Self-consistent equation of plant cell growth

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Abstract. We introduce a transcendental equation, describing the subsequent stages of plant cell/organ growth. Starting from empirically verified conclusions originating from the central limit theorem we also insert the influence of temperature on elongation growth to receive a time-dependent equation of growth parameterized by temperature. This self-consistent equation evolves with time using three cardinal parameters: t_0, T_0 and V_0. They represent the time of maximum expansion rate, the growth optimum temperature and the corresponding volume, respectively. Experimental determination of these cardinal values enables evaluation of the dynamic extensibility coefficient $\Phi = \Phi_T(t)$ in time and temperature domain.

Key words: Cell/organ extension — Transcendental equation — Extensibility coefficient

Introduction

As yet we have seen that much of experimental work dealing with plant growth has been elucidated by the Lockhart-type of equation (e.g. Lockhart 1965; Ortega 1985). Even though it could satisfactorily report on global properties of growth (in case of homogeneous and isotropic growth), it was not able to account for the local changes arising due to unidirectional stimulus (anisotropic growth). Also its applicability was quite limited to the linear in time mid-phase of elongation. However, with increasing time the exponential solution of this equation fails since it anticipates infinite cell extension. Our intent in this paper is to complete this equation with an equation capable of accounting for the elongation (and elongation rate) in the course of time and for the wall dynamics through calculation of the extensibility coefficient Φ.

Theory

In order to construct a global equation of growth, two empirical facts are taken into account: i) the sigmoid character of growth in the course of time (the sigmoid curve is followed by most plant organs) and ii) the absorption character of

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growth as a function of temperature. Thus, two main prerequisites form the foundations of the model Ansatz: one of these concerns the evolution in time (i) while the other – short-term cell expansion growth to temperature (ii).

i) It is a well-known fact in plant physiology, yet not very often used in a strict mathematical form, growth is described by the law of great growth. It is also commonly accepted that a sigmoid function, as having a non-negative first derivative in positive domain and exactly one inflection point, properly reproduces the large-scale evolution 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 ending with saturation. Such regularity can be represented by a sigmoid curve that characterizes the course of individual cell growth, the growth of plant organs, and the growth of the plant as a whole as a function of time. The sigmoid function is expressed by the hyperbolic tangent $f(t) = \frac{1}{2} [1 + \tanh(t - t_0)/t_0]$ where t_0 denotes the characteristic (inflection) time. This representation of the sigmoid function is called standard logistic cumulative distribution function (CDF). A textbook example concerning sigmoid character of growth as a function of time can be found in Fogg (1975) – its reproduction obtained by CDF interpolation (Levenberg-Marquardt procedure) is shown in Fig. 1A.

ii) Empirical data (Lewicka and Pietruszka 2008) suggest that in a quite wide range of about 5–40°C, elongation, as a function of temperature T, can be adequately described by the normal (Gauss) distribution (at least in the non-

membrane leakage regime). Briefly, from the theoretical point of view, the argument utilized therein is as follows. The central limit theorem (CLT) expresses the fact that any sum of many independent random variables will tend to be distributed according to a particular "attractor distribution". It states that if the sum of the variables has finite variance, then it will be approximately normally distributed, i.e. following a normal distribution. Since many real processes yield distributions with finite variance, this explains the ubiquity of the normal distribution. This may also apply to many different phenomena contributing to plant growth. From CLT we learn that even though the mechanisms underlying growth phenomena are often unknown, the use of the normal distribution $g(T) \cong \exp[-((T - T_0)/T_0)^2]$ can be theoretically justified by assuming that many small (or even negligible), independent or weakly coupled effects contribute to each temperature response. In order to fulfill CLT condition we assume that the individuals in the original population are normally distributed. Indeed, in a wide range of temperatures, the chemical reactions, such as metabolic processes, enzyme activity, photosynthesis, biomass production, protein denaturing etc., donate at a given temperature to the elongation growth resulting in the Gaussian dependence. At very low or high temperatures, the departure from the scenario is noticeable and CLT cannot be applied then. This is mainly expressed by asymmetric data distribution within the whole temperature range. However, as long as we are confined to ~ 5–40°C temperature interval, the acceptance of symmetric Gaussian is justified.

