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Exact analytic solutions for a *global* equation of plant cell growth

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Abstract

A generalization of the Lockhart equation for plant cell expansion in *isotropic* case is presented. The goal is to account for the temporal variation in the wall mechanical properties - in this case by making the wall extensibility a time dependent parameter. We introduce a time-differential equation describing the plant growth process with some key biophysical aspects considered. The aim of this work was to improve prior modeling efforts by taking into account the dynamic character of the plant cell wall with characteristics reminiscent of damped (aperiodic) motion. The equations selected to encapsulate the time evolution of the wall extensibility offer a new insight into the control of cell wall expansion. We find that the solutions to the time dependent second order differential equation reproduce much of the known experimental data for long– and short– time scales. Additionally, in order to support the biomechanical approach, a new growth equation based on the action of expansin proteins is proposed. Remarkably, both methods independently converge to the same kind, sigmoid–shaped, growth description functional $V(t) \propto \exp(-\exp(-t))$, properly describing the volumetric growth and, consequently, growth rate as its time derivative.

Keywords growth functional, plant cells, wall extensibility

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Introduction

Plant cells are confined by a stiff, yet flexible, polymeric wall that defines cell shape and permits high turgor pressure to develop (Cosgrove, 1993). In growing cells these walls must expand to enlarge and keep the wall strong enough to withstand the mechanical stress arising from internal hydrostatic pressure. The plant cell wall consists of a network of cellulose microfibrils glued together by a polysaccharide matrix (ibid.). The primary wall is secreted by the growing cell and is maintained in an extensible, plastic state during the period of cell growth, before the cell matures and the wall loses its ability to expand (Veytsman and Cosgrove, 1998). This process, from the physical point of view, can be described by a dynamic extensibility coefficient. In this paper, three classes of cell (tissue) growth solutions are considered under time dependent extensibility coefficient.

Lockhart (1965) model deserves a prominent place among the key milestones in the field of plant growth mechanics. The model however, has many shortcomings that limit usefulness. Among these shortcomings is the formulation of uniaxial cell growth when in fact cell growth involves strain rates along three principal directions. Moreover, the mechanical anisotropy of the cell wall was ignored. This latter aspect has been considered by many authors, and quite recently a proposal was also given (see Pietruszka, 2009 and papers cited therein) concerning a new local (coordinate dependent) tensor growth equation. Yet, there is still a need for a simple global (coordinate independent), easy applicable equation of volumetric cell/organ growth keeping positive aspects of the original Lockhart equation. This paper is an effort to complement previous efforts in the area.

Lockhart equation has been known since 1965, and it is clearly not new. However, revisiting the mathematical application of the equation can provide new insights. The Lockhart equations describe plant cell elongation, as a combination of elastic, turgor-driven extension and plastic deformation (yielding) of the cell wall. The Lockhart equation assumes that extension is driven by a constant turgor pressure due to osmotic uptake of water. The core portion of this equation has been an extensibility coefficient Φ_0, ac-

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counting of visco-elastic features of cell wall. The extensibility coefficient, Φ_0, was originally defined as a constant. This coefficient should be, however, dynamic to address the changes taking place in the walls of the growing cell of a plant. Also, numerous experiments provided evidence that the extensibility coefficient is susceptible to many environmental stimuli. These include phytohormones or growth inhibitors and temperature, and especially its pronounced change in time. From purely mathematical point of view, as well as indicated by a huge body of observational data, the extensibility coefficient magnitude should gradually decrease with time, ceasing altogether when the cell matures. In fact, the conventional treatment of the Lockhart equation (with $\Phi_0 = \text{const.}$) delivers exclusively a divergent exponential solution for the expanding volume V, which is clearly flawed. The biological meaning of this expanding volume is that growing plant cells will extend infinitely with time in the model. Closer scrutiny of the original form of the Lockhart equation also reveals that the volumetric growth of a cell is driven exclusively by the progression of time, since the product of Φ_0 and $P - Y$ is also a constant (see Eq. (1)). In other words, the cell volume expands because the time evolves. This this is indicative of a key failure of the original form of the Lockhart equation, as no inner mechanisms are responsible for growth: ongoing biological chemistry would appear to be completely ignored.

The benchmark of success must be in better descriptions of what is observed. The experiments considering wall creep (irreversible extension) (Cosgrove, 1989) or where the plastic extensibility (Cleland, 1986) experienced a kind of exponential decay with time. Unfortunately, there has been a lack of analytic description of this behavior, even at a phenomenological level, which we attempt to address herein (*vide infra*). Such modelling efforts are essential for description of dynamic features of the cell wall extension. Given the above arguments, a growth-equation, free of some serious drawbacks mentioned above, is desirable. In this paper a new consistent solution of these problems is presented in a form of two complementary models, namely biomechanical and biochemical which will be discussed later.

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Theory The Lockhart equation (Lockhart, 1965) in its raw form is given by

$$\frac{1}{V}\frac{dV}{dt} = \Phi_0(P - Y) \tag{1}$$

where V denotes the volume of a growing cell. In Eq. (1) P and Y describe the turgor pressure and turgor threshold, respectively, constant Φ_0 stands for the extensibility coefficient. Formal solution of Eq. (1) gives $V = V_0 \exp[\Phi_0(P - Y)t]$, where $V_0 = V(t = t_0)$ is the initial volume. In a more general case, Φ_0 may be assumed as time-dependent, $\Phi_0 \to \Phi(t)$, and then the integration of Eq. (1) gives

$$V(t) = \exp\left\{\int_0^t \Phi(t')(P - Y)dt'\right\} \tag{2}$$

In the biomechanical approach, heuristically as an *Ansatz* having some biomechanistic underpinning, we assume that extensibility coefficient is now a time dependent function, $\Phi_0 \to \Phi(t)$. Time-dependent wall extensibility seems a reasonable assumption, because plant cells regulate cell wall properties by secreting enzymes, including expansins. We also assume the cell wall behaves as a damped oscillator, with wall elasticity acting as a restoring force, an inertial wall mass, and a viscotic friction due to plastic deformation of the wall. Hence we postulate that the extensibility coefficient $\Phi(t)$ satisfies the second order differential equation, able to describe elastic and viscotic (plastic) features of the cell wall, in the form

$$m\frac{d^2\Phi}{dt^2} + b\frac{d\Phi}{dt} + k\Phi = f \tag{3}$$

This type of equation is recognized as the time differential equation for the damped harmonic oscillator. Expanding upon the analogy with the damped harmonic oscillator, parameter m, b and k may be called inertia, viscotic friction and restoring (elastic) coefficients, respectively, and can be bound directly with the elastic/inelastic cell wall properties. Coefficient f reflecting the role of growth hormones we put momentarily as equal to zero. Turgor pressure in Eq. (1) is treated as external force acting on the system.

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Equation Eq. (3) can be solved by standard procedures (strictly speaking, in non-isotropic case Φ should be a tensor). With $f = 0$ and $\Delta = b^2 - 4mk > 0$, the general solution has the form of aperiodic damping

$$\Phi(t) = \Phi_0 \left[c_1 \exp(\lambda_1 t) + c_2 \exp(\lambda_2 t)\right] \tag{4}$$

where $\lambda_{1,2} = -(b \pm \sqrt{\Delta})/2m$.

