Theoretical Search for the Growth-Temperature Relationship in Plants

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Abstract. In this article we deal with the definition of a new phenomenological model with physical bases for the response of short-term cell expansion growth to temperature. Although the interest on both the biomechanical bases of elongation growth and on temperature responses has a long lasting development in plant biology and biophysics, yet the question of the mode of actions of temperature is a very relevant and still open one. The purpose of our paper was not to deal with all the complexity of the possible effects of temperature on a growing cell but to concentrate on two more focused questions: i) whether it is possible to specify an optimal temperature for growth responses all along development by defining some phenomenological equations for temperature response, ii) can we learn something from that on the temperature dependence of the cell wall expansion process using a minimal analytical modelling? To answer both questions we introduce (by extending Lockhart approach) the notion of temperature by simple thermodynamical reasoning. Assuming incompressibility of water (by the constant molar density n/V) we also accounted for the role of osmosis and consequently – the role of water uptake in growing cell. This approach allowed us (by comparing theoretical solutions and experimental results) not only to determine the specific (resonance) temperature (or corresponding absorption energy $k_\mathrm{B}T^*$) of the optimal growth but also draw conclusions about the cell wall extensibility dependence on temperature and its evolution in time. A straightforward application of our method to determine optimum growth temperature for different plant species in a greenhouse practice (as its simple implication) can also be recommended.

Key words: Cell wall extensibility — Greenhouse — Modified growth equations — Optimum temperature

Introduction

The growth process 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 cell

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walls (Fogg 1975; Kutschera 2000 and papers cited therein). In the growth of a coleoptile one can differentiate three basic phases: the initial phase of slow growth, the intense growth phase and, eventually, the final phase of slow growth. The dominating length increments in time unit are observed approximately at the mid-time of growth. However, the (considered in this paper) linear period of intense growth lasts fairy short and depends on particular plant species.

Biotic and abiotic factors of environment perturb the plant growth (Wright 1966; Trewavas 1991; Edelmann 1995). The external factors that fundamentally influence plant growth are temperature, light, water and soil factors, pH and atmosphere composition. The non-linear growth dependence on temperature indicates the fact that with temperature elevation, the intensity of the biochemical reactions gradually increases, however, the disfunction of enzymes occurs at the high temperature end. The experimental relations between temperature, turgor pressure and the growth of plant cells were studied by Proseus et al. (2000).

The goal of the present paper was to introduce a phenomenological description of the temperature dependence on elongation growth and cell wall expansion process. The equations derived are adjusted next to the experimental data. We found in this manner quantitative description of the elongation of maize coleoptiles *versus* time parameterized by temperature. The foregoing major consequence of this approach was the new possibility to provide a fairly good working description of the essential features of mechanical properties of the cell wall. We must admit, however, that since the theory is based upon purely physical terms it does not consider cell wall yielding properties (e.g. elasticity and viscoelasticity) as being dependent on biochemical reactions involved in cell construction and reorganization during growth.

Temperature-dependent growth equations

Plant cell development is the result of cell production (the increase in the number of cells which is beyond the scope of this paper) and cell volume growth. Cell expansion is dependent on water uptake and on the rheology of cell walls. The regulation of the cell expansion (under condition of non-limiting hydraulic conductivity) can be described by the Lockhart equation (Lockhart 1965). Plant cell growth is described there by the dynamic balance between wall extension, which tends to dissipate turgor pressure and the water uptake acting to restore it (Cosgrove 1986, 1993). Lockhart proposed a simple (first order in time) differential equation

