# Effect of temperature on plant elongation and cell wall extensibility

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**Abstract.** Lockhart equation was derived for explaining plant cell expansion where both cell wall extension and water uptake must occur concomitantly. Its fundamental contribution was to express turgor pressure explicitly in terms of osmosis and wall mechanics. Here we present a new equation in which pressure is determined by temperature. It also accounts for the role of osmosis and consequently the role of water uptake in growing cell. By adopting literature data, we also attempt to report theoretically the close relation between plant elongation and cell wall extensibility. This is accomplished by the modified equation of growth solved for various temperatures in case of two different species. The results enable to interpret empirical data in terms of our model and fully confirm its applicability to the investigation of the problem of plant cell extensibility in function of environmental temperature. Moreover, by separating elastic effects from growth process we specified the characteristic temperature common for both processes which corresponds to the resonance energy of biochemical reactions as well as to the rapid softening of the elastic modes toward the high temperature end where we encountered viscoelastic and/or plastic behavior as dominating. By introducing analytical formulae connected with growth and elastic properties of the cell wall, we conclude with the statement how these both processes contribute quantitatively to the resonance-like shape of the elongation curve. In addition, the tension *versus* temperature "phase diagram" for a living plant cell is presented.

**Key words:** Azuki bean — Cell extension — Modified growth equation — Phase diagram — Plant elongation — Rice — Temperature

## Introduction

Growth of plants belongs to the one of the most complex physiological processes in plants (Fogg 1975; Kutschera 2000 and papers cited therein, see for a review), and is based on irreversible extension of the whole organism due to the increase in the quantity and size of cells, the mass of protoplast and the cell walls (Cosgrove 1986, 1987, 1993). The plant growth is influenced by physical (abiotic) and biotic factors of environment (Wright 1966; Trewavas 1991; Edelmann 1995). The external factors which fundamentally influence plant growth are temperature, light, water and soil factors (e.g. pH), and atmosphere composition.

The development of plant cells is comprised of two interrelated processes, growth and differentiation. The growth can be described in three steps: a) cell cycle – when new cells are formed, b) cell elongation, and c) cell maturation – cessation of cell enlargement. In b), the juvenile cells vacuolate, take up water and expand by irreversible yielding of the growth-limiting primary walls. Two independent physical processes, e.g. water absorption and cell wall yielding result in time-irreversible cell enlargement at a given temperature. A qualitative description of plant cell elongation was elaborated firstly in the mid-60's in the form of a simple (first order in time) ordinary differential equation by Lockhart (1965a). However, its main disadvantage was the absent environmental temperature at which growth takes place, as well as the lack of possible influence of above mentioned environmental factors like growth stimulators/inhibitors, constant pressure or light. In the present paper, we attempt to fulfil this absence and focus on the deficient theoretical abiotic aspects of growth (we consider only temperature here). Introducing temperature by thermodynamical reasoning and putting forward a fairly simple but very efficient and fruitful model ascribing possible influence of environmental tem-

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perature, noticeable progress toward theoretical derivation of a temperature-modified growth equation was made. We utilize the new idea that the often-described dependence of elongation rate on temperature displays clear "shape analogy" with the dependence of the output amplification factor of a harmonic oscillator submitted a range of forcing pulsation, also called the resonance curve for a damped driven linear oscillator. Indeed, the experimental data on maize seedlings elongation (coleoptile segments) could be fitted convincingly by such equation if the forcing ω is replaced by temperature $\tau$ and the amplification factor by total elongation (Pietruszka et al. 2006, 2007).

The results presented in this article partly stay in agreement with the conclusion obtained by Nakamura et al. (2002) who suggest that the environmental temperature modulates the growth rate by affecting mainly the mechanical properties of the cell wall. According to the scenario presented in this paper, based on our theoretical calculations strictly bound with experiments performed by the group of Nakamura et al. (2002), we agree with the point of view presented by Proseus et al. (1999) that the growth is not controlled only by inert polymer extension but rather by the variety of biochemical processes with the pronounced sensitivity of growth to temperature. Since these authors involve relatively high temperatures (exceeding 40°C) in their experiments, it should have also been taken into account in the developed theory. Indeed, the proper term responsible for the membrane leakage and loss of turgor at high temperature end appears in our equations.

In the present paper we concentrated on derivation of temperature-modified equation of growth and on finding its specific solutions by linearization procedure. We combined experimental and theoretical results based on the separation of elastic effects from growth and summarized our results in the "phase diagram". The high temperature limitation and the validity of our model is also discussed: when temperature is high, cell membrane tends to be leaky and turgor tends to be lost; then it is impossible for cells to expand without turgor at high temperature.

