CENTRAL LIMIT THEOREM AND THE SHORT-TERM TEMPERATURE RESPONSE OF COLEOPTILE AND HYPOCOTYL ELONGATION GROWTH

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ABSTRACT

In this contribution we deal with a new mathematical description of the response of short-term coleoptile/hypocotyl expansion growth to temperature. Although the interest of both the bio-mechanical basis of elongation growth and temperature responses has been studied in plant biology and biophysics for a long time, yet the question of the mode of actions of temperature is very relevant and still open. Here we introduce a simple idea that the normal distribution, due to the central limit theorem (CLT), is able to report on temperature-dependent elongation growth. The numerical fittings for temperature affected growth are in good agreement with empirical data. We suggest that the observation concerning a crossover effect occurring in temperature driven elongation together with CLT leads to the formulation of a hypothesis about the possible universal character of such a description, supposedly for many plant species and families. We conclude with the statement that properly constructed equations of temperature affected growth, should possibly include a specific term proportional to $\exp[-((T-T_0)/T_0)^2]$ with T_0 corresponding to the temperature of the optimum growth.

KEY WORDS: central limit theorem, coleoptile/hypocotyl, elongation, temperature.

INTRODUCTION

It has been a long search for an adequate description of the response of the short-term cell expansion growth to temperature and numerous mathematical models have been developed. Some of them concerned different issues like crop development, prediction of maize phenology, flowering dates and leaf appearance as dependent on temperature, also in the context of thermal time (heat accumulation over calendar time). Accordingly, some efforts have been made to establish corresponding mathematical models accounting for the observed phenomena (Cross and Zuber 1972; Coelho and Dale 1980; Summerfield and Roberts 1987; Olsen et al. 1993; Hunt and Pararajasingham 1995; Yan and Wallace 1996; 1998; Craufurd 1998; Yan and Hunt 1999).

The linear model was proposed by Summerfield and Roberts (1987). Nevertheless, this model is only effective when the temperature does not approach the optimum whereas the conditions frequently exceed the optimum temperature and such linear description fails to account for the suppressed growth and development at high temperatures. To resolve this contradiction Olsen et al. (1993) adopted a bilinear approach. Two different linear equations were used to describe growth responses to sub-optimum and su-

pra-optimum temperatures, separately. However, the derivations of cardinal temperatures were not always meaningful (Craufurd 1998). A multi-linear model (Coelho and Dale 1980) as less rigid than the bilinear model used for crop system simulation packages (Hunt and Pararajasingham 1995) required, in turn, five or more parameters to describe the temperature response. As we expect that the growth – temperature relationship should be a smooth curve rather than a rigid combination of linear equations, Cross and Zuber (1972) favoured exponential and polynomial models. While the exponential model can be effective in the modelling at a low to intermediate temperature range, the quadratic equation proposed by Yan and Wallace (1996, 1998), which is a symmetric parabola, can be inaccurate at extreme (high and low) temperatures. More recent attempts were presented by Yan and Hunt (1999) where the temperature response of plant growth and development has been modelled by β-distribution. Even though the authors stressed that the description employed only three cardinal numbers, no further link to biochemical basis has been given.

In this paper a concept of "normal growth" at ambient temperatures is introduced, due to CLT. In other words, the Gaussian character of elongation in function of temperature in a restricted interval of about 10-40°C is utilized. Despite that in our approach we are confined to two parame-

ters only (T_0 and σ) we are able to anticipate almost the whole plot for the growth – temperature relationship. Moreover, it is founded on inherent properties of normal distribution that are associated with many processes taking place in a growing plant.

The central limit theorem 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 a 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 taking place in plant growth. However, the extreme temperatures disturb this behavior and processes contributing to growth cannot be considered as weakly coupled or "independent". In such case the above reasoning fails and Gaussian distribution is no more applicable.

