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THE ANNUAL CYCLE OF FOREST TREES: THE SARVAS APPROACH REVISITED

HEIKKI HÄNNINEN

University of Joensuu, Department of Forestry, Joensuu, Finland.

MARKKU KANNINEN

University of Helsinki, Department of Silviculture, Helsinki, Finland.

HEIKKI SMOLANDER

The Finnish Forest Research Institute, Suonenjoki Research Station, Suonenjoki, Finland.

ABSTRACT

The approach of Sarvas to the study of the annual cycle of development of forest trees was reintroduced.

The model presented by Sarvas (1972, 1974) for the regulation of the annual cycle was put into algebraic form. The algebraic model was tested by observing whether the developmental phase predicted by the model synchronises with the season over a ten year period. The test was made with arbitrary test criteria about the permitted timing of the developmental phases. The model fulfilled the test criteria with certain parameter values.

In order to take various environmental factors into account, the model can be resolved into various forms without abandoning the basic idea underlying the model. Thus, it was concluded that the Sarvas approach is a useful theoretical and methodological framework for studying and modelling the annual cycle of forest trees.

I. INTRODUCTION

The crucial role of the annual cycle of development in the adaptation of cool and temperate forest trees is generally accepted, but there has been considerable speculation as to the mechanism controlling the cycle (e.g. Koski and Sievänen 1985). Most of the models presented incorporate only certain parts of the cycle, e.g. bud burst, anthesis, or formation of the terminal bud. Sarvas (1972,1974), however, proposed an operational model for the regulation of the annual cycle as a whole. The model consists of submodels for different parts of the cycle based on empirical data. Before his death in 1974 Sarvas was able to test his model with observations from natural stands only to a limited extent, and not at all with long-term climatic data. Later Landsberg (1977) and Fuchigami *et al.* (1982) briefly described the Sarvas approach, and J. Sarvas (1977) analysed the basis of the approach mathematically.

The purpose of the present paper is 1) to summarize Sarvas' approach to the annual cycle of forest trees, 2) to carry out a preliminary test of the model, and 3) to evaluate the approach as a theoretical framework for studies on the annual cycle of development of forest trees.

II. SARVAS' MODEL OF THE ANNUAL CYCLE OF FOREST TREES

A. The Approach

Sarvas introduced a theory of the annual cycle of forest trees and used the concepts embodied in the theory to build his model. The theory deals only with the ontogenetic development of the apical and lateral meristems of forest trees. Many physiological phenomena (e.g. gas exchange, frost resistance) vary seasonally and are dependent on the annual ontogenetic cycle (cf. Pelkonen 1980, 1981). These phenomena are not, however, elements of the annual cycle in the strict ontogenetic sense (cf. Fuchigami *et al.* 1982).

Sarvas (1972) divided the developmental phenomena of trees into two categories, and referred to these categories as "point events" and "segment events". Point events are momentary, and one can unambiguously define whether or not the event has taken place. Segment events have a definite duration, but the beginning and end of a segment event can be considered as point events.

Sarvas argued that the annual cycle is a timetable according to which specific point events are achieved. He emphasised that the timing of the developmental phenomenon should be separated from other aspects of that phenomenon. When a plant passes through a specified point event, it is said to have attained a certain stage of development defined by that point event (cf. Robertson 1968, Hari 1972). Thus two plants passing through a given point event are at the same stage of development, regardless of the calendar time at which the event occurs in each case. Another essential feature of Sarvas' concept is the irreversibility of development. In other words the annual ontogenetic cycle can either proceed or stay, but it cannot retreat.

Sarvas explored the dependence of the rate of development of the trees on temperature. The effect of temperature on the rate of development was measured as the time lapse between two point events at various constant temperatures. Sarvas defined the rate of development to be inversely proportional to the time lapse.

B. The Model

Sarvas found that the dependence of the rate of development on temperature altered as the development progressed. He ended up with three response curves, and accordingly divided the annual cycle into three phases. However, he did not formulate mathematical equations for the response curves.

The model of Sarvas can be presented as follows:

(i) The annual cycle of development of forest trees consists of three phases: an active period, dormancy I (autumn dormancy) and dormancy II (winter

dormancy) (Fig. 1). During each phase, the rate of development (v) depends only on temperature (T). We have computed an equation for each phase on the basis of data from Sarvas (1972, p. 30; 1974, p. 26,37,42).

For the active period:

$$v(T) = 27.63 \cdot F_1(T), \quad (1)$$

where F_1 is the cumulative frequency function of a normal distribution with the mean of 17.91 °C and standard deviation of 8.73 C°.

