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

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4

Abstract

5 A generalization of the Lockhart equation for plant cell expansion
6 in *isotropic* case is presented. The goal is to account for the temporal
7 variation in the wall mechanical properties - in this case by making the
8 wall extensibility a time dependent parameter. We introduce a time-
9 differential equation describing the plant growth process with some key
10 biophysical aspects considered. The aim of this work was to improve
11 prior modeling efforts by taking into account the dynamic character of
12 the plant cell wall with characteristics reminiscent of damped (aperi-
13 odic) motion. The equations selected to encapsulate the time evolution
14 of the wall extensibility offer a new insight into the control of cell wall
15 expansion. We find that the solutions to the time dependent second
16 order differential equation reproduce much of the known experimen-
17 tal data for long- and short- time scales. Additionally, in order to
18 support the biomechanical approach, a new growth equation based on
19 the action of expansin proteins is proposed. Remarkably, both meth-
20 ods independently converge to the same kind, sigmoid-shaped, growth
21 description functional $V(t) \propto \exp(-\exp(-t))$, properly describing the
22 volumetric growth and, consequently, growth rate as its time deriva-
23 tive.

24 **Keywords** growth functional, plant cells, wall extensibility

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25 Introduction

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

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

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

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

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

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

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

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, $\Phi_0 \rightarrow \Phi(t)$, and then the integration of Eq. (1) gives

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

In the biomechanical approach, heuristically as an *Ansatz* having some biomechanistic underpinning, we assume that extensibility coefficient is now a time dependent function, $\Phi_0 \rightarrow \Phi(t)$. 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

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

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.

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

$$\Phi(t) = \Phi_0 [c_1 \exp(\lambda_1 t) + c_2 \exp(\lambda_2 t)] \quad (4)$$

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

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

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

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:

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

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

94 We note that, by proposing the *model Ansatz* in the form of Eq. (3),
 95 we are far away from treating the cell wall literally as a damped harmonic
 96 oscillator. Rather, we use such *analogy*, since Eq. (3) integration produces
 97 three classes of solutions (*vide infra*) that we encounter in plant growth bio-
 98 physics. It also turned out, that these solutions complemented by one- and
 99 two-parameter (for α - and β -expansins) biochemical models form a natural
 100 basis for simultaneous mechanical and biochemical, semi-phenomenological
 101 description of cell/organ growth physiology. This is because *both approaches*
 102 result in the same kind of growth functional, where the volumetric expansion
 103 $V(t)$ is proportional to the double exponent $\exp(-\exp(-t))$ function.

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

$$\frac{dx}{dt} = -k_0x \quad (7)$$

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

$$x(t) = x_0 \exp(-k_0t) \quad (8)$$

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

$$\frac{\Phi(t)}{\Phi_0} = x_0 \exp(-k_0t) \quad (9)$$

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

equation, we arrive at the formula

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

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

106 Besides, the calculated from Eq. (10) half-time for stress relaxation, due
107 to expansins action, is $t_{1/2} = \ln 2/k_0$ and can be compared with Cosgrove
108 (1985) result (Eq. (A9), *ibid.*) to give $k_0 = \varepsilon\phi$. This relation, represented
109 in our notation by $k_0 = \varepsilon\Phi_0$, valid at least for $t_{1/2}$, combines biochemical
110 (k_0) and biomechanical (ε , Φ_0) aspects of plant growth, since ε stands for
111 the Young modulus which, by definition, is a measure of the stiffness of an
112 isotropic elastic material.

113 Results

114 Simulating plant cell growth is an important subject of research. It would be
115 especially important when we need to further improve the plant cell growth
116 properties in the future. Quite some research effort has been devoted in this
117 research area. This article introduces an extension of the Lockhart equation
118 that greatly expanded the predictive capacities of previous equation. There-
119 fore, we are motivated first to find the basic semi-phenomenological solutions
120 of growth equation that provide a better description of the time dependent
121 extensibility coefficient. The interplay of parameters in our model results in
122 three kinds of solutions (ready to use formulae are conveyed to the Appendix
123 A). First exemplary results, due to this classification, are presented in Figs
124 1-3.