Therefore, we put forward a new model based on Gaussian distribution. The important arguments for such a choice are twofold. (1) By assuming the normal distribution, we incorporate a number of fundamental chemical and biochemical processes that accelerate or decelerate growth in function of temperature (e.g. kinetics of chemical reactions, metabolism, photosynthesis – biomass production, protein denaturing, etc.). With temperature elevation, both type of these processes act simultaneously, however, with distinct intensity at different temperature ranges – a *crossover* from one type of behavior to the other should be expected. Thus, a delicate balance must exist among all contributing factors and consequently a specific, well-defined critical temperature T_0 for which the growth is optimal should appear. The outlined system (a plant cell/organ immersed in temperature reservoir) behaves similar to most systems described by a differential equation where dissipative and extortive forces are both present. In such systems there always exist a variable which is optimal at certain conditions. In the case of plant cells the external dominant factor enforcing a crossover from accelerating to decelerating growth is temperature T. Therefore, there must also exist an optimal temperature T_0 of such a crossover (and the corresponding optimal energy). This is in accordance with the fact that the optimal temperature of growth T_0 corresponds to the maximum energy absorption at $k_B T_0$ due to extreme activation of internal biochemical processes (k_B – the Boltzman constant), compare to Pietruszka et al. (2007). Such crossover is obviously present at $T=T_0$ for the peak value of the Gaussian. (2) From the central limit theorem we learn that even though the mechanisms underlying growth phenomena are often unknown, the use of the normal model can be theoretically justified by assuming that many small (or even negligible) independent effects additively contribute to each temperature-response. Indeed, in a wide range of temperature, the chemical reactions such as metabolic processes, enzyme activity, photosynthesis, biomass production, protein denaturing and many others, contribute at each temperature to the elongation growth resulting in Gaussian – like shape. Even though different enzymes from biophysical processes have different temperature coefficient Q_{10}, their values change only slightly, hence they also can be treated as normally distributed. At very low or high temperatures the departure from this scenario is noticeable and CLT cannot be applied then. This is mainly expressed by asymmetric data distribution within the whole temperature range. However, since we assumed we are confined to ~10-40°C interval, the acceptance of the symmetric Gaussian seems to be justified.

MATERIAL AND METHODS

Aiming to validate the outlined above scenario we have performed a series of experiments with different species in a broad temperature range. The experiments were carried out with four-day-old maize (*Zea mays* L.), barley (*Hordeum vulgare* L.) wheat (*Triticum vulgare* Vill.), millet (*Panicum miliaceum* L.) and bean (*Phaseolus vulgaris* L.), and five-day-old pumpkin (*Cucurbita pepo* L.). Seedlings were grown in tap water at 27°C. Seeds of all species were germinated in darkness. Five seedlings of every sample were chosen. In every case the equal length of the coleoptile was the decisive criterion; 1 cm for maize and millet, 3 cm for barley and wheat coleoptiles (initial measurement), respectively. Likewise, for bean and pumpkin the initial length of hypocotyls was 2 and 3 cm, respectively. Individual seedlings (in groups of five) were transferred to an aerated solution containing standard micro- and macro-elements. Then, they were immersed in a bath at constant temperatures: 5, 8, 16, 22, 27, 32, 37, 42 and 48°C for monocotyledones and 5, 10, 18, 22, 24, 27, 38 and 45°C for dicotyledones. Length of the coleoptiles of the Graminae seedlings was measured – 3 hours, length of the bean hypocotyls – 2 hours while length of the pumpkin hypocotyls – 4 hours after the preceding measurement. Manipulations on plants (elongation measurements and transfer to test solutions) were carried out in green light (sunlight transmitted through a green filter). The relative error has been estimated with the help of the logarithm method and indicated by error-bars in the plots. The fitting procedure was performed with the use of the non-linear Levenberg-Marquardt interpolation algorithm, and applied to the calculated relative elongation, $(L_n - L_0)/L_0$, where L_0 – the initial length, L_n – the length of coleoptiles/hypocotyls for the nth measurement.

The empirical data have been presented together with the continuous theoretical curve (dotted line) in Figure 1, where the relative elongation of monocotyledones' coleoptiles and dicotyledones' hypocotyls is plotted against temperature. The interpolation curve has been fitted convincingly by the use of the nonlinear regression method with high squared determination coefficients R^2. The optimum temperature T_0 was calculated for every species individually with the help of Levenberg-Marquardt algorithm. The original data together with the adjusted model curves are visualized in Figure 1 where the results for mono- and dicotyledones are presented, respectively. The calculated optimum temperature is depicted for every plot, also determination coefficients are indicated in the Legends.

