

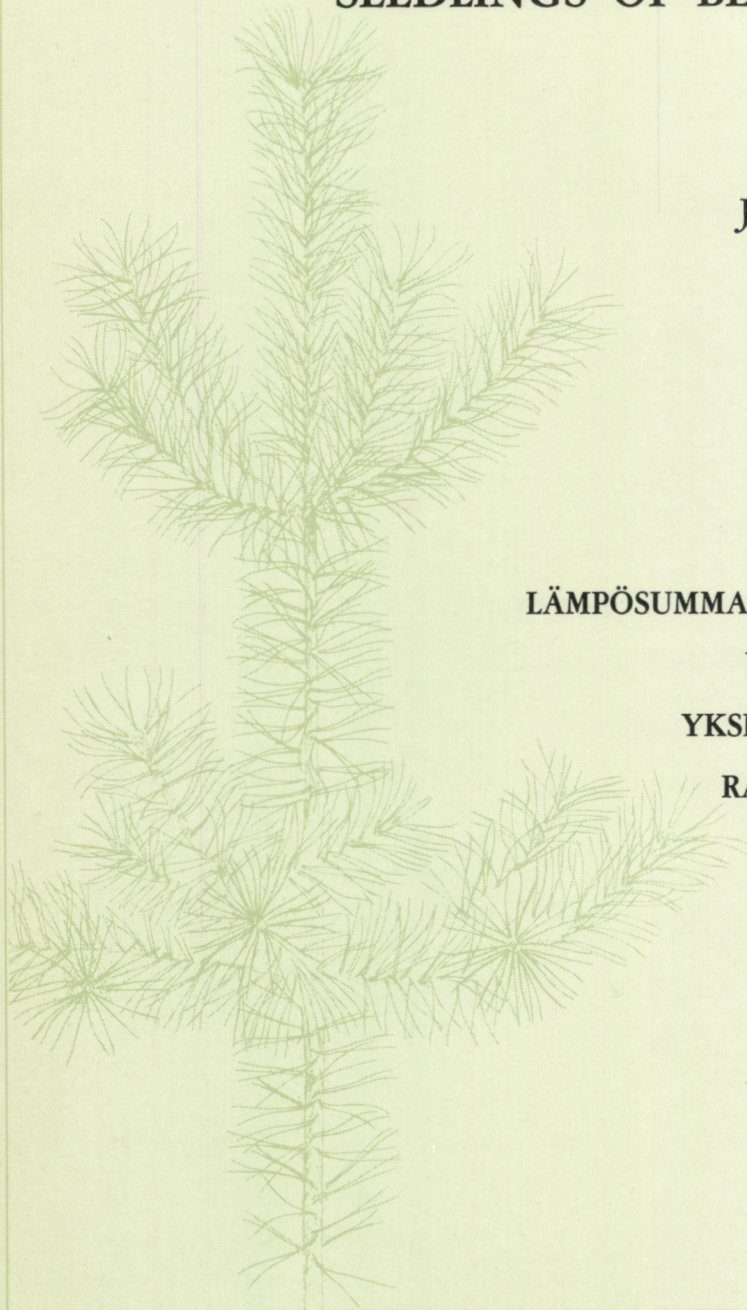
**EXPERIMENTS ON THE JOINT EFFECT OF
HEAT SUM AND PHOTOPERIOD ON
SEEDLINGS OF BETULA PENDULA**

**VEIKKO KOSKI &
JORMA SELKÄINAHO**

SELOSTE

**LÄMPÖSUMMAN JA PÄIVÄNPITUUDEN
YHTEISVAIKUTUKSESTA
YKSI- JA KAKSIVUOTIAISIIN
RAUDUSKOIVUN TAIMIIN**

HELSINKI 1982



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Cover (front & back): Scots pine (*Pinus sylvestris* L.) is the most important tree species in Finland. Pine dominated forest covers about 60 per cent of forest land and its total volume is nearly 700 mill. cu.m. The front cover shows a young Scots pine and the back cover a 30-metre-high, 140-year-old tree.

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The principle of regulation of the progress of the annual cycle is examined. Does it work autonomously, which would fit to heat sum simulations, or does it require time signals from the environment, which would be revealed in photoperiodic responses? The experimental design is based on the natural fluctuation of the photoperiod, two different growing temperatures, and replications in time throughout a year. In growth cessation both factors are involved, as well as some other modifying factors. The effect of photoperiod grows gradually without any abrupt critical value. The second year differs distinctly from the first.

Tutkimuksessa selvitetään puiden vuosirytmien säätelyn toimintaperiaatetta. Kysytään, toimiiko se autonomisesti, jolloin säätelyn toimintaa voidaan simuloida lämpösummakertymien avulla, vai perustuuko se ympäristöstä tuleviin aikamerkkeihin, jolloin päivänpituusreaktioita pitäisi ilmetä. Koejärjestely perustuu päivänpituuden luonnolliseen vuotuisen vaihteluun, kahteen eri kasvatuslämpötilaan sekä koekasvatusten aikaporrastukseen pitkin vuotta. Todettiin, että pituuskasvun päättymiseen vaikuttavat molemmat yllä mainitut tekijät sekä lisäksi jotkut muut tekijät modifioivat kasvun ajoittumista. Fotoperiodin vaikutus lisääntyy vähittäin ilman jyrkkää kynnyisarvoa. Toisen kasvukauden aikana vuosirytmien säätely on selvästi erilainen kuin ensimmäisenä.

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1. INTRODUCTION

The climatic adaptation of perennial plants in cool temperate regions can be divided into two main components: (1) the plants must be able to change to a form that is resistant to low temperatures and subsequent physiologic drying, and they must be able to become active again for the growing season. The living tissues, especially meristems, of higher plants cannot be simultaneously active and frost resistant, but they must be either active or resistant. (2) The plants must be able to match the above mentioned stages properly with the occurrence of the growing season and winter every year throughout their lifespan.

The cold and drought stress is extremely severe to trees whose meristems are largely outside the protective snow cover. Numerous provenance experiments, as well as afforestation failures, employing long distance geographic transfers of seed have shown that an adequate climatic adaptation is not ubiquitous. Obviously the climatic adaptation is genetically controlled. Natural populations display adaptation to the local pattern of the alternation of seasons. In case a gradual but permanent (in the time scale of tree generations) change of climate takes place, adaptation means a response in gene frequencies. In other words adaptation is a process at the population level, where the gene and genotype frequencies tend to follow the selection pressure. Successful geographic transfers indicate that many species have a wide capacity of acclimatization. Acclimatization means the ability of an individual to survive in a new environment without genetic changes. The recurrent annual array of different physiological phases including all visible phenological events is called the annual cycle. The unchanged sequence of those events, taking place in accordance of the alternation on seasons, is called the annual rhythm. The understanding of the genetic

background of the annual rhythm would solve many problems of adaptation and geographic transfers. The fundamental question in this connection is what is inherited in the annual rhythm. When this question has been answered we may ask what is the mechanism of inheritance.

During the last few years systems and models have been popular in the field of biology. They might be fruitful in the present connection, too, because the progress of the annual cycle can be conceived as a system of processes and regulations. Word models have in fact been applied since the 19th century (Linsser 1867). A desire to use the simplest explanation that fits the facts has lead research into blind alleys when only one factor has been accepted to explain a regulation. Much confusion has arisen because many authors have used the same term for different meanings and different terms for the same matter. A very large number of reports on biological rhythms, biological or physiological clocks, phenology, dormancy etc., dealing with many kinds of organisms from procaryotes to man have been published. The excess of terms and explanations is therefore understandable. It is impossible to keep track everything that has been said and so fix generally accepted terms. In the present report the assumption is that there is no universal biological clock system that regulates the life of all organisms. Therefore the field of interest is limited to forest trees and some other perennial plants of the cool temperate region.

The main feature of the inherited control system of the annual rhythm is its predictive capacity. In late summer the trees stop their growth and become dormant before the temperature falls below freezing point. In spring, the meristems do not turn active immediately after the first temperature rise above zero but only after the risk of late frosts has diminished.

Clearly the state of the annual cycle does not depend solely on the conditions of the moment.

The sequence of the seasons is, to a certain extent, regular from year to year. In some way, this pattern must be described in the genetic information of trees and other perennials. The explanations or word models of the regulatory systems that occur in the literature since the 18th century can be divided into two categories: (1) The regulatory system is autonomous and it does not need any time signals from the environment. In extreme forms trees are supposed to measure the normal time with a circadian rhythm (Sweeney 1969). An autonomous regulation presupposes that the genetic information contains a fixed program of the sequence and timing of all the processes during the annual cycle. In most models the rate of progress along the program depends on temperature, which means that the progress can be simulated with heat sum calculations. The program has a circular form. Thus there is no distinct zero point. Efforts to apply heat sum calculations to the annual rhythm were initiated by Reaumur (1735 cit. Sarvas 1972). Linser (1867) postulated that natural populations have adapted to the average local heat sum of the entire growing season and that the heat sum accumulated until a certain phase is in all localities, a fixed proportion of the heat sum of the whole growing season. In other words, the momentary rate of progress is proportional to the actual temperature (positive) divided by the total heat sum. Arnold (1959), obviously without knowing of Linser's work suggested that a heat sum accumulation parallels the physiologic progress of the annual cycle. Sarvas (1967, 1969, 1972, 1974) extended and refined the model of autonomous regulation and temperature dependence of the rate of progress. He stated that Linser's principle holds true in the central part of the range of distribution but not at the margins. Secondly Sarvas explained the annual variation in calendar time with heat sums. Thirdly Sarvas measured the temperature dependence of the rate of progress in all three main parts of the annual cycle: active period, autumn dormancy, and winter dormancy. He stated that the changes of

photoperiod have deliberately been excluded from the model (Sarvas 1974 p. 5). He called the model a physiological clock. More commonly the term physiological clock refers to diurnal or other fixed oscillations (Bünning 1963).

The other type of explanations presuppose that the trees are able to receive and interpret time signals from the environment. Thus the start and cessation of a physiological process require a specific impulse. As the changes in day length in spring and autumn are consistent from year to year at any latitude, the photoperiod can be considered a most reliable time signal. First attempts to explain the mechanism of the annual rhythm with photoperiodic responses were published as early as 1877 Askenasy cit. Romberger 1963). The actual rise of this theory took place at the beginning of the 20th century, when it became possible to arrange experiments with electric lights. The remarkable photoperiodic responses obtained with many plants convinced many researchers that the annual rhythm of all plants is determined by specific photoperiodic signals. Surveys of earlier studies on photoperiod as well as comprehensive lists of references can be found for instance in Romberger (1963), Sollberger (1965), Flint (1974), Vince-Prue (1975) and Kramer and Kozlowski (1978). Besides photoperiodic signals impulses based on temperature, such as thermoperiod, chilling, very low temperatures, and temperatures exceeding a certain threshold have been mentioned. A modifying effect of temperature on the photoperiodic response has been reported for instance by Heide (1974 a) and Dormling (1978) both for *Picea abies*.

Most textbooks accept the impulse model without criticism, neglecting the fact that the phenology of trees does not accurately follow the changes of the photoperiod every year. As the changes of photoperiod have exactly the same pattern relative to our calendar, the phenophases controlled by photoperiodic signals ought to take place at the same date every year. Even crude phenological observations reveal conspicuous differences between years. For example, in The Federal Republic of Germany. During a 10 year period both

Name	Location		Phenology 1968...1977			
	Latitude N	Altitude m	Flushing		Average, day from Jan. 1.	Autumn colour Difference between earliest and latest year, d.
Frankfurt aM.	50°06'	100	99	38	275	24
Bad Schwalbach	50°08'	340	112	25	263	30
Bedra	50°59'	200	111	26	285	25
Tecklenburg	52°13'	70	118	43	262	22
Wittlage	52°19'	65	113	36	287	24
Gifhorn	52°28'	50	108	25	264	44
Nienburg	52°38'	30	107	42	279	48
Hamburg	53°33'	1	110	28	269	41

the dates of flushing and the dates of autumn coloration of *Betula pendula* fluctuated several weeks in each locality.

Does all this mean that the annual rhythm of forest trees can be explained with two fundamentally different models? In fact the incompatibility factor concerning the models could not be eliminated from the experiments, even though it may have been neglected when the results were analysed. Sarvas studied the timing of flowering and other generative processes in natural conditions (1967, 1968, 1972) and took the material for the laboratory experiments on temperature dependence from trees shortly before the actual constant temperature treatments (1972, 1974). Thus the empirical material was exposed to the natural photoperiodic changes. As regards the studies on photoperiod the material has been raised in artificial conditions and the treatments were mostly carried out in phytotrones. All the time heat sums were accumulated even though the temperature was not recorded or the heat sums calculated.

A kind of hybrid between the heat sum simulation model and the photoperiod impulse model has been suggested by Stern and Roche (1974 p. 15—16), according to which the beginning of the active period parallels the heat sum accumulation whereas the photoperiodic impulses determine the timing of events in late summer and autumn.

In natural conditions, light and temperature as well as photoperiod and accumulation of heat sum during the growing season are very closely linked. On the other hand, the change of photoperiod in the South-North direction is not linear. Figure 1 gives some examples of the annual fluctuation of photoperiod in the northern hemisphere. If some results of phytotrone experiments are strictly projected on the diagram, they would suggest that terminal buds are formed earlier in the South than in the North. The observed critical night may be 3 h 30 min shorter than the shortest natural night at the latitude in question. This kind of comparison does not mean that the observed values were wrong as such. The present authors point out, to quote Romberger (1963 p. 86) "A photoperiodic response or a defined critical photoperiod to induce a certain process in artificial environment does not prove the observed numeric values valid in natural regulation". On the other hand, when seedlings of forest trees are raised in greenhouses, the accumulated heat sum can exceed by two fold the natural heat sum of the whole growing season, but the seedlings go on growing. In pilot trials, seedlings and dissected branches were exposed to close to freezing temperatures for adequate periods required to remove autumn dormancy and winter dormancy. The treatments became effective only after January, which indicates that some other factors were also involved. For further progress in

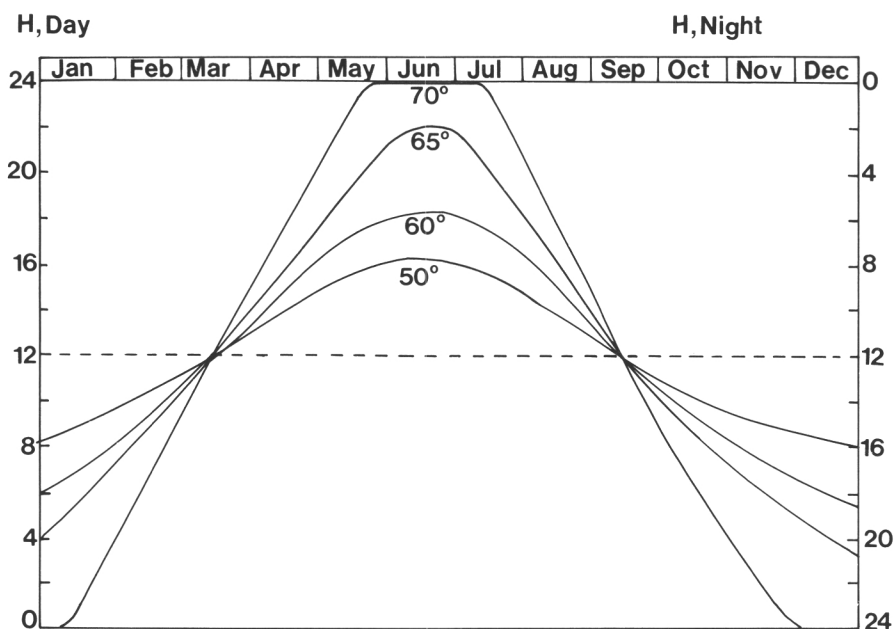


Figure 1. The annual fluctuation of photoperiod at some latitudes of the northern hemisphere. The scale on the left gives the time interval between sunrise and sunset (= day) in hours, the scale on the right gives the corresponding night lengths.