### *Temperature-modified equation of growth*

#### *General discussion*

Most of plant growth results from cell enlargement in localized growing regions. Due to the complexities of these systems, Lockhart (1965a,b) modeled the growth of single cells surrounded by water. He also assumed that the cell walls behaved as inert polymers stretched by pressure $P$ exceeding turgor $Y$, and that the wall biosynthesis is independent of growth. Ortega (1985, 1990) extended the Lockhart treatment to account explicitly for the elastic properties of the wall. However, both time-dependent equations describing

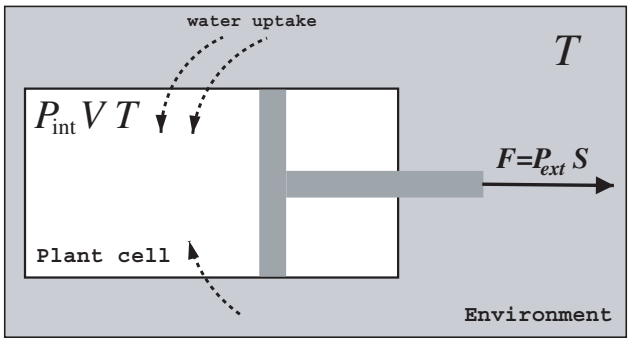


**Figure 1.** Scheme of the "gedanken experiment" set-up: movement of a piston in a cylinder reflects the extensibility properties of a cell wall. Both the water uptake and temperature influence constitutes the internal turgor pressure $P_{\text{int}}$. The external pressure acting on plant cell is represented by the applied force $F$. The whole system (the living cell) is immersed into a thermostat (environment) at a temperature $T$.

the elongation of a plant cell resulting from a dynamic balance between the water uptake and the cell wall yielding should in principle include another external factors like growth stimulators/inhibitors, the influence of light and, especially, temperature. Hence, as a differential equation taking growth temperature dependence into account, we propose the following model as an extension of the Lockhart one

$$\frac{1}{V}\frac{dV}{dt} = \Phi\left(\underbrace{P_{\text{int}} - Y}_{\text{Lockhart term}} + P_{\text{ext}}\right) \qquad (1)$$

where $P_{\text{int}} - Y$ stands for hydrostatic pressure in excess of turgor threshold and $V$ denotes the cell volume. $P_{\text{int}}$, $P_{\text{ext}}$ denote internal and external pressure, respectively. The right-hand side of Eq. (1) is linked to the growth rate by the extensibility coefficient $\Phi = \Phi(T)$ (we stress that the original form of the Lockhart equation does not contain the temperature dependence altogether). The latter term in Eq. (1) ascribes the presence of $P_{\text{ext}} = F_{\text{ext}}/S$ where $F_{\text{ext}}$ is the applied force and $S$ denotes a surface cross-section perpendicular to the force direction. So, in the framework of our theoretical model, we are also able to provide a concise description of the action of the external force (pressure) onto the elongation and, consequently, to examine the cell wall mechanical properties (see also Fig. 1).

To solve Eq. (1), we should first know the $P_{\text{int}}$ dependence on temperature ($Y$ = const.). Solution for this problem is given in thermodynamics by a state equation which provides a mathematical relationship between two or more state functions associated with matter, such as its temperature, pressure, volume, or internal energy. Here we apply the state

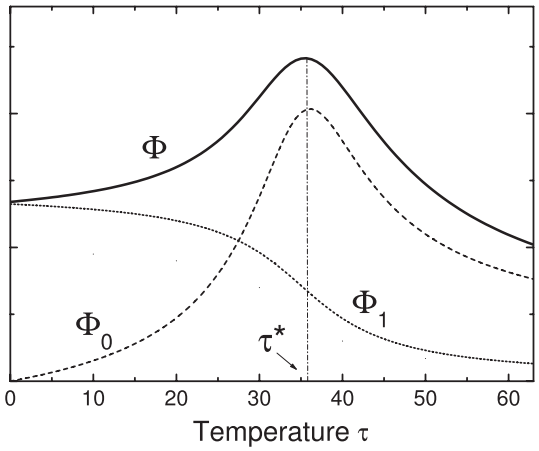


**Figure 2.** Plot of the cell wall extensibility coefficient $\Phi(\tau)$ (solid line), "growth component" $\Phi_0(\tau)$ (dashed line) and "tensile component" $\Phi_1(\tau)$ (dotted line) as functions of temperature. Plots of $\Phi_0(\tau)$ and $\Phi_1(\tau)$ are obtained through Eqs. (9) and (10), respectively. Both constituents, $\Phi_0(\tau)$ and $\Phi_1(\tau)$, superimposed result in $\Phi(\tau)$ curve. The characteristic temperature $\tau^*$ common for $\Phi_0(\tau)$ and $\Phi_1(\tau)$ functions indicates the critical point of reversible/irreversible "phase transition".

equation in the following form[1]: $P_{\text{int}} = Y + \gamma T/V$ and $\gamma$ is a constant dependent on density of water solution filling up the cell interior (it also includes the universal gas constant R). Considering Eq. (1) as only consisted of the Lockhart term, we obtain the linear solution $V = V_0 + \Phi\gamma Tt$ where $V_0 = V(t_0 = 0)$ for its unperturbed form[2]. (Indeed, also the actual experiments indicate linear growth). By inserting the state equation into Eq. (1) we receive (the detailed derivation of Eq. (2) can be found in the Appendix)

$$\begin{aligned} \frac{1}{V}\frac{dV}{dt} &= \Phi(T)\left(\gamma\frac{T}{V} + P_{\text{ext}}\right) \\ &\Downarrow \\ V(t) &= V_0 e^{\Phi P_{\text{ext}}\, t} + \frac{\gamma T}{P_{\text{ext}}}\left(e^{\Phi P_{\text{ext}}\, t} - 1\right) \end{aligned} \qquad (2)$$

where $V_0$ stands as usual for the initial cell volume. Since experimental data suggest linear time dependence of $V$ (in the ascending range in the well known sigmoid growth curve in the case of four days coleoptiles or epicotyles) we may approximate the exponent in Eq. (2) $e^{\Phi P_{\text{ext}}\, t} \simeq 1 + \Phi P_{\text{ext}}\, t$ (for full justification, see the last paragraph in the Appendix) to obtain

$$V \simeq V_0 + \Phi\left(\gamma T + V_0 P_{\text{ext}}\right)\, t \qquad (3)$$

Therefore, the elongation function reads

$$\text{Elong} = V - V_0 \simeq \Phi(T)\left(\gamma T + V_0 P_{\text{ext}}\right)\, t \qquad (4)$$

To conclude, such obtained elongation function is parameterized not only by temperature (in continuous manner) but also by the applied external pressure[3] $P_{\text{ext}}$.