$$\frac{1}{V}\frac{\mathrm{d}V}{\mathrm{d}t} = \Phi(P - Y) \tag{1}$$

where the left side of the equation is the relative expansion rate (V stands for the cell volume) which depends linearly on turgor pressure (P) in excess of a critical turgor (Y is the turgor threshold that must be exceeded in order for the cell to expand) linked by a wall extensibility coefficient Φ. The environmental factors (temperature, humidity, pH, etc.) which considerably affect cell growth rate are not
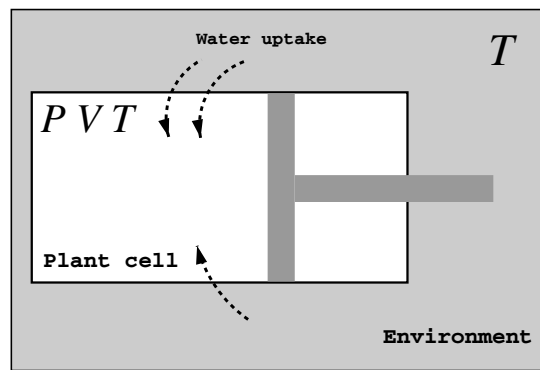
Figure 1. The "gedanken experiment". Plant cell is immersed into a surrounding bath at a constant temperature T. The piston movement reflects both the water flowing into plant cell interior and its influence onto the change of mechanical properties of the growing plant cell as well as the temperature dependence.

included in this equation. However, plants do not grow in conditions uncoupled to the real world. They are always found in a specific surroundings where one of the most important influencing growth factors is temperature. Therefore, in order to introduce the notion of temperature (as it is usually done in thermodynamics) we divided the whole system (the growing cell in the definite environment) into the investigated sample (here: plant cell) and 'the rest of the world' – a thermostat (environment) which remained at a constant temperature T (Fig. 1). In order to introduce temperature into Eq. (1) we utilize the state equation in the form: $P(T, V) = nRT/V$ where T stands for the absolute temperature (in Kelvin scale). The n coefficient here ascribes the number of water moles, R stands for the universal constant[1]. By assuming the coefficient Φ as time- and temperature-dependent we receive the following general equation

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[1] In our phenomenological (physical) model, the movement of a piston in a cylinder reflects the mechanical features of the cell wall under pressure P (see Fig. 1). However, in this scenario we are far beyond the oversimplified picture where we interpret the movement of a piston as only reflecting the compressibility/extensibility properties of the 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 conformational change, their disfunction and denaturing). Because both types of these processes act simultaneously, however, with different intensity at distinct temperature ranges, one should expect a crossover from one type of behaviour to the other. Thus, there should exist a specific, well-defined critical temperature T^* for which the growth rate is optimal. By multiplying T^* by the Boltzmann constant $k_\mathrm{B}T^*$ we also receive clear energetic interpretation which is bound with the peak energy absorption required for biological processes for the optimum growth.

$$\frac{1}{V}\frac{\mathrm{d}V}{\mathrm{d}t} = \Phi\left(P(T,V) - Y(T,V)\right) \qquad (2)$$

and $V = V(T,t)$. Since water does not change significantly its volume under pressure, we can intuitively assume nR/V as constant in time. This indeed means that the density of water is constant which is a natural consequence of its incompressibility. The fractional n/V as being constant (even though both n and V increase simultaneously) reflects in a natural way the water uptake by osmotic processes into plant cell interior (cytoplasm). Since we have $P(T,V) = nRT/V$ (linear in T) we may consequently also assume $Y = aT$, $a = $ constant (since the turgor threshold is a minimal pressure value which water must exceed to cause growth). The above equation can be rewritten as