By inserting Eq. (4) into the modified form of the Lockhart equation (see below)

$$\frac{1}{V}\frac{dV}{dt} = \Phi(t)(P - Y) \tag{5}$$

where the cell wall extensibility coefficient depends explicitly on time, and $P - Y$ is represented, as usual, by a constant average value, the general solution of Eq. (5) may be presented in the form (without the loss of generality we may put $\Phi_0 = 1$) as:

$$V(t) = V_0 \exp\left[2me^{-\frac{bt}{2m}}\left(\frac{c_1}{-b+\sqrt{\Delta}}e^{\frac{\sqrt{\Delta}t}{2m}} + \frac{c_2}{-b-\sqrt{\Delta}}e^{-\frac{\sqrt{\Delta}t}{2m}}\right)(P - Y)\right] \tag{6}$$

Remarkably, it turns out that Eq. (5) depending on the sign of the discriminant Δ one can identify three dynamic regimes (see the Appendix A for details) corresponding to various situations encountered in cell growth physiology. Some representative examples are considered in the following section.

We note that, by proposing the *model Ansatz* in the form of Eq. (3), we are far away from treating the cell wall literally as a damped harmonic oscillator. Rather, we use such *analogy*, since Eq. (3) integration produces three classes of solutions (*vide infra*) that we encounter in plant growth biophysics. It also turned out, that these solutions complemented by one- and two-parameter (for α- and β-expansins) biochemical models form a natural basis for simultaneous mechanical and biochemical, semi–phenomenological description of cell/organ growth physiology. This is because *both approaches* result in the same kind of growth functional, where the volumetric expansion $V(t)$ is proportional to the double exponent $\exp(-\exp(-t))$ function.

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The biochemical model (mechanism) of cell wall loosening, due to expansin proteins action, underlying elongation growth of plant organs represents an unsolved problem and is still a matter of current debate (see e.g. Cosgrove (2000) for review). In the simplest approximation the change of expansin proteins content in the investigated system will be proportional to its concentration x in the solution and to the kinetic coefficient k_0 responsible for the interaction of endogenous expansins with the investigated sample. Therefore, trying to tackle the problem analytically, we begin with a time differential equation for the kinetic chemical reaction in the form

$$\frac{dx}{dt} = -k_0 x \tag{7}$$

with $0 \leq x \leq 1$ - expansin concentration in the growing hypocotyl/coleoptile and k_0 - kinetic coefficient responsible for expansin interaction with the growing segment, leading to stress relaxation. Equation Eq. (7) can be easily integrated to yield

$$x(t) = x_0 \exp(-k_0 t) \tag{8}$$

where $x_0 = x(t = 0)$ describes the initial expansin concentration of the investigated system (cell or non-meristematic tissue). This equation describes the exponential degradation of an initial pulse of the wall loosening enzyme expansin. Such approach also suggests a mechanism for finite cell extension: the cell becomes rigid as the initial pulse of expansin expires. The above argument implies equation Eq. (8) may be treated as a modifying factor for Φ_0. Thus, we may substitute $\Phi(t) = \Phi_0 x(t)$, which explicitly reads

$$\frac{\Phi(t)}{\Phi_0} = x_0 \exp(-k_0 t) \tag{9}$$

where $\Phi_0 = \text{const.}$ is the Lockhart term (we put $\Phi_0 = 1$ onward). Performing insertion of Eq. (9) into Eq. (5), after integration of the resulting differential

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equation, we arrive at the formula

$$V(t) = V_0 \exp\left[-\frac{e^{-k_0 t} x_0 (P - Y)}{k_0}\right] \tag{10}$$

Above equation can be considered, similar to Eq. (6), as volumetric extension of a cell/tissue with V_0 denoting the initial volume.

Besides, the calculated from Eq. (10) half-time for stress relaxation, due to expansins action, is $t_{1/2} = \ln 2/k_0$ and can be compared with Cosgrove (1985) result (Eq. (A9), ibid.) to give $k_0 = \varepsilon\phi$. This relation, represented in our notation by $k_0 = \varepsilon\Phi_0$, valid at least for $t_{1/2}$, combines biochemical (k_0) and biomechanical (ε, Φ_0) aspects of plant growth, since ε stands for the Young modulus which, by definition, is a measure of the stiffness of an isotropic elastic material.

Results

Simulating plant cell growth is an important subject of research. It would be especially important when we need to further improve the plant cell growth properties in the future. Quite some research effort has been devoted in this research area. This article introduces an extension of the Lockhart equation that greatly expanded the predictive capacities of previous equation. Therefore, we are motivated first to find the basic semi-phenomenological solutions of growth equation that provide a better description of the time dependent extensibility coefficient. The interplay of parameters in our model results in three kinds of solutions (ready to use formulae are conveyed to the Appendix A). First exemplary results, due to this classification, are presented in Figs 1-3.

Considering the over-damped case, as in Fig. 1, we clearly see the impact of viscotic friction (b - parameter) on the shape of the function Φ (Eq. (14)) and consequently how it affects the growth functional V (Eq. (15)). This case seems to be fundamental to investigations concerning the wall creep (Cosgrove, 1989, see Fig. 5 therein), plastic extensibility (Cleland, 1986, Fig. 3) and growth kinetics (Edelman, 1995, Figs 1 and 3) observed in

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various experiments. This viscotic friction parameter also appears to apply to *growth retardation* due to inhibitors. The latter issue is clearly visualized in Fig. 1 (right column) where with increasing coefficient b the inflection point is shifted to the higher t - values and the value of V is significantly suppressed. We believe this to be a proposal worthy of further attention, as described in the Appendix B, where the functional form of $\Phi(t)$, see Fig. 9, has been substantiated by the assumptions about the sigmoid law of great growth, stay in accord with the results presented in Figs 1-2.

Now, let us consider a critical case as presented in Fig. 2. This kind of behavior seems to be expected on the brink between periodic growth oscillations, as in the case of pollen tubes (*vide infra*) and the described above over-damped case. The resulting formula, Eq. (17), involved in the critical case is comparatively simple - note, it does not contain the restoring coefficient k. It looks as though, an elastic component is not present in this case and the cell wall is in a plastic state, exclusively.

Pulsatile growth appears to be the dominant mode of extension of rapidly extending tip-growing organisms. It looks as though, at this preliminary stage, the under-damped solutions to the second order differential equation, Eq. (3), may also find a counterpart in pulsatile growth experiments (e.g. Messerli et al., 1999) through Eq. (19). Pollen tubes from a number of plants that have been studied with adequate spatial and temporal resolution have been found to grow in an oscillatory manner. Measurements of longer pollen tubes of *Lilium longiflorum* that were growing in a pulsatile manner revealed a pulsatile influx of both H^+ and K^+ at the growing tip. Calcium fluxes were also measured when pulsatile growth began, the basal Ca^{2+} influx decreased and a pulsatile component appeared, superimposed on the reduced basal Ca^{2+} flux. The Ca^{2+} oscillations have the same frequency as the growth oscillations and are nearly in phase with growth rate. It gives hope that these phenomena, by fine-tuning model parameters to receive the characteristic system oscillation spectrum (Fig. 3, mid-box), can be described in terms of time-derivative of Eq. (19), representing the modulated growth rate $V' = \frac{dV}{dt}$ corresponding to Ca^{2+} (K^+, H^+) oscillating fluxes – see also Fig. 3 (upper plot) and compare, for instance, with Figs 4-5, 7 in paper

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by Messerli et al. (1999). Furthermore, as we noticed, Eq. (5) assumes, for simplicity, a constant turgor pressure. Probably the turgor pressure will rise significantly when the wall contracts. This effect has not been included in the presented model, although it will presumably quickly damp the oscillations predicted by Eq. (19) (Ω–term). In order to overcome this difficulty and consider a cell like a closed volume filled with an incompressible fluid we propose a self-consistent solution (see the derivation in Appendix A). Hence, even more adequate results can be obtained with the use of an auxiliary transcendental Eq. (21), where more realistic system can be considered by taking into account a dampening feedback between turgor pressure and elastic wall contraction. This approach, however, demands a selfconsistent (iterative) solution as it was pointed out in Appendix A.