Kuva 1. Fotoperiodin vuotuinen vaihtelu pohjoisella pallonpuoliskolla eräillä leveyspiireillä. Vasemman puoleinen asteikko ilmaisee ajan auringon nousun ja auringon laskun välillä (= päivä) tunteina, oikeanpuoleinen asteikko antaa vastaavat yön pituudet.

the studies on type of regulation of the annual rhythm and the genetic background of adaptation a new kind of method is needed.

The aim of the present study is to introduce an experimental method that (1) takes into consideration both: the heat sum accumulation and photoperiod, and (2) removes the linkage between heat sum accumulation and the change of photoperiod. The long term goal of the study is the modelling of the regulation of the annual rhythm, and further, the determination of metric values or parameters to characterize the annual rhythm of a given genetic unit. In the beginning, when the method is investigated, only one species and one origin is to be used and the observations limited to the progress of the active period.

The study of the genetic background of the annual cycle of forest trees was inspired by the comprehensive investigations and personal communications of late professor Risto Sarvas. The senior author (Koski) carried out some pilot experiment in the mid-1970 s and then gradually came to the design presented here. The junior author (Selkäinaho) was engaged during the processing of the data from the 1978 experiments. He has formulated the graphic surveys and the model application. The experiments were carried out at the Tree Breeding Station at Punkaharju, where Mr. Jouko Lehto took care of the raising of the seedlings and Mr. Pentti Manninen attended to the measurements and observations. The computer operations were mainly carried out by Mr. Kaarlo Karvinen. The compilation of the results and preparing of the manuscript were done by Mrs. Raili Tallqvist. The figures were drawn by Miss Sisko Salminen. Professor Max. Hagman, acting professor Pertti Hari, and Dr. Paavo Pelkonen made valuable comments on the preliminary manuscript. The English language was checked by Dr. Ashley Selby. To these people we express our sincere thanks, as well as to all others who contributed to the accomplishment of the present study.

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2. MATERIAL AND METHODS

The main idea is as follows. If the progress of the annual cycle can be simulated with a proper heat sum accumulation, a population with the same genetic composition will always pass through a similar cycle interval with a constant heat sum, irrespective of the photoperiod or the actual temperature, provided that light, temperature and other environmental factors

are within the normal range. If the essential changes, such as growth cessation, are induced by specific critical photoperiods, genetically similar populations will reach a certain phenophase simultaneously in natural illumination even though they have started the active period at separate points of time and have grown at different temperature regimes.

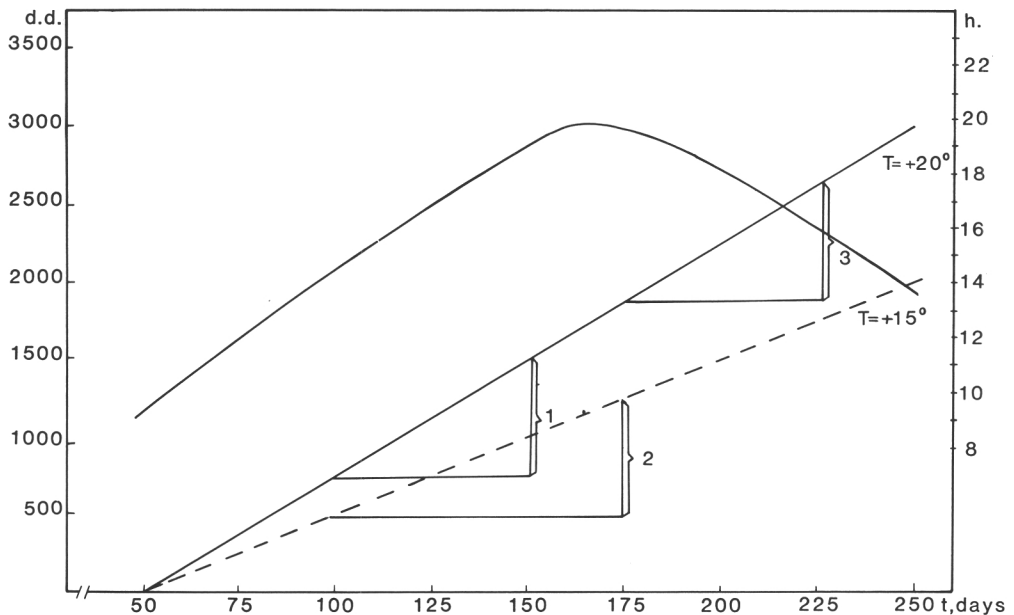


Figure 2. Schematic diagrams of the relations of heat sum accumulation and photoperiod, with natural photoperiod at Punkaharju (Lat. $60^{\circ}48'N.$) and constant temperatures of $+20^{\circ}C$ and $+15^{\circ}C$. The horizontal axis is time in days beginning from the 1st of January. The left vertical scale refers to the straight lines and denotes degree days above $+5^{\circ}C$. The right vertical scale refers to the curved line and gives the time between sunrise and sunset in hours. The curved line shows the natural change of day length. The solid straight line gives the heat sum accumulation at $+20^{\circ}C$, and the dashed straight line gives the heat sum accumulation at $+15^{\circ}C$. If an arbitrary experiment is started on day $t = 100$ simultaneously at $+20^{\circ}C$ and $+15^{\circ}C$, the same amount of degree days that is accumulated in 50 days at $+20^{\circ}C$ (1) requires 75 days at $+15^{\circ}C$ (2). If another experiment is started at $+20^{\circ}C$ on day $t = 175$ the same amount of degree days is accumulated in 50 days (3), but the photoperiod is different from the experiments started on day $t = 100$.

Kuva 2. Kaaviokuva lämpösuummakertymän ja fotoperiodin suhteista. Kaaviossa on luonnollinen fotoperiodi Punkaharjulla, Lat. $60^{\circ}48'$ pohjoista leveyttä, $+20^{\circ}C$ ja $+15^{\circ}C$ vakioämpötilat. Vaaka-akselilla on aika päivinä alkaen vuoden alusta. Pystyasiteikko vasemmalla (d.d.) liittyy suoraan kuvaajin ja ilmaisee lämpösuummakertymän d.d. yli $+5^{\circ}C$. Oikeanpuoleinen asteikko liittyy käyrään. Se ilmoittaa päivänpituuden, ajan tunteina auringon nousun ja auringon laskun välillä. Käyrä viiva osoittaa luonnollisen päivänpituuden muutoksen Punkaharjulla. Ehjä suora viiva osoittaa lämpötilan kertymän $+20^{\circ}C$ ja suora katkoviiva osoittaa lämpösuumman kertymän $+15^{\circ}C$ lämpötilassa. Jos kuviteltu koe aloitetaan päivänä 100 rinnakkain $+20^{\circ}C$ ja $+15^{\circ}C$ lämpötiloissa, sama lämpösuumma, joka kertyy $+20^{\circ}C$ 50:ssä päivässä, vaatii 15 päivää $+15^{\circ}C$ lämpötilassa. Jos aloitetaan toinen koe $+20^{\circ}C$ päivänä 175, sama lämpösuumma kertyy 50:ssä päivässä, mutta fotoperiodi on erilainen kuin päivänä 100 aloitetussa kokeessa.

These two hypotheses can be tested with an experiment that needs only very modest equipment. The elements are the natural change of photoperiod along the year and two separate greenhouses where it is possible to have two different constant temperatures. The experiments are started in late winter and finished in autumn. When parcels get started from the same initial stage with regular intervals, eg. 14 days, the replications in one greenhouse will be exposed to a constant heat sum during any fixed time interval but the photoperiod grows longer in the beginning and decreases towards the end. Parallel treatments at the other temperature mean that for each particular photoperiod there are two different velocities of heat sum accumulation. This kind of experimental design should make it possible to analyze both the separate effects of the two factors and their joint effects.

The schematic diagrams in figure 2 illustrate the idea of the experimental design. If the progress of the annual cycle can be simulated with a linear heat sum accumulation, the same amount of progress ought to be expected with a constant heat sum in both temperatures and also at any photoperiod. On the other hand, if the termination of a certain phase, for instance shoot elongation, depends on a fixed critical photoperiod, this limit value ought to appear when the experiments are repeated along the time dimension. In an extreme case the relatively short day in late winter could prevent normal development. More probably all seedlings would continue their growth until late summer when the critical night length is met, irrespective of the commencement time or the growing temperature. The hypothetical results of these mutually exclusive models are illustrated in figure 3.

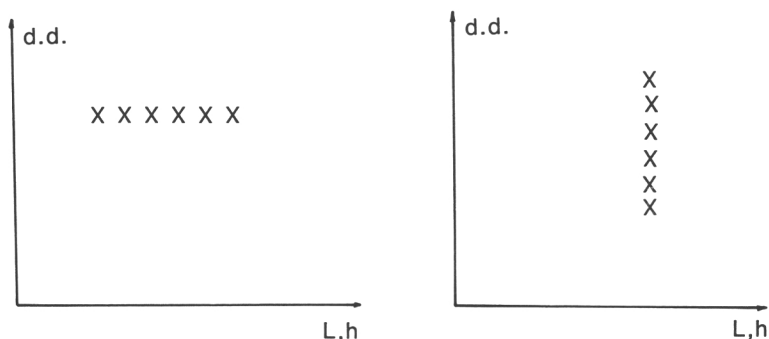


Figure 3. Hypothetical results of the experiments. a) If the progress of the active period can exclusively be explained with a heat sum (d.d.) simulation. b) If the termination of the active period can exclusively be explained with a fixed critical night length (L). In an ideal case the observed constant value should fit to the local natural conditions (cf. Figure 2).

Kuva 3. Oletetut tulokset kokeista a) mikäli aktiiviperiodin eteneminen voidaan selittää pelkästään lämpösummakertymän avulla ja b) mikäli aktiiviperiodin päättyminen voidaan selittää pelkästään kiinteän kriittisen yön pituuden saavuttamisella. Ihannetapauksessa havaittujen vakioarvojen pitäisi olla sopuoinnussa luonnossa esiintyvän tilanteen kanssa (vrt. kuvaan 2).

Common birch, *Betula pendula* Roth (syn. *B. verrucosa* Ehrh.), was chosen as an experimental species of this pilot study, because it has some obvious advantages. Seedlings of birch grow rapidly in favourable conditions. All the handling of the material as well as the measurements and observations are easier when the objects are not very small. Earlier studies have explained the behaviour of birch both concerning the heat sum model (Sarvas 1972, 1974, Raulo and Leikola 1974) and the photoperiod model (Vaartaja 1959, Häbjørg 1972, 1978). As the seedlings of *Betula pendula* can be made to flower at an age of 1–2 years from seedling with intensive growing conditions (Kärki 1976), true genetic analyses by means of controlled crossings and succeeding generations can be realistically planned.

Open pollinated seed from one tree of a local (Punkaharju) stand was used in all experiments. The seed was collected in 1975. The seedlings were raised in glass greenhouses, where the natural light penetrating the glass was the only illumination. Fertilized garden peat was used as growing substance. Watering was done manually. Two separate compartments were used, and a difference in temperature was maintained between them. Due to the modest equipment it was not possible to have accurately constant temperatures or prescribed diurnal thermoperiods. The intended temperature in one compartment was +20° C and in the other +15° C. The temperature difference between treatments was the essential matter. The actual temperature above the seedlings was continuously recorded with copper/constantane thermoelements.

During warm summer days temperature exceeded the intended values, because there was no machinery to cool the greenhouses below the outdoor air temperature.

The experiments with staggered sowings were repeated in two succeeding years, 1978 and 1979, with the same design. The same seedlings were investigated during their second growing season in 1979 and 1980 respectively. The sowings were started in both years around the middle of February, when the darkest and coldest period of the year had been passed by. The sowings were continued with regular intervals towards the end of the summer. The general outlines of the series of repeated sowings are given in the following compilation. The numbers in brackets after the dates indicate the running number of the day from the beginning of the year.

	1978	1979
The earliest sowing date	Febr. 13 (44)	Febr. 13 (44)
Time interval between sowings	7 days	14 days
The latest sowing date	Aug. 28 (240)	July 23 (202)
Number of sowing times	29	12
The date when the seedlings were moved out	Oct. 10 (283)	Sept. 9 (252)

In both years the germinating stage was carried out at 20° C temperature. Immediately after germination the seedling to be treated at 15° C were moved into the other compartment. In autumn the seedlings were moved out in the same containers where they had grown. No pretreatment or artificial shelter was applied in overwintering.

Differences in the initiation of the active period of the second year are technically much more difficult to arrange than those in sowing times. The seedlings raised at 20° in 1978 were treated as follows in 1979. During the winter dormancy each set of seedlings originating from a sowing time was divided into four parts. Four treatments were formed by taking one quarter of all sowing times separately. Treatment 1 was taken indoors on the 19th of March (day 78.), treatment 2 two weeks later (day 92.), treatment 3 again two weeks later (day 106.), and treatment 4 was left out of doors. The treatments 1, 2 and 3 were subjected to gradually rising temperature in the beginning and finally kept at +15° C. The purpose was to achieve an earlier start and consequently different combinations of heat sum accumulation and photoperiod.

One part of the seedlings raised in 1979 were subjected to an extended winter in order to cause an exceptionally small heat sum relative to the long nights in late summer. Several cubic meters of natural ice from the adjacent lake were transported into a large cellar in mid-winter. The boxes with experimental seedlings were placed in the ice basin in late winter. The close to freezing temperature could not prolong the winter dormancy by more than 3 weeks. When the buds began to swell the seedlings were given a 8 hour light period with fluorescent tubes. After the

middle of June the seedlings were trained to higher temperatures and light intensities. After a transition period the seedlings of a delayed start were moved out next to the rest of the same material that started its active period in the natural time.

