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

Risto Häkkinen & Pertti Hari

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.

Keywords: annual cycle, regulation, spring frost, temperature

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 (Liljebäck 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 temper-
2. The activation of plants in the spring

The environment directly affects the functions of plants, and besides 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.

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

Various types of the regulation principles can be introduced into the analysis by means of 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 comparison 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 $g$ in Eq.(1) as follows (Fig. 1):

1. The time principle (Bünning 1963)

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

2. The temperature sum principle (de Reaumur 1735)

$$g(T) = \begin{cases} 0, & \text{if } T(t) \leq 5^\circ C \\ T(t) - 5, & \text{if } T(t) > 5^\circ C. \end{cases}$$

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

$$g(T) = a + be^{T(t)},$$

where $a = -0.4207$, $b = 0.727$ and $c = 0.067$.

4. The period unit principle (Sarvas 1972)

$$g = \text{tabulated values (Fig.1.d).}$$

5. The feedback principle (Pelkonen & Hari 1980)

$$g(T(t), S(t)) = 100 \left[ \frac{1 + a(T(t) - 80/0)}{1 + c(T(t) - 80/0/C)} \right]$$

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 $g$ 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, 23°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 totalled 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 maximise 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, \( f(T_{min}|I(t) \geq S) \), 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.

<table>
<thead>
<tr>
<th>Regulation principle based on</th>
<th>Mean of the standard deviations, °C</th>
<th>Range of the standard deviations, °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>time</td>
<td>2.4</td>
<td>1.7–3.6</td>
</tr>
<tr>
<td>temperature sum</td>
<td>2.4</td>
<td>2.0–3.3</td>
</tr>
<tr>
<td>respiration</td>
<td>2.2</td>
<td>1.6–3.0</td>
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<tr>
<td>periods</td>
<td>2.3</td>
<td>1.8–3.2</td>
</tr>
<tr>
<td>feedback</td>
<td>1.6</td>
<td>1.4–1.8</td>
</tr>
</tbody>
</table>

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.
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 to a threshold stage, \( S^* \). For each regulation principle the threshold stage \( S^* \) is obtained as the graphical solution of the equation

\[ P(T^*, S^*) = P^* \]  \hspace{1cm} (4)

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

If the threshold risk of injury is \( P^* \) then the number of days of the active period before 1 July, when \( S(t) \geq S^* \) 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 \(-2^\circ C\). 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 ecology. 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, i.e. 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.
References


Total of 15 references

Time study on different techniques for nursery pot filling operation

Raphael E. L. Ole-Meiludie & Goodseldah K. Pamba

TIVISTELMÄ: AIKATUTKIMUS TAIMIKENNOJEN TÄYTTÖTEKNIKOISTA


Time study on different techniques in nursery pot filling operation at SUA Training Forest in Northern Tanzania was conducted. The results showed that improved tools and work place design significantly decreased the operation time, hence increased productivity. In addition, worker's comfort was generally increased.

Turkimus tehtinä Sokoine University of Agriculture harjoiteltumassa Pohjois-Tansaniassa. Tulosten mukaan paremmin työkalut ja parempin työkohteen suunnitelmasta vähensivät merkittävästi toimintoon käytettyä aikaa ja nostivat sitten tuotantonaivastoa. Lisäksi työntekijän mukavuus yleensä paranii. (Käännös toimituksen)

Keywords: nursery pot filling, time study, productivity

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1. Introduction

Seeds planted, produced in the nursery, may be transplanted either as stripplings, stumps, bare-root stock, containerized stock, in Swaziland beds, or grown in polythene tubes or other types of containers (Goor and Barney 1968, Sharpe 1971, FAO 1974). Container sowing was originally established by foresters in cold northern climates, where the difficulties of successfully producing and planting conventional bare-root seedlings were substantial (Sharpe 1971). The commonest form of container in tropics is the polythene tube; various sizes may be used depending on conditions. They have replaced containers made of clays, bamboo, baskets, banana leaves, impregnated papers or cards (FAO 1963), and are preferred because among other factors they are cheap (if large quantities are ordered), light, and have no effect on transplant growth.