Aiming to validate the outlined approach, a series of experiments with different species in a broad temperature range were performed (Lewicka and Pietruszka 2008). The experiments were carried out with maize (*Zea mays* L.), barlow (*Hordeum vulgare* L.), wheat (*Triticum vulgare* Vill.), millet (*Panicum miliaceum* L.), bean (*Phaseolus vulgaris* L.) and pumpkin (*Cucurbita pepo* L.). In all cases the determination coefficient R^2 for the Gaussian exceeded 0.98. R^2 allows us to determine how certain one can be in making predictions from a considered model (here: Gauss distribution). Since it represents the percent of the data that is the closest to the line of best fit, it is a measure of how well the regression line represents the data. Therefore, it seems that the very high value of coefficient R^2 for Gauss distribution is by no means accidental. As a typical plot, one result is presented in Fig. 1B that is based on the early work by Lehenhauer (1914) – quoted by Shaykewich (1995).

Also recent single cell measurements (Lewicka 2008, PhD thesis) on internode *Nitellopsis obtusa* L. revealed exactly the same regularity as the described above for monocotyledons and dicotyledones (a symmetric Gaussian). As it was anticipated in our papers (previously introduced as heuristic hypothesis) the elongation growth *versus* temperature plot should follow a kind of a resonance curve (Lorentzian or
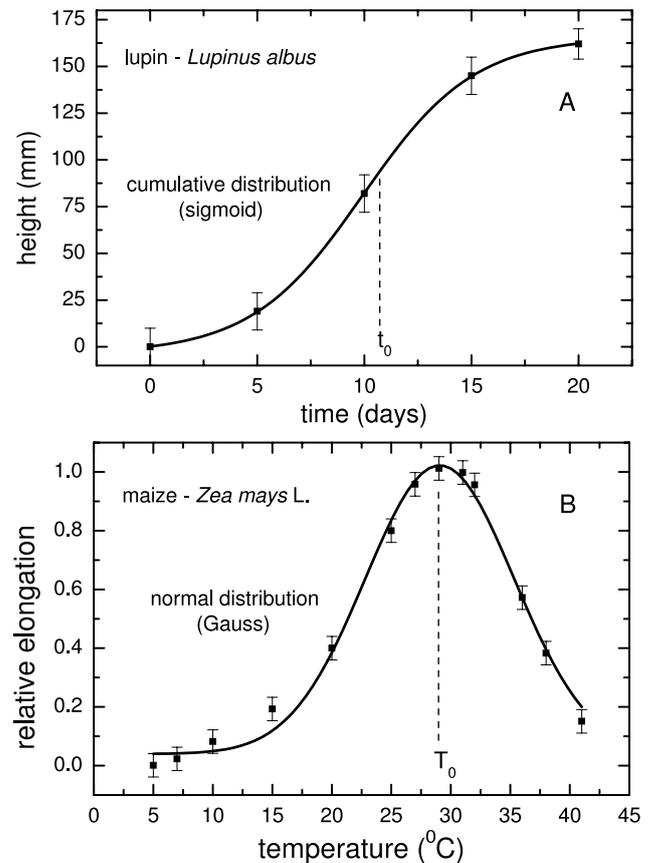

Figure 1. A. The calculated height of lupin (*Lupinus albus*) as a function of time (dotted line). The sigmoid fit yields very high squared determination coefficient $R^2 = 0.99$ for the data adapted from Fogg (1975). For clarity we present only a few original data points in the plot; t_0 indicates the characteristic time (the inflection point). **B.** Relative elongation of maize (*Zea mays* L.) coleoptile segments plotted against temperature. The experimental data points measured by Lehenhauer (1914), cited by Shaykewitch (1995), are interpolated by the normal distribution (solid line) with $R^2 = 0.99$ ($\chi^2 = 0.0001$). Normalization results from the division by the value of elongation at $T_{\max} = 29.07 \pm 0.20$.

Gaussian) centered at $k_B T_0$. Here, k_B stands for the Boltzman constant, and T_0 for the temperature of the optimum growth. (The interpretation for $k_B T_0$ is that maximum energy absorption is needed for the activation of internal biochemical processes responsible for the fastest growth). Indeed, according to our expectations, it turned out that the elongation growth *versus* temperature plot for *Nitellopsis* can be successfully described by either Lorentzian or Gaussian (both symmetric) in a broad region about the optimum temperature T_0.