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

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

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

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

164 by Messerli et al. (1999). Furthermore, as we noticed, Eq. (5) assumes,
 165 for simplicity, a constant turgor pressure. Probably the turgor pressure
 166 will rise significantly when the wall contracts. This effect has not been
 167 included in the presented model, although it will presumably quickly damp
 168 the oscillations predicted by Eq. (19) (Ω -term). In order to overcome this
 169 difficulty and consider a cell like a closed volume filled with an incompressible
 170 fluid we propose a self-consistent solution (see the derivation in Appendix
 171 A). Hence, even more adequate results can be obtained with the use of
 172 an auxiliary transcendental Eq. (21), where more realistic system can be
 173 considered by taking into account a dampening feedback between turgor
 174 pressure and elastic wall contraction. This approach, however, demands a
 175 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 ($P - Y = \text{const.}$) 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))

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

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 $P(t) - Y(t) = (P_0 - Y_0) \exp(-\xi t)$

accepted for the turgor pressure term, explicitly reads

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

176 where $P_0 = P(t = 0)$, $Y_0 = Y(t = 0)$ and ξ is a positive number called
 177 decay constant¹. The reciprocal constant $\tau = 1/\xi$ is called "mean life-time"
 178 or "scaling time" which is the time needed for the assembly (here: turgor
 179 pressure) to be reduced by a factor of $e = 2.718$ (Euler number). The plot
 180 of this exemplary solution is presented in Fig. 4. The remaining solutions
 181 to Eq. (11) are conveyed to the Appendix C.

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

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

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

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

202 be accomplished with the help of Levenberg-Marquardt algorithm. The pro-
 203 cedure was as follows: the discrete data points were taken from the figures
 204 Fig. 1a-c and then interpolated with the help of Eq. (10). As a result of
 205 the fitting procedure (x_0, k_0) pairs are obtained and new plots (Fig. 6) are
 206 created which reproduce the original data from Fig. 1. This easy fitting ex-
 207 ercise shows a good agreement between both sets of growth curves (compare
 208 plots in Fig. 1 a-c and Fig. 6), and consequently between its biomechanical
 209 and biochemical representations. By setting x_0 as fixed ($x_0 = 1$) we may
 210 repeat calculations to receive $k_0 = 0.602, 0.369$ and 0.309 corresponding to
 211 $b = 2.1, 3$ and 3.5 , respectively. A closer scrutiny reveals (see the caption)
 212 that the greater k_0 coefficient the lower b value, and the opposite, as it should
 213 be expected. Another extrapolation based on above presented numbers ap-
 214 proximately gives $k_0 = \ln b/2$, binding mechanical (b) and biochemical (k_0)
 215 model quantities together in one empirical formula. Needless to say, exactly
 216 the same routine can be performed with data taken directly from any *real*
 217 experiment, giving the opportunity to interconnect biochemical and bio-
 218 physical aspects (parameters) of volumetric plant cell growth (elongation)
 219 for a given species. Similar procedures can be conducted, depending on the
 220 experimental context, with the remaining equations presented in this paper,
 221 thus strengthening the predicative power of the presented model.

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

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

230 future study. Beneath we consider a preliminary result.

231 The environmental temperature, decisive for growth processes, can be
232 taken into account by a well justified assumption that $k_0 = k_0(T)$, where
233 T stands for the absolute temperature². The effect of temperature on rates
234 of reaction for a given plant species can be easily established empirically
235 with the help of Eq. (10), see Fig. 8. On the other hand this outcome
236 strongly supports the biochemical pathway resulting in the solution given
237 by Eq. (10).

238 Discussion

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

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

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

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

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

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

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

289 $(x_0, k_0) \longleftrightarrow (b, k)$ between biochemical and biomechanical "coordinates". It
 290 looks as though, with the help of the presented mathematical apparatus we
 291 can "tune" biomechanical parameters by changing the biochemical ones or,
 292 the opposite, draw conclusions about specific aspects of biochemical nature.
 293 Also, as in the case of Fig. 7, by knowing k_0 coefficient at $T = 20^0\text{C}$ or at
 294 $T = 30^0\text{C}$ (by interpolation to the existing empirical data) we may easily pre-
 295 dict (calculate) the plot at arbitrary temperature, below the temperature of
 296 the optimum growth (T_0), without time-consuming measurements. Among
 297 others, in this manner the "predicative power" of semi-phenomenological
 298 formulas can be employed.