The shoot elongation and the formation of the terminal buds were recorded during the first growing season. In the beginning of the second active period the opening of buds was also recorded. As a rule, 10 sound seedlings from each parcel were chosen and numbered. The total height of each of these seedlings was measured once a week. In 1978 the height measurements were not started until the seedlings had reached a height of 10 cm. In 1979 the height was measured from germination. The formation of the terminal buds was observed once a week. Each time the number of seedlings with terminal buds were counted. The opening of the buds in the spring of the second year was observed from five lateral buds next to the terminal bud. In case a seedling was damaged or it died during the period of observation its data was deleted before calculations. During the overwintering and the second growing season the parcels of the first growing season were kept separate. The height growth was described by the average of the measured seedlings of the parcel. The cessation on the shoot elongation was taken at the point of time when the average height reached 95 per cent of the final height. The points of bud opening and bud formation were defined to take place when 50 per cent of seedlings had passed the phase in question.

The first step of the data processing was a graphic survey. The diagrams of growth rhythm, growth cessation and bud formation displayed systematic trends according to the series of sowing times. The graphs indicated some kind of interrelation or mutual responses of heat sums and photoperiods but they did not provide any simple constant pattern. Therefore efforts were made to apply dynamic models. This approach is tempting, because the progress of the annual cycle can be considered a dynamic process. After trials with several types of models the following difference equation was developed to describe height growth.

$$h(t + 1) - h(t) = f(T) [h(t) + h_0] [1 - h(t)/g(L)] \quad (1)$$

where h is the cumulative height growth after the germination

h_0 is a parameter

f is a function of temperature (T)

g is a function of night length (L)

t indicates time.

The time interval is 24 h, which is a natural cycle. All quantities are daily means. Figure 4 illustrates the behaviour of the model in three different stable environments.

1. $T = 20^\circ$, $L = 6$ h
2. $T = 15^\circ$, $L = 6$ h
3. $T = 15^\circ$, $L = 10$ h

Equation (1) can be approximated in the beginning of the first growing season as follows:

$$h(t + 1) - h(t) = f(T) h_0 \quad (2)$$

A seedling has no foliage at this stage and it must grow with the aid of the resources of the seed. The magnitude of the energy storage is denoted with h_0 .

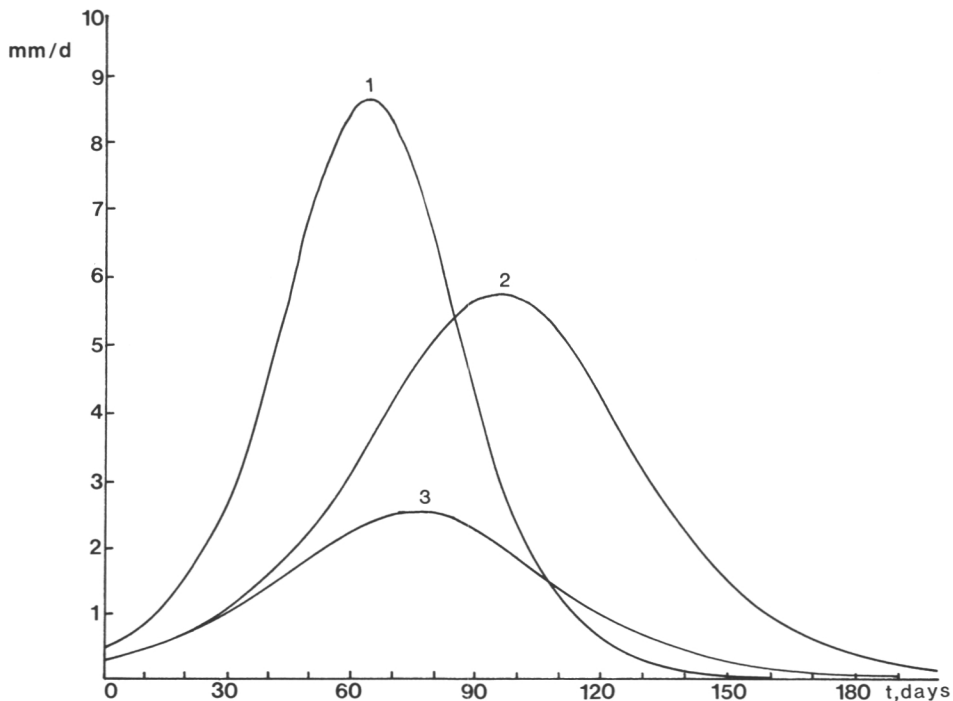


Figure 4. Schematic examples of the behaviour of the applied dynamic model in three different stable environments. The horizontal axis gives time (t) in days and the vertical axis daily height increment in millimeters. The curves illustrate the following combinations: 1. Temperature (T) = 20° C Night length (L) = 6 h, 2. Temperature (T) = 15° C, Night length (L) = 6 h, 3. Temperature (T) = 15° C, Night length (L) = 10 h.

Kuva 4. Kaaviokuva sovelletun dynaamisen mallin käyttäytymisestä kolmessa eri vakioympäristössä. Vaaka-akseli kuvaa aikaa päivinä ja pystyasteikko päivittäistä pituuskasvua millimetreinä. Käyrät havainnollistavat seuraavia yhdistelmiä: 1. Lämpötila 20° C, yönpituus 6 h, 2. Lämpötila 15° C, yönpituus 6 h, 3. Lämpötila 15° C, yönpituus 10 h.

When leaves have been formed the growth is exponential and the growth coefficient is a function of temperatures. At this stage, function (1) can be approximated as follows:

$$h(t + 1) - h(t) = f(T) h(t) \quad (3)$$

Towards the end of the growing season the rate of height growth gradually decreases and finally becomes zero. At this stage the increasing night length is supposed to accelerate the growth cessation. The model can now be approximated as follows:

$$h(t + 1) - h(t) = f(T) (g(L) - h(t)) \quad (4)$$

The height growth comes to an end when either the night length reaches a value where $h(t) = g(L)$ or temperature drops and $f(T) = 0$.

To compare the model with the observed values requires numeric estimates for the parameters. For this purpose the following relation between the growth coefficient and temperature is given.

$$f(T) = a (T - T_0) \quad (5)$$

where a and T_0 are parameters. Similarly, the function g is assumed to depend on the night length according to the following equation:

$$g(L) = b(L_0 - L) \quad (6)$$

where b and L_0 are parameters.

Formed in this way the model includes five parameters h_0 , a, T_0 , b and L_0 that must be estimated. The aim has been to determine estimates for all parameters so that the values obtained with the model have the best fit with the observed values. There is no absolute criterium for the fit. A common method is the least sum of squares.

$$\sum_i \sum_j (G_{exp} - G_{obs})^2 \quad (7)$$

where G_{exp} is the simulated and G_{obs} the observed height growth between two dates. The summation is first done through observation dates and then through sowing dates. This sum of squares stresses the parcels with tall seedlings. This bias can be reduced with a weighed sum of squares

$$\sum_i \sum_j \left[\frac{G_{exp} - G_{obs}}{H(i)} \right]^2 \quad (8)$$

where $H(i)$ is the final height of parcel i.

The minimizing of such sums of squares that are nonlinear relative to the parameters requires tedious computations.

3. RESULTS

31. Height growth and formation of terminal buds during the first growing season

The duration as well as the magnitude of height growth were distinctly different in parcels originating from different sowing dates. The mean heights and time intervals between sowing and growth cessation are given in tables 1 and 2. The number of days displays a rather regular decreasing trend from the early sowing dates towards the late ones. This result indicates that the seedlings have responded to the

change of photoperiod. On the other hand in parallel parcels from the same sowing day the same period interval generally lasted longer at the lower temperature. This result in turn suggests that the progress is proportional to the heat sum accumulation. The total height is clearly highest in the lots that were sowed in late winter. Without doubt, the amount of growth strongly depends on light intensity and day length.

The missing values at the end of the time series are explained as follows. In 1978 the height measurements were not

Table 1. The magnitude and duration of height growth of *Betula pendula* seedlings during the first growing season in 1978. Day of sowing is the running number of the day from the beginning of the year. Final height is the total height at the end of the summer. Duration is the number of days between sowing and growth cessation (95 per cent of the final height). SD means standard deviation of a sample.

Taulukko 1. Rauduskoivun taimien pituuskasvun kesto ja kokonaismäärä ensimmäisenä kasvukautena vuonna 1978. Kylöpäivä ilmoittaa päivän järjestysnumeron vuoden alusta lukien. Loppupituus on taimien kokonaispituus kesän lopulla. Pituuskasvun kesto on päivien lukumäärä kylvästä siihen päivään, jolloin 95 % loppupituudesta oli saavutettu. Keskihajonta (SD) on laskettu otoksen keskihajonnan kaavalla.

Day of sowing Kylöpäivä	Intended temperature 20° C Tavoitelämpötila 20 °C				Intended temperature 15° C Tavoitelämpötila 15 °C					
	Number of seedlings Taimien lukumäärä	Final height		Duration days		Number of seedlings Taimien lukumäärä	Final height		Duration days	
		Loppupituus		Kasvun kesto päivää			Loppupituus		Kasvun kesto päivää	
		\bar{x} cm	SD cm	\bar{x}	SD		\bar{x} cm	SD cm	\bar{x}	SD
44	20	32	11	145	23,3	5	98	6	156	4,5
51	20	39	26	136	27,2	5	78	5	148	1,6
58	20	42	34	127	20,7	5	82	22	141	2,6
65	20	34	19	125	12,7	5	77	40	147	2,7
72	20	37	18	112	9,9	5	107	6	136	7,5
79	20	78	19	103	6,5	5	111	6	117	2,9
86	20	88	16	103	—	5	109	8	113	3,8
93	19	87	20	96	4,2	5	94	14	107	2,6
100	20	74	27	97	5,8	5	107	9	107	4,3
107	20	53	19	89	4,2	5	66	12	97	1,9
114	20	73	18	89	5,2	5	102	11	104	2,9
121	20	74	16	91	7,3	5	91	8	104	2,2
128	20	36	7	73	3,6	5	82	13	91	3,8
135	20	52	12	76	4,5	5	71	10	88	0,9
142	20	55	15	76	3,1	5	69	8	86	1,8
149	20	36	16	69	2,6	5	49	12	81	1,9
156	20	29	16	71	4,6	4	36	18	77	10,5
163	20	43	12	68	4,0	5	41	6	72	2,9
170	20	29	5	62	2,5	5	21	4	66	1,9
177	20	29	7	66	3,9	5	19	3	59	3,8
184	20	17	3	60	2,4	5	12	1	55	2,3
191	19	13	3	63	3,8	5	9	1	59	7,0
198	20	12	4	61	1,8	5	8	2	54	4,9
205	19	11	4	53	2,3	5	8	1	47	3,2

Table 2. The magnitude and duration of height growth of *Betula pendula* seedlings during the first growing season in 1979. Day of sowing is the running number of the day from the beginning of the year. Final height is the total height at the end of the summer. Duration is the number of days between sowing and growth cessation (95 per cent of the final height). SD means standard deviation of a sample.

Taulukko 2. Rauduskoivun taimien pituuskasvun kesto ja kokonaisuus ensimmäisenä kasvukautena vuonna 1979. Kylypäivä ilmoittaa päivän järjestysnumeron vuoden alusta lukien. Loppupituus on taimien kokonaispituus kesän lopulla. Pituuskasvun kesto on päivien lukumäärä kylyöstä siihen päivään, jolloin 95 % loppupituudesta oli saavutettu. Keskihajonta (SD) on laskettu otoksen keskijajonnan kaavalla.

Day of sowing Kylypäivä	Intended temperature 20° C Tavoitelämpötila 20 °C					Intended temperature 15° C Tavoitelämpötila 15° C				
	Number of seedlings Taimien lukumäärä	Final height Loppupituus		Duration days Kasvun kesto päivää		Number of seedlings Taimien lukumäärä	Final height Loppupituus		Duration days Kasvun kesto päivää	
		\bar{x} cm	SD cm	\bar{x}	SD		\bar{x} cm	SD cm	\bar{x}	SD
50	8	9	6	101	8,9	9	20	7	142	18,4
64	10	17	9	98	14,7	9	17	5	119	12,9
78	10	40	7	95	11,0	9	30	7	100	9,2
92	10	44	6	85	6,0	10	34	5	89	6,5
107	10	43	7	79	6,3	9	34	6	84	4,1
120	9	43	3	73	2,7	10	39	6	76	7,6
134	10	36	7	68	3,5	9	28	4	65	3,9
148	10	33	6	61	3,6	10	33	4	67	2,6
162	10	25	4	56	2,9	10	26	3	63	2,9
176	10	17	3	55	2,8	10	18	2	57	1,8
190	6	10	4	55	6,1	9	11	2	53	2,2
204	10	6	2	52	3,9	4	4	1	52	3,9
218	5	3	0,5			6	2	0,6	47	1,4
232	6	2	0,6			9	1	0,2		

started until the seedlings attained the size of 10 cm. Seedlings sowed after day 205 did not reach that height, but they were subjected to further studies next year. In 1979 the very latest sowings were still growing when the autumn came.

A comparison of the corresponding parcels of 1978 and 1979 reveals conspicuous differences both in the duration and magnitude of height growth between years. As the temperature regulation of the greenhouse was quite restricted and the actual temperatures sometimes deviated several degrees from the intended ones it is not appropriate to make any sophisticated conclusions on the ground of the figures in tables 1 and 2. The individual variation within parcels was not analyzed further in this connection. It should be noted, however, that the withinparcel-variation of the duration of the shoot elongation was much larger in the earliest sowing lots. Their growth cessation took place before the summer solstice.

The actual heat sums accumulated between the sowing and growth cessation and the formation of the terminal bud

respectively are given in figure 5. The results show that in each case the heat sum accumulated between sowing and growth cessation or bud formation decreases gradually as the sowing day is delayed. In most cases, the accumulated heat sums conspicuously exceed the average heat sum of the whole growing season on the locality ($= 1250 \pm 110$ d.d. $> +5^\circ$). There are also clearcut differences both between years, at the same intended temperature and between the intended temperatures in each year. The smoother decline in the curves of 1979 is obviously due to a smaller random variation in observations which in turn is due to increased skill and experience.

The relationships between day length and growth cessation, as well as the formation of terminal buds, are given in figure 6. The lines show that there is no fixed day length link with growth cessation and bud formation. The day length at the time of growth cessation varied between c. 20 hours and c. 13 hours. The earliest sowings finished their shoot elongation while the day length was still increasing and approaching the annual maximum.

On the other hand the curves of growth cessation from different years and temperatures have a much better match than those of the heat sums.

The separate surveys of heat sums and day lengths showed that neither of these factors had such a critical value that could explain the timing of the growth cessation and bud formation. The next step was to study these factors together. In figure 7 the same observations that were used separately in figures 5 and 6 have been plotted in a diagram where the horizontal axis indicates the night length and the vertical axis the heat sum. Night length is used here instead of day length in order to make the values grow from left to right and also proportional to time. The general distribu-

tion reveals a rather regular and even similar pattern in all four cases. In each case the very earliest sowings, 5 in 1978 and 3 in 1979, could perhaps be separated from the rest of the parcels, because they finished the shoot elongation before the summer solstice, during the period of the shortest natural night. The large individual variation in growth cessation in the same lots suggests that an unnatural sequence of events may stir the regulation system.

