Frequency-associated transition from single-cell asynchronous motion to monotonic growth

Marcin Lipowczan¹ · Mariusz Pietruszka²

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Abstract This paper presents a Fourier analysis of the Ortega equation that examines the growth dynamics of plants, specifically the pollen tubes or non-meristematic zones of elongating coleoptiles. A frequency-induced transition from highly nonlinear (periodical) growth—like the one observed in pollen tubes—to monotonically ascending and asymptotically saturated (sigmoid-like) growth, which is anticipated within the framework of a ‘two-fluid model’, is shown. A dynamic phase diagram is calculated and presented in the form of a live video clip.

Keywords Coleoptile · Fourier analysis · Growth dynamics · Phase diagram · Pollen tube

1 Introduction

The growth of plant cells and organs has been attracting a great deal of attention for many decades. The omnipresent conviction that growth can be appropriately described by a monotonic function of time was disproved by the discovery of asynchronous growth that was observed in pollen tubes [1–4]. Many models have been proposed to illustrate the volumetric growth of cells or the elongating zones of coleoptiles [5–8] or the oscillating volume of elongating pollen tubes [9–17]. However, none of these approaches could describe the limiting cases, not to mention the continuous conversion from oscillatory to monotonic growth. The only exception can be attributed to the case presented in Fig. 4 in the paper of Pietruszka [18]

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✉ Mariusz Pietruszka
mariusz.pietruszka@us.edu.pl

¹ Faculty of Biology and Environment Protection, Biophysics and Morphogenesis of Plants, University of Silesia, Jagiellońska 28, 40032 Katowice, Poland

² Faculty of Biology and Environment Protection, Plant Physiology, University of Silesia, Jagiellońska 28, 40032 Katowice, Poland

in which the oscillatory mode can transform into a monotonic extension or even the dissociation (burst) of a pollen tube.

This work builds upon a previous paper [19] that relates the time rate of the change of the volume to the time rate of the change of the pressure and yield stress term. Basically, this model is an augmented form of the Maxwell model—a model for viscoelastic fluids. The Maxwell model can be represented by a purely viscous damper and a purely elastic spring that are connected in series [20]. The Maxwell model describes a material that behaves like an elastic object during short timescales and a fluid during long timescales. In order to perform the calculations, we decomposed a growing plant tube into two regions; a static piece (shank) and a growing region (tip). We then used Fourier analysis to investigate the frequency dependence of the plant growth rate and found that at low frequencies plant growth exhibits constant growth, whereas at higher frequencies oscillatory growth is possible. In particular, we developed a mathematical analysis of the Ortega equation of plant cell wall growth using Fourier transforms. We determined a numerical solution to a ‘two-fluid model’, specifying the growth modes that are able to describe frequency-dependent transformation (from oscillatory to monotonic growth) in an analytically satisfactory manner. In essence, the model uses a differential equation for pollen tube extension that contains viscous and elastic terms for material expansion.

As is broadly agreed in the pollen tube biophysics community, there is no consensus as to the underlying cause for the oscillations in the pollen tube growth rate. We base our modeling and results on a contentious hypothesis that oscillations in cytosolic pressure, possibly conjugated with the chemical potential induced exchange of life-vital cations or anions [21], drive the oscillations in the pollen tube growth rate. Alternative models have proposed temporal variations in cell wall properties or temporal variations in the cell wall intercalation rate (see [3] for a state-of-the-art review).

2 Results

2.1 Model summary

The growth of the plant cell wall is determined by its elastic, viscoelastic, viscoplastic, and rheological responses to internal stresses that are induced by turgor pressure P . In order to deconstruct these various wall behaviors, we start with the Ortega [7] equation:

$$\underbrace{\frac{1}{V(t)} \frac{dV(t)}{dt}}_{\text{extension rate}} = \underbrace{\frac{\Phi(P(t) - Y)}{\varepsilon}}_{\text{viscoplastic term}} + \underbrace{\frac{1}{\varepsilon} \frac{dP(t)}{dt}}_{\text{elastic term}} \quad (1)$$

which formalizes the combined effect of inelastic and elastic components to the volume V relative extension rate. By introducing the volumetric elastic modulus ε , it takes into account the elastic deformation of the cell wall in the case of a changing turgor pressure $P(t)$. In Eq. (1), Φ denotes the ‘extensibility’ of the wall, which is defined as the reciprocal of the materials’ viscosity [12]. Equation (1) describes the relative rate of change in volume as the sum of the irreversible (first term) and reversible (second term) deformation of the wall. While $P(t)$ represents the dynamic turgor pressure inside the vacuole, Y describes the yield threshold value, which is similar to that from the Lockhart [6] equation. The Lockhart/Ortega model

involves a viscoplastic term that is non-zero only for $P > Y$. Equation (1) can be solved exactly when the analytical form of turgor pressure $P(t)$ dependence on time is known or else it can be solved numerically.