299 To conclude, this paper describes a model that appears applicable to
 300 what we know empirically about the physical aspects of cell growth pro-
 301 cess. It seems clear, how realistic improvements to the modeling methods
 302 can be linked to study the biomechanical and biochemical features of cell
 303 growth. This is because of the close connection of each model with exper-
 304 iment through its free parameters that can be retrieved by standard inter-
 305 polation of the growth data. The sparse set of parameters of both models
 306 gives also hope for a wide application in comparative studies of the growth
 307 problems encountered in plant physiological experiments.

308 Acknowledgment

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311 Appendix A

312 *Special solutions – exact results*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

where

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

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

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

346 able to propose an exact model function for $Y(T)$. Nevertheless, in zeroth
 347 approximation we may surely assume $Y(T) = \text{const.}$ Based on this work
 348 (ibid.) we acknowledge that the $Y(T)$ dependence is much smaller than
 349 $P(T)$ and as such may be neglected (the assumption $Y = \text{const.}$ still holds).
 350 V is generally interpreted as cell volume but in the context of numerical
 351 recalculation of experimental data in light of our model we may also refer
 352 V to the entire organ, the coleoptile or hypocotyl. The pressure of inner
 353 cell solution is proportional to T and this is a natural consequence of the
 354 molecular energy increase with temperature³. The reciprocal proportionality
 355 of P to V we introduce as in the first approximation, which gives the linear
 356 solution $V = V(t)$ of Eq. (5). This assumption goes along with the fact
 357 that the experiments are usually performed in the linear range of the sigmoid
 358 growth curve. It is, however, evident that in more precise calculations one
 359 should solve Eq. (5) for subsequent reciprocal powers of the volume V
 360 by the iteration method. Such extension would be even more adequate,
 361 nonetheless also more complicated. However, that high accuracy in case of
 362 biological experiments where we deal with relatively high statistical error is
 363 superfluous.

Giving the above arguments together, we receive the following equation

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

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 :

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

364 Above equation can be solved by simple iterations (or other methods: bisection)

³This 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.

365 tion, regula falsi, secant, Newton-Raphson). The temperature T is, of course
 366 constant during experiment, therefore we may put $P = \text{const}/V$ in Eq. (20),
 367 and consequently also in Eq. (21). Then, the transcendental equation Eq.
 368 (21) may be solved selfconsistently by iterations. It looks as though, this
 369 is the simplest way the dampening feedback between turgor pressure and
 370 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

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

and corresponds to the volume extension in the form

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

where

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

371 Appendix B

372 *Independent estimation of the dynamic yielding coefficient*

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

377 In plant physiology growth is described by the law of great growth Fogg
 378 (1975). There is also common agreement that because the sigmoid func-
 379 tion has a non-negative first derivative in positive domain and exactly one
 380 inflection point, this functional form properly reproduces the large-scale evo-

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

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

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

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

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

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

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

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

393 **Appendix C**394 *Special solutions to Eq. (11) – Exact results*

395 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.