Even with these lots included, however, the negative correlation between night length and heat sum is quite obvious. As soon as the growth cessation took place after summer solstice, the relation between night length and heat sum follows a regular trend in each case. The longer the

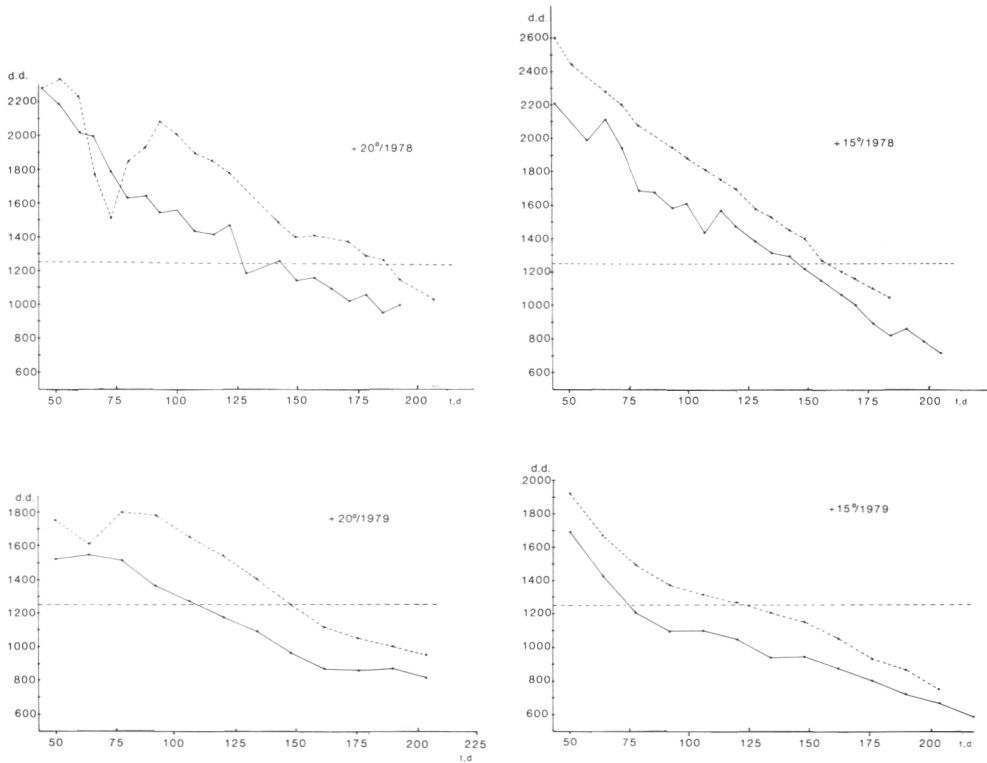


Figure 5. The heat sums accumulated between sowing and growth cessation (solid line) and between sowing and the formation of terminal bud (dotted line). Horizontal scale gives the days of sowing, vertical scale heat-sum, degree days above $+5^{\circ}\text{C}$ accumulated since the day of sowing until the state in question. The dashed horizontal line indicates the average natural heat sum of the locality.

Kuva 5. Kylvöpäivästä pituuskasvun päättymiseen (ehjä viiva) ja päätesilmujen muodostumiseen (katkoviiva) kertynyt lämpösomma eri kylvöajoille. Vaaka-asteikko ilmaisee kylvöpäivän, pystyasteikko lämpösomman d.d.:tä yli $+5^{\circ}\text{C}$, vaakasuora katkoviiva kuvaa koepaikkakunnan keskimääräistä koko kasvukauden lämpösommaa.

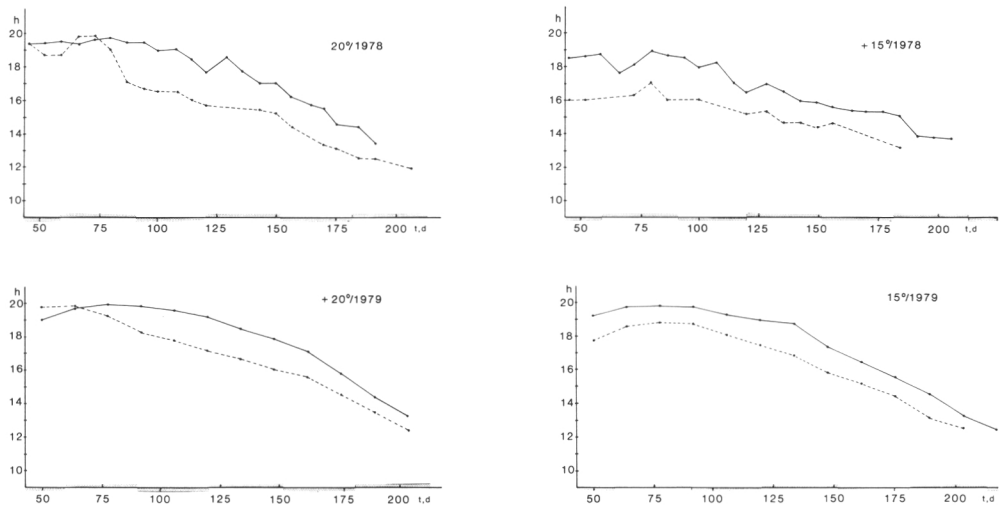


Figure 6. Day lengths of the dates when the seedlings reached 95 % of their total length (solid line) and when 50 % of them had a terminal bud (dotted line). The horizontal axis indicates the sowing days and the vertical axis shows hours between sunrise and sunset.

Kuva 6. Sen päivämäärän päivänpituus, jolloin kunkin kylvöerän koetaimet saavuttivat 95 % loppupituudesta (ehjä viiva) ja 50 % päätesilmuista oli muodostunut (katkoviiva). Vaaka-asteikko ilmaisee kylvöpäivän, pystyasteikko ilmaisee tunteina ajan auringon nousun ja auringon laskun välillä.

night, the shorter was the duration of growth, i.e. the smaller the heat sum. Similarly, the longer the growth had continued, i.e. the higher the heat sum, the shorter night induced growth cessation. In detail, the four sets of combinations do not, however, show any stable ratios between corresponding night lengths and heat sums.

The application of the dynamic model produced both estimates for the parameters and simulated growth curves. The data of 1978 was divided into two parts: (1) the seedlings that grew all the time in the original boxes at +20°C, and (2) the seedlings that were transplanted and moved to +15°C after the initial growth at +20°C. The transplanted seedlings were here omitted because they had been exposed to an extra stress when transplanted. The seedlings raised in 1979 grew all the time in the same containers and they were subjected to one and the same analysis. As there were two parallel series grown at two different temperatures the parameters (T_0) and (a) describing the

temperature dependence ought to be unambiguous. The minimizing of the weighed square sums gave the following parameters:

Parameter	Year	
	1978	1979
h_0	6,3 mm	1,1 mm
a	$0,0046^\circ\text{C}^{-1}\text{d}^{-1}$	$0,0058^\circ\text{C}^{-1}\text{d}^{-1}$
T_0	$5,0^\circ\text{C}$	$1,9^\circ\text{C}$
b	$0,07 \text{ m h}^{-1}$	$0,03 \text{ m h}^{-1}$
L_0	13,0 h	11,8 h

The difference in the values of h_0 originates mainly from the change in the initiation of the height measurements. As regards T_0 , the degree of explanation would have been almost as good if T_0 were fixed at 5°C . The smaller value of night length parameter (L_0) in 1979 is probably due to the deliberately lower level of fertilization in 1979. This was also reflected in the final heights of the seedlings. It is possible that the difference in the level of fertilization caused the deviations in parameters a, b, and L_0 , but it is not certain. In any case the applied

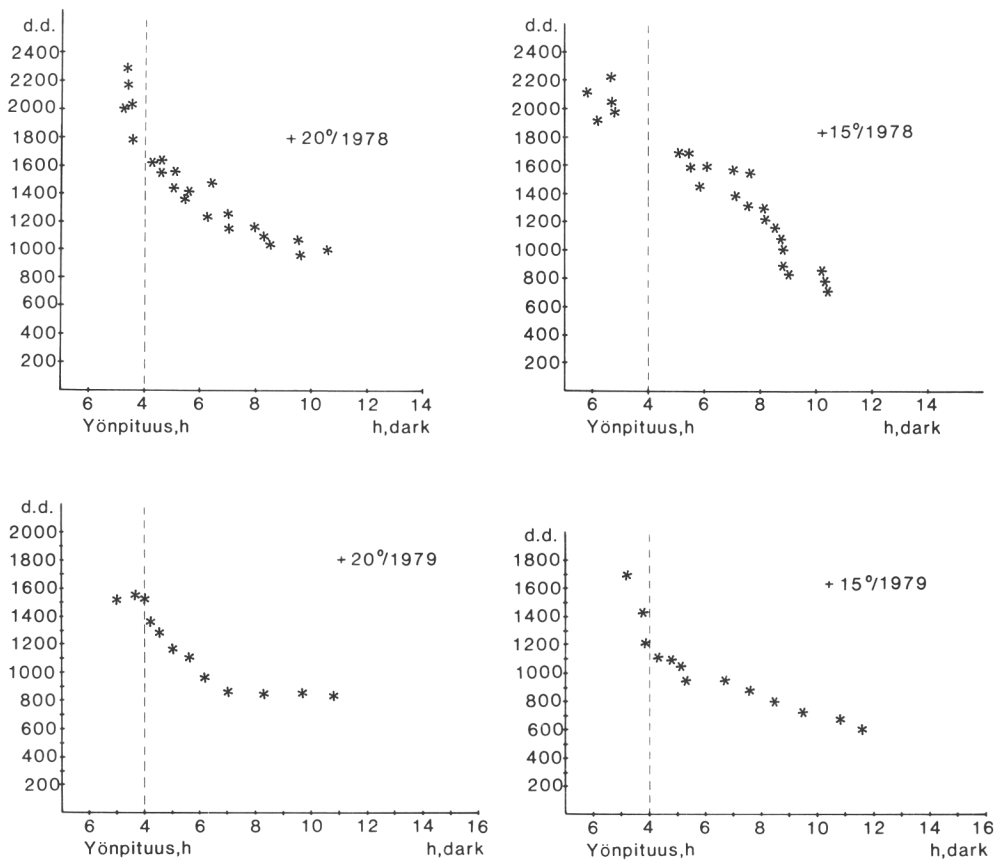


Figure 7. The joint effect of heat sum accumulation and night length on the cessation of shoot elongation during the first growing season. The horizontal scale gives the time between sunset and sunrise in hours, the vertical scale gives the accumulated heat sum (d.d. > + 5° C) from sowing to growth cessation. The minimum natural night length is indicated with the vertical dashed line. The sequence of sowing times goes from the upper left end to the lower right.

Kuva 7. Lämpösomman kertymän ja yönpituuden yhteinen vaikutus pituuskasvun päättymiseen ensimmäisenä kasvukautena. Vaaka-akseli ilmoittaa ajan aurigon laskun ja auringon nousun välillä tunteina, pystyasteikko ilmaisee kylöpäivästä pituuskasvun päättymiseen kertyneen lämpösomman. Lyhin luonnollinen yönpituus on kuvattu pystysuoralla katkoviivalla. Kylvöaikojen mukaan havainnot kulkevat järjestyksessä vasemmalta ylhäältä oikealle alas.

model could not produce consistent parameters for the night length factor. In fact, the model does not include a specific term for critical heat sums but, on the other hand, it is of cumulative character.

The model could simulate the timing of height growth fairly well and in most cases also the amount of growth. The diagrams of the observed and simulated daily height increments are given in figures 8. . .11.

mm/d

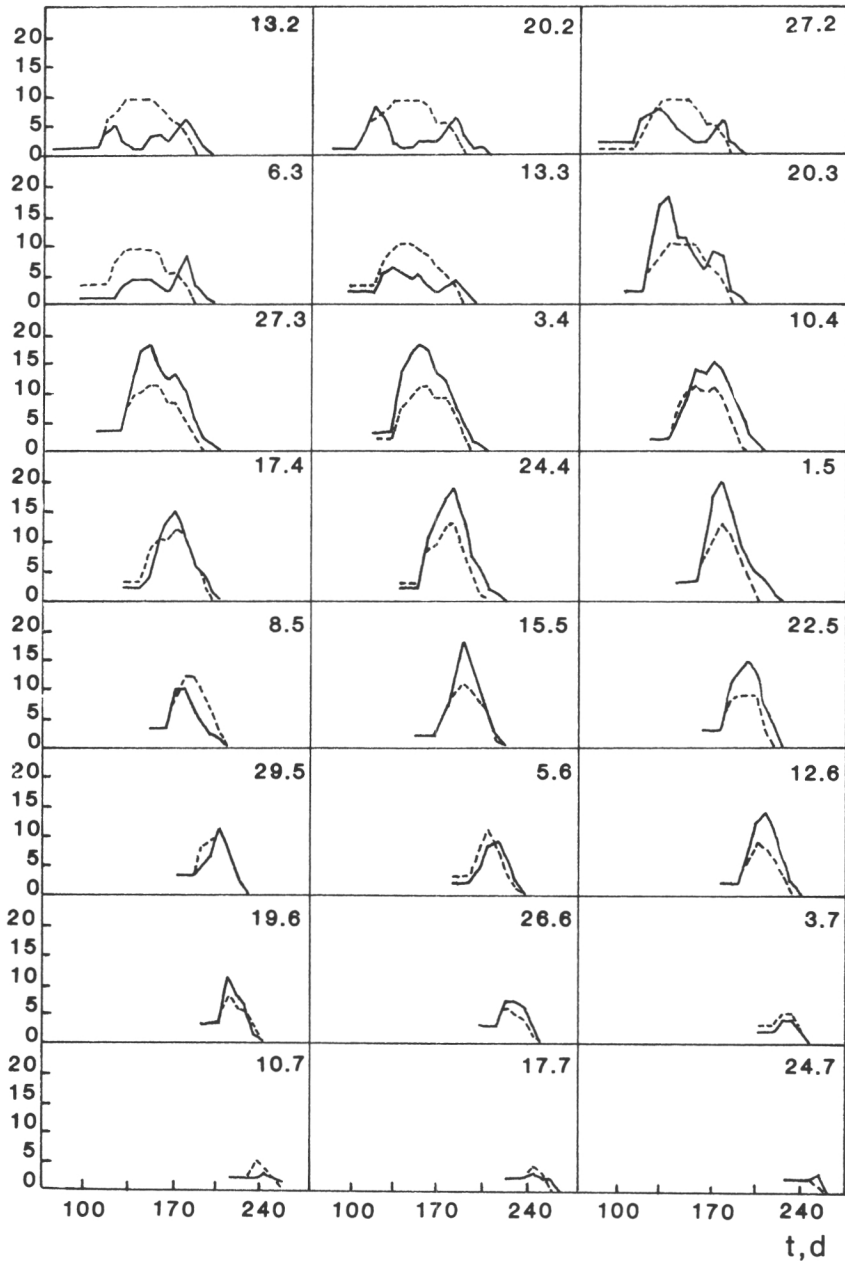


Figure 8. The pattern of daily shoot elongation after different sowing dates in 1978. Horizontal scales give the time in days from the beginning of the year. Vertical scales give the daily shoot elongation in millimeters. Solid lines indicate observed values, broken lines indicate the values obtained from the model. Figures in the upper right corner give the date of sowing (day, month). Intended growing temperature + 20°C, natural photoperiod.