$$\frac{1}{V}\frac{\mathrm{d}V}{\mathrm{d}t} = \Phi(T,t)\left(\frac{nR}{V}T - aT\right) \qquad (3)$$
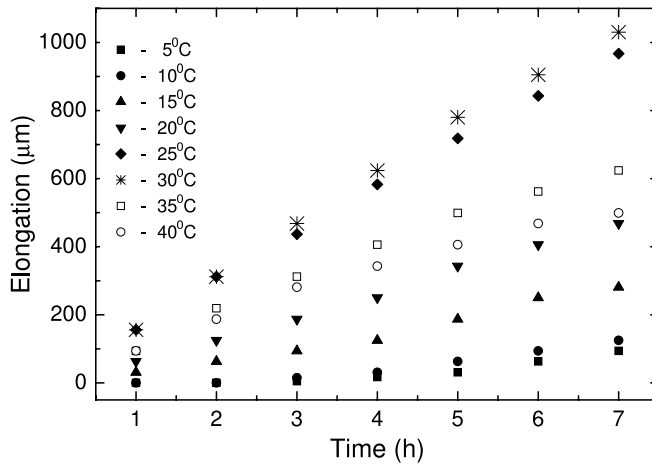

Figure 2. Elongation of maize (*Zea mays* L.) coleoptile segments *versus* time at eight different temperatures.

From the experiment (Fig. 2) we have an additional argument that $b = \dfrac{nR}{V} - a$ > 0 which expresses the fact that plant cell does not contract while growing in the normal conditions (due to cell turgor). The above equation yields after integration the following solution

$$V = V_0 \exp\left(bT \int \Phi(T,t)\mathrm{d}t\right) = V_0 \exp\left(b(\tau + 273.15) \int \Phi(T,t)\mathrm{d}t\right) \qquad (4)$$

where $V_0 = V(t = t_0)$ stands for the initial volume of the cell and $T = \tau + 273.15$ (τ is the temperature in Celsius scale). The above presented result is a general solution of Eq. (3) for the volume in function of both time and temperature. From our model calculations, the coefficient $\Phi(\tau, t)$ could be received. We can adopt a modified (by a linear factor τ) Lorentz distribution function (the resonance curve) by writing[2]

$$V(\tau, t) - V_0 = V_0 \frac{\phi_0 \tau}{\sqrt{(\tau - \tau^*)^2 + \alpha^2}} \tag{5}$$

(see the comment in the footnote beneath) where we are dealing with three fitting parameters: the peak height (amplitude) ϕ_0, its half-width α and temperature τ^* which stands for the optimum (resonance) growth temperature (energy). The first two parameters in general depend on time. The latter one is time-independent and can be treated as a characteristic constant parameter for a given species. We stress that temperature enters the model by the state equation and by the Lorentz-like function, Eq. (5).

By comparing Eqs. (4) and (5) we receive

$$V_0 \exp\left(b(\tau + 273.15) \int \Phi(\tau, t) \mathrm{d}t \right) = V_0 \frac{\phi_0 \tau}{\sqrt{(\tau - \tau^*)^2 + \alpha^2}} + V_0 \tag{6}$$

and finally we arrive formally at

$$\Phi(\tau, t) - \Phi(\tau, t_0) = \frac{1}{b(\tau + 273.15)} \frac{\partial}{\partial t} \ln\left(\frac{\phi_0 \tau}{\sqrt{(\tau - \tau^*)^2 + \alpha^2}} + 1 \right) \tag{7}$$

Knowing (from the fit to the experimental data) the time dependencies for the coefficients ϕ_0 and α (linear), we eventually receive the function $\Phi(\tau, t)$ which would possibly allow us to draw further conclusions about the cell wall mechanical properties (e.g. extensibility in function of temperature).

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[2] Let us justify the choice of such a function: the outlined system (plant cell) behaves similarly to the most systems where both dissipative and extortive forces are present. In such systems there always exist a variable which is optimal at certain conditions (like the resonance frequency ω^* for the harmonic oscillator). In our case, the factor enforcing the crossover from growth acceleration to deceleration is temperature τ. One can suspect, in analogy to the harmonic oscillator, that also in our case there must exist a critical (resonance) temperature ($\tau = \tau^*$). Consequently, elongation may be described by a resonance curve, the Lorentz distribution function (see also Discussion and Fig. 6), however, modified by a linear factor τ. The latter adjustment is due to the fact that at $\tau = 0\,°C$, growth must cease altogether.

