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Cell mechanics of pollen tube growth

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The pollen tube features particular traits that can only be understood when integrating cell biological with cell mechanical concepts. Firstly, regular temporal variations in the growth rate are governed by a feedback mechanism thought to involve mechanosensitive ion channels. Secondly, the tube uses invasive growth to penetrate the flower tissues with the aim to transport the male sperm cells to their target. Thirdly, the pollen tube is able to reorient its growth direction upon exposure to a guidance cue; the steering mechanism involves the sophisticated choreography of intracellular transport processes. Sophisticated imaging and micromanipulation techniques have been instrumental for the advancement in characterizing the biomechanical features of this crucial cell in the plant reproductive cycle.

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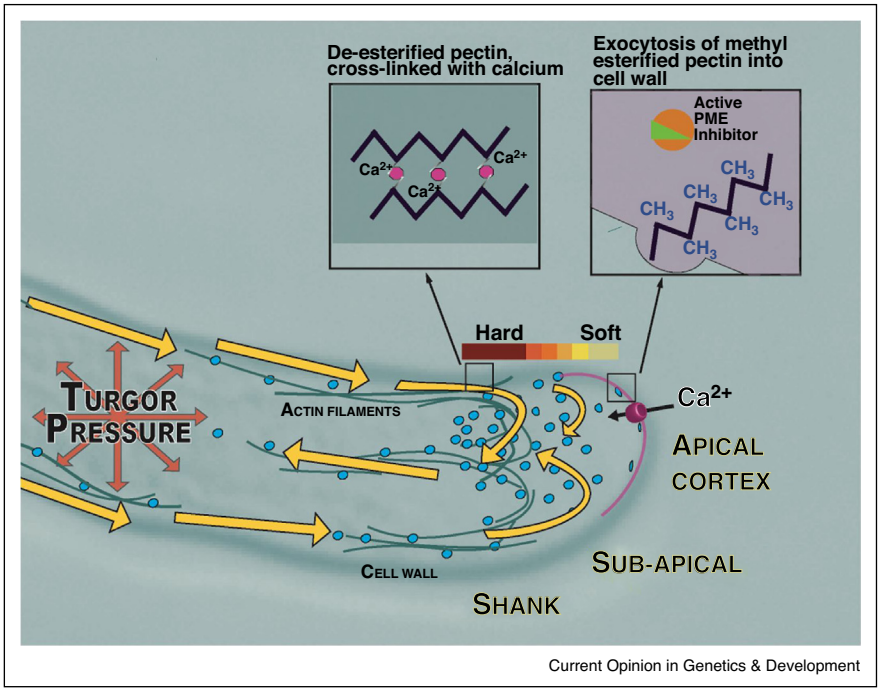
Introduction

Male gametes in plants are delivered to the female partner by way of a mobile intermediate generation, the male gametophyte or pollen grain [1]. The final step of this delivery entails a transport of the gametes from the top of the flower pistil where the pollen grain lands, to an ovule containing a female gametophyte, nestled deeply within the ovary [2]. Delivery is executed through elongation of a conduit: the pollen tube, that penetrates the transmitting tract of the pistil, growing at unparalleled rates to precisely hone in on its target [3]. Formation of the pollen tube is governed by the general principles of plant cell growth, but optimized for the purpose of invasive and directional growth by confining the growth activity to the very tip of the cell [4]. It is here that cell wall gets assembled through both exocytosis and membrane-located polysaccharide synthesis [5]. Cell wall assembly is fueled by precisely choreographed cytoplasmic streaming of vesicles which deposit cell wall material and synthesizing enzymes at the tip [6,7] (Figure 1). The rapid polar elongation of the pollen tube depends on the superb coordination of multiple cellular processes that have been investigated over the past few decades including cytoskeletal dynamics, cell polarity and intracellular transport [8–11]. The physical interplay between the cell wall and internal turgor pressure has an important role in invasive growth which motivates researchers to consider the fundamental cell mechanical underpinnings of the growth process [12]. Several remarkable features characterizing pollen tube growth have garnered particular attention in recent years, due to technological developments that have finally allowed studying them in more detail. Some of the most recent trends are briefly summarized in the following.