Giving together arguments (i) and (ii) results in a proposal of time and temperature dependent phenomenological equation of growth. One remark concerning cell inner pressure needs

to be made. In most plant cells, turgor pressure (P) is required for growth (Proseus et al. 2000). Pressure must be above certain minimum (Y), and growth appears as a steady increase in size if P is steady (Cleland 1971). Hence we put $P(t) - Y = \text{const}(t)$, since we assume a constant water intake. However, no formal constraints limit the value either of P or Y during growth. Both magnitudes can vary slightly during time evolution.

Recalling the argumentation presented above, we receive (step 1) the approximate expression for the expanding volume in the form $v = v_0 f(t)g(T)$ which explicitly reads:

$$v = \underbrace{\frac{1}{2}\{1 + \tanh(\tau - 1)\}}_{f(t)}\underbrace{\exp\left\{-\frac{(T - T_0)^2}{T_0^2}\right\}}_{g(T)}$$

$$\Downarrow \tag{1}$$

$$v = \frac{1}{2}\{1 + \tanh(\tau - 1)\}\exp\left\{-\frac{(Pv - P_0 + (1 - v)Y)^2}{(P_0 - Y)^2}\right\}$$

The form-factor $f(t)$ is time-dependent, in accordance with point (i) of our derivation, while all temperature modifications, that enter through the reduced volume v, are due to the exponential term (point (ii)). In the exponential term we have already inserted the thermodynamic relations $P - Y = nRT/V$, $P_0 - Y = nRT_0/V_0$ into $g(T)$; R is the universal constant, and n is the number of moles. We have also attributed $v = V/V_0$ and $\tau = t/t_0$. The thermodynamic relations can be received from the equation of state at zero-th approximation. We accommodate here the argumentation given by Stanley (1971) concerning the linear term of the virial theorem we followed in all our recent papers where the full justification of the use of these state equations is presented (e.g. Pietruszka et al. 2007, p. 18). In Eq. (1) V stands for the volume of elongating plant cell/organ at temperature T. The value of P can be taken from experiment. It approximately equals 0.5 MPa, while Y is usually of about 0.1 MPa.

However, Eq. (1) is incomplete yet. In order to bring the wall mechanics into it we need to perform (step 2) the "rescaling" of the time variable in the logistic function f. This is accomplished by recalling the Lockhart equation and assuming that the extensibility coefficient Φ is temperature-dependent $\Phi = \Phi(T)$

$$\frac{1}{v}\frac{dv}{dt} = \Phi(P - Y) \Leftrightarrow \frac{d\ln v}{dt} = \Phi(T)G(v, T) \tag{2}$$

In Eq. (2) we have introduced the unknown temperature- and volume-dependent function G instead of $P - Y$ (such change of variables can be accomplished by virtue of a state equation). Integrating Eq. (2) yields

$$\underbrace{\int_0^v \frac{d\ln v'}{G(v', T)}}_{I(v)} = \Phi(T)t \tag{3}$$

Denoting the definite integral on the left side by $I(v)$ we get $I(v, T) = \Phi(T)t$. By solving Eq. (3) with respect to v, we formally obtain $v(t, T) = I^{-1}(\Phi(T)t)$.

In order to introduce time scaling in Eq. (1) we may rewrite it to the following form

$$\underbrace{2v\exp\left\{\frac{(Pv - P_0 + (1 - v)Y)^2}{(P_0 - Y)^2}\right\}}_{F(v)} = \{1 + \tanh(\tau - 1)\} \tag{4}$$

where the left side we have denoted as $F(v)$. By expanding the hyperbolic tangent on the right to the linear term about one ($\tanh(x) \approx x + O(x)^3$ – such approximation is fully justified in the broad linear range of growth) the above equation reads $F(v) = \tau$. By inverting this relation we get $v = F^{-1}(\tau)$. On the other hand we have already obtained from Eq. (3) the relation $v = I^{-1}(\Phi(T)\tau)$. Then, by comparing the latter, we see that the time argument differs by a factor of $\Phi(T)$. Therefore, in order to introduce Φ into Eq. (1) we may postulate its final form as

$$v = \frac{1}{2}\underbrace{\left\{1 + \tanh\left[\frac{\Phi}{\Phi_0}(\tau - 1)\right]\right\}}_{\text{cell-wall-dynamics}}\underbrace{\exp\left\{-\frac{(Pv - P_0 + (1 - v)Y)^2}{(P_0 - Y)^2}\right\}}_{\text{cell-sap-thermodynamics}} \tag{5}$$

where $\Phi_0 = \Phi(t_0, V_0)$ has been introduced for normalization. Equation Eq. (5) represents an irreversible increase in the volume at fixed temperature. Here t_0 denotes the time of the maximum expansion rate and $V_0 = V(t_0)$.