Another question arises concerning constant $P - Y$ term. The assumption that P and Y are unchanging ($P - Y =$ const.) is valid only under steady growth conditions. What are the consequences of this assumption to apply the equation at a long time scale under fluctuating conditions (say, over few weeks)? For instance Lechaudel et al. (2007) reported a non-constant threshold pressure Y during fruit growth. To answer this question the general solution of Eq. (5) in the following form may be introduced (with the use of Eq. (4))

$$V(t) = V_0 \exp\left[\int_0^t \left(c_1 e^{\lambda_1 t'} + c_2 e^{\lambda_2 t'}\right)\left(P(t') - Y(t')\right) dt'\right] \tag{11}$$

where either P or Y may vary with time. This equation, among other possibilities, may also report on turgor decrease due to water deficiency, applicable in case of a previously growing plant cell that is deprived of its water resources. Thus, by accepting the adequate, specific form of $P - Y$ term it can be solved analytically. The solution of Eq. (11), for the most suitable form of the exponential decay $P(t) - Y(t) = (P_0 - Y_0)\exp(-\xi t)$

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accepted for the turgor pressure term, explicitly reads

$$V(t) = V_0 \exp\{(P_0 - Y_0)\left[\frac{c_1}{\lambda_1 - \xi}\left(e^{(\lambda_1-\xi)t} - 1\right) + \frac{c_2}{\lambda_2 - \xi}\left(e^{(\lambda_2-\xi)t} - 1\right)\right]\} \tag{12}$$

where $P_0 = P(t = 0)$, $Y_0 = Y(t = 0)$ and ξ is a positive number called decay constant[1]. The reciprocal constant $\tau = 1/\xi$ is called "mean life-time" or "scaling time" which is the time needed for the assembly (here: turgor pressure) to be reduced by a factor of $e = 2.718$ (Euler number). The plot of this exemplary solution is presented in Fig. 4. The remaining solutions to Eq. (11) are conveyed to the Appenix C.

Last but not least, Lockhart equation has been derived for elongation growth and was intended to describe a single cell elongation by assuming steady growth conditions (constant turgor). Since no constraint regarding turgor pressure is imposed onto Eq. (11), not only it can describe the single cell growth in varying external conditions, but can also be useful in single cell simulations. A good example is presented in the Fishman and Genard model (1998), where the growing fruit is assimilated to one big cell separated from the exterior by a composite membrane (see also Liu et al., 2007). Also the influence of ξ parameter, as in Eq. (12), onto the volumetric growth, visualized in Fig. 4, can be useful in this case.

The importance of plant *growth regulators* in plant tissue culture is well documented. Plant hormones (also known as phytohormones) are chemical compounds that regulate plant growth. The action of such external stimuli should also be recognized in solutions of Eq. (5). This can be accomplished by considering a positive f-term on the right side of Eq. (3). The solutions of such modified equation are shown in the explicit form in the Appendix A, as Eqs (22) and (23). An illustration of the influence of plant hormones onto the volumetric growth is presented in Fig. 5 (note, the volume V is still normalized, and does not exceed one in the case of $f = 0$).

It seems tempting to link both models presented in this paper. This can

[1]Equation Eq. (12) will be finite for long times if $\xi \geq \lambda_1, \lambda_2$. Then we receive: $\lim_{t\to\infty} V(t) = \exp\{(P_0 - Y_0)\left[\frac{c_1}{\xi-\lambda_1} + \frac{c_2}{\xi-\lambda_2}\right]\}$.

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be accomplished with the help of Levenberg-Marquardt algorithm. The procedure was as follows: the discrete data points were taken from the figures Fig. 1a-c and then interpolated with the help of Eq. (10). As a result of the fitting procedure (x_0, k_0) pairs are obtained and new plots (Fig. 6) are created which reproduce the original data from Fig. 1. This easy fitting exercise shows a good agreement between both sets of growth curves (compare plots in Fig. 1 a-c and Fig. 6), and consequently between its biomechanical and biochemical representations. By setting x_0 as fixed ($x_0 = 1$) we may repeat calculations to receive $k_0 = 0.602$, 0.369 and 0.309 corresponding to $b = 2.1$, 3 and 3.5, respectively. A closer scrutiny reveals (see the caption) that the greater k_0 coefficient the lower b value, and the opposite, as it should be expected. Another extrapolation based on above presented numbers approximately gives $k_0 = \ln b/2$, binding mechanical (b) and biochemical (k_0) model quantities together in one empirical formula. Needless to say, exactly the same routine can be performed with data taken directly from any *real* experiment, giving the opportunity to interconnect biochemical and biophysical aspects (parameters) of volumetric plant cell growth (elongation) for a given species. Similar procedures can be conducted, depending on the experimental context, with the remaining equations presented in this paper, thus strengthening the predicative power of the presented model.

Also, in order to support our analysis let us take some real, experimental growth data from Lewicka and Pietruszka (2006) - see Fig. 2 therein. The result of calculations is given in Fig. 7 (see the caption). It shows, among others, that we may obtain quantitative (numerical) values for the relevant biochemical parameter (k_0). More than this, since we have here considered data for the elongation growth of maize at two different temperatures, we can bind these numbers (k_0) directly with temperature change. The problem of temperature, in this context, is of great interest and may be subjected to

rate. Temperature is a measure of the kinetic energy of a system, so higher temperature implies higher average kinetic energy of molecules and more collisions per unit time. A general rule of thumb for most (not all) chemical reactions is that the rate at which the reaction proceeds (Q10) will approximately double for each 10^0C increase in temperature. Once the temperature reaches a certain point, some of the chemical species may be altered (e.g., denaturing of proteins) and the chemical reaction will slow or stop.

[2]Usually, an increase in temperature is accompanied by an increase in the reaction

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future study. Beneath we consider a preliminary result.

The environmental temperature, decisive for growth processes, can be taken into account by a well justified assumption that $k_0 = k_0(T)$, where T stands for the absolute temperature[2]. The effect of temperature on rates of reaction for a given plant species can be easily established empirically with the help of Eq. (10), see Fig. 8. On the other hand this outcome strongly supports the biochemical pathway resulting in the solution given by Eq. (10).

Discussion

Lockhart equation was conceived to explain growth for water immersed cells with negligible suction for which only turgor is required to calculate the stretching forces involved in plant growth. Our improved approach extends the idea of growth by relaxation of viscoelastic cell walls to plants subjected to suction by introducing the dynamic extensibility coefficient of the cell wall. In this sense the assumption made by introduction of Eq. (3) may be justified and accepted. Even though in this paper we focus primarily on the time evolution of wall samples the problem of the yield stress is not neglected. Green and coworkers (1971) provided experimental evidence on *Nitella* that the most labile material property in the context of Lockhart equation is the yield stress of the wall, not the extensibility. Nonetheless, it is easy to notice that all presented solutions, either of biomechanical or biochemical origin, have preserved the structure of the original Lockhart equation (also by retaining the $P - Y$ term). Therefore, not only they can report on the wall properties, but also over the changes regarding the yielding threshold (cf. e.g. Eq. (11) and its exemplary solutions).

Cell expansion plays a crucial role in shaping the form and size of plants. Expansins are plant cell proteins first discovered in studies of plant cell enlargement (Cosgrove, 1998). They have unique loosening effect on plant cell walls and enhance stress relaxation. Consequently, they induce a long-term, irreversible extension (creep). Even though their mechanism of action still remains enigmatic there exist temptation to link their influence with the

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presented model. This is made possible by invention of the analytic expressions (as Eq. (10)) for the wall extensibility including free parameters (x_0, k_0) that can also be attributed to the action of expansins. Moreover, further equipment of our model by a gravitational force term (representing load), as a natural extension, may supposedly account for the results obtained by the experimental layout of the cell-wall extension assay (Cosgrove, 1989). This in turn can easily be linked to the expansin action. This issue, concerning – among others – similar models for a more realistic case of α– and β–expansins, is presently under study.