Oscillatory pollen tube growth

Pollen tube growth kinetics exhibits oscillatory changes, suggesting that the temporal regulation of the growth process underlies a feedback mechanism [13,14]. In parallel with the growth rate, many cellular parameters in the pollen tube fluctuate including the cytoplasmic Ca^{2+} concentration, ion fluxes across the plasma membrane, the thickness of the apical cell wall and local enzyme concentrations suggesting some of these processes may be linked [6,15,16]. One pivotal parameter is the exocytosis rate which has been documented to oscillate along with cell growth and is suspected to be a key factor involved in mediating spatio-temporal growth regulation [17]. Correlating with exocytosis, the amount of cell wall material at the tip shows temporal variations and it has been observed that the status of the cell wall predicts the magnitude of pollen tube growth [17]. The deformability of the cell wall at the apex is determined by both its biochemical composition and its thickness, and only quantitative, real-time monitoring of both will allow determining any true causal relationship governing temporal control, similar to the question of spatial control of growth [17,18]. Whether or not the oscillatory phenomenon has a biological purpose is up for debate, but it has inspired many to investigate the regulatory network controlling the rapid growth process [19,20]. Oscillatory phase delays of individual processes have been used to deduce relationships between these different phenomena [13]. However this approach is not without fallacies, as elegantly pointed out by Damineli *et al.*, who provide an excellent overview of the current state of research on oscillatory growth and propose two distinct oscillatory systems: one at the tip and the other at the shank [20].

Figure 1



Pollen tube elongation is driven by turgor. At the apex, where the wall yields the cylindrical cell elongates. Only where the wall yields is the force created by the pressure effective against external obstacles. Wall assembly at the tip is fueled by the delivery of intracellular vesicles, transported in a reverse fountain stream (indicated by the yellow arrows). The vesicles contain cell wall material as well as cell wall synthesizing enzymes which are released through exocytosis at the tip. The cell wall at the tip is made up of methyl esterified pectin that is pliable allowing for deformation and continued elongation. Maturation of the pectin involves de-methyl esterification by pectin methyl esterases (PME), secreted at the tip. Ca^{2+} influx occurs at the tip through calcium channels.

Prominent among the oscillating features, and therefore incorporated into many of the modeling approaches, are the cytoplasmic concentration and the transmembrane flux of Ca^{2+} [15,21]. Calcium has a particularly complex role in plant cell growth both outside of the plasma membrane, where it influences the biochemical properties of the cell wall by cross-linking pectin, as well as inside the cytoplasm, where it influences the dynamics of the actin cytoskeleton, for example mediated by actin-binding proteins or Rho GTPase interactions [22]. The concentration of cytoplasmic free Ca^{2+} has been observed to oscillate [15,23], but the concentration peak was found to be delayed with respect to growth [24]. The result was initially puzzling, but a feedback mechanism relating exocytosis, cell wall mechanics and mechanosensitive calcium channels provided a possible explanation [14,25]. The reality is likely to be more complex, however [13,20,26,27]. As the modeling attempts progress, it becomes increasingly obvious that the quality and quantity of experimental data are limiting factors when investigating the regulation of pollen tube growth. One particular challenge is posed by the physical limitations of the optical microscope which limit the spatial and temporal resolution at which oscillatory phenomena can be detected. This is a challenge in particular for *Arabidopsis thaliana*, the primary model organism for plant cell biology, whose pollen tubes are small in diameter and grow slower than those of many other species. Progress was recently made through the development of a novel computational method named CHUKNORRIS which was used to investigate the correlation between oscillatory tip growth and calcium dynamics in *A. thaliana* pollen tubes [28•]. Using this image processing technique, frequent high amplitude Ca^{2+} oscillations in non-growing pollen tubes were detected suggesting that calcium oscillations can occur independently of growth oscillations [28•] (Figure 2). In addition, Ca^{2+} spikes were recorded during the slowed growth of the pollen tube toward the embryo sac, suggesting a possible role for calcium signaling in ovular perception [28•] (Figure 2). These observations confirm that the role of calcium in regulating pollen tube growth is more complex than previously thought.

Mechanics of invasive growth

In order for successful fertilization to occur, the pollen tube must push through the pistil matrix to overcome the mechanical resistance of pistillar and ovular tissues [12,29]. Until recently, it was unknown how the pollen tube generates the requisite invasive growth force.