Kuva 8. Päivittäimen pituuskasvu eri kylvöajoille vuonna 1978. Vaaka-asteikko ilmaisee ajan päivinä vuoden alusta. Pystyasteikko kuvaa päivittäistä pituuskasvua millimetreinä. Ehjä viiva esittää havaittuja arvoja, katkoviiva osoittaa mallin mukaan laskettuja arvoja. Numero ruudun oikeassa yläkulmassa ilmaisee kylvöpivän. Tavoitelämpötilä + 20°C, luonnonmukainen valojakso.

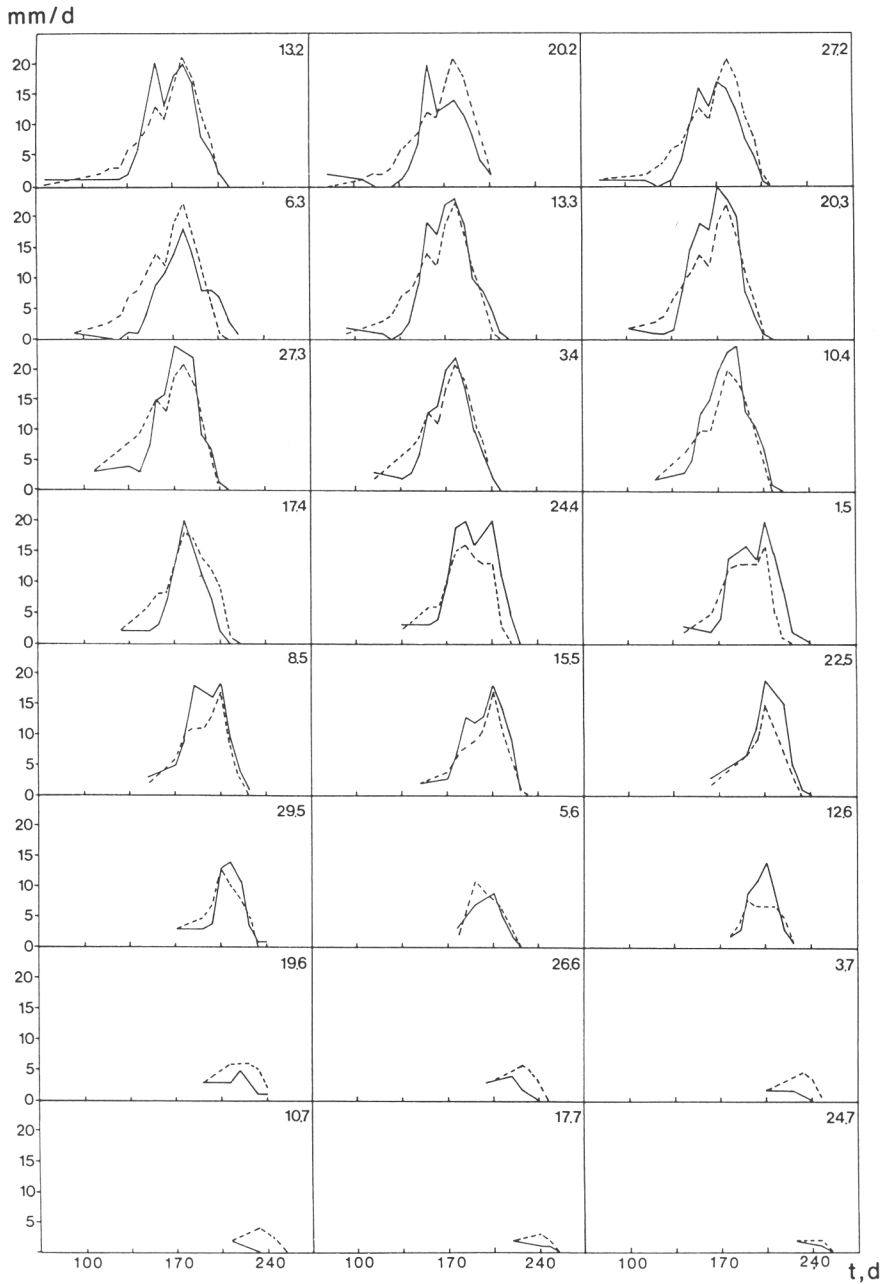


Figure 9. The pattern of daily shoot elongation after different sowing dates in 1978, intended growing temperature $+15^{\circ}\text{C}$, natural photoperiod. Scales and symbols as in Fig. 8.

Kuva 9. Eri kylvöaikojen mitattu ja mallin mukaan laskettu päivittäinen pituuskasvu $+15^{\circ}\text{C}$ ta-voitelämpötilassa vuonna 1978. Vaaka-asteikko ilmaisee ajan päivinä vuoden alusta. Pystyasteikko kuvaa päivittäistä pituuskasvua millimetreinä. Ehjä viiva esittää havaittuja arvoja, katkoviiva osoittaa mallin mukaan laskettuja arvoja. Numero ruudun oikeassa yläkulmassa ilmaisee kylvö-päivän.

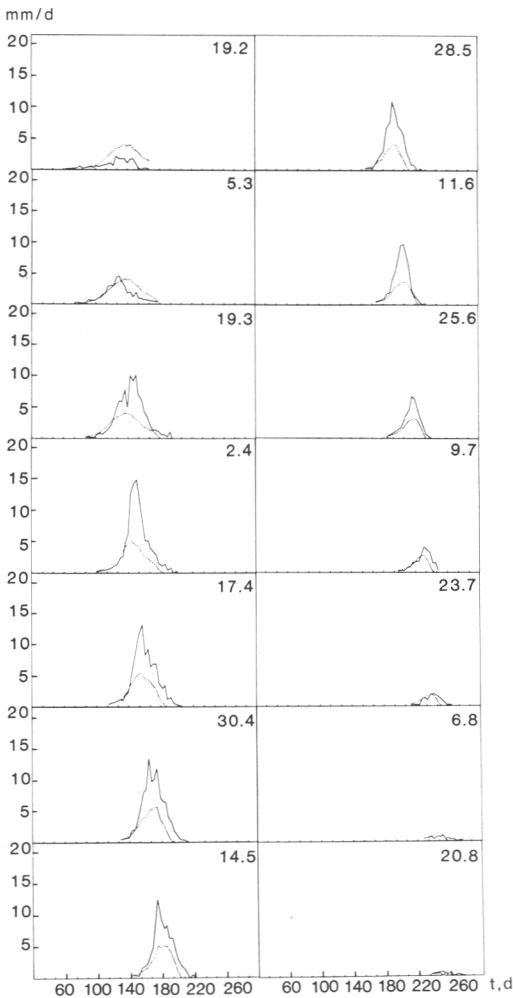


Figure 10. The pattern of daily shoot elongation after different sowing dates in 1979. Intended temperature +20°C, natural photoperiod. Scales and symbols as in Fig. 8.

Kuva 10. Eri kylvöaikojen mitatut ja lasketut päivittäiset pituuskasvut +20°C tavoitelämpötilassa vuonna 1979. Selitykset kuten kuvassa 8.

32. The timing of the shoot elongation and bud formation during the second year

The developmental path of the second growing season deviates essentially from that of the first year because it starts from an existing seedling with a history. If the idea of an autonomous program is used, a starting point at the beginning of the active period is required from which the heat sum is accumulated. In the present case

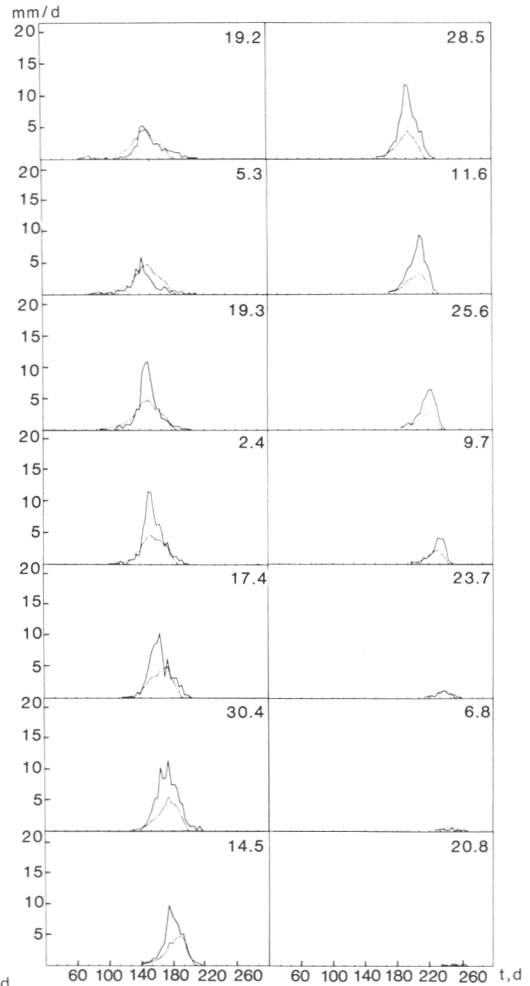


Figure 11. The pattern of daily shoot elongation after different sowing dates in 1979. Intended growing temperature +15°C, natural photoperiod. Scales and symbols as in Fig. 8.

Kuva 11. Eri kylvöaikojen mitatut ja mallin mukaan lasketut päivittäiset pituuskasvut +15°C tavoitelämpötilassa vuonna 1979. Selitykset kuten kuvassa 8.

the opening of the buds was taken as the starting point. The intervals from bud opening to growth cessation and the formation of terminal bud were each studied. The seedlings raised in 1978 at +20°C were taken into the greenhouse in late winter 1979 in three batches at two week intervals. The fourth part of the material was left out of doors. Observations and measurements were carried out separately by original parcels (sowing days) of 1978.

As the sowing date in 1978 varied from

February 13th to August 28th, a rather heterogenous behaviour could be expected during the second growing season. The first question to arise was whether all lots start their second year from the same line or do they "remember" the differences of the first summer. In figures 12 and 13 the results are shown relative to heat sums and day lengths. In all treatments there are differences between parcels of the previous year, but no such trends as in the first year (cf figures 5 and 6). The number of seedlings per parcel was originally rather small and it was still reduced during the winter.

Therefore the variation is considered to be random and to originate mainly from the small size of the samples.

The effect of synchronization during the dormancy was given further support by another experiment in 1980 in which the corresponding parcels of 1979 were compared with each other. These results are given in figure 14. It was concluded that the differences of the annual rhythm had disappeared during the dormancy period. Consequently each treatment of the 2nd year could be described by the average of all the seedlings of all the parcels of the first year.

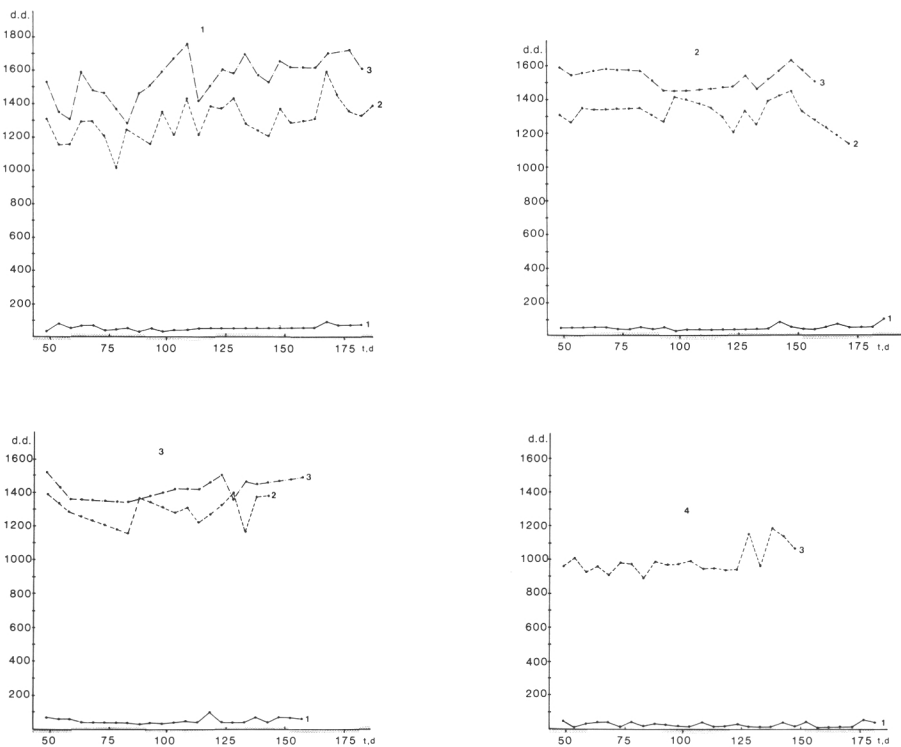


Figure 12. The behaviour of the seedlings during the second growing season (1979) in four treatments. Each treatment consists of seedlings of different sowing dates in 1978. Horizontal scale in each treatment refers to the day of sowing. Vertical scales give the accumulated heat sums (d.d. + 5° C). The line 1. indicates bud opening, the line 2. Growth cessation and the line 3. formation of terminal buds. Treatment 1 taken into greenhouse on the 19th of March, 1979, treatment 2 into greenhouse on the 4th of April, treatment 3 into greenhouse on the 19th of April, and treatment 4 was control out of doors. Treatment 4 was damaged by late frost and no top shoots developed. Bud formation was observed at the lateral shoots.

Kuva 12. Eri aikoina kylvettyjen taimien käyttäytyminen talvilevon jälkeen toisena kasvukautena. Taimet kasvatettiin vuonna 1978 ja koe tehtiin vuonna 1979. Vaaka-asteikko viittaa vuoden 1978 kylvöpäivään. Pystyas- teikko viittaa lämpösummaan vuonna 1979. Kuvaaja 1. viittaa silmujen avautumiseen, viiva 2 pituuskasvun päättymiseen ja viiva 3 päätesilmujen muodostumiseen. Käsitely 1 otettiin kasvihuoneeseen 19.3.1979, kä- sittely 2 otettiin kasvihuoneeseen 4.4.1979, käsittely 3 otettiin kasvihuoneeseen 19.4.1979 ja käsittely 4 oli ulkona kasvanut vertailuerä. Myöhäistalven pakkaset vikuuttivat käsittelyn 4 päätesilmuja, joten pituuskas- vua ei voitu mitata. Päätesilmut havaittiin uusista sivuversoista.