It is worth also to emphasize that the solution of Eq. (5) possesses an important normalization property

$$V(t) \propto \lim_{t \to +\infty} \exp\{-\exp[-t]\} = 1 \tag{13}$$

not present in hitherto solutions. We see, we are dealing with the natural (and expected) upper bound corresponding to growth cessation when the growing cell matures. Hence, the maximum growth is treated in the model as normalized to unity. Therefore, in order to obtain significant results the control value should be always subtracted, as it is usually done in experiment. It is clear that this result extends from the over-damping to critical case as well as for all solutions of Eq. (10) kind.

I realize, the presented semi–phenomenological approach does not bring a new *biological* insight, either elucidate *biological* mechanisms. Phenomenology usually serves as qualitative and quantitative description of the observed phenomena. Sometimes, it leads to discovery of new solutions that can be verified experimentally or carry important hints for experimentalists or theoreticians. Also here exploited phenomenology gives such directions about changing properties of the cell wall during the process of growth. Moreover, in our case it provides interchangeable information about mechanical and biochemical aspects of expanding cell walls, also in terms of calculated numbers and empirical relations ($k_0 = \ln b/2$) or mathematically derived rules ($t_{1/2} = \ln 2/k_0$ or $k_0 = \epsilon\Phi_0$). Also, easy but precise fitting procedures allow indirect (through experimental data) transformation of the following kind:

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$(x_0, k_0) \longleftrightarrow (b, k)$ between biochemical and biomechanical "coordinates". It looks as though, with the help of the presented mathematical apparatus we can "tune" biomechanical parameters by changing the biochemical ones or, the opposite, draw conclusions about specific aspects of biochemical nature. Also, as in the case of Fig. 7, by knowing k_0 coefficient at $T = 20^0$C or at $T = 30^0$C (by interpolation to the existing empirical data) we may easily predict (calculate) the plot at arbitrary temperature, below the temperature of the optimum growth (T_0), without time–consuming measurements. Among others, in this manner the "predicative power" of semi–phenomenological formulas can be employed.

To conclude, this paper describes a model that appears applicable to what we know empirically about the physical aspects of cell growth process. It seems clear, how realistic improvements to the modeling methods can be linked to study the biomechanical and biochemical features of cell growth. This is because of the close connection of each model with experiment through its free parameters that can be retrieved by standard interpolation of the growth data. The sparse set of parameters of both models gives also hope for a wide application in comparative studies of the growth problems encountered in plant physiological experiments.

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Appendix A

Special solutions – exact results

Based on the sign of the discriminant Δ solutions to Eq. (3) may be divided into three categories.

Over-damping case: if $\Delta > 0$, the solution is written explicitly as

$$\Phi(t) = \Phi_0 \left[c_1 \exp\left(-\frac{b - \sqrt{\Delta}}{2m} t \right) + c_2 \exp\left(-\frac{b + \sqrt{\Delta}}{2m} t \right) \right] \tag{14}$$

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To evaluate c_1 and c_2, the initial conditions are needed, in order to seek for these coefficients. When a damped oscillator is subjected to a damping force which is linearly dependent upon the velocity, such as *viscous* damping, the oscillation have exponential decay terms which depend on damping coefficient. By introducing Eq. (14) into Eq. (5) the resulting differential equation may be solved to get

$$V(t) = V_0 \exp\left[\exp\left(-\frac{b+\sqrt{\Delta}t}{2m}\right)\left[\frac{2c_1 \exp\left(\frac{\sqrt{\Delta}}{m}\right) m}{-b+\sqrt{\Delta}} - \frac{2c_2 m}{b+\sqrt{\Delta}}\right](P-Y)\right] \tag{15}$$

which is the explicit analytical solution for the expanding volume of the cell in the over-damped case. Here $V_0 = V(t = t_0)$ describes the initial volume. The term $P - Y$ is of the order of several tenths of MPa, and can be directly measured. Parameter b, m and Δ (k) are to be determined from experiment by interpolation of growth data by Eq. (15) with the help of e.g. Levenberg-Marquardt procedure. These values then can be inserted back in Eq. (14) thus producing complete analytic expression for the dynamic yielding coefficient $\Phi(t)$.

Critical damping: if $\Delta = 0$, the general solution takes a form

$$\Phi(t) = \Phi_0 \left[(c_1 + c_2) \exp\left(-\frac{b}{2m}t\right)\right] \tag{16}$$

and c_1 and c_2 are to be obtained from initial conditions. By inserting Eq. (16) into Eq. (5) the evaluation of the differential equation results in

$$V(t) = V_0 \exp\left[-\frac{2m}{b}(c_1 + c_2) \exp\left(-\frac{b}{2m}t\right)(P-Y)\right] \tag{17}$$

Again, this is the explicit analytical solution for the expanding volume of the cell in the critical (maximum damping) case. Here V_0 describes the initial volume. The only parameter b and m are to be determined from experiment by interpolation of growth data with Eq. (17). These values then can be plugged in Eq. (16) to receive analytic expression for the dynamic yielding coefficient.

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Under-damping (hereafter referred also to as *cell growth (rate) oscillations*): if $\Delta < 0$, the solution reads

$$\Phi(t) = \Phi_0 \left[\exp\left(\frac{-b}{2m}t\right) \left[A\cos\left(\frac{\sqrt{|\Delta|}}{2m}t\right) + B\sin\left(\frac{\sqrt{|\Delta|}}{2m}t\right)\right]\right] \tag{18}$$

where from the given initial conditions, the coefficients A and B can also be evaluated numerically. By inserting Eq. (18) into Eq. (5) the integration of the resulting differential equation yields

$$V(t) = V_0 \exp\left\{ \frac{m\exp\left(-\frac{bt}{2m}\right)}{b^2 - 2mk}(P - Y)\,[\Omega]\right\} \tag{19}$$

where

$$[\Omega] = \left[-(Ab + B\sqrt{\Delta})\cos\left(\frac{t\sqrt{\Delta}}{2m}\right) + (A\sqrt{\Delta} - Bb)\sin\left(\frac{t\sqrt{\Delta}}{2m}\right)\right]$$

Eq. (19) is the explicit analytical solution for the expanding volume of the cell in the oscillatory case. It exploits the sigmoid growth double exponent in the form of $\exp(-\exp(-t))$ in a superposition with a periodic function (Ω – pulse); b, m, k are free parameters to be determined from experiment by interpolation. Constants A and B contribute to the superimposed pulse amplitude whereas $\frac{\sqrt{\Delta}}{2m} = \omega = 2\pi\nu$ – represents its frequency ν in Hz, respectively. These values can be inserted in Eq. (18) to get an expression for the dynamic yielding coefficient in this case.

