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The efficiency of time and temperature driven regulation principles in plants at the beginning of the active period

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TIIVISTELMÄ: KASVIEN AIKAAN JA LÄMPÖTILAAN PERUSTUVIEN SÄÄTÖPERIAATTEIDEN TEHOKKUUDESTA KASVUKAUDEN ALUSSA

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The distributions of the minimum temperatures after the beginning of the active period (one temperature for each spring) have been calculated for each principle using daily meteorological data collected during the years 1883-1980. The efficiency criterion is the variance of the minimum temperature distributions and the length of the active period. The most efficient regulation principle is found to be based on the temperature sum which includes a feedback component.

Jokaiselle periaatteelle määritettiin kasvukauden alkamisajankohdan jälkeisten minimilämpötilojen (yksi havainto kevättä kohti) jakauma vuosien 1883–1980 sääaineiston perusteella. Eri säätöperiaatteiden tehokkuutta verrattiin toisiinsa minimilämpötilajakaumien varianssien ja eri vaurioitumisriskeillä saatavien kasvukausien pituuksien perusteella. Tehokkaimmaksi säätöperiaatteeksi osoittautui lämpösummaan perustunut periaate, johon sisältyi sään kylmenemisen huomioiva takaisinkytkentä.

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1. Introduction

Long continuous series of weather observations for different locations are available and the weather statistics are good, especially for Europe. Those for England (Manley 1974) and Sweden (Liljequist 1950) cover over two centuries. Despite this, the utilization of weather records has so far been rather poor in biology. The main emphasis has been on the monthly or daily means of temperature.

Cannell & Smith (1984) and Cannell (1984,1985) estimated the risks of damaging frost in Scotland utilising weather records. Their ideas are formulated and further developed in the present paper.

The phenological development of plants in the spring is strikingly regular in the temperate zone. For instance, the budburst and flowering of each species occur synchronously if the genetical properties of the plants are similar, providing there are no major differences in the temperature conditions between the different locations. The sequence of events is also rather similar from one year to another. The regularity of the phenological development is generated by the self-regulation of the functions of plants. One of the major research tasks in the study of annual cycle is to detect the regulation principle which operates at the onset of the active period in the spring.

Several regulation principles have been presented during the last two centuries. Their analysis can be carried out either experimentally or theoretically. The main emphasis during recent decades has been on experimental work; theoretical argumentation has received very little attention. Thus the new opportunities generated by the development of modelling and the accumulation of weather data have not yet been fully exploited.

The aim of the study is to compare the efficiency of different regulation principles at the beginning of the active period using daily weather observations for the period 1883–1980.

2. The activation of plants in the spring

The environment directly affects the functions of plants, and besides of it plants themselves regulate their own functions. Accordingly, the analysis is based on the following four features:

1. The stage of the annual development can be described by one variable.
2. The development of the annual cycle is described by the time derivative of the stage of the annual development.
3. The development of the annual cycle depends on the state of the environment and on the stage of the annual development.
4. The active period begins and the resistance to low temperatures disappears when the annual cycle has proceeded long enough.

The above four statements allow mathematical descriptions of the development of the annual cycle. Let S(t) denote the stage of the development of a plant at time, t. The rate of change in the stage of the development, dS/dt, depends on the environmental factors u(t) and on the stage S(t), itself, i.e.

$$dS/dt = g(u(t),S(t)). \qquad (1)$$

Various types of the regulation principles can be introduced into the analysis by means of the alternative functions, g, in Eq. (1). If the function g is known then the stage of the development, S(t), can be determined by integration using the history of environmental factors.

A wide range of different types of models describing the activation of plants in the spring are used in the literature. Models are based on temperature sum, daylength, time etc. These models can be analysed using Eq. (1) (Hari 1972). The rather simple mathematical formalism of the functions g enables the comparision of the efficiency of the different regulation principles.