Considering the volume of the elongating pollen tube, we partitioned the total cell volume V_T into two compartments – V_A and V_B , where V_B is the volume of the cylindrical pollen tube basal to the hemi-spherical apex and V_A is the volume of the apical region itself, which is known to undergo volume oscillations [22] in the following way: $V_T(t) = V_B(t) + V_A(t)$ (see [19] for details). To describe the apical volume oscillations in the pollen tube, we used Eq. (1) in a modified form in which the time dependence of turgor pressure P is shifted to the pressure fluctuation term $\delta P(t)$, so $P(t) - Y = P + \delta P(t) - Y \geq P - Y$. It is also possible to couple the Ortega equation to the equation for the change in the cell wall properties by taking the extensibility coefficient Φ , which is responsible for the viscoplastic wall properties, as a dynamic variable. This operation is justified by the fact that the mechanical properties of the wall can be modified by the intercalation of specific new cell wall materials into the wall [23]. By taking $\Phi = \Phi(t)$ and $\varepsilon = \text{constant}$, we followed Pietruszka's [8] model equation to introduce the dynamic cell wall mechanical properties by the inclusion of the wall-loosening chemical activity factor in the form of diffusion rate (k_0). Cell wall viscoelasticity is then expressed by the $\Phi(t) = \Phi_0 x_0 \exp(-k_0 t)$ term, where $\Phi_0 = \text{constant}$ is the extensibility coefficient that was originally proposed by Lockhart [6] with the dimensionality $[\Phi_0] = 10^{-6} \text{ (s} \cdot \text{MPa)}^{-1}$. The dimensionless coefficients x_0 and k_0 [1/s] represent the initial polymer density [$x_0 = x(t = t_0)$] and the cell wall intercalation rate (diffusion rate), respectively. Furthermore, we assumed that the intracellular osmotic pressure can be changed in response to changes in the extracellular osmotic potential and therefore the osmotic pressure interaction, which is included in $\delta P(t)$, is justified. Hence, after a simple computation, we obtained:

$$\frac{1}{V_A + V_B} \frac{dV_A}{dt} = \underbrace{\Phi_0 x_0 (P + \delta P(t) - Y) e^{-k_0 t}}_{\text{viscoplastic}} + \underbrace{\frac{1}{\varepsilon} \frac{d(\delta P(t))}{dt}}_{\text{elastic}} \quad (2)$$

Because the Y time-derivative vanished in the calculations, Eq. (2) shows that the relative change V_A'/V_A in the apical volume V_A is dependent on the sum of the viscoplastic term that is proportional to the total turgor pressure $P + \delta P(t) - Y$ plus the elastic term (acting within the range of the applicability of Hooke's law) conjugated to the pressure fluctuations time-derivative $d[\delta P(t)]/dt$. The material constants that are responsible for the properties of the growing wall are included in Φ and ε , thus combining irreversible (viscoplastic) growth and reversible (elastic) cell extension, respectively. Equation (2) takes into account the effective (total) pressure in the system as well as the cell wall elastic and viscoplastic properties. The constant turgor pressure P is connected to the 'first fluid', while the pressure fluctuation term $\delta P(t)$ stands for the 'second fluid'. Together, they form the so-called 'two-fluid' model.