DISCUSSION

Many papers have been written on the short-term growth response to temperature. Even though they touched the very essence of the problem from the biological (biochemical, biomechanical, genetic, etc.) point of view they still need
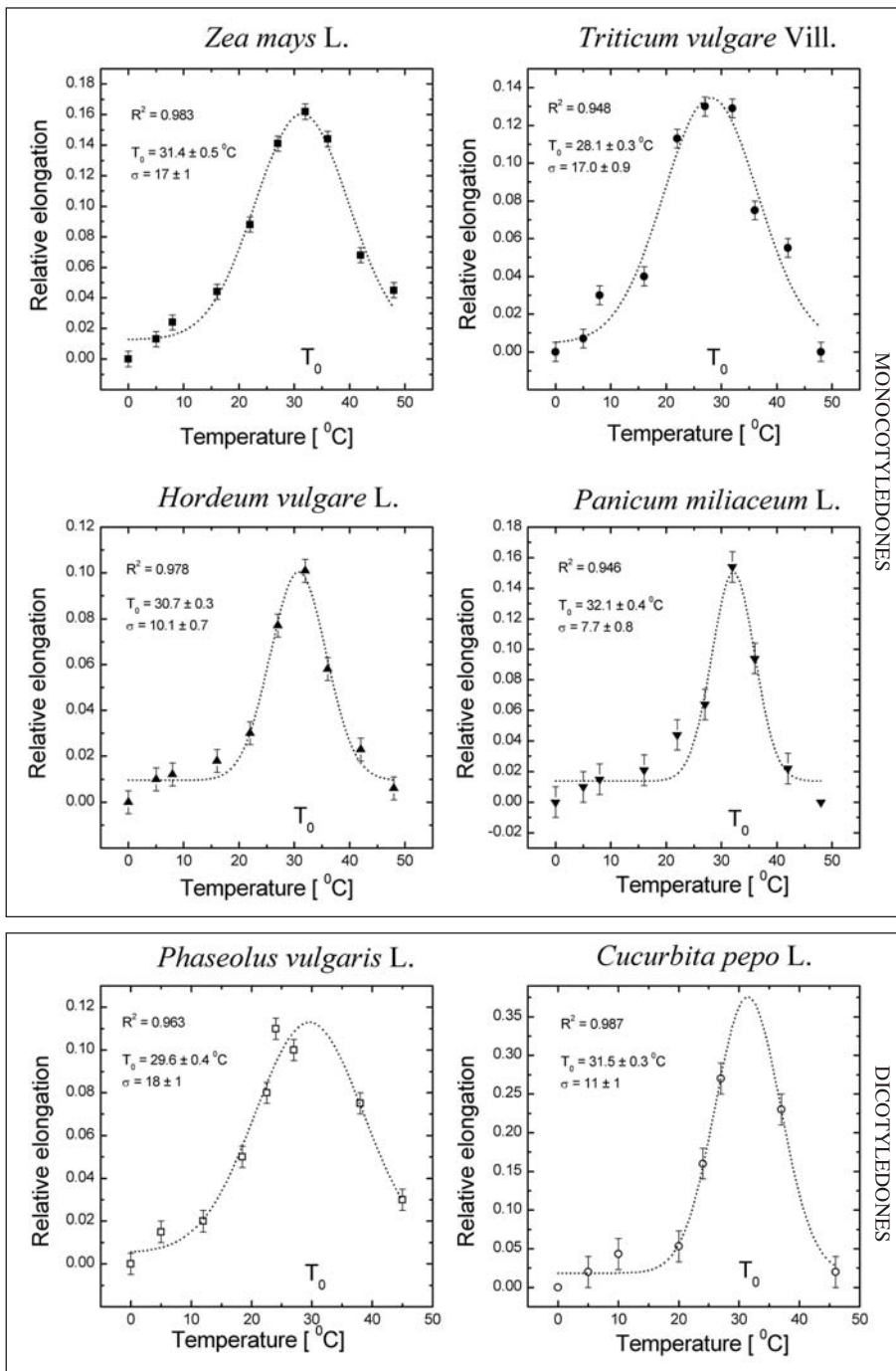
Fig. 1. Relative elongation of maize (*Zea mays* L.), barley (*Hordeum vulgare* L.), wheat (*Triticulm vulgare* Vill.) and millet (*Panicum miliaceum* L.) coleoptiles, bean (*Phaseolus vulgaris* L.) and pumpkin (*Cucurbita pepo* L.) hypocotyls in function of temperature. The model parameters and corresponding determination coefficients are indicated in the figures.