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

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

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

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

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

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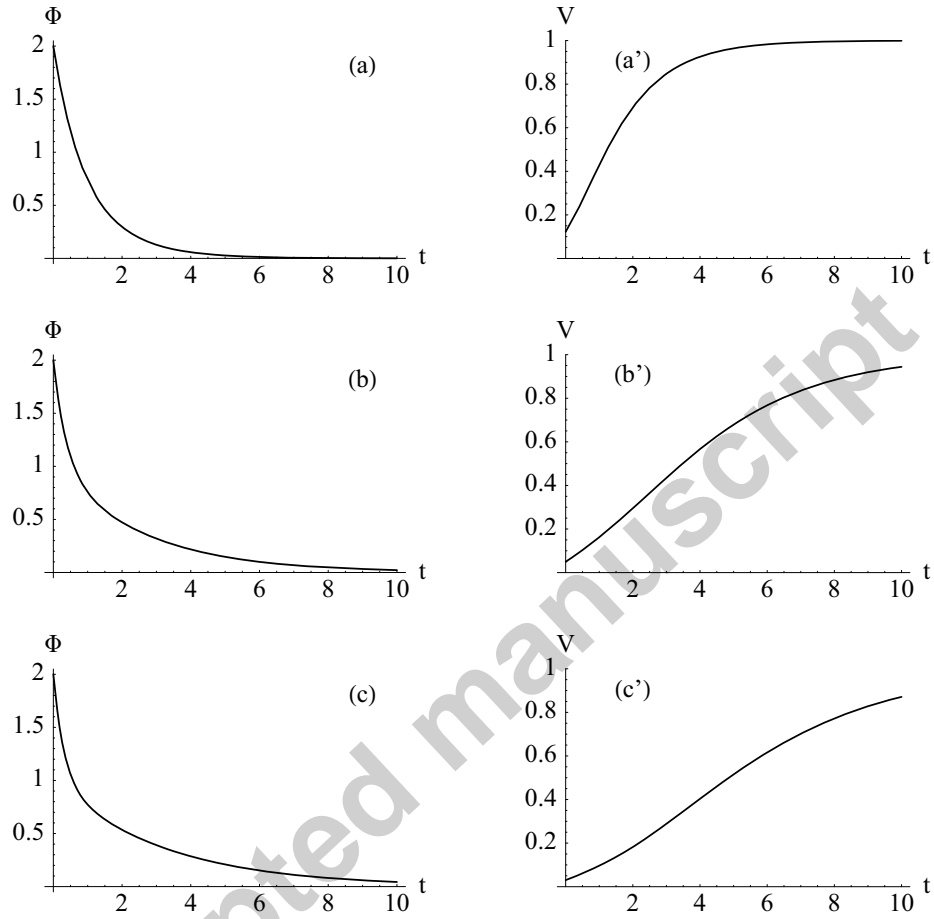


Figure 1: Dynamic cell wall extensibility Φ , as defined by Eq. (14), and the corresponding volumetric growth V , Eq. (15), as a function of time t . *Over-damping case*. The parameters are: $P - Y = 1$, $m = 1$, $k = 1$, $b = 2.1$ (a and a'), $b = 3$ (b and b'), $b = 3.5$ (c and c'). All figures are 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 .