The five regulation principles to be examined in this study are based on time t and on time-dependent temperature, T(t). The principles are described by means of the corresponding functions g_i in Eq.(1) as follows (Fig. 1):

1. The time principle (Bünning 1963)

$$g_1(t) = c \text{ (constant).}$$

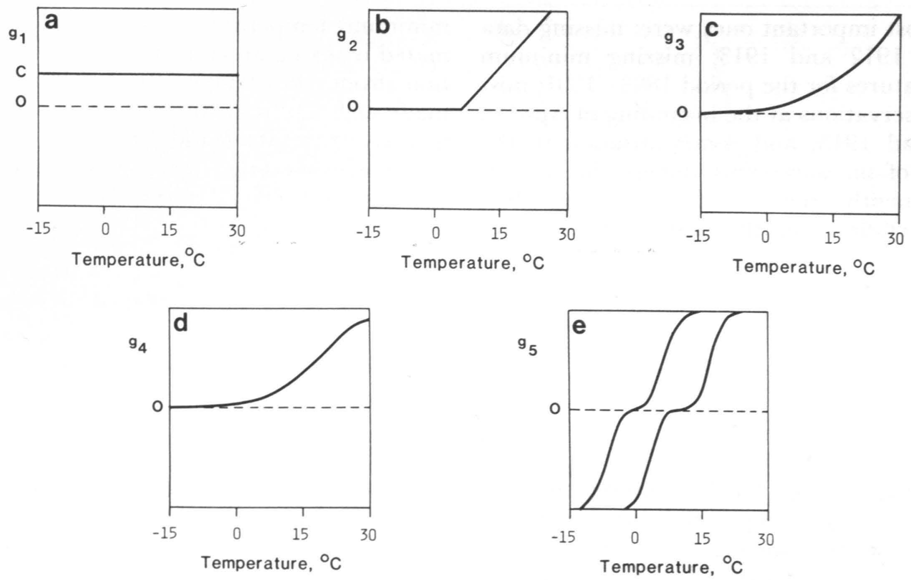

Fig. 1. The rate of change, g_i , of the stage of the development as a function of temperature: a) The regulation is based on time, b) on temperature sum, c) on respiration, d) on period units, e) on feedback principle. The function g_5 depends on temperature as well as on the stage of development S(t), which is demonstrated by two alternative curves corresponding the values S(t)=0 (on the left) and S(t)=6000.

2. The temperature sum principle (de Reaumur 1735)

$$g_2(T(t)) = \begin{cases} 0, \text{ if } T(t) \leq 5°C \\ T(t)-5, \text{ if } T(t)>5°C. \end{cases}$$

3. The respiration principle (Hari et al. 1970)

$$g_3(T(t)) = a+be^{cT(t)},$$
where a=−0.4207, b=0.727 and c=0.067.

4. The period unit principle (Sarvas 1972)

g_4 = tabulated values (Fig.1d).

5. The feedback principle (Pelkonen & Hari 1980)

$$g_5(T(t),S(t)) = \frac{100}{1+a^{-(T(t)-S(t)/c)}} - \frac{100}{1+a^{(T(t)-S(t)/c)}},$$
where a = 2 and c = 600.

The principles 2–5 are all some kind of temperature sum models. The feedback principle differs from the others in the manner that it allows the plant to develop back towards the winter stage if cold period occurs after a warm one. The functions g_i are shown graphically in Fig. 1.

3. Meteorological data

The study is based on official weather statistics collected by the Finnish Meteorological Institute in the city of Jyväskylä in Central Finland (62°14′ N, 25°44′ E, 86 m asl) during the period 1883–1980. Temperatures recorded 2 m above the ground at 8 am, 2 pm and 8 pm each day, and the daily minimum temperature, were utilised.

The development of the measuring procedure and practical arrangements generated shortcomings in the long-term weather data .

The most important ones were: missing data during 1912 and 1913; missing minimum temperatures for the period 1883–1901; missing observations at the beginning of April in 1914 and 1915; and some variation in the timing of measurements during the period. Consequently, the data for 1912 and 1913 were excluded from the analysis; the missing minimum temperature values were approximated by using an empirical regression function from the temperature measurements made at 8 am; and the missing observations in early April 1914 and 1915 were replaced with corresponding average temperatures for the data set. The number of observations utilised totaled 34944.