A more subtle approach requires introduction of a dampening feedback between turgor pressure and elastic wall contraction. In order to bring this feedback between turgor pressure and elastic wall contraction into Eq. (5) we utilize the state equation (we accommodate argumentation as given by Stanley (1971) and restrict to the first approximation in the virial theorem). Thus, we may assume $P = \gamma T/V$ where T is the absolute temperature (in Kelvin scale). The latter assumption needs a comment. There exist a few empirical data (e.g. Proseus et al., 2000) revealing weak turgor threshold Y dependence on temperature T. Despite this sparse information we are not

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able to propose an exact model function for $Y(T)$. Nevertheless, in zeroth approximation we may surely assume $Y(T) = \text{const}$. Based on this work (ibid.) we acknowledge that the $Y(T)$ dependence is much smaller than $P(T)$ and as such may be neglected (the assumption $Y = \text{const.}$ still holds). V is generally interpreted as cell volume but in the context of numerical recalculation of experimental data in light of our model we may also refer V to the entire organ, the coleoptile or hypocotyl. The pressure of inner cell solution is proportional to T and this is a natural consequence of the molecular energy increase with temperature[3]. The reciprocal proportionality of P to V we introduce as in the first approximation, which gives the linear solution $V = V(t)$ of Eq. (5). This assumption goes along with the fact that the experiments are usually performed in the linear range of the sigmoid growth curve. It is, however, evident that in more precise calculations one should solve Eq. (5) for subsequent reciprocal powers of the volume V by the iteration method. Such extension would be even more adequate, nonetheless also more complicated. However, that high accuracy in case of biological experiments where we deal with relatively high statistical error is superfluous.

Giving the above arguments together, we receive the following equation

$$\frac{1}{V}\frac{dV}{dt} = \Phi(t)\left(\frac{\gamma T}{V} - Y\right) \tag{20}$$

instead of Eq. (5), where T is the absolute temperature and γ is a constant. Returning to the problem of cell oscillations we may also change the right side of Eq. (19) in analogous fashion, replacing P by $\gamma T/V$, to receive the self-consistent transcendental equation for the fluctuating volume V:

$$V(t) = V_0 \exp\left\{\frac{m\exp\left(-\frac{bt}{2m}\right)}{b^2 - 2mk}\left(\frac{\gamma T}{V} - Y\right)[\Omega]\right\} \tag{21}$$

Above equation can be solved by simple iterations (or other methods: bisec-

[3]This statement stays also in agreement with the state equation in the general form of $P = w\rho = w\frac{k_B T}{V}$, where ρ is the energy density and w is a constant; k_B is the Boltzmann constant.

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tion, regula falsi, secant, Newton-Raphson). The temperature T is, of course constant during experiment, therefore we may put $P = \text{const}/V$ in Eq. (20), and consequently also in Eq. (21). Then, the transcendental equation Eq. (21) may be solved selfconsistently by iterations. It looks as though, this is the simplest way the dampening feedback between turgor pressure and elastic wall expansion (contraction) may be taken into account.

Stimulator present One of the most important solutions, taking into account the role of growth regulators (phytohormones), can be obtained by adding a non-vanishing exerting force f on the right side of Eq. (3). Then, the solution of Eq. (3) reads

$$\Phi(t) = \Phi_0 \left[c_1 \exp\left(-\frac{b - \sqrt{\Delta}}{2m} t \right) + c_2 \exp\left(-\frac{b + \sqrt{\Delta}}{2m} t \right) + \frac{f}{k} \right] \tag{22}$$

and corresponds to the volume extension in the form

$$V(t) = V_0 \exp\left\{ \left[\exp\left(-\frac{b + \sqrt{\Delta} t}{2m} \right) [\Upsilon] + \frac{ft}{k} \right] (P - Y) \right\} \tag{23}$$

where

$$[\Upsilon] = \left[\frac{2c_2 \exp\left(\frac{\sqrt{\Delta} t}{m} \right)}{-b + \sqrt{\Delta}} - \frac{2c_1 m}{b + \sqrt{\Delta}} \right]$$

Appendix B

Independent estimation of the dynamic yielding coefficient

Based on the Lockhart model and the assumption that the cell volume variation follows a sigmoid curve a formula for the extensibility coefficient can be constructed. Thus, one can explain, in a semi–phenomenological manner, the shape of the cell wall extensibility experimental plots encountered.

In plant physiology growth is described by the law of great growth Fogg (1975). There is also common agreement that because the sigmoid function has a non-negative first derivative in positive domain and exactly one inflection point, this functional form properly reproduces the large-scale evo-

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lution in time. In fact, growth of any plant organ can be split into three basic phases: the initial phase of slow growth, the intense growth phase and, eventually, the final phase of slow growth. Such regularity can be represented by a sigmoid curve that characterizes the time evolution of individual cell growth and the growth of plant organs as a whole.

Recalling the Lockhart equation Eq. (1) and assuming Φ_0 as time-dependent $\Phi_0 \to \Phi(t)$, integration of Eq. (1) yields

$$V(t) = V_0 \exp\left[\int_0^t \Phi(t')(P-Y)dt'\right] \tag{24}$$

On the other hand, assuming sigmoid character of growth, one gets

$$V(t) = \frac{1}{2}V_0\left[1+\tanh\left(\frac{t}{t_0}-1\right)\right] \tag{25}$$

By comparing Eqs (24) and (25), assuming the hydrostatic pressure constant $P-Y$=const=c, calculating log of both sides and taking the time-derivative, we arrive at an analytic expression for the dynamic yielding coefficient in the form

$$\Phi(t) = \frac{\sec^2\left(\frac{t}{t_0}-1\right)}{ct_0\left[1+\tanh\left(\frac{t}{t_0}-1\right)\right]} \tag{26}$$

In the above equation t_0 denotes the inflection point of the elongation/growth curve that corresponds to the time of the maximum extension rate. The dimension of Φ follows: $[\Phi]$=(MPa)$^{-1}$(time unit)$^{-1}$, consistently with the Lockhart equation. Providing the application of a proper time-scale (minutes, hours or days) to a particular growth problem, the above formula can be interpreted as an approximated expression for the dynamic yielding coefficient Φ (see also Fig. 9).

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Appendix C

Special solutions to Eq. (11) – Exact results

Among others, we may consider the following special cases.

1. $P(t) - Y(t) = P_0 \exp(-\xi_1 t) - Y_0 \exp(-\xi_2 t)$, with separate decay constants ξ_1 and ξ_2 by P and Y processes, respectively.

$$V(t) = e^{\frac{c_1\left(-1+e^{t\,(\lambda_1-\xi_1)}\right)P_0}{\lambda_1-\xi_1}+\frac{c_2\left(-1+e^{t\,(\lambda_2-\xi_1)}\right)P_0}{\lambda_2-\xi_1}-\frac{c_1\left(-1+e^{t\,(\lambda_1-\xi_2)}\right)Y_0}{\lambda_1-\xi_2}-\frac{c_2\left(-1+e^{t\,(\lambda_2-\xi_2)}\right)Y_0}{\lambda_2-\xi_2}}\,V_0 \tag{27}$$

2. $P(t) - Y(t) = P_0 - Y_0 \exp(-\xi_2 t)$, $P_0 = P(t=0) = \text{const.}$

$$V(t) = e^{\frac{c_1\left(-1+e^{\lambda_1\,t}\right)P_0}{\lambda_1}+\frac{c_2\left(-1+e^{\lambda_2\,t}\right)P_0}{\lambda_2}-\frac{c_1\left(-1+e^{t\,(\lambda_1-\xi_2)}\right)Y_0}{\lambda_1-\xi_2}-\frac{c_2\left(-1+e^{t\,(\lambda_2-\xi_2)}\right)Y_0}{\lambda_2-\xi_2}}\,V_0 \tag{28}$$

3. $P(t) - Y(t) = P_0 \exp(-\xi_1 t) - Y_0$, $Y_0 = Y(t=0) = \text{const.}$

$$V(t) = e^{\frac{c_1\left(-1+e^{t\,(\lambda_1-\xi_1)}\right)P_0}{\lambda_1-\xi_1}+\frac{c_2\left(-1+e^{t\,(\lambda_2-\xi_1)}\right)P_0}{\lambda_2-\xi_1}-\frac{c_1\left(-1+e^{\lambda_1\,t}\right)Y_0}{\lambda_1}-\frac{c_2\left(-1+e^{\lambda_2\,t}\right)Y_0}{\lambda_2}}\,V_0 \tag{29}$$

