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SPOTLIGHT

A crucial step toward understanding tip growth in plants

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In this issue, Ryken et al. (https://doi.org/10.1083/jcb.202506021) show that three Ca^{2+} pumps (ACAs) play an important role in the maintenance of the tip-focused Ca^{2+} gradient in moss tip-growing cells. The steepness of this gradient promotes the secretion of the new cell material needed for tip growth.

Tip growth is an extreme version of polarized growth, where new material is deposited in only one part of the cell, allowing for directional elongation. While not common, this type of growth is present across multiple branches of the evolutionary tree, including plants, various algae, and fungi (1, 2, 3). In land plants, several types of cells with vital functions are characterized by this type of growth, including pollen tubes in flowering plants, root hairs in vascular plants, rhizoids in mosses and ferns, and protonema cells in mosses (1). Despite these cells playing some of the most crucial functions in plant growth and reproduction, we still do not fully understand the molecular mechanisms underlying tip growth. Several important players have been identified over the years, including cytosolic Ca^{2+}, pH, cytoskeleton, vacuoles, and cell wall machinery (4).

Cytosolic Ca^{2+}, or more specifically, a highly dynamic tip-focused Ca^{2+} gradient, has emerged as an important regulator of tip growth in many plant species. For example, these oscillating Ca^{2+} gradients are important for the proper growth and cell integrity of both Arabidopsis pollen tubes and root hairs (4, 5). To test if tip-growing cells from nonflowering plants also possess tip-focused Ca^{2+} gradients, the Bezanilla group has previously developed a novel microfluidic device for long-term growth and imaging of moss (*Physcomitrium patens*) (6). They found that moss tip-growing caulonemal cells indeed have a steep tip-focused Ca^{2+} gradient, with pronounced oscillations (7). Their analysis revealed that the Ca^{2+} oscillations during normal growth are composed of 6 discrete periods, called intrinsic mode functions, suggesting that many different mechanisms contribute to the Ca^{2+} oscillations in moss cells. This is a much more complex situation than in pollen tubes and root hairs, whose tip-focused Ca^{2+} oscillations are typically comprised of one or two discrete periods (8, 9). Furthermore, Bascom et al. (7) found that the Ca^{2+} oscillations in the tips of moss cells are anticorrelated with the dynamics of the actin spot in the same region. More specifically, the intensity of the apical actin spot, which plays an essential role in tip growth, is predicted by the preceding Ca^{2+} levels. In turn, the growth status of moss cells affected the Ca^{2+} oscillatory profile, suggesting a possible feedback regulation. These findings were an important step in understanding the molecular mechanisms behind tip growth in mosses.

In a new paper (10), published in this issue, the Bezanilla group takes a crucial next step in understanding the molecular mechanisms underlying tip growth in moss. They take an innovative approach to consider not only the importance of Ca^{2+} oscillations, as previously done, but also the importance of the shape of the tip-focused Ca^{2+} gradient itself. In doing so, they found that the temporal (oscillatory profile) and spatial (gradient steepness) components of Ca^{2+} signaling independently contribute to the proper tip growth in moss cells.

Ryken et al. used the approach previously developed by the group (7) to investigate the role of three autoinhibitory calcium-ATPases (ACAs) in tip growth and Ca^{2+} signaling in moss caulonemal cells. They found that two of them localized to the plasma membrane (ACA1 and ACA2) and one to the vacuolar membrane (ACA5). ACA3 and ACA4 are not expressed in moss protonema tissue (7). These three Ca^{2+} pumps are redundantly required for proper cell growth and maintenance of the Ca^{2+} gradient steepness. They remove excess cytosolic Ca^{2+} in the regions away from the tip (Fig. 1 A). Surprisingly, while the disruption of the three pumps made the gradient shallower, it did not affect the complex Ca^{2+} oscillatory profile nor the related tip actin spot dynamics (see above). This suggests that the ACA-regulated Ca^{2+} gradient affects the tip growth in an actin-independent manner. Indeed, Ryken et al. found that the ACA-dependent Ca^{2+} gradient promotes growth, likely by controlling the deposition of membrane proteins, such as cellulose synthase-like D3, at the cell tip. Furthermore, in the current and previous work, the Bezanilla group found that actin disruption affected the Ca^{2+} oscillatory profile (7) but not its gradient steepness (10), supporting the notion that the two are independently controlled. Based on these findings, the authors propose an exciting model wherein tip growth is controlled by two independent mechanisms, one where ACA-regulated tip-focused Ca^{2+} gradient promotes secretion and consequently cell growth, and another where Ca^{2+} and actin

