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Understanding pollen tube growth dynamics using the Unscented Kalman Filter[☆]

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ABSTRACT

In the process of pollination, a pollen tube grows from a pollen grain that has fallen on the stigma of a flower. This tube grows towards the ovary of the flower where it will deliver male reproductive material. Knowledge of the dynamics of pollen tube growth will provide a basis for understanding more complex cells that exhibit similar growth behavior. Current pollen tube growth models are a collection of differential equations that represent the level of understanding that biologists have concerning apical growth. Due to their complex nature, these models are not used to verify observed behavior in living cells as seen under a microscope. We present a model that can be used to describe the behavior of growing pollen tube cells in actual experiments. We propose biologically relevant functions based on knowledge of the growth process to explain the dynamics of model parameters. Our model uses an affine transformation to propagate the tip of the cell and statistical parameter estimation to measure necessary parameters during growth. Using experimental videos of pollen tube growth, we show that our model can adapt to various growth scenarios while extracting growth parameters from the videos.

1. Introduction

Sexual reproduction in flowering plants produces seeds that ensure the continuation of the plant life cycle. This process is initiated by pollination: the transfer of pollen grains from the male part of the flower (anther) to the female part of the flower (stigma). The pollen tube grows from the grain into the style of the flower, navigating female tissue to deliver sperm for fertilization (Fig. 1). Unlike most cells, the pollen tube grows through polar extension wherein cell membrane and cell wall expansion is limited to the apical/tip region of the cell. To prevent the cell from bursting, new cell wall material is deposited at the growth site. The cycle of growth/deposition continues until the cell tip reaches the ovary where it bursts and fertilization occurs. Biologists study these processes to identify key ingredients and their functions. Mathematical models are an important tool in this study because they are able to measure and make predictions on how the shape of the cell evolves throughout the growth/deposition cycles. In the development of these tools, engineers/mathematicians require knowledge of the various pathways leading to cell growth as understood by the biologists.

Pollen tube growth oscillates between periods of activity and inactivity. When plant cells grow, they absorb water and increase the flexibility of their cell walls, allowing for expansion followed by reinforcement of those same cell walls ([22]). Tip growth is the result of two key systems: the first system provides a balance of forces between internal pressure (Turgor, Osmotic) and the stiffness of the cell wall resisting deformation. The second system deals with internal protein and ion dynamics that lead to the deposition of material at the growth site ([5,23]) by vesicles. Callose is a cell wall component that adds structure and flexibility that is selectively deposited in the shank providing rigidity to the cell wall while its absence in the tip provides a flexible domain that can flex and grow ([8]). In a slightly more complicated mechanism, pectin is deposited throughout all regions of the tube, however it exists in a *soft* form at the apex and transitions to a *hard* form as the shank forms through the action of enzymes that promote the pectin molecules to bind to each other. This binding creates a dense matrix that provides both the rigidity and plasticity needed for proper pollen tube growth ([16]). The transportation of material is facilitated by a network of dynamic cable-like fibers (F-actin network) that act as tracks on which vesicles travel and is highly responsive to the active cytosolic gradient of free calcium concentrated at the tip ([24]). Furthermore, the influx of intracellular calcium oscillates with pollen tube growth showing a spike in influx a few seconds after the burst of growth most likely promoting the rest phase ([11]).

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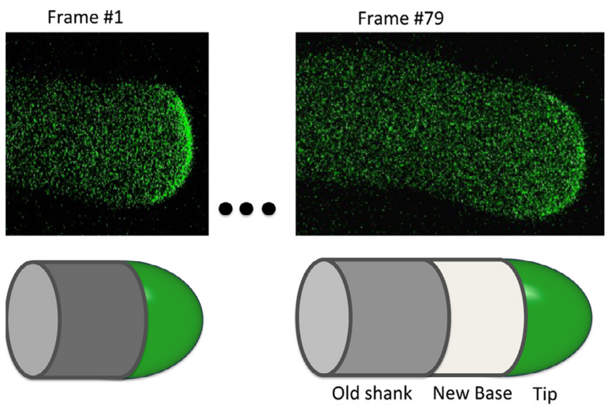
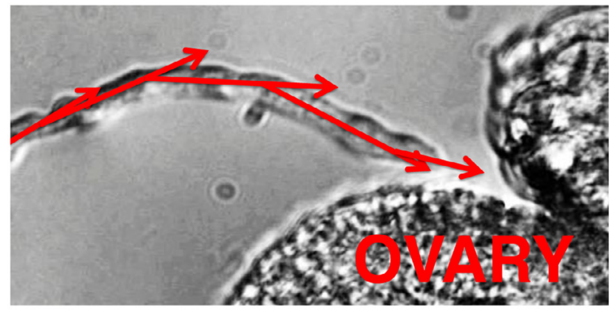


(a) Sample images and their corresponding representations using a standard model



(b) Cell turning towards ovary

Fig. 1. (a) Fluorescence images of a growing pollen tube from an experimental video with accompanying 3D rendition. (b) Enhanced bright field image of a pollen tube cell turning towards the ovary. Arrows show changes in tip orientation over time.