At a first glance, Eq. (5) acquires reasonable interpretation. The time-evolution of the volume V in Eq. (5) is governed by two factors, namely the cell wall extensibility properties entering the logistic-like function through Φ and cell sap thermodynamics represented by the exponential (temperature enters implicitly by $V = V(\Phi(T))$. Because parameters t_0 and V_0 can be taken from experiment, Eq. (5) may serve as an equation to determine Φ as a function of time.

Solutions and Applications

Eq. (5) can be solved either by graphical methods (see the drawing in Fig. 3) or iterations (we will discuss later). Plotting separately left hand side and right hand side of Eq. (5) we can see that they intersect exactly at one point (the volume V is always a positive quantity). This means that Eq. (5) has always a unique solution for the volume V.

The internal "degrees of freedom" are represented implicitly by the dependence of the volume on the cell wall extensibility $V = V(\Phi)$ in Eq. (5). In particular, the "material coefficient" Φ can be dependent on temperature, $\Phi = \Phi_T$. The specific functional form of $V(\Phi_T)$, as taken from experiments, can either be inserted to Eq. (5) to report on
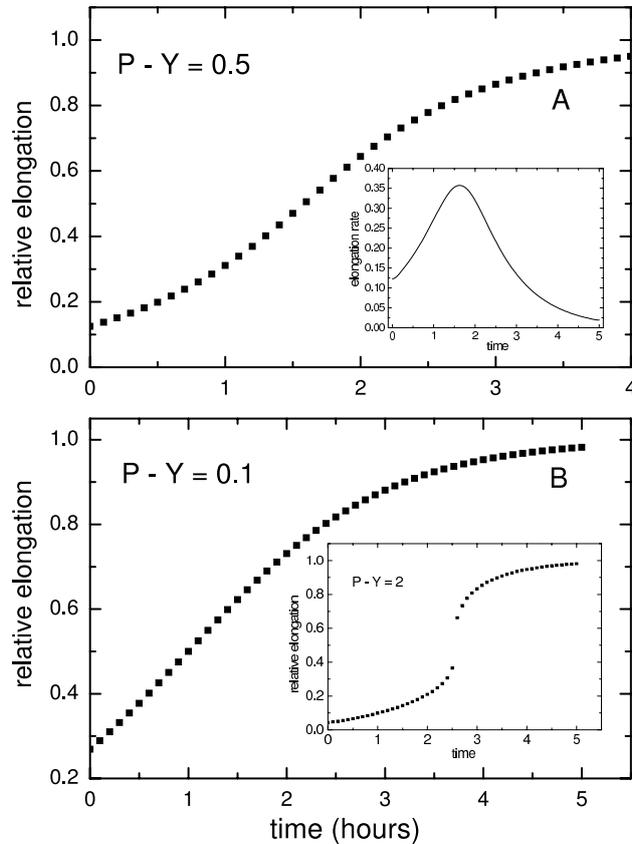
Figure 2. Numerical solutions of transcendental equation Eq. (1). The calculated relative elongation is plotted in function of time for different values of the turgor pressure difference $P - Y$. **A.** A typical sigmoid curve for $P - Y = 0.5$ MPa (the insert in the upper plot presents the corresponding solution of Eq. (1) for the elongation rate). **B.** Example solutions for the lower and greater (inset) $P - Y$ value. The turgor pressure difference (in MPa) is indicated in all plots for the relative elongation, respectively.

Figure 3. Schematic diagram of a graphic solution for transcendental equation Eq. (5) with $\Phi/\Phi_0 = 1$. The solution is found where the two lines representing left (lhs) and right (rhs) side of Eq. (5) intersect.

elastic/viscoelastic/plastic phases of elongation (Pietruszka and Lewicka 2007, Fig. 2) and the discussion therein) or deduced from the solution of Eq. (5) completed with the empirically estimated cardinal values. Beneath, we consider the case when $\Phi = \Phi_T(t)$ is unknown.