*Separating elastic effects from growth*

This part of our study is undertaken to determine whether growth can be distinguished from elastic deformation when plants enlarge. Both processes are always present but they occur together and are superimposed on each other when plant becomes larger. Nevertheless, they are fundamentally different because growth results from irreversible enlargement whereas elastic extension is not permanent and reverses when the deforming force is removed. The literature data (Proseus et al. 1999) stress that the elastic deformation is independent of growth as it also occurs in mature cells. Even though growth at low temperature is eliminated, however, it does not alter elastic effects. The authors emphasize that they have performed such experiments that allowed subtracting elastic deformation from elongation that resulted in the fact that growth could be distinguished. Following this idea, we undertake in our study a problem how to establish a physical model, which can report on above-mentioned features. In our opinion, it can be accomplished by the assumption that the extensibility coefficient $\Phi$ responsible for growth and the elastic properties of the cell wall consists of two terms

$$\Phi = \Phi_0 + \Phi_1\left(\frac{E}{E_0}\right) \qquad (5)$$

[1] It is evident that in more precise calculations one should solve Eq. (1) for subsequent reciprocal powers of the volume V by the iteration method. Such extension would be even more adequate nonetheless also more complicated. However, high accuracy in case of biological experiments, where we deal with relatively high statistical error, is superfluous. The method based on making reasonable simplifying assumptions that allows for analytical solutions which yield clear interpretations is always the best to start with. Such methodology (here utilized) is commonly accepted in science. In this paper, we follow the reasoning concerning the introduction of temperature *via* the equation of state as in Stanley (1971).

[2] The integration of Eq. (1) can be accomplished since, similar to the original Lockhart approach, the parameters appearing in this equation are time-independent. We also follow this line considering $\Phi(T)$ as also constant in time which is commonly accepted typical treatment, see also Cosgrove (1985).

[3] It is worth stressing that based on experimental data for the elongation at low temperature range we observe vanishing of this magnitude while approaching 0°C. In accordance with Eq. (5) also the cell wall extensibility coefficient $\Phi$ should reach zero since we have $\Phi(T) = \text{Elong}/(\gamma T + V_0 P_{\text{ext}})t$. Let us notice that the denominator is always positive even for $P_{\text{ext}} = 0$ (no added pressure).

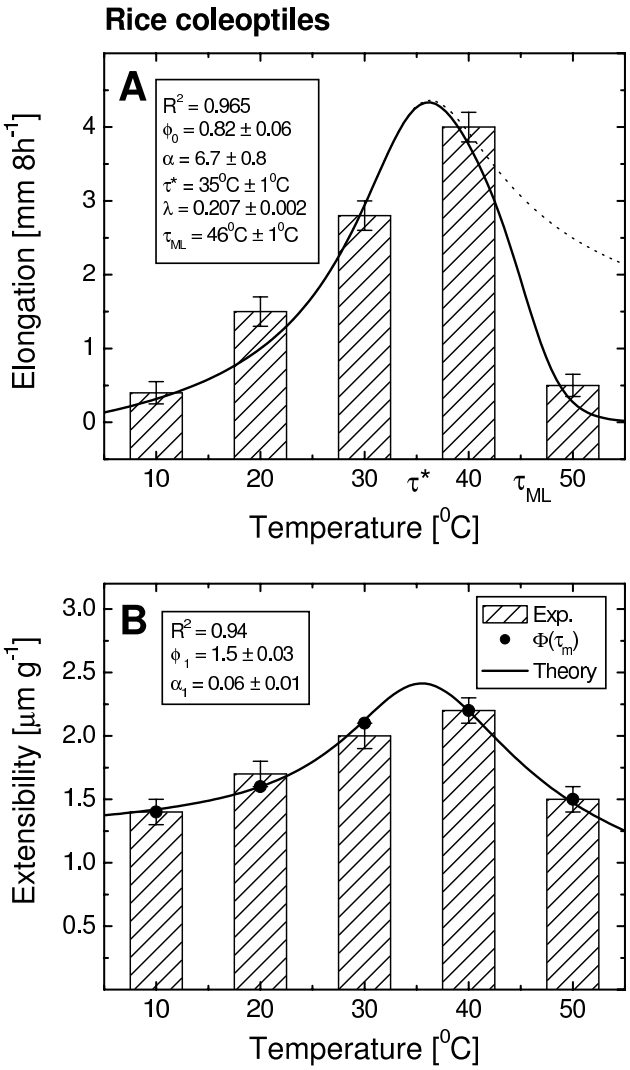


**Figure 3.** Elongation (A) and extensibility (B) *versus* temperature for rice coleoptiles. Bars denote experimental results obtained by Nakamura et al. (2002) (Exp.) while the solid curves result from our model (Theory); $\tau_m$ is the measured temperature. The dotted line corresponds to the case when the membrane leakage and loss of turgor are not considered.