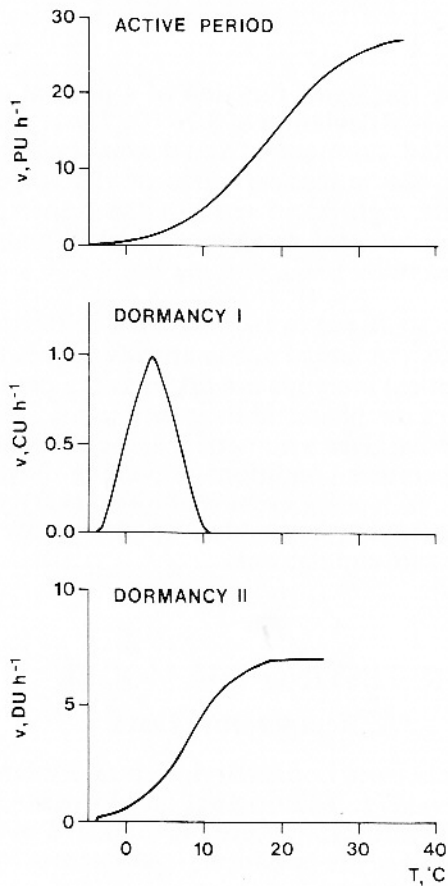


Fig. 1. The dependence of the rate of development (v) on mean hourly temperature (T) in the three developmental phases. PU (period unit), CU (chilling unit) and DU (dormancy unit) are the developmental units of the phases.

For dormancy I:

$$v(T) = \begin{cases} 0, & T \leq -3.40 \\ 0.14 \cdot T + 0.49, & -3.40 < T < 3.50 \\ -0.15 \cdot T + 1.57, & 3.50 \leq T \leq 10.36 \\ 0, & 10.36 < T \end{cases} \quad (2)$$

and dormancy II:

$$v(T) = \begin{cases} 0, & T < -4 \\ 9.01 \cdot F_2(T), & -4 \leq T \leq 19 \\ 7.06, & 19 < T \end{cases} \quad (3)$$

where F_2 is the cumulative frequency function of a normal distribution with the mean of 11.66 °C and standard deviation of 8.76 °C. The r^2 values were 0.997, 0.95 and 0.97 for the active period, dormancy I and dormancy II, respectively.

(ii) At a given instant, the numerical value of the stage of development is obtained by integrating the right-hand term of the respective equation, i.e. by summing hourly values of the term using mean hourly temperatures. The three phases cumulate in period units (*PU*), chilling units (*CU*), and dormancy units (*DU*), respectively.

(iii) When the integral calculated in (ii) reaches a critical value specific to the genotype, tissue and phase, the model automatically moves onto the next phase. The values of the three critical integrals are taken as the parameters of the model and represent the lengths of the phases in their own units.

The model presented above gives a numerical value of the stage of development as a function of the temperature conditions prevailing during the development. The model postulates that each point event is attained every year at a specific *PU*, *CU* or *DU* sum. The reasoning resembles, to some extent, that underlying conventional temperature sum simulations.

III. TESTING THE MODEL

A. Temperature Data

We used temperature data from Luonetjärvi, Central Finland (62°55'N, 25°39'E) covering the period 1962—1971. The original data consisted of daily minimum, mean and maximum temperatures measured in standard meteorological screens. As the response curves involved are nonlinear, it was necessary to approximate the daily temperature distributions.

A graphical survey of air temperature measured in every two minutes at the Forest Field Station of Helsinki University, Hyytiälä (61°51'N, 24°17'E) revealed that a beta distribution corresponded roughly to the daily temperature distribution observed. The beta distribution is completely defined when minimum, maximum,

mean and variance are known. In the original data the variance is the only unknown parameter. The following relationship between the variance and the temperature range was obtained: $s^2 = 0.078 \cdot (T_{\max} - T_{\min})$. This approximation was found to be satisfactory for the purposes of the present study.

B. The Test of the Model

Our test was based on the synchronisation between the developmental stage of a tree and the actual weather conditions. The point is that the thermal conditions vary considerably from year to year, but the annual cycle has to match them every year.

We simulated the annual cycle of development of an arbitrary genotype with the model. Various parameter (critical PU , CU and DU sum) combinations were used in search for parameter combinations which enable the predicted developmental phase to be properly synchronised with the seasonal rhythm over the whole test period. The test criteria about the synchronisation is given in Table 1.

Table 1. The test criteria applied in the simulation. + = permitted, — = non-permitted timing of a phase.

| Month | Active | Dormancy I | Dormancy II |
|-------|--------|------------|-------------|
| Jan | — | — | + |
| Feb | — | — | + |
| Mar | — | — | + |
| Apr | + | — | + |
| May | + | — | + |
| Jun | + | — | — |
| Jul | + | — | — |
| Aug | + | + | — |
| Sep | + | + | + |
| Oct | + | + | + |
| Nov | — | + | + |
| Dec | — | — | + |

Sarvas (1974, p. 64) states that in Southern Finland the active period of the flower buds of many tree species is usually complete by the end of August. In a preliminary test, the simulations were started on August 1, September 1 and October 1. The results differed from each other only slightly, so that subsequent simulations were always started on September 1, 1962.