The main merit of Eq. (5) concerns the possibility of numerical evaluation of cell extensibility coefficient Φ in function of temperature and time. The procedure is straightforward, yet it demands a) growth experimental data and b) numerical investigations. Eq. (5) is a deterministic equation, it means – the knowledge of its parameters (t_0, V_0) returns the whole $V_T(t)$ plot. However, in what follows we leave Φ as an unknown function that must be determined.

In order to accomplish this issue, the following algorithm is to be performed. The average turgor pressure $P - Y$ difference may be assigned constant throughout, say 0.4 MPa.
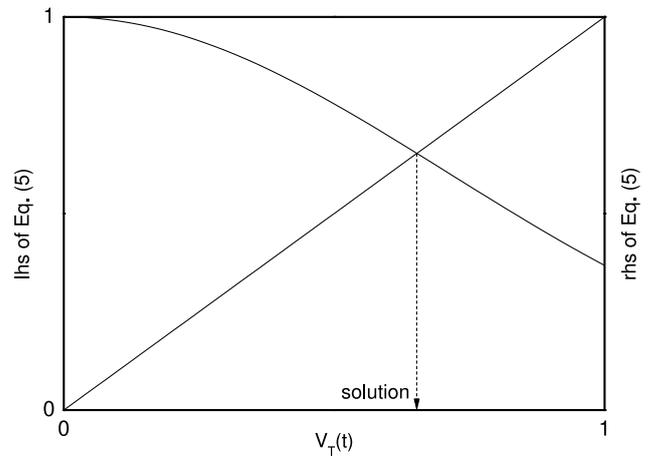
The credibility of this assumption is justified at least for the linear in time phase of growth (Kutschera and Kohler 1993, Fig. 1 where the authors conclude that the linear phase of growth in darkness, days 4 and 5 after sowing, is characterized by a constant cell turgor pressure). However, for special purposes the turgor pressure P or turgor threshold Y may vary, since Eq. (5) imposes no limitations with respect to this issue.

The simple procedure is as follows:
1. Measure the (volumetric) growth of an organ (or cell) at fixed temperature in the course of time $\{t_i, V_i = V(t_i)\}$, $i = 1,..., n$. This step also yields the set of unknown optimum parameters.
2. Use the values measured in 1 to solve numerically the nonlinear Eq. (5) with respect to $\Phi_{T=\text{const}}(t)$ in the course of time. Adopt iteration method (see the paragraph beneath), to extract Φ.
3. Change the temperature in the experiment. Go to step 1, or exit.