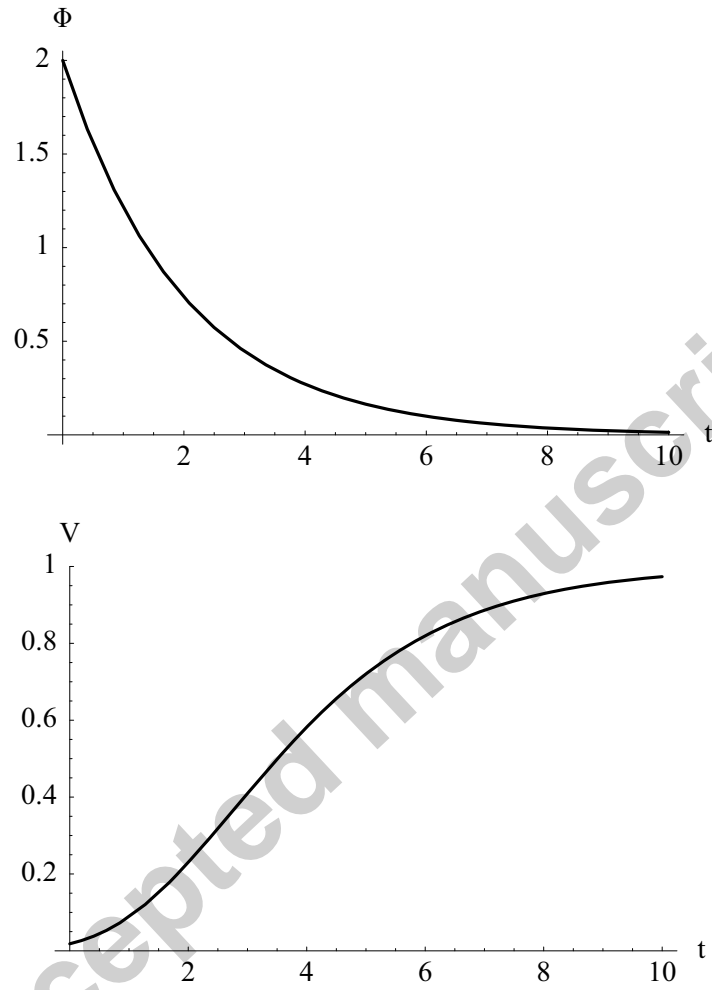


Figure 2: Dynamic cell wall extensibility Φ , as defined by Eq. (16), and the corresponding volumetric growth V , Eq. (17), as a function of time t . *Critical damping case*. The parameters are: $P - Y = 1$, $m = 1$, $b = 2$.

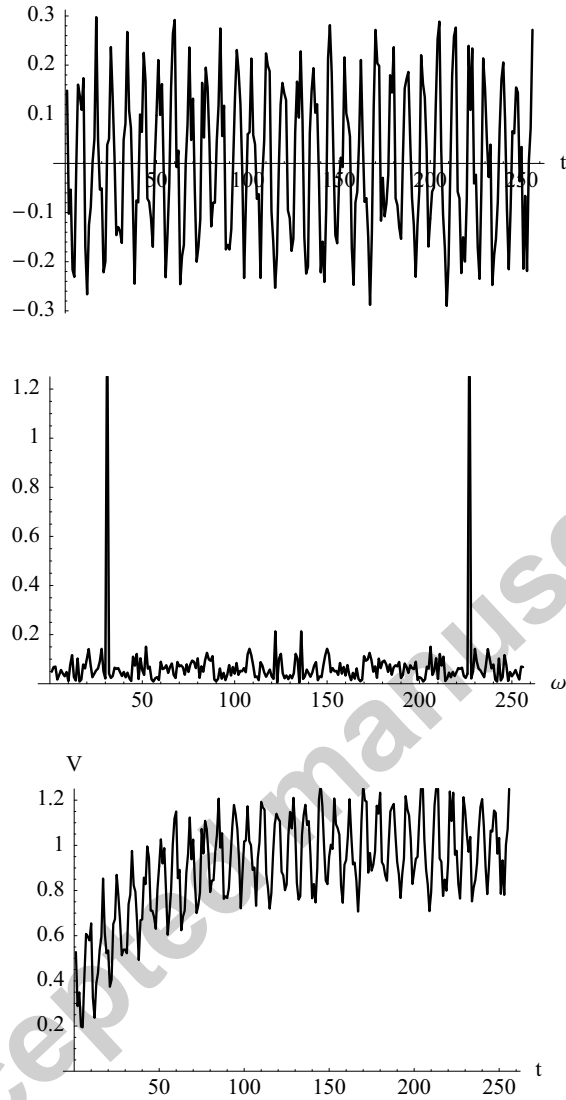


Figure 3: Numerical simulation ($A = B = 1$, $\Delta < 0$) based upon Eq. (19) resembling tip-measured pollen tube influx of Ca^{2+} - a periodic signal with random noise added. The tubes show pulsatile growth (lower plot) and pulsatile Ca^{2+} influx (upper plot). The Ca^{2+} oscillations have the same 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.