Materials and Methods

The experiments were carried out with 4-day-old maize plants *Zea mays* L. grown on Hoagland's medium (Hoagland 1948) at 27 °C. Seeds of maize were cultivated in darkness. Then individual seedlings were transferred to an aerated solution containing standard micro- and macro-elements and coleoptiles were cut into segments. The segments were divided into eight groups growing at different temperatures (see the legend in Fig. 2). Each group was represented by 5 segments. The experiment was carried out within 7 h, the measurements were taken at every 1 h. Elongation was measured under microscope. The individual values presented in Fig. 2 are the averages obtained from ten measurements. The standard deviation error was estimated as not exceeding 20 μm.

Results

The almost linearly alined points of elongation of maize *versus* time from authors' performed experiments are presented in Fig. 2. The cross-sections for three different times have resulted in elongation *versus* temperature plots in Fig. 3. Each figure represents the experimental results for elongation $(V - V_0)$ dependence on temperature for three selected times (4, 5 and 6 h) fitted by the Lorentz-like function (Eq. (5)). The characteristic maximum at τ well below 30 °C is clearly visible in all cases obtained in the measurement. However, the same characteristic value of temperature (resonance temperature $\tau = \tau^*$) we acquire from our model. The latter is obtained from the fit to the experimental data. We have performed the following procedure: the Lorentz-like fit with the parameters ϕ_0, α and τ^* was made for all given times. These parameters were estimated by the method of non-linear least square fitting; the non-linear regresion method was based on Levenberg–Marquardt algorithm. The fit with the best determination coefficient ($R^2 = 0.997$) was chosen (here, in the case of 5 h) – in this case the credibility of the fit was the best, and the optimum temperature τ^* was fixed ($\tau^* = 26.9 \pm 0.2$). For all remaining times, the fit was performed with the other two parameters only: ϕ_0 and α (the value of τ^* was taken from the case of $t = 5$ h). Further calculations were made using the linear regression for the height ϕ_0 and width α (see Fig. 4). By assuming $\phi_0(t) = A + Bt$ we have obtained $A = 1.0 \pm 0.2$, $B = 26.3 \pm 0.5$ values with the determination coefficient $R = 0.999$; for $\alpha(t) = C + Dt$ we have received $C = 3.71 \pm 0.05$ and $D = 0.10 \pm 0.01$ with $R = 0.978$ (for the remaining values see Table 1). One can see that the width α changes slightly in the course of time while the height ϕ_0 pronouncedly increases. Even though the model we have introduced is simple, it succesfully reproduces the data obtained in the measurement within the 5 % experimental error (see Fig. 3).