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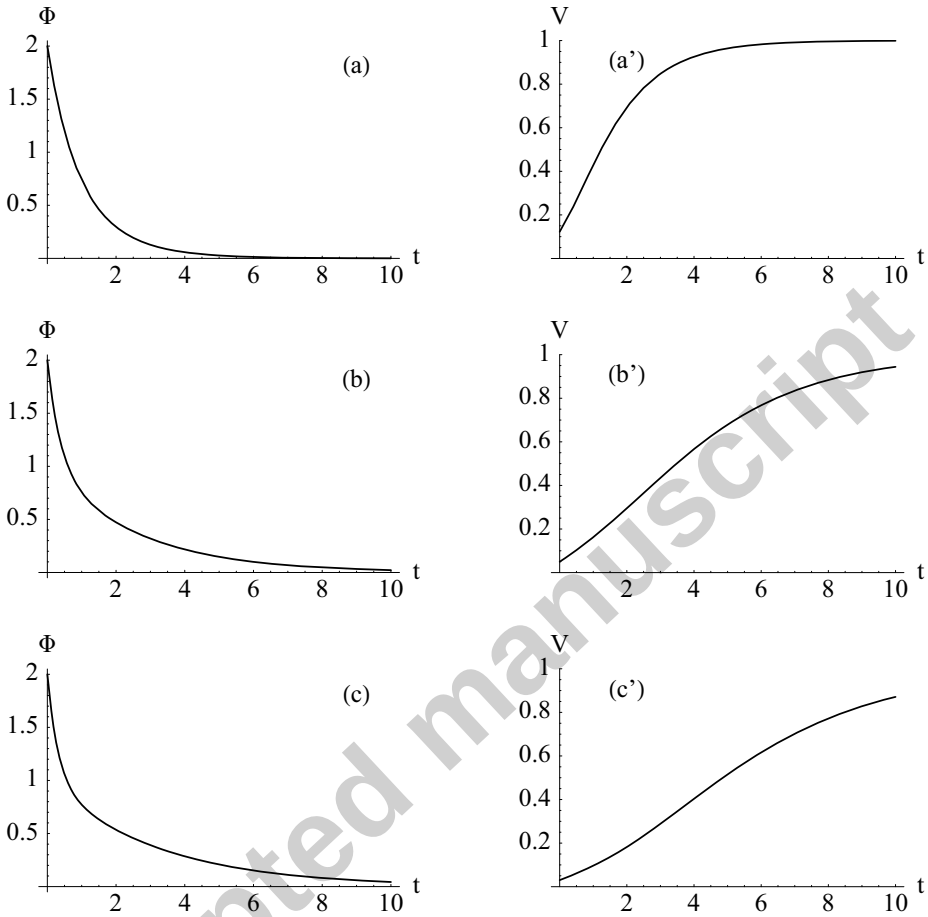

Figure 1: Dynamic cell wall extensibility Φ, as defined by Eq. (14), and the corresponding volumetric growth V, Eq. (15), as a function of time t. *Over–damping case.* The parameters are: $P - Y = 1$, $m = 1$, $k = 1$, $b = 2.1$ (a and a'), $b = 3$ (b and b'), $b = 3.5$ (c and c'). All figures are described in terms of suitable units for the considered time-scale; also we adopt such units that $\Phi_0 = 1$. We put $c_1 = c_2 = 1$ in Figs 1-2, 4-5 and $V_0 = 1$ in Figs 1-4. It is easy to notice how slightly changing wall mechanical properties (b - parameter) drastically change the shape of the growth functional V.

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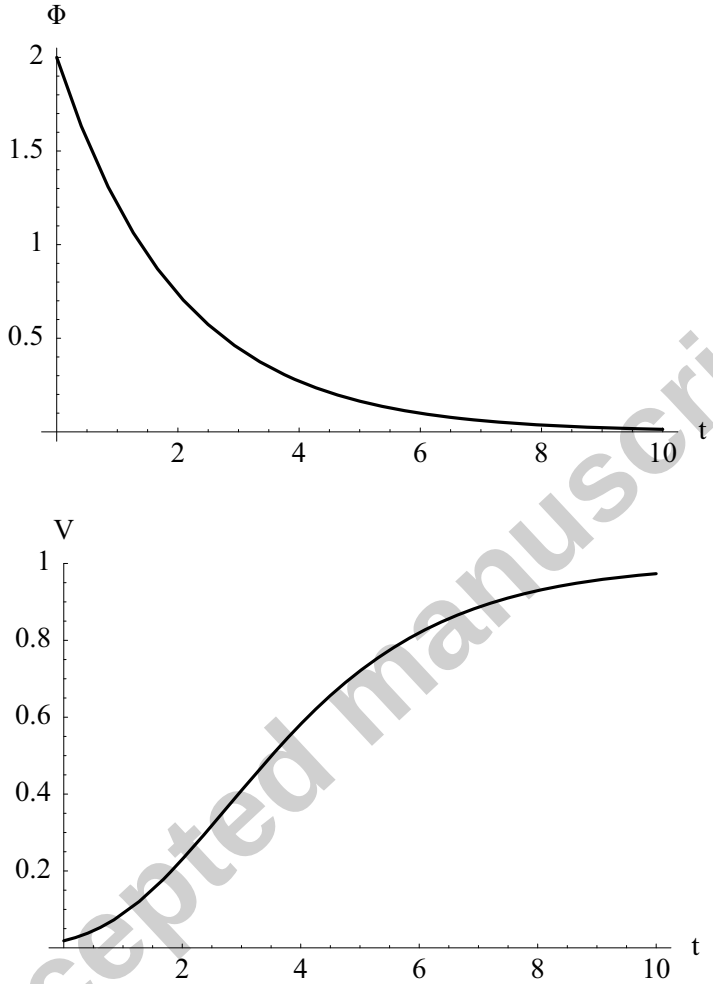

Figure 2: Dynamic cell wall extensibility Φ, as defined by Eq. (16), and the corresponding volumetric growth V, Eq. (17), as a function of time t. *Critical damping case.* The parameters are: $P - Y = 1$, $m = 1$, $b = 2$.

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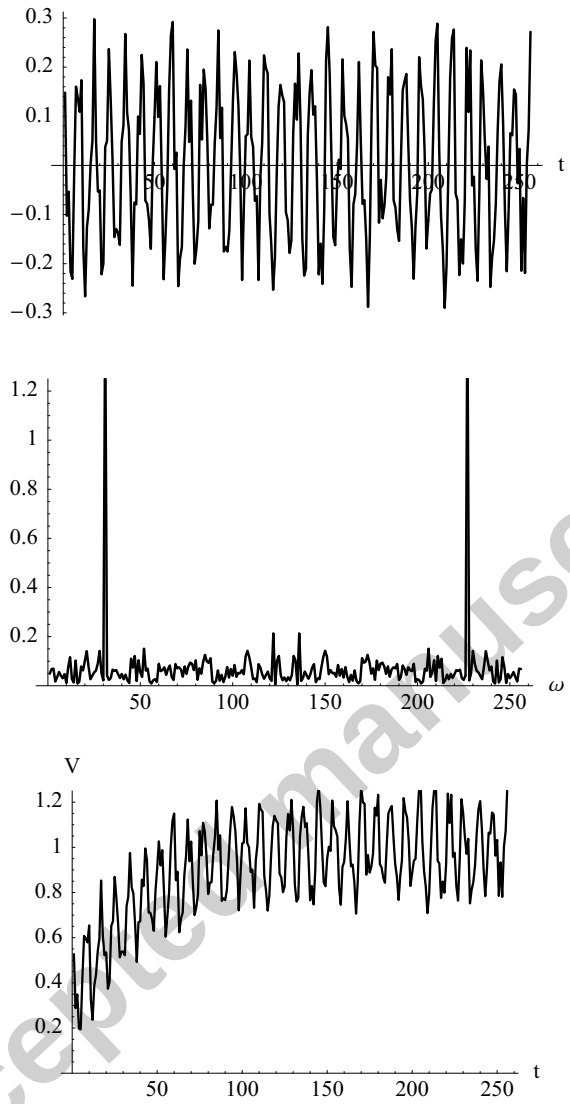