Eq. (5) is, in fact, a complicated transcendental equation, since it involves the implicit time (and fixed temperature) dependence not only on its left side but also in the exponential term (*via* $V = V_{T=\text{const}}(t)$), and therefore it must be solved by self-consistent (iterative) numerical methods. Solution by simple iterations is the procedure that serves our purpose best. Thus, the convergence (self-consistent solution) is reached while $|V^{(n)}(t) - V^{(n-1)}(t)| < \varepsilon$ where $V^{(n)}(t)$ corresponds to the nth iteration for the volume at a given time and fixed temperature and ε denotes the accepted accuracy. However, it turns out, that a few iteration steps are required to converge to a very high accuracy of the order of 10^{-4} that is even superfluous in the case of plant cell/organ extensibility measurements. In the first iteration we can simply insert the
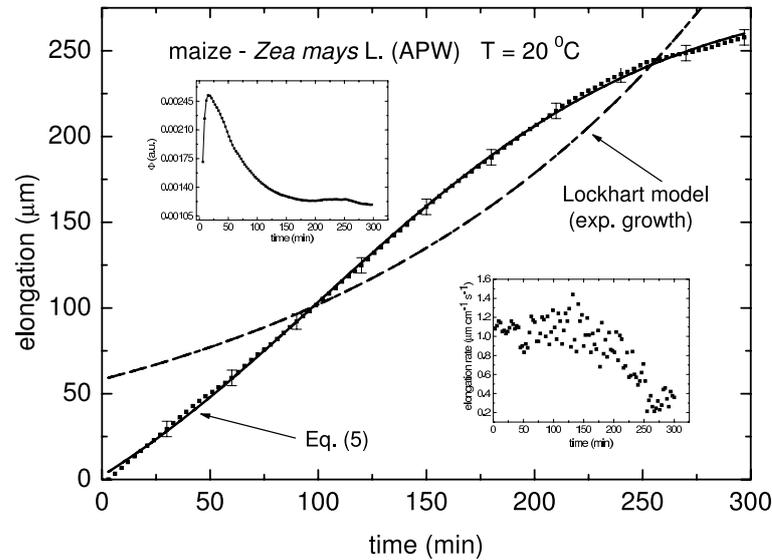
Figure 4. Elongation of maize coleoptile segments (APW – artificial pond water) in function of time (solid squares) as interpolated by Eq. (1) (hyperbolic tangent – solid line). The original data (ambient temperature) for the elongation rate are plotted in the inset (right). The dashed line representing the corresponding Lockhart solution is shown for comparison. The squared determination coefficient R^2 equals 0.9996 for Eq. (1) and 0.8909 for the Lockhart model. The extensibility coefficient Φ (arbitrary units) is plotted as a function of time in the inset (left) where the calculated through equation Eq. (5) data points are represented by the solid squares.
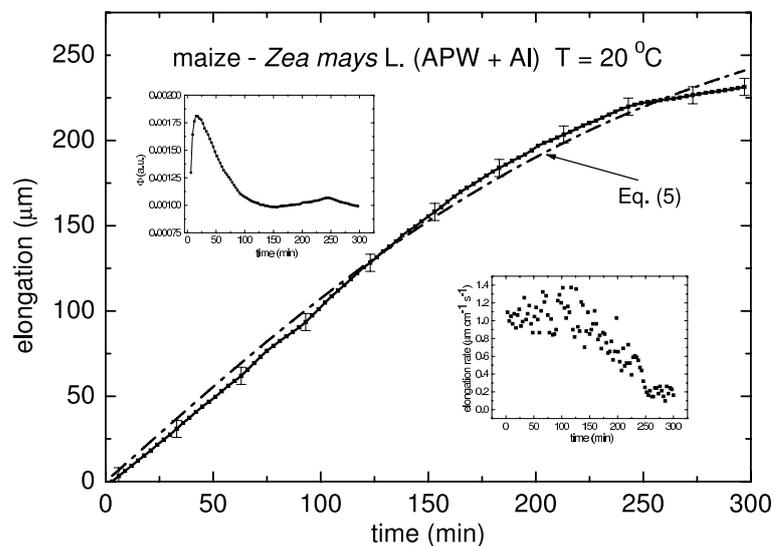

Figure 5. Elongation of maize coleoptile segments (APW + Al) in function of time (solid squares) as interpolated by Eq. (1) (hyperbolic tangent – solid line). The calculated through Eq. (5) extensibility coefficient Φ for APW+Al medium is slightly suppressed compared to APW (see the insets in Figs. 4 and 5).

initial volume of the cell $V^{(0)} = V(t = t_0)$ in the right side of Eq. (5). Then the iteration process continues by introducing the output of such calculation to the right side of this equation until the convergence condition is reached.

Some possible solutions are presented in Figs. 2A,B. It turns out, a moderate pressure difference $P – Y$ results in a kind of sigmoid curve (Fig. 2A) while the low pressure reveals linear growth with characteristic saturation ending (Fig. 2B) also present in Fig. 2A (compare with Mohr and Shopfer 1995). When turgor pressure $P – Y$ is too high a kind of discontinuity starts to appear (see the inset in Fig. 2B). The numerically calculated elongation rate corresponding to the

elongation plotted in Fig. 2A is shown in the inset and reproduces qualitatively the usually obtained data (also compare with the inset in Fig. 4, where the data for the elongation rate of maize is shown).

Furthermore, in Figs. 4–5 we present the possible applicability of Eq. (5) for typical data analysis like e.g. for elongation growth of maize (coleoptile segments). The solid line is obtained from the raw data for the elongation rate (see the inset in Figs. 4–5) through the following procedure. These data (elongation rate) has been numerically integrated to reconstruct of the primordial function – the elongation points (solid squares in the main plot). Then the elongation points were interpolated (solid line) with the use of Eq. (5). Similar procedure has been performed for the Lockhart model. The resulting curve (dashed line) is plotted in order to compare with our result. It looks as though, the exponential growth due to Lockhart equation is less adequate when noticing that the elongation data (solid squares) almost coincide with continuous curve. The discrepancy is pronouncedly bigger at greater times due to exponential increase of the Lockhart solution, contrary to saturation effect (exponential decay corresponding to maturation) observed in experiments and more properly described by logistic function. The high determination coefficient R^2 also favors the presented approach (see the caption of Fig. 4). Last but not least, the calculated through Eq. (5) extensibility coefficient Φ is shown in the inset in both figures.

