



Mechanical signaling in plant morphogenesis

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To control changes in shape during development, the molecular regulatory networks have to interact with the mechanical, structural components of the individual cells, in particular the cytoskeleton and the cell wall. A widely accepted hypothesis proposes that molecular regulation interferes with wall synthesis and stiffness, causing the wall polymers to yield to the internal turgor pressure. However, growth is not only the result of a rigid molecular program instructing the cells precisely what to do. Local differences in growth rates between neighboring cells generate mechanical constraints that can feed back on the regulatory networks and the cytoskeleton. A number of components involved in the perception of these constraints have been identified, although their precise function remains to be determined.

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Introduction

The control of size and shape during the development of multicellular organisms is a major topic in biology. Growth patterns emerge from the interactions between the molecular regulatory networks and the structural, physical elements of cells and tissues. Whereas the regulatory networks have received considerable attention, the biophysical basis of morphogenesis has only quite recently received the renewed attention it deserves, although it has been recognized for more than a century that forces and mechanical properties are fundamental in growth control (see for example [1] and references therein). This is at least in part because it has been very challenging to measure with sufficient precision both physical and geometrical parameters. Several developments, including methodological and conceptual advances, have led to this renewed interest. These involve not only the possibility to

visualize and quantify with unprecedented precision the behavior of molecules, molecular assemblies, cells and tissues even *in vivo*. In addition, novel computational approaches have been developed that integrate information coming from multiple scales, taking into account both biochemical and biophysical processes. As a result, impressive advances have been made in both the animal and plant field during the last decade and we can start to study in an integrated manner how complex geometrical structures emerge from the interaction between biochemistry and biophysics (e.g. see Hofhuis *et al.* as an excellent illustration [2]). Since it is not possible to give a full overview of the field within this opinion article, we will focus here on a limited number of well-characterized examples coming from work on higher plants. First, however, we will briefly review our current understanding of plant growth control.

Translating genetic regulation into geometry: the structural elements of the cell

In higher plants, the cells are, with a few exceptions, surrounded by a wall that mainly consists of cellulose microfibrils, embedded in a viscoelastic matrix of other polymers, in particular pectins and hemicelluloses [3]. In a growing tissue, all the walls are under tension, generated by the turgor pressure within each cell. In equilibrium, the wall exactly counteracts these forces and undergoes reversible (elastic) deformation. Growth occurs when the cell walls within a tissue yield to the forces causing their irreversible (plastic) deformation [4]. This is the case when the forces exceed a particular threshold, which depends on the mechanical status of the cell wall. This threshold is subject to regulation and depends on a range of enzymes involved in the weakening or strengthening of the bonds between the polymers [5]. In addition, synthesis and insertion of novel polymers in the wall contribute to this process, keeping the walls at a particular thickness and stiffness while the cells are growing. Whereas growth rates largely depend on the synthesis and crosslinking of the wall polymers, growth direction is mostly defined by the orientation of the cellulose microfibrils, which are often aligned and restrict growth along their length. They are therefore playing a major role in the definition of growth direction. In turn, the alignment of the cellulose polymers depends on the microtubules, which guide the cellulose synthases that move in the membrane [6]. Although growth anisotropy has been mostly associated with cellulose deposition, recent evidence indicates that the pectin/hemicellulose matrix might also contribute to determining both growth rates and growth directions [7,8].

The capacity of plant cells to modulate the mechanical properties of their walls is apparently under very strict control, although the precise molecular basis of this regulation is poorly understood. The differential distribution of pectins with a variable degree of stiffness has been associated with organ outgrowth at the meristem and the formation of leaves [9–11,12**]. Cell wall properties can even vary considerably within one cell. For instance, the outer walls of the cells at the surface of the meristem can be several times thicker than the internal walls (e.g. [13]). Recent work by Majda and colleagues suggests that the mechanical properties can be even modulated along single, anticlinal walls of epidermal cells in leaves [14**].