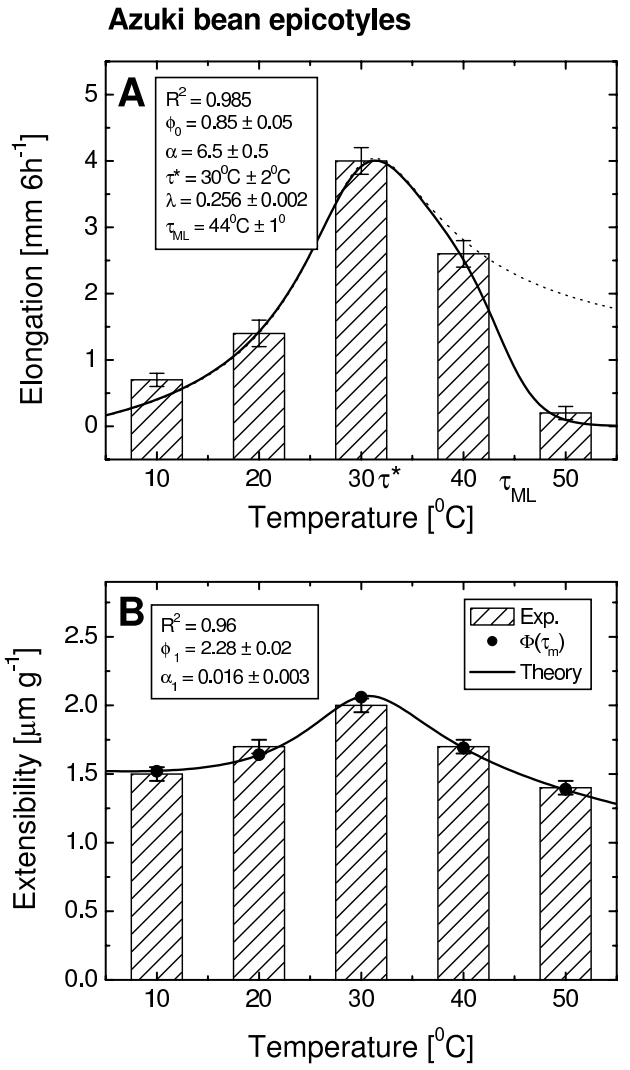


**Figure 4.** Elongation (A) and extensibility (B) *versus* temperature for Azuki bean epicotyles. Bars denote experimental results obtained by Nakamura et al. (2002) (Exp.) while the solid curves result from our model (Theory); $\tau_m$ is the measured temperature. The dotted line corresponds to the case when the membrane leakage and loss of turgor are not considered.

where $\Phi_0$ stands for the irreversible ("growth") coefficient as in the original Lockhart equation $1/V\,\mathrm{d}V/\mathrm{d}t = \Phi_0\,(P_{\mathrm{int}} - Y)$ while the second ("tensile") coefficient $\Phi_1 = \Phi_1(E/E_0)$ reflects the cell wall mechanical properties itself and depends on the fraction $E/E_0$. The inertial factor $E/E_0$ in Eq. (5) is bound with the rheology of cell wall (tensile modulus) and is defined as the slope of the stress-strain curve normalized to its value at zero temperature. The proposed approach in graphical form is presented in Fig. 2. The first term, $\Phi_0$, we associate with biochemical reactions (with the energy absorption peak at the optimum temperature) while the second one, $\Phi_1$, is attributed successively (with increasing temperature) to the elastic/viscoelastic/nonelastic mechanical properties of the cell wall. This representation, Eq. (5), is due to the fact that according to Proseus et al. (1999) growth is not controlled only by inert polymer extension ($\Phi_1$) but rather by biochemical reactions with the marked sensitivity of growth to temperature (the resonance-like asymmetric $\Phi_0$ term). On the other side, $\Phi_1$ is strictly dependent on $E/E_0$. It is worth stressing that the tensile modulus depends on temperature because the cell wall does not satisfy the Hook's law in the whole temperature range but obviously only at low tem-

perature end ($E_0 = E(\tau = 0°C)$), like the typical amorphous materials. Thus $E/E_0$ at low temperatures is almost constant (like in the solid state materials) and strongly decreases with temperature at a specific transition range (see Fig. 5). By inserting Eq. (5) into the Lockhart equation and taking into account the relevant considerations from the previous section, we receive

$$\frac{1}{V}\frac{dV}{dt} = \left(\Phi - \Phi_1\left(\frac{E}{E_0}\right)\right)\cdot(P_{\text{int}} - Y + P_{\text{ext}}) \quad (6)$$

Hence, after inserting $P_{\text{int}} - Y = \gamma T/V = \gamma(\tau + 273.15)/V$ and integrating Eq. (6), we get the following expression for the elongation function

$$\text{Elong}(\tau) \simeq (\gamma(\tau + 273.15) + V_0 P_{\text{ext}})\cdot \cdot\left[\Phi(\tau) - \Phi_1\left(\frac{E}{E_0}(\tau)\right)\right] t \quad (7)$$

The above solution takes into account the existing partition of Φ onto two components: the "growth" and the "tensile" one.