4. Results

The criteria used for determining the efficiency of a regulation principle are derived on the basis of the following deliberations. During the winter dormancy period, plants are resistant to low temperatures. When they enter the active period they lose this cold resistance. It is reasonable to assume that during the course of evolution plants have adopted the most efficient regulation principle which enables them to maximize the length of the active period at a certain risk of injury. Hence the criteria of the efficiency of the regulation used in this study are: 1. the reliability of estimating the risk of injury, and 2. the length of the active period.

4.1. Reliability of the regulation principles

The daily minimum temperature is characterised by great random variation and by a trend-like increase during each spring. The risk of injury can be approximated utilising the long continuous weather statistics available. Regulation based on time is studied in the first phase and the analysis is subsequently expanded to include other principles.

Let t denote time counted from the beginning of the year, T(t) temperature at the moment t, and T_{min} the minimum of the temperatures T(t) of the year before 1 July. The conditional frequency distribution of the minimum temperatures, $f(T_{min} \mid t \geq t°)$, after the fixed time, t°, is determined using weather statistics for years 1883–1980. Thus, the frequency distribution is based on 96 minimum temperature observations, one for each year. Changing the condition time t° different conditional distributions are formed (Lindgren 1976). The increase in temperature during the spring can clearly be seen in a shift in the location of the empirical histograms (Fig. 2a).

The method of applying conditional distributions is expanded to include any other regulation principle as follows. By integrating Eq. (1) we obtain the stage of the development, S(t), at the moment t :

$$S_i(t) = \int_0^t g_i(T(t) \mid S(t))dt, \qquad (2)$$

where i refers to the regulation principle. The value of S(t) can be computed at any moment t for each year and for each regulation principle utilising the weather statistics. Let S° be a fixed value of the stage of the development. The conditional frequency distributions of minimum temperatures, $f(T_{min} \mid S(t) \geq S°)$, according to each principle is determined in an analogous way as was applied previously when the condition was based on time. The practical computations were done with Riemann sum approximation of the integral in the Eq. (2) using the time step of 6 h (Apostol 1963).

The reliability of the regulation principles was measured by means of the standard deviation of the conditional frequency distribution. The smaller the standard deviation the more precise is the information about the coming minimum temperatures, thus small standard deviation means good reliability. The conditional distributions (Fig. 2) were computed for each regulation principle with varying values S° of the conditional stage of the annual cycle. The number of computed distributions for each principle equaled 12. The means and the ranges of the standard deviations of the distributions for each regulation principle are shown in Table 1.

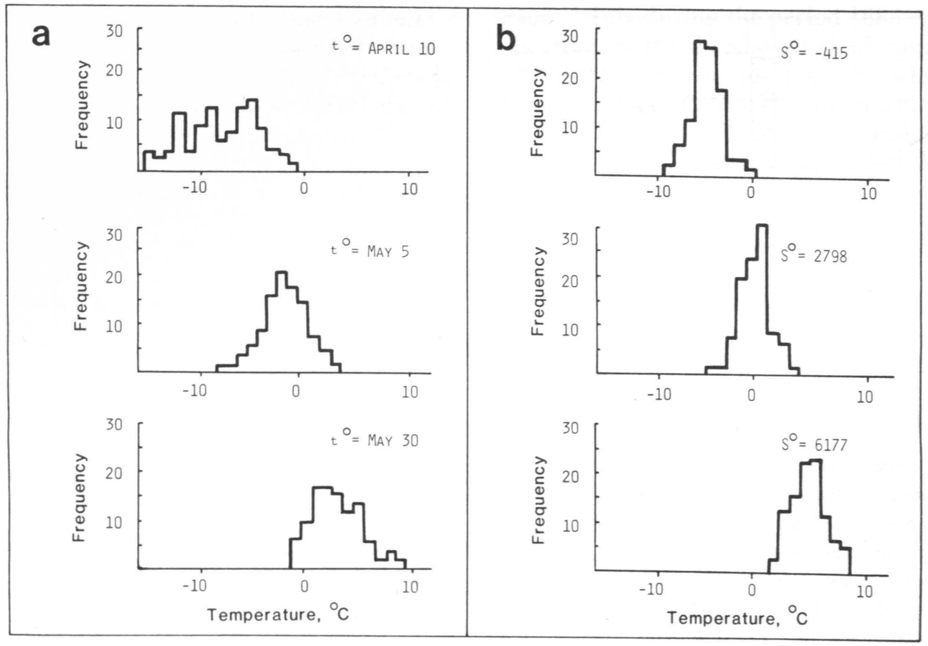

Fig. 2. Conditional distributions of minimum temperatures during spring (years 1883–1980). Examples of empirical histograms, each based on 96 temperature values, one for each year: a) Regulation is based on time (three alternative condition dates were applied). b) Regulation is based on the feedback principle (three alternative condition stages of the development were applied).