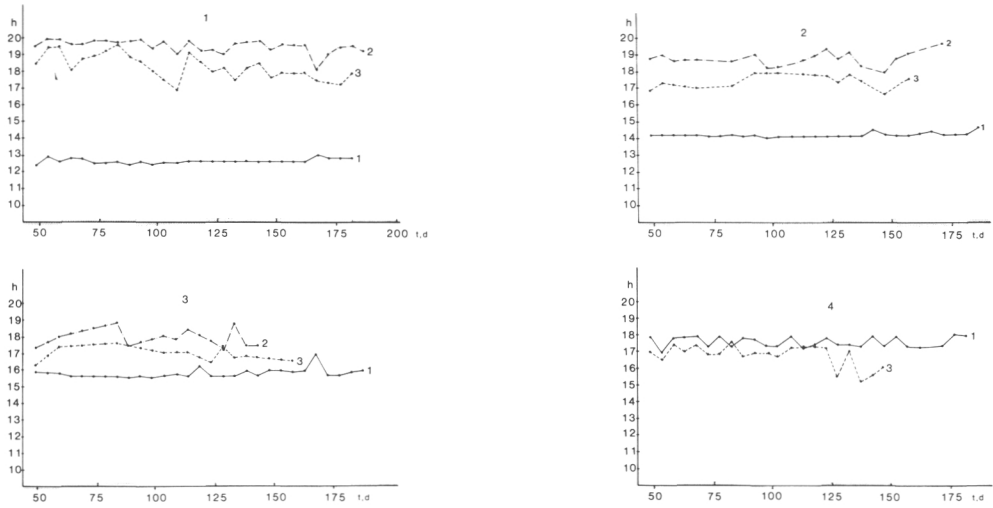


Figure 13. The behaviour of the seedlings during the second growing season (1979) relative to day length. Treatments and symbols as in Fig. 12.

Kuva 13. Eri aikoina kylvettyjen taimierien käyttäytyminen talvilevon jälkeen suhteessa päivänpituuteen. Taimet kasvatettiin vuonna 1978 ja kokeet tehtiin vuonna 1979. Käsitteilyt ja merkien selitykset kuten kuvassa 12.

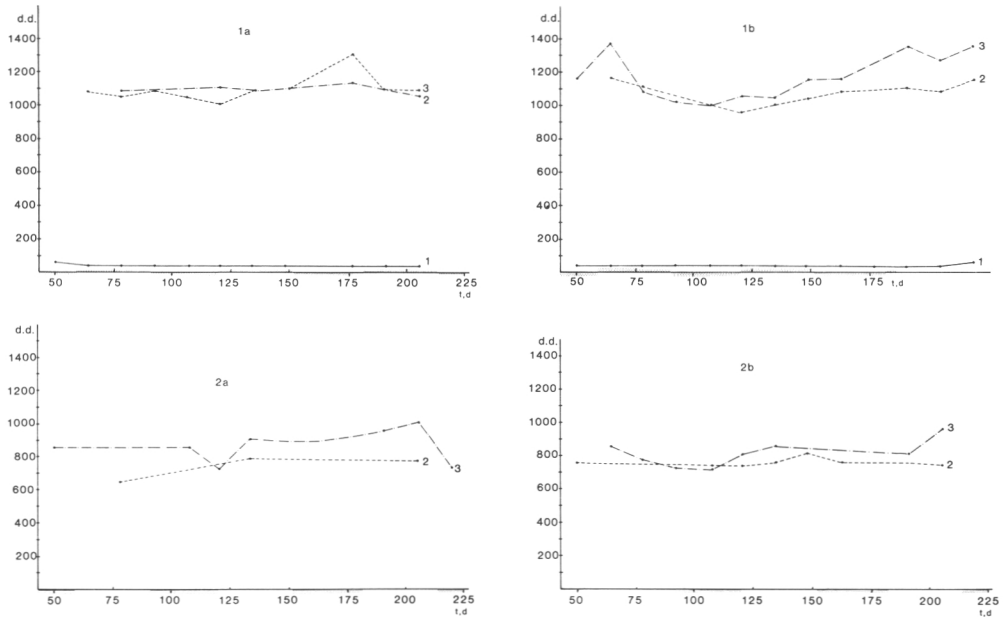


Figure 14. The behaviour of the seedlings during the second growing season (1980) in two different treatments. Each treatment consists of seedlings of different sowing days in 1979. Treatment 1, out of doors, natural temperature and photoperiod. Treatment 2 extended winter, transferred out on the 17th of June. Horizontal scale refers to the sowing days in 1979. The vertical scale show the accumulated heat sum (d.d. > + 5°C) in 1980. For symbols of the treatments see table 4.

Kuva 14. Eri aikoina kylvettyjen taimierien käyttäytyminen talvilevon jälkeen toisena kasvukautena. Taimet kasvatettiin vuonna 1979, kokeet tehtiin vuonna 1980. Käsitteilyt on selostettu taulukossa 4 ja asteikot ja muut merkit kuten kuvassa 12.

The treatments in 1979 and 1980 with the seedlings raised during the previous growing season were considered analogous to the repeated sowing times of the first year. Due to the small number of seedlings the growing within greenhouse was carried out only in one temperature. In fact the total number of seedlings was large enough, but there was no evidence concerning the synchronization in advance.

The results of the experiments in 1979 are given in table 3. In all treatments, started considerably before the normal spring the buds opened in 5 or 6 days in the greenhouse, which equalled around 50 d.d. heat sum accumulation. Out of doors the heat sum of bud opening was only 25 d.d. The difference was probably due to the rest of the winter dormancy that staggered the start in greenhouse treatments. Nevertheless, the problem of the true starting point could be evaded when the opening of the buds was taken as a milestone. The interval from bud opening to growth cessation is rather similar in all greenhouse treatments and particularly in terms of heat sum.

Unfortunately the shoot elongation and growth cessation could not be measured out of doors because of the damages to terminal buds of the first year. In the formation of terminal buds there were indications of a trend of decreasing heat sums and shortening durations. The most clearcut difference was between the natural development out of doors and all the greenhouse treatments with regard to duration. The date, and consequently the day length, of bud formation was almost the same in the latest greenhouse treatment as out of doors.

In the experiment of 1980 the time difference in the beginning of the active period was arranged towards the opposite direction. The beginning was postponed with an extended artificial winter. The temperature of the melting ice could not maintain the winter dormancy, and after some weeks the buds began to swell. The time difference from the natural start was about 20 days. The timing of the bud opening, growth cessation and formation of terminal buds is given table 4. This time the experimental material was composed of

Table 3. The timing of bud opening, growth cessation and the formation of terminal buds during the second growing season. Seedlings raised in 1978. Treatments 1, 2 and 3 were taken into greenhouse at two weeks' intervals in late winter 1979. Each treatment consists of seedlings from several sowing times of the previous year.

Taulukko 3. Silmujen avautumisen, kasvun päättymisen ja päätesilmujen muodostumisen ajoittuminen toisena kasvukautena vuonna 1979. Taimet kasvatettiin kesällä 1978. Käsitellyt 1, 2 ja 3 otettiin sisälle kasvihuoneeseen loppupalvelle vuonna 1979 kahden viikon välein. Kussakin käsittelyssä on mukana taimia usealta kylvökerralta edellisestä vuotena.

Treatment Nr and description Käsitellyn N:o ja kuvaus	50 per cent of buds open			95 per cent of shoot elongation			50 per cent terminal buds		
	day number	d.d.	day length, h	after days	bud burst d.d.	day length, h	after days	bud burst d.d.	day length, h
	50 % silmuista puhjennut			95 % pituuskasvusta			50 % päätesilmuista muodostunut		
	Pv n:o	d.d.	Päivän pituus	Päiviä	d.d.	Päivän pituus	Silmujen puhke- misen jälkeen Päiviä	d.d.	Päivän pituus
1. start on day 78, in greenhouse <i>1. tuotu kasvihuoneeseen päivänä 78</i>	84	55	12,6	101	1 236	19,5	121	1 499	18,2
2. start on day 94, in greenhouse <i>2. tuotu kasvihuoneeseen päivänä 94</i>	99	49	14,2	99	1 270	18,7	116	1 481	17,4
3. start on day 109, in greenhouse <i>3. tuotu kasvihuoneeseen päivänä 109</i>	115	55	15,8	94	1 252	17,8	105	1 383	16,9
4. natural start out of doors <i>4. luonnonmukainen liikkeelle läbrö ulkona</i>	134	25	17,6	*—	*—	*—	86	966	16,8

*) Late frost damaged terminal buds out of doors. That is why the shoot elongation could not be measured. The formation of terminal buds was observed in the new leaders.

*) Loppupalveln pakkaset vikuuttivat päätesilmuja ulkona. Tästä syystä ei pituuskasvua voitu mitata. Päätesilmujen muodostaminen havaittiin uusista versoista.

Table 4. The timing of bud opening, growth cessation, and formation of terminal buds during the second growing season. Seedlings raised in 1979. Treatment 1 was growing out of doors. Treatment 2 was kept in ice basin in order to extend the winter dormancy. Each treatment consisted of two sub-sets as the seedlings raised in 1979 at 20° C and at 15° C were measured separately.

Taulukko 4. Silmujen avautumisen, pituuskasvun päättymisen ja päätesilmujen muodostumisen ajoittuminen toisena kasvukautena vuonna 1980. Taimet kasvatettiin kesällä 1979. Käsitely 1 kasvoi ulkona. Käsitely 2 tapabrui jääkellarissa, sen tarkoituksena oli jatkaa talvilepoa. Kumpikin käsittely sisälsi 2 erää, koska vuonna 1979 20° C ja 15° C lämpötiloissa kasvatetut taimet mitattiin erikseen.

Treatment Nr and description Käsittelyn N:o ja kuvaus	50 per cent of buds open			95 per cent of shoot elongation			50 per cent terminal buds		
	day number	d.d.	day length, h	after days	bud burst d.d.	day length, h	after days	bud burst d.d.	day length, h
	50 % silmuista puhjennut			95 % pituuskasvusta			50 % päätesilmuista muodostunut		
	Pv n:o	d.d.	Päivän pituus	Päiviä	d.d.	Päivän pituus	Silmujen puhke- misen jälkeen Päiviä	d.d.	Päivän pituus
1a; 1 st year at +20°C, 2 nd year out of doors <i>1a, ensimmäinen kasvukausi 20°C, toinen ulkona</i>	130	37	17,1	96	1 059	16,3	93	1 055	16,6
1b; 1 st year at +15°C, 2 nd year out of doors <i>1b, ensimmäinen kasvukausi 15°C, toinen ulkona</i>	131	38	17,2	97	1 043	16,1	111	1 141	14,7
2a; 1 st year at +20°C, 2 nd year extended winter, growing out of doors <i>2a, ensimmäinen kasvukausi 20°C, toisena vuotena pidennetty talvilepo, kasvat- tus ulkona</i>	154	*0	**—	74	738	16,1	78	798	15,7
2b; 1 st year at +15°C, 2 nd year extended winter, growing out of doors <i>2b, ensimmäinen kasvukausi 15°C, toisena vuotena pidennetty talvilepo, kasva- tus ulkona</i>	149	*0	**—	78	762	16,2	102	928	13,8

*) The temperature in the basin was about zero and no temperature sum above +5° C was accumulated. As reported by Sarvas (1972) the active period can proceed slowly even at this temperature.

*) Lämpötila jääkellarissa oli lähellä nollaa, joten lämpösomaa yli +5° C ei voisi kertyä. Sarvaksen (1972) mukaan aktiiviperiodi etenee hitaasti myöskin tässä lämpötilassa.

**) The seedlings were kept in darkness that was interrupted occasionally when checkings and observations were made. Thus there was no regular photoperiod.

**) Taimet olivat kellarissa pimeässä ja ne saivat valoa ainoastaan satunnaisesti silloin, kun tarkistuksia ja mittauksia tehtiin. Niillä ei siis ollut mitään säännönmukaista fotoperiodia.

seedlings raised at either 20°C or 15°C in the previous year. Those sub-sets were also measured and calculated separately. The difference in heat sums and day length of bud opening from those of the previous year was small compared to the accuracy of the results. In the ice cellar, no heat sum above +5° C was accumulated until bud opening. The accumulated amount of period units Sarvas (1972), could here be neglected as the bud opening itself was used as the starting point of further calculations. The results from the two sub-sets in each treatment were slightly different. Relative to the accuracy of the means these differences do not allow any conclusions. The two treatments, however, resulted in different values of heat sums,

but in fact equal day lengths for growth cessation. Even though there was a difference of about three weeks in the initiation between treatments they finished their shoot elongation simultaneously. In other words, after the artificially extended winter the seedlings passed the same period interval with 300 d.d. units smaller heat sum than the seedlings growing permanently out of doors. The results for bud formation display a larger scatter, but the same kind of tendency is still visible. Because of the technical limitations the number of treatments was small and the time shifts to opposite directions could be arranged only in different years. For this reason the combination of the data and its plotting together was made with

reservations. Figure 15 shows the observed relationships of growth cessation to increasing night length and heat sum during the second growing season. The diagram has quite a different form from the corresponding ones of the first growing season in figure 5. Unfortunately observations between 6 and 7,5 hour night lengths and 1100. . . 1200 d.d. heat sums did not occur in the experiments.

The few points of the second year would suggest that as long as the night was

shorter than 6 hours the shoot elongation continued until a heat sum of about 1250 d.d. had accumulated, but as soon as the night length was close to 8 hours the shoot elongation ceased with a distinctly smaller heat sum. The highest heat sums were essentially lower than those of the first growing season. Even in greenhouse treatments the shoot elongation ceased when the accumulated heat sum was of the same magnitude as the average local heat sum of the whole growing season.

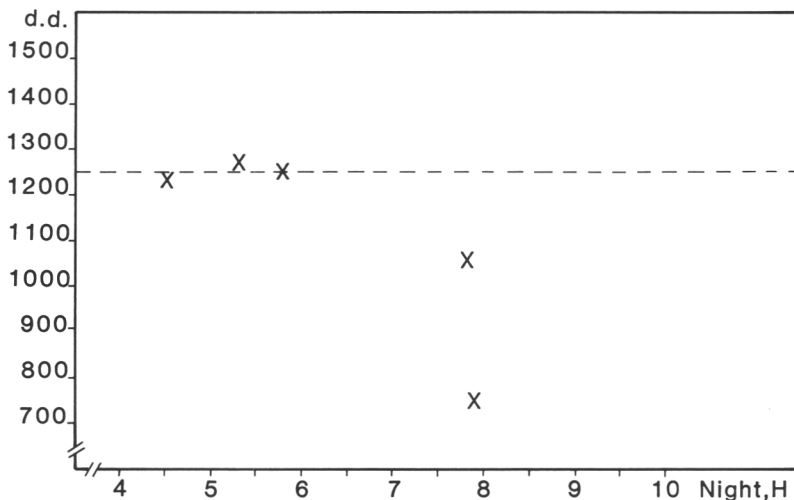


Figure 15. The relation of growth cessation to the combination of night length and heat sum accumulation during the second growing season. The horizontal axis gives the natural night length in hours on the day when the average height of the seedlings reached 95 per cent of the final height. The vertical axis gives the accumulated heat sum above + 5° C from bud opening to growth cessation. The dashed horizontal line indicates the average heat sum of the whole growing season in Punkaharju.