## Results

### *Fitting procedure*

To make our paper complete, we add some comments about the way how we have fitted the adopted empirical data (Nakamura et al. 2002) in order to bind them with Eq. (7) (see also Figs. 3A, 4A). The model equation[4] used for the fitting procedure for the elongation function is (for full justification, see also Pietruszka et al. 2006, 2007)

$$\text{Elong}(\tau) = \underbrace{\frac{\phi_0\tau}{\sqrt{\alpha^2 + (\tau - \tau^*)^2}}}_{\text{non-dissipative}}\cdot\underbrace{\exp\left(-\lambda\vartheta(\tau - \tau_{\text{ML}})\right.}_{\text{dissipative}} \quad (8)$$

where the function ϑ is defined as follows

$$\vartheta(\tau - \tau_{\text{ML}}) = \begin{cases} 0 & \text{for } \tau < \tau_{\text{ML}} \\ \tau - \tau_{\text{ML}} & \text{for } \tau \geq \tau_{\text{ML}} \end{cases}$$

and the parameter $\tau_{\text{ML}}$ is the temperature at which the loss of turgor and membrane leakage processes become dominating. The first term in Eq. (8) is associated with non-dissipative term where the Lockhart equation holds, while the second term is bound with dissipative processes occurring at high temperatures, e.g. loss of turgor due to leaky membrane and denaturation of its protein components. Even though the intuitive explanation for the first term in Eq. (8) can be found in the footnote 4, nevertheless it should be derived from the first principles. A tempting way to obtain such dependence, the authors bind with the application of stochastic resonance in biological systems in which random perturbations (temperature fluctuations) play a useful role in enhancing energy absorption in non-linear systems (the whole complexity of basic processes stimulating plant to grow). This mathematically very difficult task is presently

[4] By introducing our physical model (see Fig. 1), we are far beyond the oversimplified picture where we interpret the movement of a piston as only reflecting the compressibility/extensibility properties of water solution inside the plant cell. In contrary, in such a way we incorporate rather a number of basic chemical and biochemical processes which accelerate or decelerate growth in function of temperature (kinetics of chemical reactions, metabolism, photosynthesis (biomass production), protein denaturing, etc.). Because both type of processes act simultaneously, however, with different intensity at distinct temperature ranges, one should expect a crossover from one type of behavior to the other. Thus, there should exist a delicate balance among all those factors and consequently a specific, well defined critical temperature for which the growth rate is optimal. We may justify the choice of such a function in a following way. The outlined system (a plant cell) behaves similarly to the most systems described by a differential equation where both dissipative and extortive forces are present. In such systems, there always exists a variable which is optimal at certain conditions. In the case of plants, the factor enforcing the crossover from accelerating to decelerating the growth is temperature $\tau$ – there must exist a critical ("resonance") temperature $\tau = \tau^*$ of such a crossover. Consequently, the plant elongation (in function of temperature) may be described by a resonance curve – the Lorentz distribution function, however, modified by a factor $\tau$. The latter correction is due to the fact that at $\tau = 0°C$, the growth must cease altogether. This is also in accordance with the fact that the Celsius scale is a natural temperature scale for higher plants. Also due to high intensity and steep "onset" of the underlying biochemical processes responsible for membrane leakage and loss of turgor, the real curve of the temperature dependence of plant elongation is not symmetric like the Lorentz distribution but asymmetric, and this is our case. In the work of Boyer (1993), temperature and growth associated with water uptake were studied. He found that water permeability in membranes and water viscosity were limiting factors for cell elongation at relatively lower temperature. Also, considering the "resonance temperature" we are very well aware that such magnitude is meaningless unless we treat it in the energetic context: multiplying temperature by the Boltzmann constant $T \to k_B T$. This is in accordance with the fact that the optimum temperature of growth ("resonance temperature" $\tau^*$) corresponds to the maximum energy absorption $k_B T^*$ due to activation of internal biochemical processes.

under study. The parameters $\alpha$, $\phi_0$ and $\tau^*$ denote the half-width, height and resonance (optimum) temperature (energy) of the Lorentz-like distribution, respectively. (Note that $\phi_0$ should not be confused with $\Phi_0$). By comparing the first term[5] of Eq. (8) with Eq. (7) we receive the cell wall extensibility coefficient $\Phi(\tau)$ which is parameterized by external pressure $P_{\text{ext}}$ as follows

$$\Phi(\tau) = \underbrace{\frac{1}{(\gamma(\tau + 273.15) + V_0 P_{\text{ext}})\, t} \cdot \frac{\phi_0 \tau}{\sqrt{\alpha^2 + (\tau - \tau^*)^2}}}_{\Phi_0} + \\ + \Phi_1\left(\frac{E}{E_0}(\tau)\right) \tag{9}$$

where the absolute temperature (in Kelvin scale) $T = \tau + 273.15$. The symbol $t$ in this equation should not be confused with continuous time but it serves only as a parameter which takes on the values from paper of Nakamura et al. (2002): 8 and 6 h, respectively for rice and azuki bean. For both cases of rice and azuki bean considered in the paper by Nakamura et al. (2002) we have obtained two distinct sets of coefficients $\phi_0, \alpha, \tau^*, \lambda$ and $\tau_{\text{ML}}$ for the elongation function (Eq. (8), see the legends in Figs. 3A, 4A and compare to Figs. 1A and 2A in Nakamura et al. (2002)). All parameters were estimated by the method of non-linear least square fitting. The non-linear regression method was based on the Levenberg–Marquardt algorithm.