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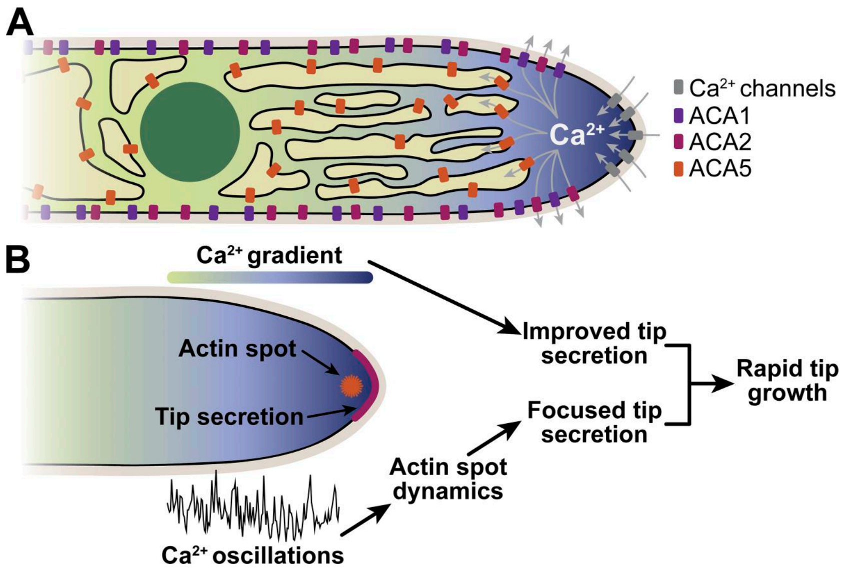

Figure 1. **Cytosolic Ca^{2+} signaling plays a crucial role in tip growth in moss. (A)** A summary of Ca^{2+} flow in the tip of moss caulonemal cells. Ca^{2+} enters the cell via several channels at the tip and is removed from the cytosol by Ca^{2+} pumps (ACAs) further down the cell shaft, generating a concentration gradient. **(B)** A model of Ca^{2+} contributions to the tip growth. Ca^{2+} gradient directly promotes secretion of new cell material at the tip. In a parallel pathway, Ca^{2+} oscillations modulate the dynamics of the actin spot, which in turn help promote and focus the material secretion.

spot oscillations control tip secretion and growth (Fig. 1 B). In support of this hypothesis, Ryken et al. showed that the disruption of these two independent mechanisms led to a dramatic and cumulative reduction in tip secretion and overall growth.

In summary, Ryken et al. uncovered one of the mechanisms essential for the maintenance of the tip-focused Ca^{2+} gradient in tip-growing moss cells. Interestingly, both plasma and vacuolar membranes play, via embedded ACAs, a partially redundant role in this process (Fig. 1 A), and hence both contribute to cell growth. This finding highlights that the role of vacuoles in plant cell growth is not limited to just a space-filling mechanism (11), but rather they likely contribute to cell growth in multiple ways. Overall, this work, together with previous work from the same group, makes a crucial contribution to our understanding of the interplay between key players in tip growth, Ca^{2+} signaling, actin dynamics, secretion, etc. This will undoubtedly be an important baseline for future investigations. This work also highlights that the molecular mechanisms behind tip growth likely diverged between different plant lineages. For example, while in mosses the Ca^{2+} gradient is not affected by actin disruption; this is not the case in Arabidopsis pollen tubes and root hairs, where the two seem to be interconnected (12, 13). This divergence presents an excellent opportunity for us to gain a broader insight, through cross-lineage comparative studies, into the evolution of tip growth in plants as well as other lineages.

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