Kuva 15. Pituuskasvun päättymisen suhte yönpituuteen ja kertyneeseen lämpösummaan toisena kasvukautena. Vaaka-asteikko antaa luonnollisen yönpituuden tunteina sinä päivänä, jolloin 95 % loppupituudesta oli saavutettu. Pystyasteikko ilmaisee kertyneen lämpösumman silmun puhkeamisen ja pituuskasvun päättymisen välillä. Vaaka-suora katkoviiva osoittaa paikkakunnan keskimääräisen koko kasvukauden lämpösumman.

4. DISCUSSION

The main result of the experiments was that the simple method used could elucidate the influence of both the temperature dependant progress of the active period and photoperiodic changes. At the beginning of the growing season, in long day conditions, growth cessation and formation of terminal buds took place because the program of the active period autonomously reached a certain stage. Increasing night lengths, however, resulted in accelerated spans of growth cessation and bud formation. The experiments were mainly made with first year seedlings. They did not indicate any fixed critical values of heat sums or photoperiods. The effect of the photoperiod seemed to increase gradually and to be proportional to the night length. The observations on the seedlings of the second year were few. They suggested, however, that both the temperature dependent progress of the cycle and the influence of photoperiod are involved. The relations of these two factors seemed to deviate from those of the first year.

As regards the genetic background of the climatic adaptation and modelling of the progress of the annual cycle, no factual characteristics could be obtained. The observed values of heat sums were not in accordance with the local natural growing season and neither were they consistent from year to year. Neither a combination of night length and heat sum nor a dynamic model including both temperature and night length resulted in applicable parameters. Obviously still other factors, such as nutrition concentrations, modify the progress of the active period. The experiments of the seedlings behaviour of the second growing season had not been repeated at this stage for, except the synchronizing effect of the dormancy. No information can therefore be given concerning the stability of the growth cessation responses. In any case, after the present results all one factor explanations of the

regulation of the annual rhythm seem unrealistic. The method introduced in this paper needs much further development. The mathematical procedures also require considerable refinement before an invariant description of the regulatory system is available.

In his model of the annual cycle of forest trees, Sarvas (1972, 1974) took into consideration the entire year. His starting point was the fact that in the nature the date of certain phenological phase, above all, anthesis, is not constant from year to year. The unpredictable variation which can mean differences of several weeks between years greatly hampers field work of the studies on flowering as well as controlled crossings. It was then determined that the flowering took place every year when a certain heat sum above $+5^{\circ}\text{C}$ had accumulated irrespective of the date. From this simple coincidence the model was gradually extended to the whole active period (Sarvas 1967, 1969, 1972), and finally it included also the autumn dormancy and the winter dormancy Sarvas (1974). The function of the model, called the physiological clock by Sarvas (op.cit. and J. Sarvas 1977), seemed to be independent of external impulses like photoperiodic changes. The name of the model was unfortunately the same that has been used generally in another meaning. The term physiological clock usually refers to periodic diurnal or circadian phenomena in many kinds of organisms (Bünning 1963). The term biological clock has been used for fixed oscillations (see eg. Sollberger 1965). In the general the stress in the above terms is on the word "clock". The organisms are supposed to contain a pace maker whose oscillation is insensitive to environment and that regulates physiological processes. Sarvas (op.cit) in turn stressed the word "physiological". The rate of physiological processes depends on temperature, and the progress of the annual cycle is made up of completed physiological processes. The an-

nual cycle and the physiological clock in the meaning of Sarvas are auxiliary concepts that need not have physical counterparts in trees. Accumulation of heat sums or period units simulates the sequence of events in plants without an image of the trees calculating heat sums (see Sarvas 1972 p. 68 and Landsberg 1977). The model of Sarvas presupposes that each of the main phases is homogenous relative to its temperature response (J. Sarvas 1977).

The experimental methods of Sarvas did not detect the possible effects of external impulses. Obviously the role of photoperiod or other impulses were masked by the conspicuous climatic variation in natural populations. The technique used in the present study also could not reveal the timing or magnitude of the photoperiodic signal *per se*. The response to photoperiod or any other signal from the environment was naturally initiated a certain time previous to the visible outcome. So far, it is not certain that the time lapse or the accumulated heat sum between the impulse and the final result would be constant. As regards studies on photoperiod, which have mainly been carried out in phytotrones or growth chambers, the extreme light conditions have probably masked the temperature dependent rate of progress.

A very difficult problem in the study of climatic adaptation and its genetic background is the lack of objective traits that can be directly measured. We can speak about earliness, lateness, the depth of the dormancy etc. without any specific units. A biological clock system based on day units and permanent durations and predetermined dates of all phases is out of question. The suggestions by Sarvas (1972, 1974) to describe the annual cycle and its progress by means of special units of cycle intervals is a valuable idea as such regardless, as to whether the units are absolutely correct. Sarvas (*op.cit.*) included in his units the joint effect of temperature and time. Finally he described the non-linear regression of the rate of progress of the annual on temperature in the three main phases of the annual cycle. Of the main phases, the active period provides the most obvious visible incidents, but the exact be-

ginning and ending of it are still obscure. Obviously the limits towards dormancy periods are not very sharp. In the present work the problem of the total length of the active period has been avoided by studying certain period intervals within the active period. By definition the meristems are active only during the active period and consequently the active period comes to an end after growth cessation and bud formation. On the other hand the timing of growth cessation must be related to the end of the whole active period. In the same way the opening of buds is related to the beginning of the active period. In studies of adaptability to a certain climate, the numeric characteristics of all three main phases, as well as the limits between active and dormant phases, must be properly defined. In the present study the principle of the regulation of the progress of the active period has been dealt with. The observed joint effect has not, to the authors' knowledge been reported earlier.

Unfortunately the earlier literature neither contains such results that could be compared with the values obtained in the present study. Reports concerning photoperiodic responses of birch (Vaartaja 1959, Håbjørg 1972, 1978) do not contain detailed temperature data. In the study by Raulo and Leikola (1974), which was carried out at the same locality as the present study, the photoperiod was not mentioned and the growth cessation was defined in a different way. There are several observations of the interaction of photoperiod and temperature for birch (Håbjørg 1972) and for spruce (Heide 1974 a, b, Dormling 1978, Magnesen 1969, 1971, 1972), but temperature was considered only a modifying temporal factor.

The idea of repeated starts has been used earlier in studies connected with the termination of the active period, Tumanov et al. (1972), Pohtila (1977), and Hulten (1980) but not for the same purpose as in the present study.

The establishing of experiments with repeated starts at regular intervals is easiest when the initial material is seed. On the other hand the first growing season after germination contains no such sharp phenological events that could be

accurately observed. Frequent measurements of the total height give the possibility to calculate, afterwards, the time of any relative height. In this study 95 per cent of the final height was used as the point of growth cessation. The terminal bud is a concrete morphological feature, but still the limit between alternatives not-formed — formed is arbitrary. Autumn coloration and leaf abscission did not take place in an ordinary way in the greenhouse and hence did not provide any further information.

The second growing season is operationally more difficult than the first one. In addition to the technical problems with shortened or extended winter rest, there is the uncertainty of the influence of the winter dormancy and of invisible damages. The opening of buds provides quite a sharp phase in the beginning of the active period. Stages of the reproductive development would also be of special interest because of their timing and also in order to study their linkage to vegetative processes. Birch flowering can be promoted at a young age (Kärki 1977), but the saplings are then at least 2 m tall, which in turn causes technical difficulties with space.

The observed difference between the first and second year in the growth cessation versus heat sum — photoperiod combinations was not unexpected. Intuitively it seems useful that the program of the very first active period is rather flexible. In that case the period for successful germination is longer. According to Sarvas (1972 p. 18) *Betula pendula* has no seed dormancy and the seed dispersal takes place mainly in late summer. Differences in the photoperiodic reactions of the first year seedlings and those of subsequent years were observed eg. by Heide (1974) and Eriksson & al. (1978) at spruce. The behaviour of the first year is certainly linked with free growth and non-existence of buds, but this correlation does not prove any causal relations. The difference may as well be at gene level and is being expressed in several different ways.

In the present study the heat sums were calculated with a simple linear function and threshold temperature of $+5^{\circ}\text{C}$. As regards linear heat sums, Arnold (1959)

and Sarvas (1972) have studied the significance of the base temperature and they have both come to the conclusion that $+5^{\circ}\text{C}$ is the most suitable base temperature. The non-linear period unit (p.u.) scale suggested by Sarvas (op.cit.) is more sophisticated than the degree day (d.d.) scale, but within the temperature regime $+10^{\circ}\text{C}$. . . $+25^{\circ}\text{C}$ the difference between the two approximations is negligible (see Sarvas 1972 p. 63). It would have been possible to find specific base temperatures and coefficients of temperature dependence by means of iterative calculations. For instance, Skjelvåg (1981) has applied such a method. With complex heat sum equations the results of separate experiments can be made to fit to one pattern but the benefit is questionable. It is hard to believe that the regulatory systems of trees could be labile in this respect.

The mathematical model developed for the present study explains the daily height increment with the actual temperature and photoperiod. In its present form the model does not include a term for the progress of the active period in terms of heat sum accumulation. However, as visualized in figure 4, the model leads to growth cessation even in a constant environment. Predecessors of the model were published earlier by Mork (1941), Dahl and Mork (1959), Robertson (1968), Hari et al. (1970), Pohjonen and Hari (1973), Parviainen (1974).

The idea of simulating the annual development with heat sum accumulations can be traced back to Reaumur (1735 cit Sarvas 1972). As early as 1867 Linsser suggested that native plant species have been adapted to the average heat sum of the growing season and that the heat sum required to reach a certain phenological phase is always proportional to the average heat sum of the entire growing season. This report was, however, unknown for a century. Langlet (1967) and Sarvas (1969) reintroduced Linsser's principles into scientific discussion. In agriculture and horticulture heat sums were found useful practical measures of the time of flowering and of the ripening of the crop. Arnold (1959) stated that the heat sum accumulation actually simulates the

physiological progress of the annual cycle. Robertson (1968) introduced the "biometeorological time scale" that is analogous to the active period of Sarvas (1967). Robertson (op.cit.) included both day and night temperatures as well as photoperiod in his model. Recently Skjelvåg (1981) introduced a model that is based on similar assumptions as those of Sarvas (1972, 1974), i.e. the additivity and irreversibility of the progress. In his study on the rate of CO₂ uptake on pine Pelkonen (1981) came to the conclusion that the "rate of maturation" may sometimes be negative. This is an interesting observation, but it need not be contradictory to the irreversibility of the progress of the annual cycle. The rate of metabolic processes as well as the absolute growth rate during the cambial activity are not directly elements of the annual cycle. They are certainly influenced quite strongly by the temporal environmental factors.

The annual rhythm of perennial plants and the progress of development of annual plants have been comprehensively investigated since the beginning of the modern science. Separate approaches or schools of research can be detected in

retrospect. A very effective isolation seems to have occurred between forest research, botany, and agriculture. A surprising contradiction or ignorance has existed between the photoperiod school and the heat sum school. An attempt to incorporate both models was made by Stern and Roche (1974 pp. 15—16) who suggested such a combination where the heat sum simulation is valid in spring whereas the timing of the events in late summer is based on photoperiod. The results of the present report actually support this kind of hybrid model for birch. The active period proceeds due to the autonomous regulation even without any external signals. The rate of progress depends on temperature. In late summer, if the autonomous progress is too slow relative to the approaching autumn the increasing night length accelerates the progress. There is, nevertheless, no abrupt critical value for the night length. The sensitivity to night length increases gradually towards the end of the active period. On the other hand gradually increasing night length produces a response at a more and more early stage of the active period.

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SELOSTE

Lämpösunnan ja päivänpituuden yhteisvaikutuksesta 1- ja 2-vuotisiin rauduskoivun taimiin

Johdanto

Puiden sopeutuminen vuodenaikojen vaihteluun viileässä ilmastovyöhykkeessä perustuu kahteen ilmiöön. Ensiksi puiden, kuten kaikkien monivuotisten kasvien, täytyy pystyä muuttamaan aktiivisesta tilasta pakkasia ja fysiologista kuivumista kestäväään tilaan talven ajaksi ja taas palautumaan aktiiviseen tilaan kasvukauden ajaksi. Toiseksi, siirtymisen aktiivisesta tilasta lepo- ja horrosvaiheeseen ja päinvastoin täytyy joka vuosi puun koko elinaikana tapahtua oikeaan aikaan vuodenaikojen vaihtuessa. Tässä tutkimuksessa selvitettiin sitä periaatetta, jolla puut ohjaavat vuotuista päävaiheiden ja yleensä kaikkien vuosijakson tapahtumien ajoitusta.

Erilaisista eliöillä esiintyvistä säännöllisesti toistuvista eli rytmillisistä ilmiöistä on julkaistu tavattoman paljon tutkimustuloksia. Luonnonvaraiset puulajit noudattavat hämmästyttävän hyvin vuodenaikojen vaihtelua siitä huolimatta, että sääsuhteet eri vuodenaikoina eivät ole samanlaisia. Puut eivät kuitenkaan pelkästään mukaudu sen hetkiseen säättilaan, vaan ennakoivat tulevan muutoksen, esim. siirtyvät loppukeksällä lepotilaan jo ennen pakkasten tuloa. Vuosirytmien säätelyä on pyritty selittämään jo 1700-luvulta lähtien. Selityksistä voidaan löytää kaksi kovin erilaista ajatusmallia. Toisaalta on oletettu, että vuosirytmii toimii autonomisesti, eikä tarvitse kasvin ulkopuolelta tulevia signaaleja eri vaiheiden ajoituksen ohjaukseen. Koska elintoimintojen nopeus riippuu lämpötilasta, vuosijakson etenemistä voidaan kuvata lämpösunnan kertymän avulla. Toisaalta on oletettu, että kasvit tarvitsevat luotettavia aikamerkkejä, jotta niiden vuosirytmii pysyisi oikeassa tahdissa vuodenaikojen vaihtelun kanssa riippumatta sään oikullisuudesta. Tärkeimpänä aikamerkinä on pidetty päivänpituuden eli fotoperiodin säännöllistä vuotuista vaihtelua. Lämpösunnan ja vuosirytmien yhteenkuuluvuutta esitti Reaumur jo 1735, mutta tämä teoria ei tullut yleisesti tunnetuksi. Joitakin uusia lämpösunnakehitelmiä esitettiin myös 1800-luvulla. Metsäpuiden suhteen tunnetaan nyt parhaiten Linsserin julkaisu vuodelta 1867. Tämän vuosisadan alkupuolella keksittiin fotoperiodin vaikutus kasvien vuosirytmii, kehitykseen ja kukkimiseen. Tämän jälkeen vuosirytmii on lähes yksinomaan pyritty selittämään ulkopuoliseen ohjaukseen perustuen. Fotoperiodisia reaktioita puilla on tutkittu hyvin paljon Ruotsissa ja Norjassa (esim. Dormling ja muut, Heide, Håbjørg, Magesen) fytotronikokeilla. Suomessa Sarvas lähti siitä tosiasista, ettei tietty fenologinen vaihe luonnossa satu joka vuosi samalle päivämäärälle, kuten fotoperiodiohjauksen mukaan pitäisi tapahtua. Sen sijaan samaan fenologiseen vaiheeseen mennessä kertynyt lämpösunna pysyi vuodesta toiseen vakiona. Tältä pohjalta Sarvas kehitti

mallin, joka edelleen on lajissaan ainutlaatuinen. Malli käsittää ensinnäkin koko vuosijakson ja toiseksi siinä on määritelty mitattavat yksilöt vuosijakson etenemiselle ja etenemisnopeuden lämpötila riippuvuudelle.