Despite the loss of turgor, caused by the increasing membrane leakage at higher temperatures, we have not omitted the high temperature end point at 50°C in this procedure. The reason was the authors' conviction that nonelastic properties of the cell wall still remained even though in this temperature most of biological processes in plant cease altogether (see Figs. 3A, 4A and compare to Figs. 3B, 4B). The validity of the asymmetric Lorentz-like fit (Figs. 3A, 4A) is in fact limited to the temperature region where the Lockhart equation holds and this is surely well below the high-temperature edge. Nonetheless, the fitting curve would be more adequate providing that the data points were more dense at least in the supraoptimal region. Our observations are also in accordance with other literature data: Ikeda et al. (1999) measured growth rates of kidney beans at various temperatures together with water potential, osmotic potential and turgor, and they found that at 40°C turgor was lost due to leaky membrane. Additionally, water uptake related to cell expansion, was inhibited at the same temperature. In the work of Nakamura et al. (2002), the similar behavior seemed to be happening at 50°C. If turgor is lost completely

[5] The second term can be omitted here since even though its influence onto plant elongation is decisive at high temperatures, nonetheless its impact on extensibility features within the same temperature regime can be neglected.

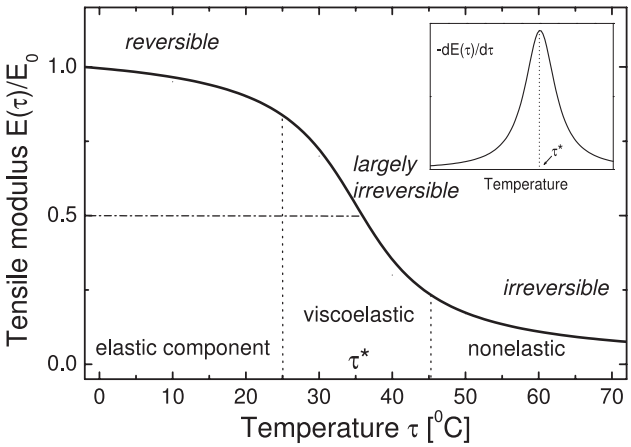


**Figure 5.** Phase diagram for plant cell wall and the plot of tensile modulus $E/E_0$ *versus* temperature $\tau$. The characteristic temperature $\tau^*$ is also pointed out. The inset shows the negative temperature derivative of tensile modulus.

at high temperature, Lockhart equation will not be valid at such temperature any longer. This is the limitation (high-temperature edge limit) of our Lorentz-like model and the reason for the discrepancy as seen in both figures (Figs. 3A, 4A) at the high temperature end (the solid *versus* dotted plots in Figs. 3A, 4A). Therefore, from the biophysical point of view, it is more adequate to choose such a type of fitting function which is able to account for the steep decrease in plant elongation at high temperature regime. This, however, demands some modification of the Lorentz-like non-dissipative term in Eq. (8) by multiplying it by the dissipative term which takes into account the loss of turgor due to increasing membrane leakage at higher temperatures. The appearance of the dissipative term introduces two additional parameters, namely $\lambda$ (which denotes how steep the slope is) and $\tau_{\text{ML}}$ (the threshold temperature at which the loss of turgor is a dominating process affecting the growth, mathematically expressed as a value for which the elongation decreases $e \approx 2.78$ times. The values of $V_0$ and t are given as input while $\gamma$ and $P_{\text{ext}}$ can be easily calculated. One may have doubts as to whether our treatment is adequate and the close fits to experimental data notwithstanding. It is worth stressing that authors' performed experiments for *Zea mays* L. (Lewicka and Pietruszka 2006) for more numerous (eight temperatures) elongation data also confirmed this analysis. An additional remark needs to be made here: the calculated maximum is slightly shifted with respect to the experimental value, however, it looks as though this is the actual optimum temperature at least within the estimated accuracy range ±1°C. Accordingly, such a fit which delivers the continuous Lorentz-like curve is always more exact in estimating the optimum temperature than the discrete set of experimental values (here measured at every ten degrees).

The following step of our considerations focus on mechanical properties of the cell wall which are also included in Eq. (9). Taking into account the rheological properties of the cell wall, we may treat it as a kind of elastic material at low temperatures and viscoelastic (amorphous) material above. Accordingly, the tensile modulus $E/E_0$ part of Eq. (9) can be represented (here as Ansatz, based on the experimental data for amorphous materials in Angell and Boehmer (1998), Fig. 3; also Sperling (2006), Fig. 1.6) by

$$\Phi_1\left(\frac{E}{E_0}(\tau)\right) = \frac{1}{3}\phi_1\left(\frac{\pi}{2} + \arctan\left[\alpha_1(\tau - \tau^*)\right]\right) \quad (10)$$

where the $\phi_1 = \Phi_1(E/E_0(\tau = 0))$ parameter stands for the height of the curve, $\alpha_1$ decides how steep the slope is, and $\tau^\star$ ($T_g$ in Fig. 3, Angell and Böhmer (1998) and in Fig. 1.6, Sperling (2006)) specifies the position of the inflection point which we assume as exactly the same as the optimum temperature in the Lorentz-like distribution (see also Fig. 2). The 1/3 factor is due to normalization. These last mentioned parameters and $\phi_1$ have been fitted to the adopted experimental data (Nakamura et al. 2002) for the extensibility (see the legends in Figs. 3B, 4B and compare to Figs. 1B and 2B in Nakamura et al. (2002)).