Inserting the calculated coefficients (A, B, C and D) from linear regression to Eq. (7) we may easily calculate the time derivative ($\frac{\partial}{\partial t}$ in the right side of Eq.
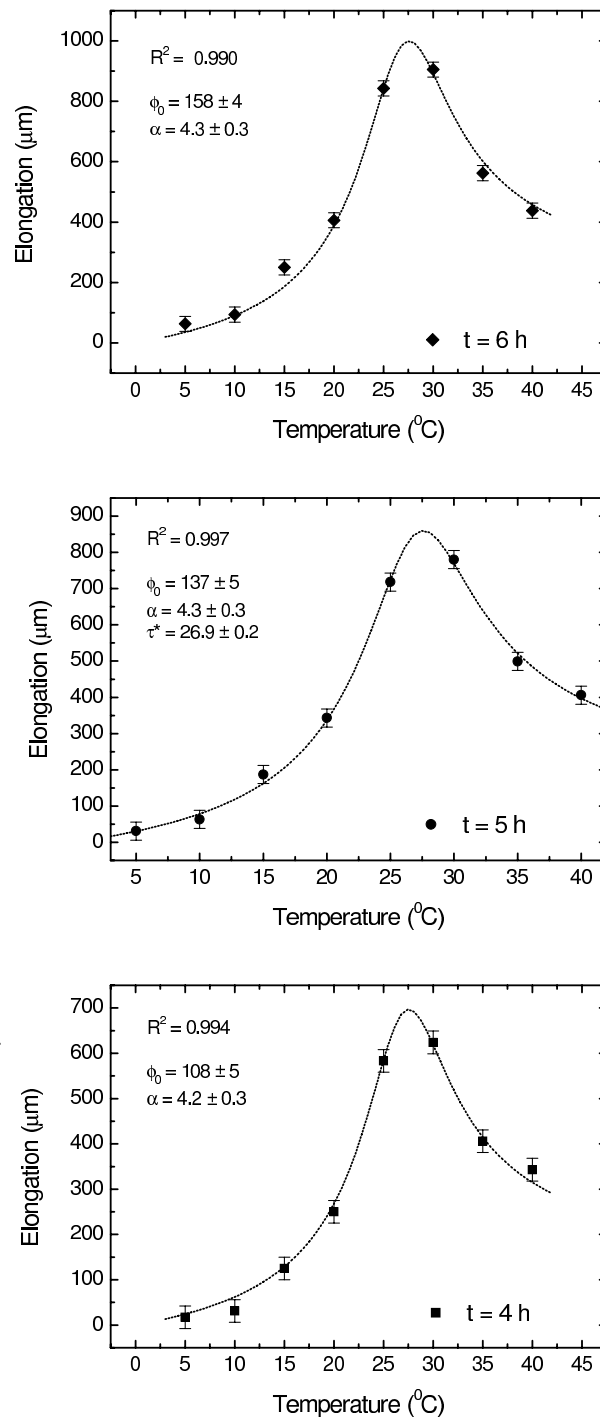
Figure 3. The elongation of maize coleoptile segments *versus* temperature for three different times ($t = 4, 5, 6$ h). The dotted lines represent the fit to the experimental data (solid points with error bars). The parameters ϕ_0 (height), α (half-width) and τ^* (optimum temperature) are estimated by the method of non-linear least square fitting. The value of R^2 stands for the determination coefficient squared.
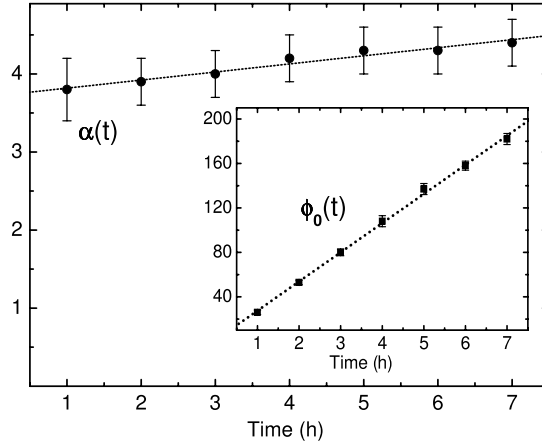
Figure 4. Time dependencies of the peak height ϕ_0 and the half-width α coefficients. The linear increase in both cases is noticeable. The functions $\phi_0(t)$ and $\alpha(t)$ are estimated by the linear regression method of least squares.

Table 1. Values of ϕ_0 and α parameters as obtained in the fitting procedure

Time (h)	Height ϕ_0	Width α
1	26 ± 2	3.8 ± 0.4
2	53 ± 2	3.9 ± 0.3
3	80 ± 3	4.0 ± 0.3
4	108 ± 5	4.2 ± 0.3
5	137 ± 5	4.3 ± 0.3
6	158 ± 4	4.3 ± 0.3
7	182 ± 5	4.4 ± 0.3

(7)) and thus proceed further with conclusions concerning the cell wall extension coefficient $\Phi(\tau, t)$ itself:

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\Phi(\tau, t) - \Phi(\tau, t_0) = \frac{1}{b(\tau + 273.15)} \frac{\tau}{\sqrt{(C + Dt)^2 + (\tau - \tau^*)^2} + (A + Bt)\tau} \\
\cdot \left(B - \frac{(A + Bt)D(C + Dt)}{(C + Dt)^2 + (\tau - \tau^*)^2} \right)
\tag{8}
$$

where $\Phi(\tau, t_0)$ denotes an initial value of extensibility coefficient for a juvenile cell and the whole function expresses the change of cell wall expansion in the course of time and its dependence on temperature. It is worthwhile to stress that this novel equation combines the theoretical predictions with our empirical data (which enter this equation *via* fitting constants A–D). We can see from Eq. (8) that the
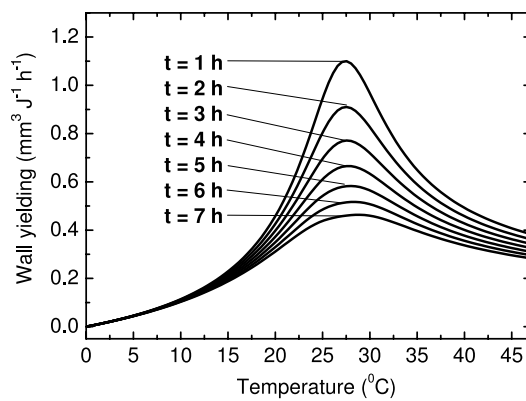
Figure 5. Model calculations of the cell wall extensibility $\Phi(\tau, t)$. The diminishing of the crest height in the course of time t is clearly visible.

extensibility of the cell wall has a resonance form with the peak localization at $\tau^* = 26.9\,°C$ (for details, see Fig. 5) which also stays in good agreement with experimental results on maize common in the literature. This observation may lead us to conclusion that, in fact, there exists a specific critical temperature τ^* (energy $k_B T^*$) of the optimum growth which can be estimated with the help of our model and which, in addition, can reflect the physical properties of the cell wall. This fact, however, would provide us with a new research tool, which has two basic functions. Firstly, by starting from experimental data points we can specify the diagram (plot) for the whole spectrum (range) of temperatures thus enabling us to predict theoretically the optimum growth temperature for a given species (we can foresee theoretically the optimum temperature τ^* of plant cell growth). Secondly, by having obtained theoretical results (specific values of parameters ϕ_0 and α) in the particular case (species) one can draw further qualitative and, especially, quantitative conclusions (through the Eq. 8) about the normal and critical behaviour of the cell wall. We also noticed that from the calculated plots of the wall extensibility $\Phi(\tau, t)$ against temperature the peak heights of the individual plots decreased with increasing time. This result remains in agreement with the fact that the plant cell after the period of intense growth decelerates its rate in the course of time; a cessation of cell enlargement takes place (cell maturation).

Discussion

Consider plant cell enlargement focussing our attention on biomechanical point of view. In this context plant cell membrane equipped with ionic and water channels, ionic pumps and ligand receptors is of the most direct significance. The period of optimal growth occurs when cell membrane is in a liquid-crystall (semi-liquid) phase. In such a state of matter, the endogenous auxin activates H^+-ATPase, acidification
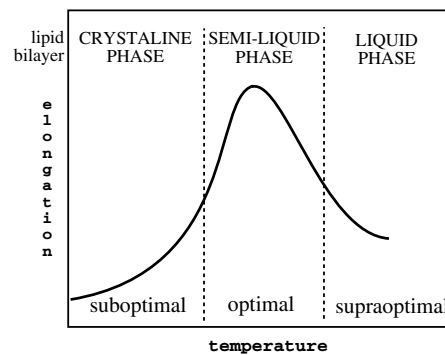
Figure 6. Elongation *versus* temperature phase diagram. The vertical dashed lines introduce division into three phases at inflection points of the Lorentz-like distribution (where the second derivative equals zero). In the suboptimal temperature range plasmalemma is in crystalline phase, in the optimal range – in semi-liquid phase while in the supraoptimal range – in liquid phase.

