita Gross-Hardt, Christina Kägi, Nadine Baumann, James M Moore, Ramamurthy Baskar, Wendy B Galiano, Gerd Jürgens and Ueli Grossniklaus
LACHESIS restricts gametic cell fate in the female gametophyte of *Arabidopsis*.

Signal transduction

Ullrich Dubiella, Anne-Claire Cazale, Mirko Glinski, Wolfram Weckwerth and Tina Romeis
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