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Cellulose Microfibril-Mediated Directional Plant Cell Expansion: Gas and Brake

Directional cell expansion is a fundamental process that is involved in virtually all cellular processes. Divergence from isotropic growth is commonly associated with cell fate transition, organ shaping, or cell maturation. To obtain continuous directional cell growth, and tissue and organ growth as well, positive feedback loops are needed to lock anisotropic cell expansion. On the other hand, antagonistic mechanisms are needed to terminate directional cell expansion. Many genes affecting cell shape have been identified, but only in a few cases do we understand the precise chains of molecular events to some extent. Recently, a cortical microtubule (CMT)-mediated mechanical feedback loop has been recognized that amplifies tensile stress anisotropy and leads to expansion perpendicular to the stress direction (Sampathkumar, 2020; Zhao et al., 2020) (Figure 1A). By contrast, passive reorientation of cellulose microfibrils (CMFs) may form a combative mechanism that cancels directional cell expansion (Figure 1B). However, passive CMF reorientation is insufficiently recognized by developmental biologists who are interested in directional cell expansion, anisotropic tissue growth, and organ shaping.

Plant cells are under turgor pressure, the force that pushes the plasma membrane against the cell walls, in a range of 0.2–5 MPa to drive cell expansion (Long et al., 2020). On the other hand, cell expansion is restricted by plant cell walls, which consist of CMFs embedded in matrix polysaccharides and structured in a lamellar arrangement (Cosgrove, 2018). The orientation of stiff semi-crystalline CMFs confers mechanical anisotropy on the cell wall, which can be instrumental for directional expansion. Fast-growing cells commonly expand predominantly in the direction perpendicular to the net orientation of cell wall CMFs. Multimeric cellulose synthase (CESA) complex polymerizes individual β-1,4-glucan chains, which subsequently assemble into microfibrils. CMT plays a key role in guiding the movement of CSEA complexes and microfibril organization (Paredez et al., 2006). CMT can sense the tensile stress direction along each individual wall and orient parallel to this direction (Hamant et al., 2019). Although the molecular mechanism underlying CMT alignment remains to be explored, katanin-dependent microtubule severing has been proposed to promote CMT alignment with the tensile stress (Hamant et al., 2019). Strikingly, this chain of events would lead to cell expansion perpendicular to the tensile stress direction, which often forms a positive feedback loop to enable directional expansion (Figure 1A). Taking an isolated cuboid-shaped cell as an example, a uniform turgor pressure would lead to higher tensile stress perpendicular to the long axis, align CMTs, and guide CMF deposition more in the direction of higher stress. As a result, the cell expands more in the long axis, which does not change the higher stress perpendicular to the long axis. Together, this chain of molecular events closes a feedback loop (Figure 1A). Recent studies have shown profound influences of the CMT-mediated mechanical feedback loop on cell and organ shape deformation, such as in pavement cells, trichome cells, leaves, and stems (Sampathkumar, 2020; Zhao et al., 2020).

By contrast, passive reorientation of CMFs provides a counteracting molecular mechanism that has the potential to terminate directional expansion at the cell and tissue levels (Dyson and Jensen, 2010). Formerly called the multinet growth hypothesis, the passive reorientation hypothesis postulates that CMFs are passively reoriented during wall extension (Preston, 1982). Although difficult to test experimentally, recent breakthroughs have explicitly demonstrated CMF reorientation under stretch, which leads to tensile strain, in seed plants. By using confocal microscopy in combination with fluorescent carbohydrate-binding Pontamine Fast Scarlet 4B dye, it was shown in real-time that CMFs in *Arabidopsis* root cells reorient as predicted by the passive reorientation hypothesis (Anderson et al., 2010). An independent study used atomic force microscopy (AFM)-based imaging of microfibril movement in cell-free strips of the outer epidermal wall of onion (Zhang et al., 2017). When cell walls were extended by a stretching device, microfibril reorientation was recorded during forced mechanical extension. For a directional expanding cell, the cell wall stretch direction is often perpendicular to the net orientation of CMFs. CMFs can be remodeled and reoriented by stretch (Figure 1B), resulting in reduced CMF network anisotropy and more isotropic cell expansion. Together, passive CMF reorientation reduces directional cell expansion, counteracting the CMT-mediated mechanical feedback loop. Note that passive CMF reorientation reduces stretch anisotropy and would end up with more isotropic cell expansion.