of cell walls and, as a result, their loosening. Simultaneously, the K^+ ions flow in through ion channels pulling behind the water molecules (through the reduction in the potential of the water solution filling up the plant cell interior). However, at low temperatures we deal with a kind of a phase transition from semi-liquid to crystalline phase. The diminishing of temperature causes membrane depolarization and the K^+ loss, water out-flow and consequently growth inhibition. Moreover, for $\tau \approx 0\,^{\circ}\mathrm{C}$, the reservoir of liquid water becomes almost empty because of crystallization process into the ice phase. On the other hand, at high temperatures, the phase transition from the semi-liquid to liquid phases occurs. It causes the malfunction of ionic and water channels as well as ionic pumps. Effectively, we deal with the ionic leakage and a secondary water stress, and consequently – growth cessation. Additionally, under the influence of high temperatures, the auxin receptor proteins change their conformation and functionality (up to the denaturing), which obviously causes growth deceleration and eventually its cessation. All these processes are reflected in the elongation curve (see Fig. 3) and specific division of the phase diagram (Fig. 6). We believe that such biological arguments justify the choice of the Lorentz-like distribution for the phenomenological description of plant cell growth (see also the foot-notes 1 and 2 for physical basis), however, it is obvious that it should be derived from the first principles.

In this paper we deal with the coaction of temperature and time in plant cell growth connected with cell wall mechanical properties. We also argue that the existence of the optimum temperature at which plant cells grow the fastest can be obtained from our model by fitting the experimental data to the analytical solutions. Indeed, it is obvious that such an optimum must exist if one observes slow growth at both high and low temperatures which implicates the high rate

growth at the crossover region about τ^*. The potential interest of our paper was to determine this conclusion theoretically and predict the optimum temperature using elementary thermodynamical mechanisms. The modified growth equations not only thoroughly reproduced the experimental growth data but also lead to determine of the optimum (resonance) temperature $\tau = \tau^*$ of growth rate. However, another competitive result of our paper is using elementary thermodynamical mechanisms for theoretical investigation of the physical properties of the cell wall, namely the dependence of its extensibility on temperature and its evolution in time. From the Fig. 5 we can easily observe the damping of cell wall expansion (and consequently of growth intensity) and that such suppression for the optimum temperature is the strongest. This in turn is strictly bound with the rheology of the cell wall (through Eq. (8)) and also results from our thermodynamical approach. We are well aware that the relation (8) should be proven by data obtained from cell wall elasticity experiments. However, these difficult to perform experiments requiring dedicated equipment are inaccessible in our laboratory so that problem of confrontation of the model with experiment leaves still open to experimentalists.

Besides the factors of external nature like temperature (humidity, etc.), the growth regulators are of fundamental importance in cell growth and development (see also Cleland 1986). These substances stimulate or inhibit the processes of growth. Further study of subsequent particular experiments, where we consider the case of linear and non-linear response under external perturbation (growth inhibitors/stimulators introduced at a time $t = t_1 > t_0$) in the light of our thermodynamical approach in both cases, has been conducted elsewhere (Pietruszka et al. 2006).

The main contribution of the present paper lies in presenting a new tool (analytical function) describing actually observed growth-temperature relationship which can be eventually used in mathematical models of plant growth to express formally needed particular parameters (characterizing plant properties). The empirical results from elongation measurements should be inserted into the model equations in order to obtain relevant parameters characterizing, among others, the optimum growth temperature as well as time and temperature dependence of cell wall extensibility. The main limitation of our approach is obvious: it does not account for the role of biochemical reactions involved in cell building process (even though these are intrinsic in the postulated Lorentz-like distribution). This is, however, due to the confinement in the model to the physical aspect.

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