2.2 Fourier analysis

In order to further investigate Eq. (2), we completed the Fourier analysis. After taking the Fourier transform [24] of Eq. (2), the left side becomes the Fourier transform of the relative growth rate $F(\text{GR})$ and the right side can be split into three contributing terms, which we refer

to as viscoplastic, coupling (fluctuating-plastic) and fluctuating-elastic, respectively. After performing some calculus, the corresponding spectral intensity (magnitude) contributions are equal to:

$$I_{\text{viscoplastic}} = \Phi_0^2 x_0^2 (P-Y)^2 \frac{1}{k_0^2 + 4\pi^2 f^2} \quad (3)$$

$$I_{\text{coupling}} = \frac{1}{\varepsilon^2} P_0^2 \Phi_0^2 x_0^2 (P-Y)^2 \left| F(\delta P(f)) * \frac{1}{k_0 + 2\pi i f} \right|^2 \quad (4)$$

$$I_{\text{elastic}} = \frac{1}{\varepsilon^2} P_0^2 f^2 |F(\delta P(f))|^2 \quad (5)$$

In Eqs. (3)–(5), we omitted the ‘A’ indices on the left side for the sake of generality (the validity of these final equations is universal and *not* only limited to the pollen tube apex). Here f stands for the oscillation frequency (in Hz), ‘*’ denotes convolution and F represents the Fourier transform. Terms (3)–(5) stand for all of the model contributions to the energy distribution spectrum (Fig. 1). The viscoplastic Fourier component has its maximum at $f = 0$ Hz and a Lorentz form for higher frequencies. This term may be responsible for steady elongation. The fluctuating-elastic term, Eq. (5), will have an envelope of $f^2 F(\delta P)$. This will be 0 at $f = 0$ Hz and increases with the frequency. This term will promote the oscillatory state naturally. The fluctuating-viscoplastic component, Eq. (4), will act as effective coupling between the first and last terms. The interplay between these terms will, among others, define the effective frequency of the oscillations in the pollen tube. In the paper

Fig. 1 Frequency dependence of power spectral density at $k_0 = 0.015$ and $\varepsilon \in [200 \text{ MPa}, 1 \text{ GPa}]$. **a** Several selected values of ε . **b** Continuous range of ε . Comparison with the relaxational spectrum for Maxwell material

of Haduch-Sendecka et al. [25], the response of a single pollen tube to the changes in the extracellular osmotic potential and fluctuating elastic term that promoted the oscillatory state was analyzed. Indeed, one should pay special attention to the phase difference between the transverse and longitudinal fluctuation. Provided that they are in phase, the oscillatory growth should be dominant. The observed frequency for *Nicotiana tabacum* (ibid.) ranges from 0.03 Hz (hypertonic), through 0.06 Hz (hypotonic) to 0.13 Hz (isotonic). In the present work, we assumed the value of 0.066 Hz for calculations.

Experimental data suggest that there exists a continuous transition in the mechanical properties of the cell wall between the apical and basal regions [26]. Interestingly, another continuous transition takes place in tip-growing plants—from periodic motion (as in pollen tubes, e.g., [22]) to a smooth (monotonic) elongation of plant organs (as in the elongating zones of the coleoptiles in maize, e.g., [8]). Because pollen tube growth offers an easily observed example of the time-variable growth behavior in a single cell, there exists a unique opportunity to explore the dynamics of more complex cell wall behavior through harmonic analysis. By implementing Fourier analysis into a computer code (Supporting Information), we calculated the frequency dependence of power spectral density (PSD) for the diffusion rate k_0 and changing ε (Fig. 1) in order to show the supremacy of the fluctuating-viscoplastic term over the fluctuating-elastic one or the opposite for several selected frequencies (Fig. 2).

By proceeding with the frequency as in Fig. 1, three main growth modes are observed.

1. At very low frequencies, the viscoplastic phase that is responsible for monotonic extension and irreversible deformation is the dominating one. The diffusion rate k_0 (at a constant turgor pressure P) is the main device that is responsible for growth.
2. At slightly higher frequencies but still well below the arbitrarily accepted value of a ‘resonance’ frequency $f_0 = 0.066$ Hz, the fluctuating-viscoplastic phase (extension accompanied by weak oscillations) plays the main role. The coexistence of fluctuating pressure and viscoplastic phases may lead to growth fluctuations with an extended oscillation period. The oscillation amplitude is lower (Fig. 1) for higher values of the elastic constant ε . Note that it is well known that pollen tube oscillations have been observed to oscillate across a wide range of frequencies. For our purposes, the example value of 0.066 Hz was used, however it has also been reported elsewhere for Ca^{2+} ionic oscillations [27] that accompany growth.
3. In the immediate vicinity of the ‘resonance’ frequency $f_0 = 0.066$ Hz, the fluctuating-elastic phase dominates and the oscillatory mode of the plant growth prevails. The energy for growth is accumulated and dissipated in the oscillations and growth can be resumed in each cycle. The non-marginal contribution of the viscoplastic phase allows for the superposition of growth oscillations and monotonic growth (growth is ‘parallel’ to the oscillations, as in the elongating pollen tubes).