Discussion

In this article a nonlinear equation for growing plant cell/organ has been introduced. This transcendental equation incorporates a number of features necessary to describe growth in the presence of environmental temperature or additional external/internal positive or negative pressure. It is quite easy to anticipate that Eq. (5) can be correspondingly supplemented to report on the implementation of phytohormons or influence of abiotic factors on the growth of plants. This can be accomplished by inserting proper terms in Eq. (5) in a similar fashion as in our recently published papers (see e.g. Pietruszka et al. 2007). Furthermore, careful analysis of Eq. (5) may deliver a new tool to extract information about the extensibility coefficient Φ.

Closer examination of Eq. (5) reveals that both terms on the right can be identified as corresponding to the Lockhart equation. The exponential part can serve simultaneously as a "higher order correction" due to the temperature-volume-dependence (V depends both on time and temperature). Notwithstanding, the correction term is difficult to overestimate since it should be present to describe the elongation growth (and elongation growth rate) properly. Indeed, both terms are required to describe different phases of elongation

growth: acceleration of growth with maximal velocity up to saturation and, next, cessation of cell expansion (see also Fogg 1975 and Cosgrove 2000 regarding large-scale growth). We also realize that the validity of the above solution for elongation growth ranges for the whole time interval, contrary to the Lockhart equation which is valid only for the linearly ascending interval of elongation. In addition, we notice that the applied constant pressure in the Lockhart equation implies exponential growth and, formally, the solution "blows up" with increasing time (Fig. 4).

It would be interesting to explain how the equation proposed here differ (except that it includes temperature effects) from the Lockhart equation in which the cell wall extensibility would not be constant. The answer is as follows. Providing that $\Phi = \Phi(t)$ then the solution of the Lockhart equation reads

$$V = V_{init} e^{\int \Phi(t)(P-Y)dt}$$

and the time dependence of the coefficient Φ must be known in order to calculate V.

Another point is that in Eq. (5) two experimental facts are included, namely the sigmoid character of growth as a function of time and the Gaussian dependence of growth as a function of temperature. This additional input is reflected by the existence of some cardinal numbers that anchor Eq. (5) to experiment.

Moreover, we should recall that the growth process is a non-equilibrium process and, in principle, should not be described by a Lockhart time differential equation. In contrary, the transcendental Eq. (5), through its structure, must be solved self-consistently, i.e. its subsequent solutions with increasing time are being found for quasi-equilibrium conditions at a given temperature. This fact may be interpreted as corresponding to such physiological situation that many internal processes must coincide to let the plant grow.

It is also important to mention that in the original Lockhart equation the coefficient Φ is independent of time and temperature, which is obviously not the case. In contrary, the extensibility coefficient Φ, decisive for the mechanical properties during growth, depends strongly on time (see Liu et al. 2007, Fig. 1A) and temperature (Nakamura et al. 2002, Figs. 1 and 2). Therefore, Eq. (5) can also serve as a new mathematical tool to determine the behavior of Φ in function of time at a given temperature.

In Eq. (5) the elongation (volumetric) growth can be adequately described by two characteristic parameters, namely t_0 (corresponding to the maximum rate of elongation) and the volume V_0 at t_0. Further development of this model may assimilate some other "material constants" bound with the elastic/viscoelastic/plastic properties of plant cell wall (Pietruszka and Lewicka 2007) through the coefficient Φ.

Last but not least, Lockhart equation has been derived for elongation growth in a particular (cylindrical) geometry and was intended to describe a single cell elongation. Since no geometrical assumptions are imposed onto Eq. (5), not only it can describe the single cell growth, but also some single cell simulations. A good example presents a Fishman and Genard model (Fishman and Genard 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).

In this article we have presented an equation to describe cell or organ growth as a function of time, which includes the influence of temperature. This kind of development can be useful to describe complex processes with fairly simple equations integrating different levels of knowledge. Since it has the advantage to yield the temporal dynamic of cell wall extensibility, it seems this equation may be used instead of the Lockhart equation largely used in plant sciences.

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