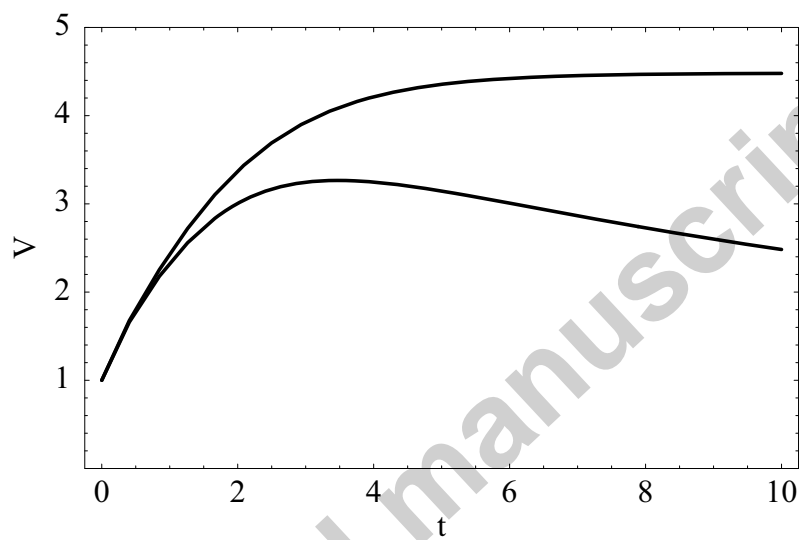


Figure 4: Volumetric growth V as defined by Eq. (12) as a function of time t . The parameters are: $m = 1$, $k = 1$, $b = 3$, $\xi = 0$ (upper curve), $\xi = 0.05$ (lower curve) – applicable in case of a previously growing plant cell that is deprived of its water resources due to water deficiency (slightly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

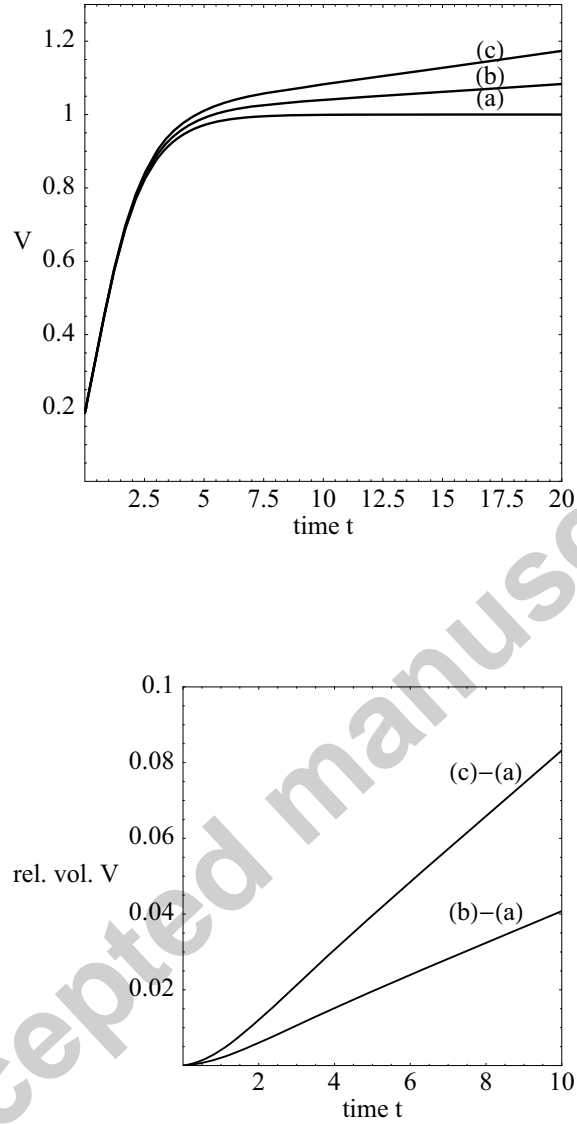


Figure 5: Volumetric growth V (upper plot), in presence of growth regulators, as defined by Eq. (23), as a function of time t . Net growth $V - V_0$ (lower plot), where V_0 corresponds to $f = 0$ – control, as an example of linear reaction due to the use of growth stimulator. The parameters are: $P -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