All of these cases can lead to unidirectional growth, either due to the changes in symmetry [28] or the anisotropy of the cell wall properties and reinforcement [26].

Creating a continuously changing phase diagram was not, however, an easy task. This is because a four-dimensional presentation is then required in our three-dimensional space. This task was resolved in the form of a video clip (SI Movie 1) in which the time of the presentation corresponds to the frequency f . Hence, SI Movie 1 presents a dynamic phase diagram in which the difference between the fluctuating-viscoplastic and fluctuating-elastic parts at a continuously changing oscillation frequency belongs to the $[0, 0.32]$ Hz interval in (k_0, ε) coordinates.

Fig. 2 The supremacy of a fluctuating-viscoplastic term (green) over a fluctuating-elastic one (blue) and vice versa for several selected frequencies. **a** $f \in [0, 0.0591]$ Hz, domination of a fluctuating-viscoplastic term (green). **b** $f = 0.0596$ Hz, coexistence of both a fluctuating-viscoplastic term (green) and a fluctuating-elastic one (blue). **c** $f = 0.0601$ Hz, coexistence of both a fluctuating-viscoplastic term (green) and a fluctuating-elastic one (blue). **d** $f \in [0.061, 0.071]$ Hz, domination of a fluctuating-elastic term (blue). **e** $f = 0.0718$ Hz, coexistence of both a fluctuating-viscoplastic term (green) and a fluctuating-elastic one (blue). **f** $f = 0.0723$ Hz, coexistence of both a fluctuating-viscoplastic term (green) and a fluctuating-elastic one (blue). **g** $f = 0.0728$ Hz, coexistence of both a fluctuating-viscoplastic term (green) and a fluctuating-elastic one (blue). **h** $f \in [0.073, 0.5]$ Hz, domination of a fluctuating-viscoplastic term (green)

In a narrow (close to resonance) frequency window in which the fluctuating-elastic phase dominates (see Fig. 2 and SI Movie 1 at about 0.066 Hz), amplified oscillatory growth is allowed. In the remaining situations, monotonic growth prevails. This result explains, among

others, why growth rate oscillations are present in small (μm in scale) single-cell systems (elongating pollen tubes) that have a peculiar mechanical and rheological structure.

The aim of this study was to understand what leads to the oscillations in pollen tube growth. We merely showed that if the plant wall is like a viscoelastic fluid, then it will respond to an oscillating pressure that has a specific frequency dependence. Low frequencies favor the fluid behavior of the model that damps out oscillations and higher frequencies (shorter timescales) allow for an oscillating behavior. The proposed model does not answer the more interesting question of what mechanism determines the variations in pressure, since to some degree this was the subject of our recent investigations [27]. However, in agreement with the presented model, we explain how the quantities P and Φ can fluctuate. Thus, the following scenario can be realized.

The increased involvement of H^+ -ions in cell-wall building and exocytosis [21, 29], which change the inner volume by a small $-\delta V$ amount within the cell, raises the turgor pressure inside the cell by δP . The increased pressure by δP at the apical plasma membrane induces the stress relaxation of the cell wall (allowing to replace Φ by $\Phi(t)$ in Eq. (1)), a relaxation-driven cell expansion by δV and thus triggers the start of the next growth cycle with a lowered turgor pressure to the $\sim P$ level. Then, the system can restore the initial configuration in order to allow a new growth cycle to begin (explicit in pollen tube oscillations).

In order to cut through the numerous conceptual models published in the biophysical community, the determination of the spectral value of the peak intensity can serve as a litmus test that can be delivered for a given model parameter set (especially applicable for different values of ε). The interrelation of spectral intensity at f_0 and ε , can—at least in principle—be measured. Because in our model the platform for oscillatory growth is prepared and the mechanical or chemical interpretation can be delivered, the dependence between the wall mechanical properties and oscillation frequency can be established. Each model that contains these parameters can be validated in experiments.