Figure 3: Numerical simulation ($A = B = 1$, $\Delta < 0$) based upon Eq. (19) resembling tip-measured pollen tube influx of Ca^{2+} - a periodic signal with random noise added. The tubes show pulsatile growth (lower plot) and pulsatile Ca^{2+} infux (upper plot). The Ca^{2+} oscillations have the same frequency ω as growth oscillations and are nearly in phase with growth; that is, the peaks of tip-localized Ca^{2+} nearly coincide with growth rate. The calculated spectrum *via* Fourier transform (mid-plot) shows a very strong peak at 30, the calculated "frequency" of the calcium influx originating the periodic signal and oscillatory growth response. There is a second peak, which is essentially a consequence of aliasing.

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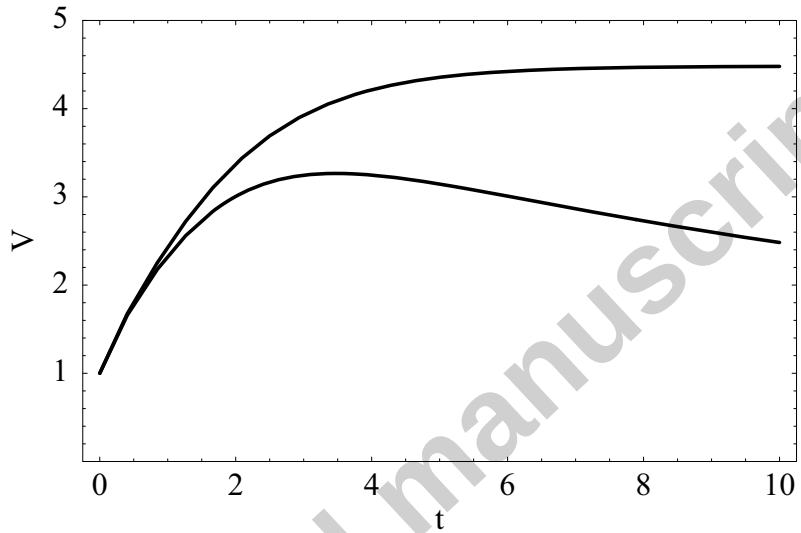

Figure 4: Volumetric growth V as defined by Eq. (12) as a function of time t. The parameters are: $m = 1$, $k = 1$, $b = 3$, $\xi = 0$ (upper curve), $\xi = 0.05$ (lower curve) – applicable in case of a previously growing plant cell that is deprived of its water resources due to water deficiency (slightly exaggerated to highlight the effect).

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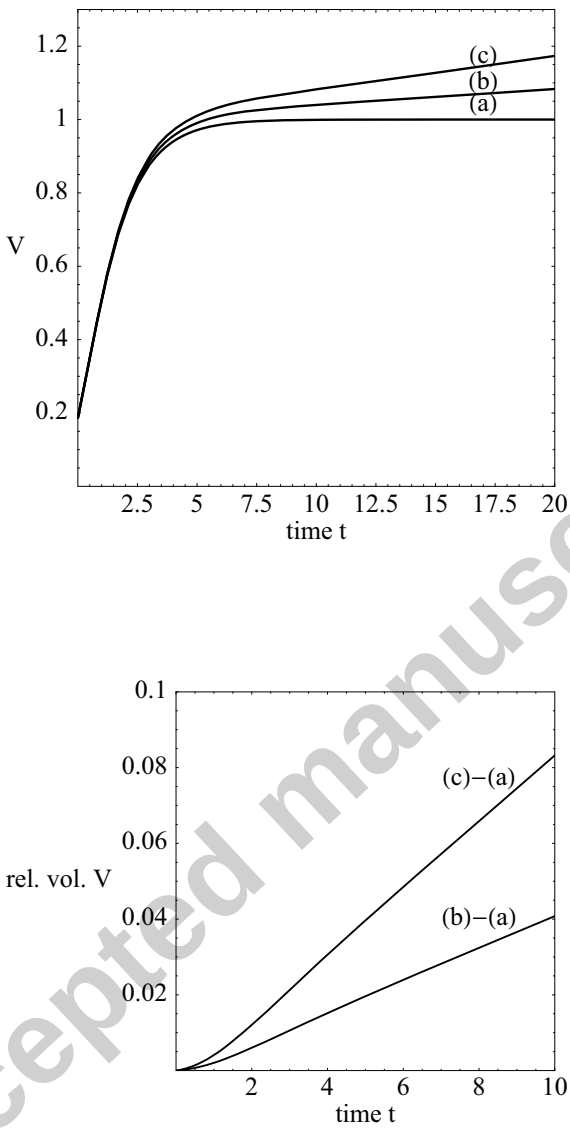

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Figure 5: Volumetric growth V (upper plot), in presence of growth regulators, as defined by Eq. (23), as a function of time t. Net growth $V - V_0$ (lower plot), where V_0 corresponds to $f = 0$ – control, as an example of linear reaction due to the use of growth stimulator. The parameters are: $P - Y = 0.8$, $m = 1$, $k = 1$, $b = 2.1$; (a) $f = 0$ (no stimulator), (b) $f = 0.005$ and (c) $f = 0.01$

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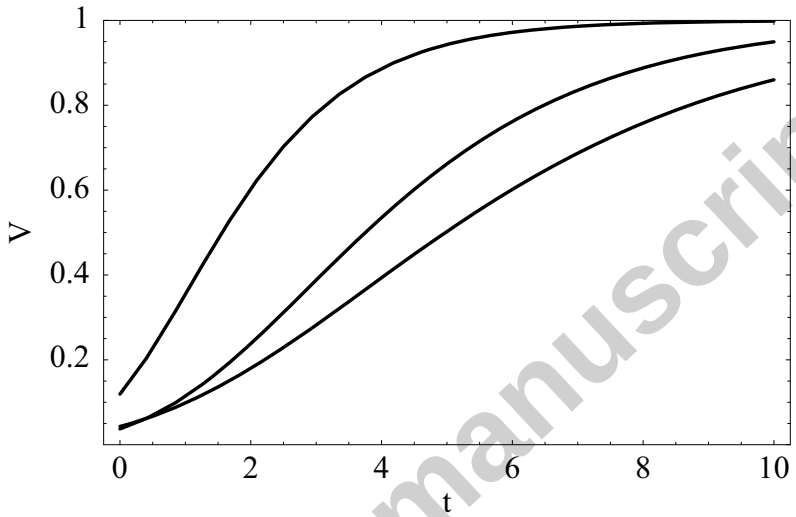

Figure 6: Volumetric growth V as defined by Eq. (10) as a function of time t. The parameters are: $P - Y = 1$, $V_0 = 1$. The estimated *via* Levenberg-Marquardt procedure parameters of Eq. (10) are: $k_0 = 0.718533$, $x_0 = 1.52802$ (upper curve, corresponding to $b = 2.1$ in Fig. 1a'), $k_0 = 0.415263$, $x_0 = 1.367$ (middle curve, corresponding to $b = 3$ in Fig. 1b') and $k_0 = 0.303804$, $x_0 = 0.955824$ (lower curve, corresponding to $b = 3.5$ in Fig. 1c'). An exponentally decaying pool of expansin results in a mechanism for finite growth.