We began the simulation at the beginning of dormancy I. The test program accumulated daily CU values to a fixed critical value (see below), moved onto dormancy II, and accumulated the daily DU values from the following day onwards. After the fulfillment of a fixed DU sum, the programme started to accumulate daily PU values for the active period. Having reached a critical PU sum, the tree was assumed to move onto dormancy I, thus beginning new cycle.

The above procedure was repeated with a set of fixed parameter combinations. The critical PU values tested ranged from 8000 — 28000 (step 2000, 11 values), critical CU values from 50 — 750 (step 50, 15 values) and critical DU values from 1000 — 10000 (step 1000, 10 values). Thus in all, we examined 1650 parameter combinations.

IV. RESULTS AND DISCUSSION

With certain parameter combinations, a rough correspondence was found between seasons and the predicted developmental phase over the entire test period (Fig. 2). When the parameters were plotted within a three-dimensional system of coordinates, acceptable combinations of parameter values bounded a fairly large uniform space. (In Fig. 2 the three-dimensional system of coordinates is broken down into four two-dimensional planes. This is for the sake of visual clarity). The model was thus not sensitive to variation in the value of any of the three parameters.

The fairly satisfying performance of the model is due to the synchronising effect of dormancy I. Without such a phase, the development after an unusually warm summer would proceed very early to dormancy II, and too early to the subsequent active period. This might even happen in the autumn, or early the next spring. Dormancy I prevents the cycle from proceeding until temperatures fall close to zero, and thus keeps the developmental cycle synchronised with the seasons.

The range of acceptance of each of the three parameters depended on the values of the two other parameters. When the value of one of the parameters is low, the tree tends to move onto the next phase too early, in other words the predicted development is too rapid. This could be corrected to some extent by increasing the values of the other two parameters. This procedure cannot be continued

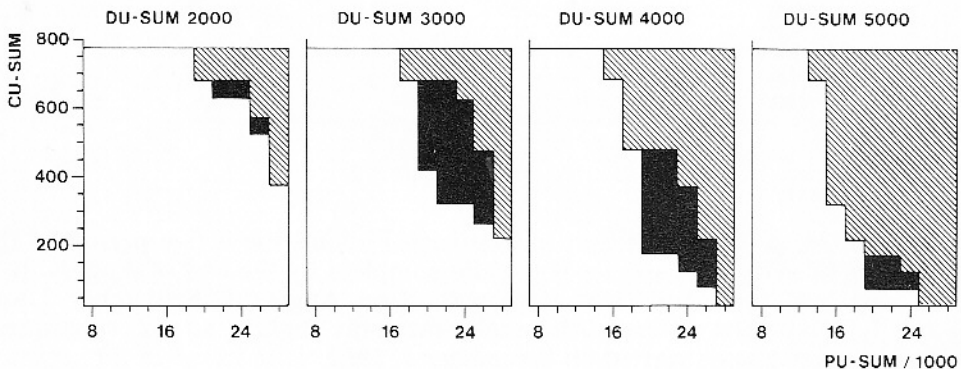


Fig. 2. Functioning of the model with various combinations of parameters. □: the simulated development was too rapid (the model moved onto the next phase too early), ■: the simulated development kept properly synchronised with the seasons (the test criteria were fulfilled) during the test period, ▨: the simulated development was too slow (the model moved onto the next phase too late).

indefinitely, because too large an increment in the value of either of the compensating parameters will cause the model to move onto the next phase too late in another part of the cycle. When the value of one or several of the parameters is too large, the predicted development tends to be too slow.

The test outlined above is the first step in testing the Sarvas' model. We aimed to study the logical structure and performance of the model, rather than the timing of specified phenological events or the phenology of a certain tree species. The small amount of data is an additional limitation to the inferences one can make. We can only conclude, that the model proposed by Sarvas continues to provide a plausible means of accounting for the regulation of the annual cycle of forest trees under the climatical conditions the test was performed.

The basic idea of Sarvas' approach is the concept of irreversible quantitative development, whose rate depends on environmental factors. The specific model presented by Sarvas can be resolved into various forms. A synergetic approach based on a joint effect of photoperiod and temperature sum has been reported (Koski and Selkänaho 1982, Koski and Sievänen 1985). Nonetheless, the rate of development can be modelled to depend also on photoperiod without abandoning the basic idea underlying Sarvas' approach. Thus, his approach provides an useful theoretical and methodological framework for studying and modelling the annual cycle of development of forest trees.

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