a strict thermodynamic model which would be able, in a quantitative way, to describe the observed phenomena. Lockhart (1965), Ortega (1985), Lewicka (2006) and others put forward phenomenological equations and suggested solutions of short- and large-scale time dependent plant growth. However, almost all attempts of theoretical description treated the growth as independent of temperature. Only a few papers have theoretically challenged the problem of temperature induced growth (e.g. Proseus et al. 1999, 2000; Lewicka and Pietruszka 2006; Pietruszka et al. 2007). Even though a progress has been made in phenomenological description of growth related issues, the lack of time- and temperature-dependent differential equation describing plant cell growth, free of the abundance of essential assumptions, has been noticed. It looks as if the simple proposal presented in this paper, expressed by the implementation of central limit theorem to the description of

temperature affected growth, may be accepted as a first step. Notwithstanding, the normal distribution may be recognized as a good candidate to report on a core portion of temperature response.

CONCLUSIONS

Based on our considerations, it looks as though a term proportional to $\exp[-((T-T_0)/T_0)^2]$ should be present in the properly constructed thermodynamical equation of growth. Such thermodynamic equation, likely to represent changes of volumetric growth in various external conditions (e.g. pH, water and soil factors or light) will be subjected to further studies. We believe that this contribution will help explaining the phenomenon of temperature affected growth, despite the fact that many questions remain open.

LITERATURE CITED

COELHO D.T., DALE R.F. 1980. An energy-crop growth variable and temperature function for predicting maize growth and development: planting to silking. Agron. J. 72: 503-510.

CRAUFURD P.Q., QI A., ELLIS R.H., SUMMERFIELD R.J., ROBERTS E.H., MAHALAKSHMI V. 1998. Effect of temperature on time to panicle initiation and leaf appearance in sorghum. Crop Sci. 38: 942-947.

CROSS H.Z., ZUBER M.S. 1972. Prediction of flowering dates in maize based on different methods of estimating thermal units. Agron. J. 64: 351-355.

HUNT L.A., PARARAJASINGHAM S. 1995. CROPSIM-WHEAT: A model describing the growth and development of wheat. Can. J. Plant Sci. 75: 619-632.

LEWICKA S., PIETRUSZKA M. 2006. Theoretical search for the growth-temperature relationship in plants. Gen. Physiol. Biophys. 25: 125-136.

LEWICKA S. 2006. General and analytic solutions of the Ortega equation. Plant Physiol. 142: 1346-1349.

LOCKHART A. 1965. An analysis of irreversible plant cell elongation. J. Theor. Biol. 8: 264-275.

OLSEN J.K., MCMAHON C.R., HAMMER G.L. 1993. Prediction of sweet maize phenology in subtropical environments. Agron. J. 85: 410-415.

ORTEGA J.K.E. 1985. Augmented growth equation for cell wall expansion. Plant Physiol. 79: 318-320.

PIETRUSZKA M., LEWICKA S., PAZURKIEWICZ-KOCOT K. 2007. Temperature and the growth of plant cells. J. Plant Growth Regul. 16:15-25.

PROSEUS T.E., ORTEGA J.K.E., BOYER J.S. 1999. Separating growth from elastic deformation during cell enlargement. Plant Physiol. 119: 775-784.

PROSEUS T.E., ORTEGA J.K.E., BOYER J.S. 2000. Turgor, temperature and the growth of plant cells: using *Chara corallina* as a model system. J. Exp. Bot. 51: 1481-1494.

SUMMERFIELD R.J., ROBERTS E.H. 1987. Effects of illuminance on flowering in long- and short-day grain legumes: a reappraisal and unifying model. In: Manipulation of flowering, ed. Artherton J.G., London, Great Britain.

YAN W., WALLACE D.H. 1996. A model of photoperiod x temperature interaction effects on plant development. Crit. Rev. Plant Sci. 15: 63-96.

YAN W., WALLACE D.H. 1998. Simulation and prediction of plant phenology for five crops based on photoperiod by temperature interaction. Ann. Bot. 81: 705-716.

YAN W., HUNT L.A. 1999. An equation modelling the temperature response of plant growth and development using only the cardinal temperatures. Ann. Bot. 84: 607-614.