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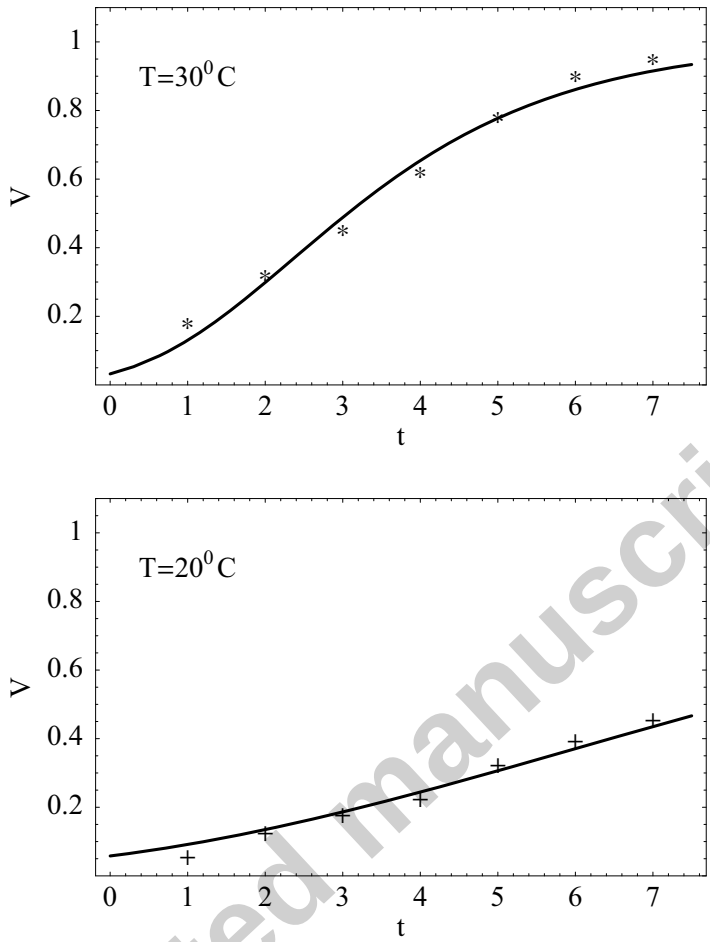

Figure 7: Elongation growth of maize (*Zea mays* L.) coleoptile segments *vs* time at two different temperatures. Both curves are fitted, with the help of Levenberg-Marquardt interpolation routine *via* Eq. (10), to the original data (*, +) taken from Lewicka and Pietruszka (2006), Fig. 2. The expansin pool is assumed to be at the same level for the initial time, corresponding to $x_0 = 1$. The resulting kinetic coefficient k_0 leading to wall stress relaxation and subsequent volumetric growth equals: $k_0 = 0.252611$ (smaller) for $T = 20^0$C and $k_0 = 0.418721$ (greater) for $T \approx 30^0$C , as expected. The determination coefficient R^2 for the fitting procedure exceeds 0.99 (R^2 allows us to determine how certain one can be in making predictions from a considered model: here a differential equation $V^{-1}V'(t) = x_0 \exp(-k_0 t)(P - Y)$ leading to Eq. (10)). Left scale in [mm] – we take the coleoptile cross-section equal to 1 mm^2. The procedure is valid for all temperatures up to the optimal growth temperature.

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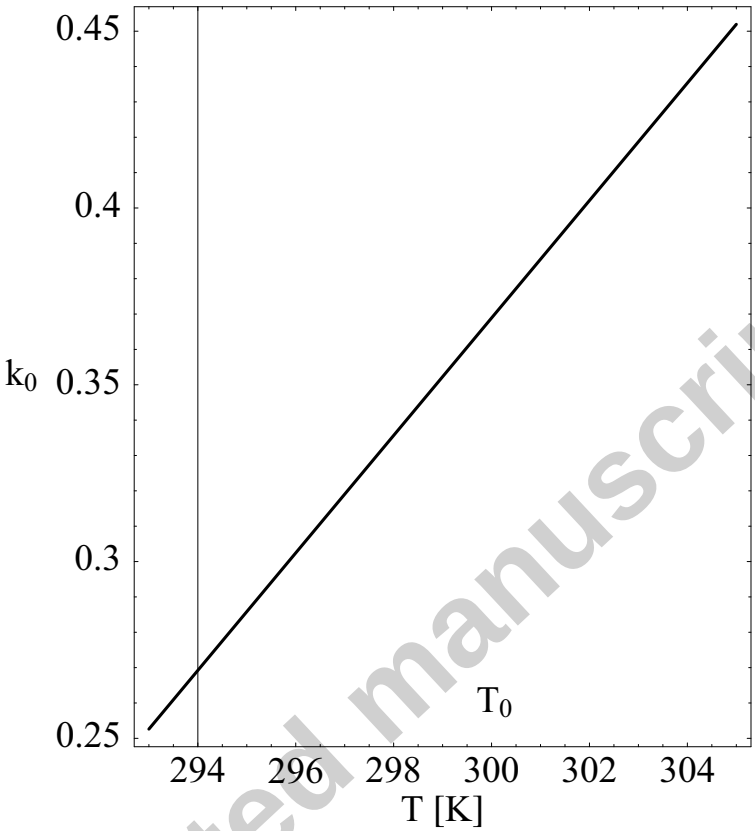

Figure 8: Kinetic coefficient k_0, linearly interpolated with the use of the least squares method (Levenberg-Marquardt procedure), as a function of temperature for maize *Zea mays* L. (input data: see the caption to Fig. 7). The optimum growth temperature for maize approximately equals $T_0 = 300$ K. The kinetic coefficient k_0 changes in the interval of 20–30^{0}C about two times. This is in agreement with "Q10 law" stating the rate at which the reaction proceeds will approximately double for each 10^{0}C increase in temperature. The procedure is valid in ascending part of growth/elongation *vs* temperature curve (below T_0).

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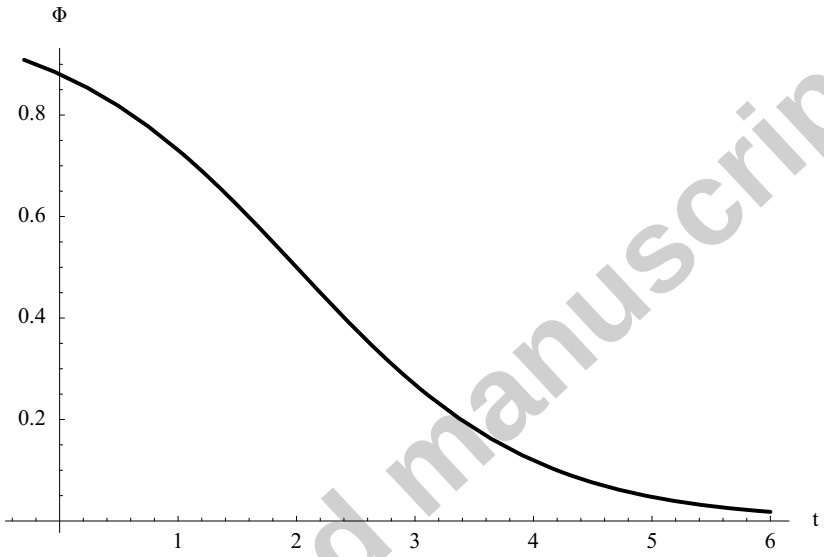

Figure 9: Estimated dynamic extensibility Φ, as defined independently by Eq. (26) in the Appendix B. The inflection time $t_0 = 2$.

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