These dynamic processes are highly regulated and connected to one another through signaling cross talk by way of known and unknown mechanisms. Fig. 2 shows an artist's rendition of the components involved in the regulation of tip growth in pollen tubes. These known biological phenomena can then be used to inform mathematical models giving biologists a tool to predict the response to changes in the biological system and better design hypothesis and experiments.

In this paper, we discuss a mathematical model for the growth of pollen tubes as witnessed in experimental videos. We explicitly model those biological process that are observable in the videos, and make meaningful assumptions of other underlying processes that are not observable. In the following sections, we summarize current mathematical models of tip growth in Section 2. Section 3 covers the theoretical development of the proposed method including assumptions made about the growth process. Section 4 covers experimental results and discussion of these results, and Section 5 presents the conclusions of the paper.

2. Related work and contributions

2.1. Related work

There are many factors that affect the growth of pollen tubes, some of which are ion concentrations (e.g. K^+, Ca^{2+}, H^+, Cl^-), turgor pressure and osmotic pressure. The net result of the interactions between these agents is a change in the cell size (i.e. increase in cell length and volume). The complex nature of apical growth has been addressed by a few models in recent literature: ([3,7,10,14,17]). Each model explains pollen tube growth by proposing differential equations to represent what is known about some aspects of the growth process. These models can be divided into two classes based on their area of focus: internal dynamics vs. cell wall dynamics.

Hill et al. [10] approach cell growth as the result of changing osmotic pressure when water from the surrounding enters the cell and causes swelling. This influx is caused by changes in ion concentrations within the cell which establishes an osmotic pressure gradient. Simulations of their model show similar growth (change in volume) patterns as those of *in vitro* pollen tubes. Since the pollen tube can be divided into two main parts: a hemispherical tip and a cylindrical shank (Fig. 1), [17] develop an integrated and self-regulatory two-compartment model whose ion dynamics lead to cell growth. Ion transporters connect these compartments to each other and the surrounding media. In this model, cell growth is the change in tip and shank volumes which are related to the dynamics of K^+, Ca^{2+}, H^+ and Cl^-) through a power law formalization of the cell growth rate.

Unlike the previous two models that focused mainly on internal dynamics, [3] present a model that focuses more on cell wall dynamics. The cell wall is modeled as an inhomogeneous viscous fluid shell

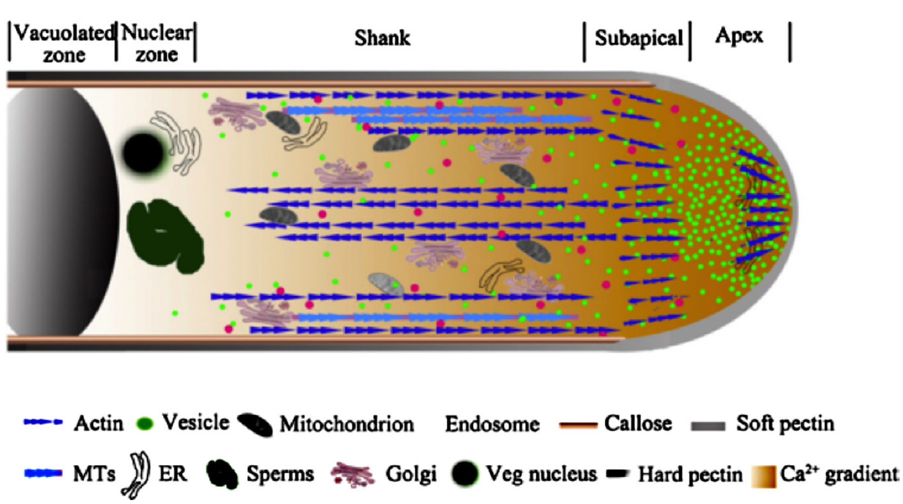


Fig. 2. Artists rendition taken from [21] of the cytoplasm of a pollen tube including cytoplasmic contents. Vesicles are produced from the golgi bodies and then make their way to the cell tip via actin filaments. The filaments indicate direction of vesicle traffic.