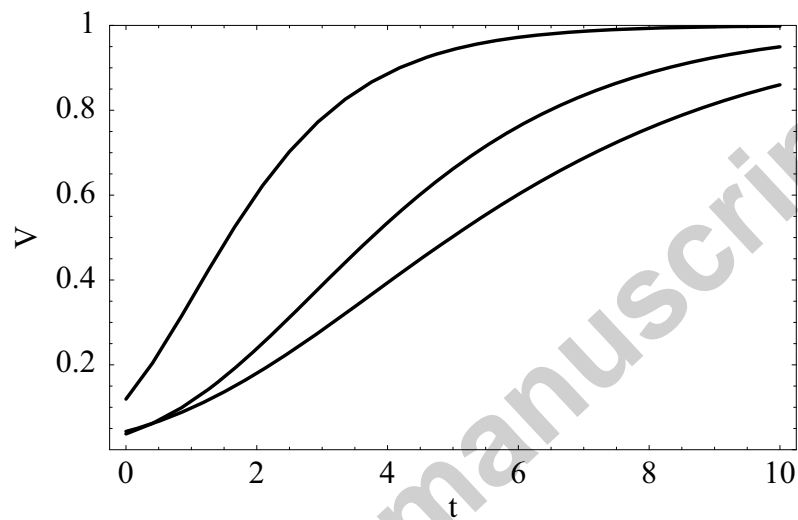


Figure 6: Volumetric growth V as defined by Eq. (10) as a function of time t . The parameters are: $P - Y = 1$, $V_0 = 1$. The estimated *via* Levenberg-Marquardt procedure parameters of Eq. (10) are: $k_0 = 0.718533$, $x_0 = 1.52802$ (upper curve, corresponding to $b = 2.1$ in Fig. 1a'), $k_0 = 0.415263$,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

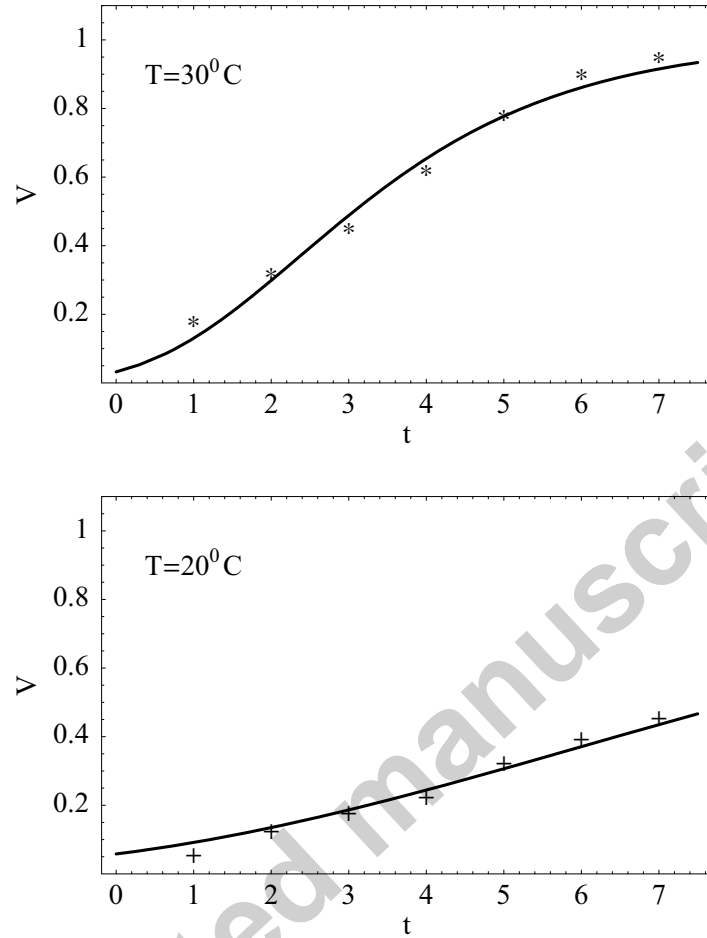


Figure 7: Elongation growth of maize (*Zea mays* L.) coleoptile segments *vs* time at two different temperatures. Both curves are fitted, with the help of Levenberg-Marquardt interpolation routine *via* Eq. (10), to the original data (*, +) taken from Lewicka and Pietruszka (2006), Fig. 2. The expansin 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 $T = 20^\circ\text{C}$ and $k_0 = 0.418721$ (greater) for $T \approx 30^\circ\text{C}$, 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.