We focus the readers' attention on the important issue that in our description temperature enters the modified Lockhart equation in three ways: by a state equation (which causes modification of the Lockhart term), by the temperature dependence of elongation (model Ansatz, Eq. (8)) and by definition of a "tensile" component of cell wall extensibility, Eq. (10).

## Discussion

In experiments performed by Proseus et al. (1999), the cell walls of *Chara corallina* internodes displayed elastic deformation which was inevitable consequence of the attached external force. This kind of change was observed as parallel to the growth to create a complex response of early rapid elongation, viscoelastic deformation and steady elongation. The authors claimed that because elastic and viscoelastic deformation occurred when the cells were not growing, both could be easily separated from the process of growth. As inert polymers display stable elastic behavior over a considerable temperature range, the thermal stability suggests that elastic behavior of cell walls is of purely physical nature and can consequently be treated by these methods. Such behavior can be expected to manifest in all plant cells. According to Proseus et al. (1999), the viscoelastic behavior was present in mature cells and was independent of growth. They claimed that in contrast to the reversible elastic responses, it was largely irreversible and can be attributed to a displacement of wall polymers, which was not reversed whenever applied force returned to its original level. Indeed, the same situation as described in the previous paragraph we encounter in our theoretical model, Eq. (9), where the first term $\Phi_0$ was associated mostly with biochemical reactions (with the energy absorption peak at $\tau = \tau^\star$) while the second one $\Phi_1$ was assigned to the elastic/viscoelastic/nonelastic mechanical properties which reflect the rheology of the cell wall. The Lorentz-like shape of the $\Phi_0$ from Eq. (9) is plotted in Fig. 2 and the short outline about it can be found in the footnote 4 or elsewhere (Lewicka and Pietruszka 2006; Pietruszka et al. 2006). However, $\Phi_1$ in Eq. (9), as presented in Fig. 2, is related to the mechanical properties of the cell wall. By assuming Eq. (10) we are able to divide the area of Fig. 5 into three main stripes: a) elastic (reversible), b) viscoelastic (largely irreversible) and c) nonelastic (irreversible) in function of temperature. The reversible elastic component lies at low temperatures range where the Hook's law is merely satisfied. Mostly irreversible viscoelastic component spreads about the characteristic resonance temperature $\tau^\star$ (absorption energy $k_B T^\star$). The irreversible nonelastic part occupies the high-temperature end of our diagram. (Careful reader can notice, that we propose a "phase diagram" usually created for condensed matter systems for a (living) plant cell). We put the temperature $\tau^\star$ as common both for the maximum energy exchange (absorption) with environment (Lorentz-like distribution) and for the maximum rate of change ($1/E_0$ $\mathrm{d}E(\tau)/\mathrm{d}\tau$ reaches its extremal value, see the inset in Fig. 5) of the character of the cell wall mechanical properties where (exactly at the critical point $\tau^\star$) the reversible – irreversible (temperature driven) continuous phase transition takes place. Accordingly, the kink-like shape of the tensile modulus curve ($\Phi_1$) with the important character change at $\tau^\star$ (reversible/irreversible behavior – the inflection point where the curvature changes its sign) and the resonance-like shape of $\Phi_0$ with the maximum at $\tau^\star$ entitles to think about the growth process in the vicinity of "resonance" (optimum) energy $k_B T^\star$ as of about a special kind of qualitative "phase transition" taking place in a growing plant cell.

## Appendix

Notice that for the choice of state equation $P_{\mathrm{int}} - Y = \gamma T/V$, $Y =$ const. the Lockhart equation gives the solution linear in time

$$\frac{1}{V}\frac{dV}{dt} = \Phi\gamma\frac{T}{V} \quad (11)$$

$$\Downarrow$$

$$V(t) = V_0 + \Phi\gamma T\, t \quad (12)$$

which satisfies the initial condition $V_0 = V(t_0 = 0)$. Next, as we will see later, the additional constant pressure $P_{\mathrm{ext}}$ disturbs this linear behavior

$$\frac{dV}{dt} = \Phi(\gamma T + P_{\text{ext}} V) \tag{13}$$

We solve Eq. (13) by a standard method. Firstly, we find solution for homogeneous equation

$$\frac{1}{V}\frac{dV}{dt} = \Phi P_{\text{ext}} \tag{14}$$

$$\Downarrow$$

$$V(t) = V_0 e^{\Phi P_{\text{ext}} t} \tag{15}$$

(here we notice that the applied constant pressure implies exponential growth). Secondly, we perform the constant variation (we differentiate Eq. (15) and compare to Eq. (13)) to obtain

$$\begin{aligned} \Phi\gamma T &= \frac{dV_0}{dt} e^{\Phi P_{\text{ext}} t} \\ V_0 &= \Phi\gamma T\left(-\frac{1}{\Phi P_{\text{ext}}} e^{-\Phi P_{\text{ext}} t}\right) + C \end{aligned} \tag{16}$$

$$\Downarrow$$

$$V_0 = V_0(t_0) + \frac{\gamma T}{P_{\text{ext}}} \cdot \left(1 - e^{-\Phi P_{\text{ext}} t}\right) \tag{17}$$