3 Discussion

Numerous studies have dealt with tip-growing organ morphology combined with their mechanical properties or molecular dependencies. Among others, morphological studies assumed a model that generates the shape of a straight hypha with a regular shape and size [30], where a stationary VSC (vesicle supply center) releases vesicles that reach the cell surface in approximately equal numbers in all directions and the cell grows as a sphere. Any displacement of the VSC from its original central position distorts the spherical shape. A sustained linear displacement of the VSC generates the typical cylindrical shape of fungal hyphae. Also, the cell wall was modeled biomechanically as a stretchable elastic membrane using large-deformation elasticity theory [31]. Tip growth was also modeled with the aid of thin shells and anisotropic viscoplasticity [12]. The viscoplastic properties of the cell wall affected the shape of the cell at steady-state and non-steady changes in cell shape. Moreover, the anisotropy of mechanical properties were taken into account for observed patterns of wall expansion in plant cells. Here, the oscillations in cell shape were also observed. Recent approaches have dealt, among others, with the finite element method [14]. In such cases, the phase diagram from our study can play a role in checking the physical conditions in the simplest considered elements. All the works mentioned above yield useful predictions concerning the nature of the cell's deposition machinery and the shape and dynamics of tip-growing cells [10]. In this context, since our study is primarily focused on physically measurable parameters, it can help to discern if the considered model is applicable/suitable or not.

The phenomenon of oscillatory tip growth in the context of constitutive and kinematic equations for computational modeling has been reviewed in Chapter 14 by [32] in a newly published book entitled *Pollen Tip Growth*. What is important from our point of view is the number of pulsatile and non-pulsatile cells as a function of the average elongation rate of lily pollen tubes. Interestingly, all (more energetic) lily pollen tubes elongating faster than $0.2 \mu\text{m s}^{-1}$ were observed to oscillate (Fig. 14.1, *ibid.*). A transition from monotonic to pulsatile growth at approximately this value of elongation speed should be observed. Whether this is the same kind of transition as suggested in this work remains an open question. Nonetheless, the properties ascribed by the parameters from constitutive Eq. (2) may play an essential role. Also, the coupling term, expressed explicitly for the growth rate intensity by Eq. (4), can possibly lead to different growth rate profiles, from stationary cell, to various pulsatile cell profiles (Fig. 14.2, *ibid.*). A unique set of mechanistic couplings (material constants such as Φ and ε) should, in principle, deliver such a solution, at least at the phenomenological level. On the other hand, one should note that an additional requirement mentioned earlier in this work should be fulfilled, namely that the transverse and longitudinal oscillations [25]—if not in phase—can also contribute to different wave profiles (Fig. 14.2 C-D). Consequently, one can speculate that the case of stationary cell profile (steady growth, Fig. 14.2 A) may originate from a total phase difference (180 deg.), while the symmetric pulsatile profile (Fig. 14.2 B) may be a consequence of a near-zero phase offset.

‘Another brick in the cell wall’ that considers—at the microscopic level—cytosolic approaches to oscillations has been reviewed by Portes et al. [33]. The authors, seeking a missing pendulum, reviewed the pollen tube oscillator as integrating biophysical and biochemical aspects of cellular growth. Also, a proposal that the variation of the chemical potential of protons (note e.g., a visible H^+ influx at the tip of a growing pollen tube) represents a ‘still-missing’ regulatory mechanism either of the oscillating or non-oscillating elongating system has been put forward by Pietruszka [21]. This view is in accord with pH oscillations observed recently on single hyacinth pollen tubes [27]. Furthermore, the global $1/f$ characteristic of the PSD, which corresponds to the membrane channel noise, was found (*ibid.*).

4 Conclusions

This work lies at the heart of the controversies surrounding pollen tube growth [34–36]. However, this paper focused on a general mathematical model that can describe a process (growth in plants: pollen tubes) by developing a new description—Fourier analysis—and then applying it to a specific example. Therefore, it is of interest as it provides the tools to relate this model to other more complex structures in plants. Based on the Fourier analysis of the augmented Ortega equation expressed in the form of a ‘two-fluid model’, we proposed a theoretical basis for a postulated continuous transition—in the frequency domain—from oscillatory to monotonic growth in extending plant cells or elongating organs.

Author contributions MP conceived of the project. ML wrote the MATLAB code for the movie. MP performed the analytical calculations and wrote the paper. Both authors reviewed the manuscript.

Compliance with ethical standards

Competing financial interests The authors declare no competing financial interests.

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