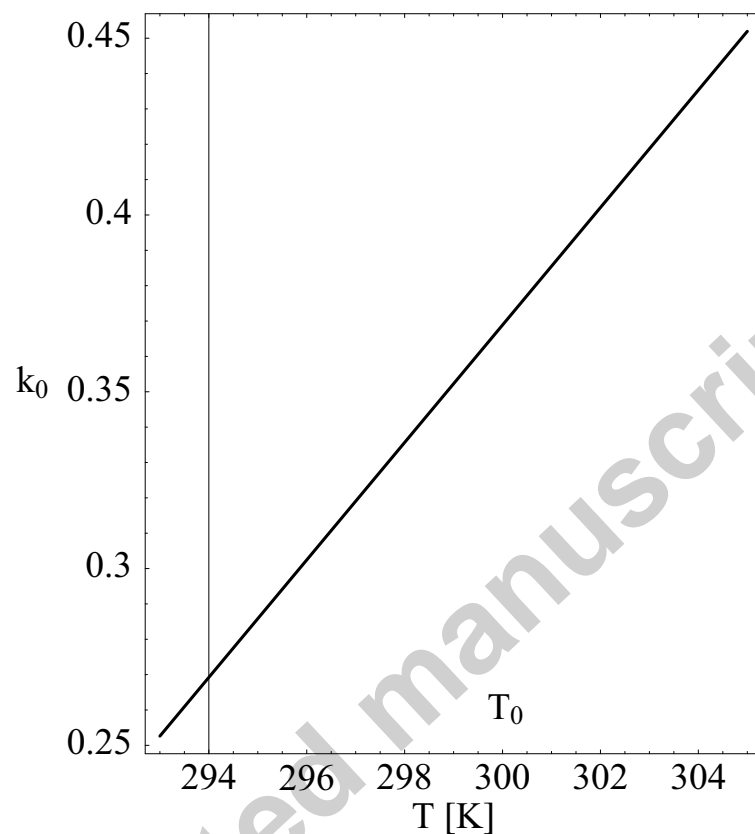


Figure 8: Kinetic coefficient k_0 , linearly interpolated with the use of the least squares method (Levenberg-Marquardt procedure), as a function of temperature for maize *Zea mays* L. (input data: see the caption to Fig. 7). The optimum growth temperature for maize approximately equals $T_0 = 300$ K. The kinetic coefficient k_0 changes in the interval of 20–30°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°C increase in temperature. The procedure is valid in ascending part of growth/elongation *vs* temperature curve (below T_0).

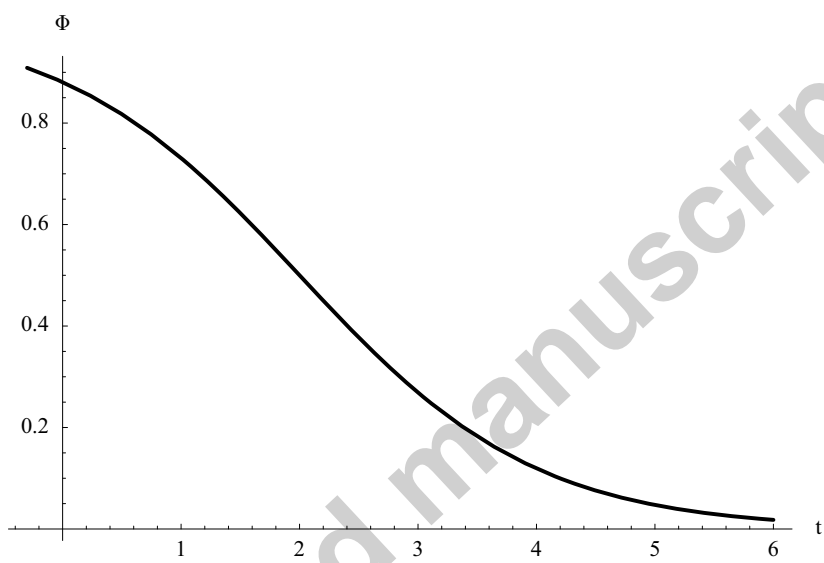


Figure 9: Estimated dynamic extensibility Φ , as defined independently by Eq. (26) in the Appendix B. The inflection time $t_0 = 2$.