Mechanical signaling: from changes in geometry back to genetic regulation

So far, we have mainly considered a scenario where the genetic regulatory system acts on the capacity of the wall to yield to the forces that are exerted on it. However, shape changes are not just governed by a top-down genetic program ordering the structural elements what to do. By modifying local growth rates, genetic regulation will also modify the force pattern and thus generate a feedback on the local tension felt by the cell walls (Figure 1). Indeed, the forces that act on the wall are likely to be highly dynamic, in particular in a growing plant tissue. This is because they do not only depend on the local turgor pressure, but also on global, tissue wide properties. Geometrical parameters such as tissue curvature, or differences in growth rates between neighboring cell populations will contribute to the formation of particular force patterns. Since growth depends in part on the forces that are exerted on the cells, these force patterns can, in turn, feedback on local growth rates. In this context the work of Paul Green and co-workers is relevant. They proposed that stress (defined as force exerted per unit area) induced by local differences in growth rate induce out of plane deformations, or buckling of the tissues [15]. These deformations could be particularly important during organ initiation. Recent work by Rebocho *et al.* has put this concept in a more general framework, proposing how neighboring tissues with conflicting growth patterns can generate complex out of plane deformations [16**].

Importantly, the feedback is not just limited to modifying local force patterns. May be not surprisingly, there is strong evidence that information from the stress patterns acts on the molecular regulatory network and thus on the capacity of the cells to react to stress. This is again illustrated by work of Green and colleagues, who observed that externally applied constraints modify the pattern of organ formation in sunflower [17]. This implies, that changes in mechanical constraints can even affect gene expression and patterning. Recent findings have further confirmed the existence of such a mechanical

feedback on molecular regulation. The pattern of cell polarity during stomata formation in leaves can be modified by the application of external, directional stress [18*]. More correlative evidence was found in meristems, where specific genes are activated in meristematic domains under high mechanical stress, in particular in organ boundaries. Interestingly, a promoter driving GFP expression in organ boundaries was also activated by externally applied stress [19]. This link is largely indirect, however. The response of promoter activity to stress took up to several days, and the precise chain of events linking mechanics to gene expression in plants remains completely unknown.

Whereas the previous examples link mechanics to gene expression, stress also has an effect on cytoskeleton organization. There is compelling evidence that cortical microtubules at the meristem surface align along the predicted directions of main force intensity [20]. By doing so, they in principle also orient cellulose microfibril deposition in this direction, thus causing the cells to resist to the main stress direction [21]. The existence and modulation of this mechanical feedback can potentially account for a number of morphogenetic events, including organ initiation or the formation of cylindrical organs. Hervieu *et al.* suggested that cortical microtubules at the surface of the outgrowing sepal might be involved in growth arrest [22*]. A model was proposed where a mechanical feedback loop, via microtubules acting both as stress sensor and growth regulator, channels the growth and shape of the sepal tip.

Mechano-signal transduction

In the previous section, we have argued that stress patterns could feed back on transcriptional regulation and the properties of structural components such as the cytoskeleton. How do the cells perceive these mechanical signals? In animal systems, a plethora of factors involved in mechano-transduction have been identified [23,24]. These include membrane localized stress-activated channels, but also cytoskeletal elements, able to sense the direction of the forces acting on a cell. Actin polymerization, for instance, is stimulated under stress [25]. Although less well-documented and certainly less well understood, this also seems to be the case for microtubules, as illustrated for example by the microtubules in the mitotic spindle which align also along force directions [26]. In animals, Rho proteins could be implicated downstream of mechanical forces in regulating cytoskeleton dynamics [27,28]. How this occurs remains to be elucidated.

Several of these mechanisms also seem to operate in plants [29,30]. Mechanosensitive channels have been identified, although their precise roles in development are not well understood. As discussed in another review in this issue, DEK1 (DEFECTIVE KERNEL1), a protein

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