Table 1. The mean values and ranges of the standard deviations of the conditional minimum temperature distributions of different regulation principles during the spring.

Regulation principle based on	Mean of the standard deviations, °C	Range of the standard deviations, °C
time	2.4	1.7–3.6
temperature sum	2.4	2.0–3.3
respiration	2.2	1.6–3.0
period units	2.3	1.8–3.2
feedback	1.6	1.4–1.8

The conditional distributions based on the feedback principle had the smallest standard deviations. Also the shape of the empirical histograms generated by the feedback principle appeared to be rather stable compared to others (Fig. 2). This fact can also be seen in the variation (ranges) of the standard deviations of the distributions (Table 1).

4.2. The length of the active period

Plants cannot be in an active state and cold resistant at the same time. Plants have to compromise between the length of the active period and the risk of frost injury. The risk of frost injury can be determined using the conditional distributions. We may assume that the active period of plants begins when the risk of the injurious cold night temperature is low enough. This permits the calculation of the mean length of the active period at each risk level in accordance to each regulation principle.

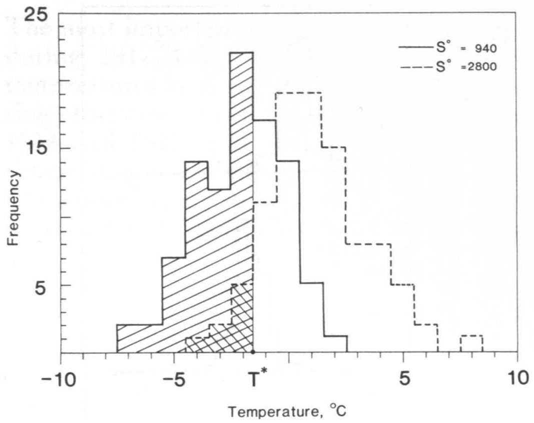

Fig. 3. Determination of the risk of injury. The conditional minimum temperature distributions in the example were generated by the period unit principle. Two empirical histograms corresponding to the stage of the development, S° = 940 and S° = 2800, are presented. The threshold temperature of injury, T* , was assumed to be −2°C. The areas representing the risk of injury, P, are indicated by shading: P = 0.62 when S(t) ≥ 940 and P = 0.08 when S(t)≥ 2800.

When plants are in the active stage they are injured if the temperature falls below a certain species-specific threshold temperature, T*. There is always a slight risk that the night temperature will fall below the injuring temperature T* . But the risk of injury decreases during the spring.

Let $P(T^*, S^\circ)$ denote the risk of injurious temperature during the spring when the threshold temperature is T* and the stage of the development is S°. The risk $P(T^*, S^\circ)$ is determined using conditional distributions f as follows:

$$P(T^*, S^\circ) = \int_{-273}^{T^*} f(T_{min} \mid S(t) \geq S^\circ)dT. \qquad (3)$$

Computation of the risk of injury is demonstrated in Fig. 3.

The risk $P(T^*, S^\circ)$ is a decreasing function of the stage of the development S°. The dependence of the risk of injury P on the stage S for each principle was determined using Eqs. (2) and (3) and graphical curve fitting (Fig. 4).

Let us assume that the active period begins when the risk of injury falls below some specified threshold risk, P*. Each pair of the threshold temperature T* and the threshold risk P* corresponds a threshold stage, S*. For each regulation principle the threshold stage S* is obtained as the graphical solution of the equation

$$P(T^*, S^*) = P^* \qquad (4)$$

using the fitted curves defined above (Fig. 4).