Besides CMT, existing CMFs could also guide the CESA complex, forming an additional feedback loop. It has been shown that CESA complexes autonomously follow trails left by previous complexes (Chan and Coen, 2020). This simple mechanism would result in a positive feedback, through which the level of CMF anisotropy is passed to newly synthesized ones. Thus, the existing level of directional cell expansion is reinforced. Nevertheless, this autonomous guidance can be overridden by the CMT-based guidance when there is a conflict.

The CMT-mediated mechanical feedback loop is a "gas" mechanism to initiate and even amplify directional cell expansion. By

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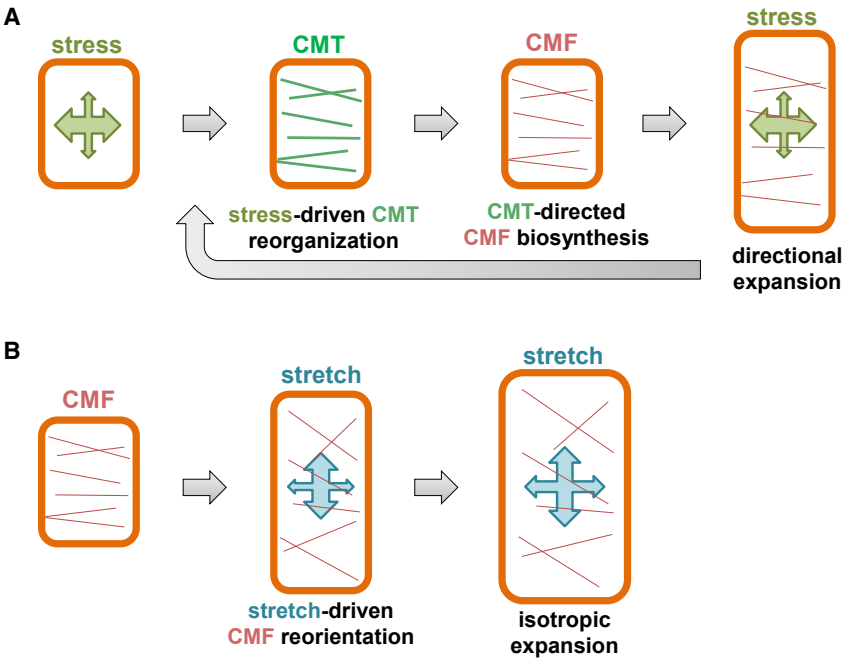

Figure 1. Possible Mechanisms Promoting and Inhibiting Directional Cell Expansion.
(A) CMT-mediated mechanical feedback leads to directional cell expansion. Cells can sense the main force direction along each wall and orient their CMTs parallel to this direction. This would in turn lead to the CMT-guided deposition of CMFs and wall reinforcement restricting cell expansion in the orientation of maximal tension stress.
(B) CMFs passively reorient by the main stretch direction of the wall, which is perpendicular to the net orientation of CMFs. This would lead to reduced CMF anisotropy and promote isotropic cell expansion.

contrast, passive CMF reorientation serves as a "brake" mechanism to reduce and terminate directional cell expansion. It remains to be answered how these counteracting mechanisms are balanced. Analyses of CMF orientation in different cell groups found that less differentiated cells tend to have anisotropic CMFs, and fully differentiated cells tend to have isotropic CMFs (Kerstens and Verbelen, 2003). It is plausible that the CMT-mediated mechanical feedback loop is the dominating mechanism during early cell expansion, which is overridden by passive CMF reorientation later on. The underlying molecular reactions that balance these two mechanisms remain elusive. Within the cell walls, CMFs are surrounded by networks of polymers, commonly including hemicelluloses, pectins, and arabinogalactan proteins (Cosgrove, 2018). Cell wall components, their chemical modification, and physical conditions, such as pH, may affect the kinetics of passive microfibril reorientation (Zhang et al., 2017, 2019). In addition, cell wall plasticity, elasticity, and time-dependent extension (termed creep) may relate to the positive feedback strength. Auxin is another key factor affecting cell walls. It has been demonstrated that mechanical forces also play a role in affecting local accumulation of auxin at the shoot apical meristem through the polar localization of the PIN1 auxin transporter (Heisler et al., 2010), and that the local accumulation of auxin can also promote CMT reorientation (Sassi et al., 2014). It is tenable that auxin may affect passive CMF reorientation; auxin induces cell wall acidification, which presumably reduces interactions between CMFs (Cosgrove, 2018). Identifying additional molecular components that affect CMF reorientation would help us exploit additional layers of regulation of directional cell expansion and anisotropic tissue growth.

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