The integration constant $C$ has been chosen to satisfy the initial condition $V_0 = V_0(t_0)$ for $t = t_0 = 0$. Now, by substituting the "constant" $V_0$ into Eq. (15) we finally get the particular solution for the inhomogeneous Eq. (13)

$$V(t) = V_0 e^{\Phi P_{\text{ext}} t} + \frac{\gamma T}{P_{\text{ext}}}\left(e^{\Phi P_{\text{ext}} t} - 1\right) \tag{18}$$

Now, if we have good reasons (see the comment beneath) to expand the exponent into the linear term $\exp(\Phi\, P_{\text{ext}}\, t) \approx 1 + \Phi\, P_{\text{ext}}\, t$, we may eventually receive the solution which is linear in time

$$V(t) = V_0 + \Phi\left(\gamma T + V_0 P_{\text{ext}}\right) t \tag{19}$$

Aiming to justify such approximation, let us calculate the order of magnitude for $\Phi P_{\text{ext}}$: $\Phi \sim 4 \times 10^{-8}$ $\mu$m s g$^{-1}$ and $P_{\text{ext}} = mg/S$, where $m \approx 10$ g, $g \approx 10$ ms$^{-2}$ $= 10^7$ $\mu$m s$^{-2}$, $S \approx 4$ mm$^2$ $= 4 \times 10^6$ $\mu$m$^2$. Thus $\Phi P_{\text{ext}} \sim 10^{-3}$ h$^{-1}$. Accordingly, the experiment would need to take at least 300 h ($\approx$13 days) to cause visible time-exponential behavior of plant growth.

## References


Angell C. A., Böhmer R. (1998): Mechanical spectroscopy of glassy systems. In: Mechanical Spectroscopy (Ed. B. Magalas), Chapman & Hall, UK http://www.public.asu.edu/~caangell/inaccessible/mechspec.pdf

Boyer J. S. (1993): Temperature and growth-induced water potential. Plant, Cell Environ. **16**, 1099–1106

Cosgrove D. J. (1985): Cell wall yield properties of growing tissue. Plant Physiol. **78**, 347–356

Cosgrove D. J. (1986): Biophysical control of plant cell growth. Annu. Rev. Plant Physiol. **37**, 377–405

Cosgrove D. J. (1987): Wall relaxation and the driving forces for cell expansive growth. Plant Physiol. **84**, 561–564

Cosgrove D. J. (1993): How do plant cell walls extend? Plant Physiol. **102**, 1–6

Edelmann H. G. (1995): Wall extensibility during hypocotyl growth: a hypothesis to explain elastic-induced wall loosening. Physiol. Plant. **95**, 296–303

Fogg G. E. (1975): The Growth of Plants (Ed. R. Clay) The Chaucer Press, Bungay, Suffolk, UK

Ikeda T., Nonami H., Fukuyama T., Hashimoto Y. (1999): Hydraulic contribution in cell elongation of tissue-cultured plants: growth retardation induced by osmotic and temperature stresses and addition of 2,4-dichlorophenoxyacetic acid and benzylaminopurine. Plant, Cell Environ. **22**, 899–912

Kutschera U. (2000): Cell expansion in plant development. Rev. Bras. Fisiol. Veg. **12**, 65–95

Lewicka S., Pietruszka M. (2006): Theoretical search for the growth-temperature relationship in plants. Gen. Physiol. Biophys. **25**, 125–136

Lockhart J. A. (1965a): An analysis of irreversible plant cell elongation. J. Theor. Biol. **8**, 264–275

Lockhart J. A. (1965b): Cell extension. In: Plant Biochemistry (Eds. J. Bonner and J. E. Varner), pp. 826–849, Academic Press, New York and London

Nakamura Y., Wakabayashi K., Kamisaka S., Takayuki H. (2002): Effects of temperature on the cell wall and osmotic properties in dark-grown rice and azuki bean seedlings. J. Plant Res. **115**, 455–461

Ortega J. K. E. (1985): Augmented growth equation for cell wall expansion. Plant Physiol. **79**, 318–320

Ortega J. K. E. (1990): Governing equations for plant cell growth. Physiol. Plant. **79**, 116–121

Pietruszka M., Lewicka S., Pazurkiewicz-Kocot K. (2006): Thermodynamics of irreversible plant cell growth. Acta Soc. Bot. Pol. **75**, 183–190

Pietruszka M., Lewicka S., Pazurkiewicz-Kocot K. (2007): Temperature and the growth of plant cells. J. Plant Growth Regul. **26**, 15–25

Proseus T. E., Ortega J. K. E., Boyer J. S. (1999): Separating growth from elastic deformation during cell enlargement. Plant Physiol. **119**, 775–784

Sperling L. H. (2006): Introduction to Physical Polymer Science. p. 8, John Wiley & Sons Inc., New Jersey

Stanley H. E. (1971): Introduction to Phase Transitions and Critical Phenomena. p. 67, Oxford University Press

Trewavas A. J. (1991): How do plant growth substances work? Plant, Cell Environ. **14**, 1–12

Wright S. T. C. (1966): Growth and cellular differentiation in the wheat coleoptile (Triticum vulgare): II. Factors influencing the growth response to gibberelic acid, kinetin and indolyl-3-acetic acid. J. Exp. Bot. **17**, 165–176


Final version accepted: November 20, 2006