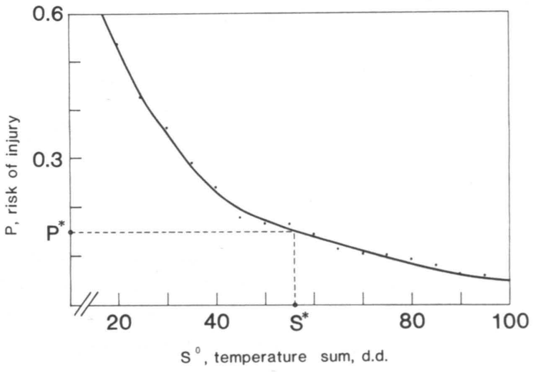

Fig. 4. The dependence of the risk of injury on the stage of the development. In this example the regulation is based on temperature sum principle. The threshold temperature of injury is T*= −2°C. The threshold state S* corresponding to the given threshold risk of injury,P* , is found graphically.

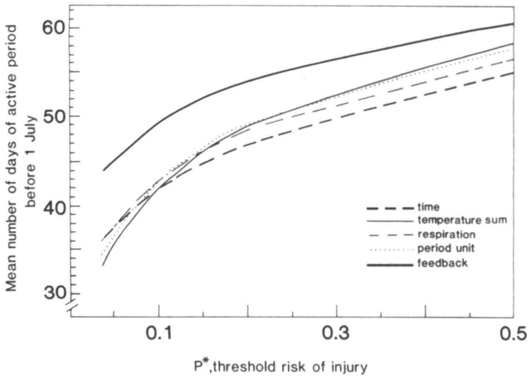

Fig. 5. The mean length of the active period before 1 July as function of threshold risk of injury, P*, for the five regulation principles.

If the threshold risk of injury is P* then the number of days of the active period before 1 July, when S(t) ≥ S* can be computed for each principle for each year using weather statistics. The efficiency of the regulation principles can now be evaluated by comparing the mean number of days in active period before 1 July during the period 1883−1982 as a function of the threshold risk of injury. The results are shown in Fig. 5, when the threshold temperature T* was assumed to be −2°C. The principle based on feedback resulted a clearly longer active period than the others.

5. Discussion

Theoretical concepts which are not directly measurable, have been used to analyse the development of plants (Hari 1968,1972, Robertson 1968, Sarvas 1972). This type of analysis has, however, met resistance because empirical thinking seems to be dominant in this field. The empirical requirement of direct measurability is generally accepted as a reasonable basis for theories in plant ecophysiology. The empiricist philosophy has, however, been questioned in the literature of philosophy of science (Bunge 1973). In addition, the use of nonmeasurable state variables, such as S in the present study, is also a general praxis in the system theory (Ashby 1976).

Theoretical concepts should have their basis in more fundamental sciences. Evolution theory and biochemistry could serve as a background for studies of the annual cycle. The present paper is an attempt to introduce evolutionary argumentation to studies of the annual cycle in an operational form. The stage of development makes it possible to utilize weather records in a new way by comparing the efficiency of different regulation principles. The biochemical background of annual cycle is still rather obscure and it will probably take decades before it is well understood.

Annual cycle of plants involves two types of phenomena, ie. development and growth. These two are to some extent parallel but they are different. Development refers mainly to the status of the regulation system, and growth to the formation of a new structure, especially concerning the division of cells. Perhaps the most prominent difference between the development and growth rates is that development may obtain negative values, as in the feedback principle, but the growth rate is always non-negative. This means that the stage of the annual cycle may retreat towards the winter stage during cold periods in the spring, but the disappearance of cell walls is not possible.

The utilization of dynamic models and conditional distributions enabled the efficiency of different regulation principles to be compared in the temperature conditions of Central Finland. The result was rather clear. The feedback principle (Pelkonen & Hari 1980) gave the most reliable prediction in estimating the risk of frost injury and it also resulted in the longest active period at a given frost injury risk at the beginning of the active period. The sequential daily minimum temperatures are strongly autocorrelated, i.e. a cold night is probably followed by another one. Unlike the others, the feedback principle is able to utilise this autoregressive information.

The differences in the efficiencies were so large that the regulation principle appears to be an important factor in the evolution of species. If the principles in question have been subjected to evolutionary forces then the feedback principle has most probably been selected.

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