Kahden tässä mainitun selitysmallin — "lämpösunnateorian" ja "fotoperioditeorian" vastakkaisuus on metsäpuiden kohdalla mennyt niin pitkälle, etteivät eri suuntien tutkijat siteeranneet toistensa töitä julkaisuissaan. Peltokasvien tutkijat ovat olleet avarakatseisempia (Robertson 1968, Skjelvåg 1981). Tosin Stern ja Roche (1974) esittivät lämpösunnan ja fotoperiodin yhdistämistä metsäpuiden vuotuisen jakson ohjauksessa.

Luonnossa valotekijä ja lämpötekijä ovat niin kiinteästi yhteydessä toisiinsa, että pelkkien havaintojen ja mittausten avulla kysymystä autonomisen ohjauksen ja ulkoisten aikamerkkien suhteista tuskin voidaan ratkaista. Fytotronikokeet on tehty niin paljon luonnosta poikkeavissa olosuhteissa, että niistä saadut lukuarvot eivät ole sopuisuudessa todellisuuden kanssa. Tämän tutkimuksen tarkoituksena oli selvittää saadaanko uudenlaisella koejärjestelyllä ilman kalliita erikoisvälineitä selvyyttä autonomisen ohjauksen ja ulkoisten aikamerkkien osuuteen vuosirytmien säätelyssä.

Materiaali ja menetelmät

Koejärjestelyn idea perustuu siihen, että aloittamalla koekasvatukset kasvihuoneissa eri aikoina vuotta ja käyttämällä vain luonnollista päivänvaloa, saadaan yhtä suurilla lämpösunnakertymiä vastaamaan erilaisia päivänpituuksia. Toiseen suuntaan saadaan eroja kasvattamalla rinnakkaisia koe-eriä kahdessa eri lämpötilassa, jolloin kullekin päivänpituudelle muodostuu kaksi erilaista lämpösunnakertymää. Mikäli vuosirytmien säätely on täysin autonomista, tietyn vaiheen saavuttamiseen mennessä kertyvä lämpösunna pysyy vakiona riippumatta päivänpituudesta tai kasvatuslämpötilasta. Mikäli taas säätely perustuu pelkästään ns. kriittiseen fotoperiodiin, kyseinen vaihe ilmenee kaikissa koe-erissä samana ajankohtana riippumatta kasvatuksen kestosta tai kasvatuslämpötilasta.

Kokeet tehtiin Punkaharjun jalostuskoekesmen kasvihuoneissa vuosina 1978—80. Koekasvina käytettiin rauduskoivua. Lähtömateriaalina oli yhdestä Punkaharjulla kasvavasta puusta kerätty vapaapölytyssemen. Siementä kylvettiin kasvuturpeeseen säännöllisin väliajoin helmikuun puolivälissä loppukesään. Taimet kasvatettiin kahtena rinnakkaiseränä kasvihuoneen erillisissä osastoissa. Toisessa osastossa lämpötila oli noin 20° ja toisessa noin 15°. Koska kasvihuoneiden laitteisto oli varsin vaatimaton, ei lämpötila pysynyt tarkoin näissä ohjearvoissa. Varsinkin kuumina

kesäpäivinä lämpötila nousi korkeammaksi. Ilman lämpötila taimien yläpuolella rekisteröitiin jatkuvasti monipistepiirurilla.

Taimien kokonaispituus mitattiin säännöllisesti ja päätesilmujen muodostumisen ajankohdasta tehtiin havainnot. Syksyllä taimet siirrettiin ulos talvehtimaan. Kevättalvella 1979 edellisenä vuotena kasvatettuja taimia otettiin sisälle kasvihuoneeseen kahden viikon välein, yhden erän jäädessä ulos vertailueräksi. Taimista tehtiin havainnot silmujen avautumisesta, pituuskasvusta ja päätesilmujen muodostumisesta. Kevättalvella 1980 puolet vuonna 1979 kasvatetuista taimista siirrettiin jääkellariin, jotta niiden talvilepo jatkuisi ja aktiiviperiodin alku siirtyisi myöhemmäksi. Aikanaan taimet siirrettiin ulos kellarista vertailuerän viereen. Taimista tehtiin havainnot silmujen avautumisesta, pituuskasvusta ja päätesilmujen muodostumisesta.

Tulosten käsittely tapahtui kunkin koe-erän mitattujen taimien keskiarvon perusteella. Pituuskasvun päättymisen ajankohdaksi määriteltiin se vaihe, jossa 95 % loppupituudesta oli saavutettu. Päätesilmun muodostumisen ja silmujen aukeamisen ajankohdaksi määriteltiin se vaihe, jossa 50 % tutkituista silmuista oli muodostunut tai vastaavasti avautunut. Pituuskasvun päättymisestä, päätesilmujen muodostumisesta ja silmujen avautumisesta saatuja tuloksia tarkasteltiin graafisesti. Päivittäisiä pituuskasvuja analysoitiin myös tätä työtä varten kehitetyn dynaamisen mallin avulla.

Tulokset

Ensimmäisen vuoden pituuskasvun kesto ja kokonaisuus vaihtelivat suuresti kumpanakin vuotena eri kylvöajankohtien välillä. Lukuarvot ovat taulukoissa 1 ja 2. Lukuarvoissa on kaksi selvää suuntausta. Ensimmäinen pituuskasvun kestoajaksi oli sitä lyhyempi mitä myöhemmin liikkeelle lähtö, ts. kylvö, tapahtui. Toiseksi samaan aikaan kylvetyillä erillä pituuskasvun kesto oli pidempi alhaisemmassa kasvatuslämpötilassa. Pituuskasvun päättymisen ja päätesilmun muodostumisen suhdetta kertyneeseen lämpösommaan ja kyseisen ajankohdan päivänpituuteen osoitetaan kuvissa 5 ja 6. Kaikissa neljässä tapauksessa (2 vuotta, 2 kasvatuslämpötilaa) ilmeni, ettei sen paremmin kylvöstä kasvun päättymiseen tai päätesilmun muodostumiseen kertyneellä lämpösommalla kuin ilmiön ajankohdan päivänpituudellakaan ole vakiosuuruista arvoa. Kuvassa 7 tulokset on yhdistetty siten, että akseleina ovat vuorokauden valojaksoa kuvaava yönpituus ja kylvöstä kasvun päättymiseen kertynyt lämpösomma. Havaintopisteiden järjestäytyminen tähän koordinaatistoon osoittaa selvää säännönmukaisuutta. Siinä vaiheessa, kun päivä on vielä pitenevässä tai pisimmillään pituuskasvun päättymiseen mennessä kertynyt lämpösomma on paljon suurempi kuin paikkakunnan koko kasvukauden keskimääräinen lämpösomma. Yön pidentyessä kohti kesän loppua pituuskasvun päättymiseen mennessä kertynyt lämpösomma pienenee vähittäin. Mitään jyrkkiä kynnyksarvoja kumpankaan tekijän suhteen ei ilmennyt. Se, etteivät piste-parvet eri vuosilta ja eri kasvatuslämpötiloista kuitenkaan satu täsmällisesti samalle kohdalle, viittaa siihen, että pituuskasvun ajoittumiseen vaikuttavat muutkin seikat kuten kasvualustan ravinteisuus, kastelu, valaistuksen intensiteetti jne. Kuvissa 8...11 verrataan kunkin kylvöerän pituuskasvua dynaamisen mallin avulla saatuihin odotusarvoihin. Mallissa esiintyvillä parametreilla lasketut lukuarvot erosivat vuo-

sien 1978—1979 tuloksissa jonkin verran toisistaan. Dynaamisella mallilla nykyisessä muodossaan ei siis saavutettu sellaisia numeerisia tunnuslukuja, joilla voitaisiin kuvata käytetyn koivualkuperän vuosirytmien ohjailua.

Taimien toinen elinvuosi on olennaisesti erilainen kuin ensimmäinen siitä syystä, että on jo olemassa valmis taimi, jolla on oma kehityshistoriansa. Aikaporrastukseen perustuvassa koejärjestelyssä esiintyy tällöin ongelmia, joita ei ole siemenistä lähdettäessä. Kokeiden toteutus on teknillisesti paljon vaikeampaa. Ennen normaalin kasvukauden alkua käynnistettävissä kokeissa on ongelmana se, ettei talvihorrokseen päättymistä pystytä määrittelemään. Tässä työssä alkupisteeksi osoitettiin silmujen avautuminen, jolloin käsittelyn alussa mahdollisesti jäljellä ollutta talvihorrorsta ei tarvinnut ottaa lukuun.

Varsinaiset käsittelyt toisena vuotena perustuivat aikaeroihin liikkeelle lähdössä keväällä. Koeaineistona käytettiin edellisenä vuotena eri aikoina kylvettyjä taimia. Ensiksi selvitettiin millä tavoin silmujen avautuminen, pituuskasvun päättymisen ja päätesilmun muodostuminen ajoittuivat eri aikaan kylvetyillä taimilla. Tulokset vuonna 1979 tehdyistä jatkokokeista ovat kuvissa 10 ja 11 ja vuonna 1980 tehdyistä kuvassa 12. Edellisen vuoden kylvöaikojen välillä on kaikissa tapauksissa vaihtelua, mutta mitään sellaista selvää suuntausta kuin ensimmäisen vuoden tuloksissa ei esiinny (vrt. kuvaan 5 ja 6). Erojen katsottiin aiheutuneen pienistä taimimääristä ja olevan sattumanvaraisia. Tulos tulkittiin siten, että ensimmäisenä kasvukautena syntyneet erot olivat hävinneet horrosvaiheiden aikana. Itse käsittelety tapahtuivat vuonna 1979 siten, että taimia otettiin ulkoa talvehtimispaikalta kasvihuoneeseen loppupalvelulla kahden viikon välein. Vuonna 1980 talvilepoa jatkettiin osalle taimista, jolloin niiden liikkeellelähtö saatiin myöhäisemmäksi. Yhdistämällä kahdelta vuodelta kertyneet tulokset voitiin todeta, että pituuskasvun päättymisen ja päätesilmujen muodostuminen toisenakin kasvukautena ovat yhteydessä sekä lämpösomman kertymiseen että päivänpituuden muutokseen. Näiden kahden tekijän suhde oli kuitenkin erilainen kuin ensimmäisenä kasvukautena (kuva 13). Toista kasvukautta koskevien kokeiden määrä oli toistaiseksi niin pieni, ettei pitkälle meneviä päätelmiä voida tehdä. Tulokset viittaavat kuitenkin siihen suuntaan, että jo toisena kasvukautena aktiiviperiodin sisältö on siinä määrin vakiintunut, että pituuskasvu päättyy pitkänkin päivän tilanteessa, kun lämpösomman kertymä vastaa paikkakunnan keskimääräistä koko kasvukauden lämpösommaa. Yön piteneminen loppukesällä aikaansaa pituuskasvun päättymisen tuntuvasti pienemmän lämpösommakeritymän jälkeen.

Tulosten tarkastelu

Merkittävin tulos oli, että yksinkertaisella koejärjestelyllä ja ilman kallista erikoislaitteita voitiin selvittää sekä lämpötilasta riippuvan etenemisnopeuden että päivänpituuden muutoksen aiheuttamia vaikutuksia vuosirytmien säätelyssä. Lämpösommasimulointia ja päivänpituuden vaikutusta ei tulosten mukaan pidä tarkastella toisiaan pois sulkevana vaihtoehtoina, vaan toisiaan täydentävinä mekanismeina. Koejärjestely ja tulosten analysointi, mm. dynaamisen mallien avulla, ei tässä vaiheessa johtanut käyttökelpoisiin tunnuslukuihin vuosirytmien kuvaamiseksi. Tämä merkitsee sitä, että vielä muut tekijät ilmeisesti vaikuttavat vuo-

siryttiin. Pituuskasvun ajoittumista käytettiin tässä tutkimuksessa metodisista syistä, koska ensimmäisenä ja toisena vuotena taimissa ei vielä ole käyttökelpoisia ns. pistetapahtumia. Tässä tutkimuksessa ei pyritty selvittämään kasvun kokonaismäärää tai päivittäistä kasvua sinänsä.

Sarvaksen kehittämä ajatusmalli puiden koko vuosijaksosta on merkittävä edistysaskel ilmastoon sopeutumisen tutkimuksessa. Hänen käyttämänsä tutkimusmenetelmä ei kuitenkaan paljastanut fotoperiodin tai pakkasen vaikutusta koko vuosijakson säätelyssä. Sarvaksen toteamat etenemisnopeuden lämpötilariippuvuudet lyhyen ajan puitteissa ovat sinänsä varmasti oikeita. Nyt saatujen tulosten valossa joutuu asettamaan kyseenalaiseksi sen perusoletuksen, että kukin päävaihe on homogeeninen etenemisnopeuden lämpötilariippuvuuden suhteen. Toisaalta tässä tutkimuksessa

saadut tulokset tekevät ymmärrettäväksi fytotronikoissa todetut fotoperiodin ja lämpötilan yhteisvaikutukset. Todettu ero ensimmäisen ja toisen kasvukauden pituuskasvun päättymisen ajoittumisessa oli aikaisemmin julkaistujen tietojen perusteella odotettavissa. Ensimmäisenä kasvukautena syntyneiden vaihe-erojen häiviäminen syys- ja talvihorroksen aikana oli Sarvaksen mallin perusteella odotettavissa, mutta ns. jälki-vaikutuksesta on myös julkaistu havaintoja (esim. Heide 1974). Yhteenvetona voidaan todeta, että tässä tutkimuksessa saadut tulokset tukevat Sternin ja Rochen (1974) esittämää käsitystä, jonka mukaan kasvukauden alussa vuosijakson etenemistä voidaan kuvata pelkällä lämpösumman kertymällä, mutta kasvukauden lopulla pitenevät yöt alkavat asteittain vaikuttaa tapahtumien kulkuun.

KOSKI, V. & SELKÄINAHO, J. 1982. Experiments on the joint effect of heat sum and photoperiod on seedlings of *Betula pendula*. Seloste: Lämpösumman ja päivänpituuden yhteisvaikutuksesta yksi- ja kaksivuotiaisiin rauduskoivun taimiin. Commun. Inst. For. Fenn. 105:1 — 34.

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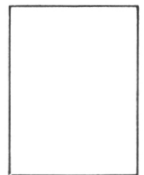
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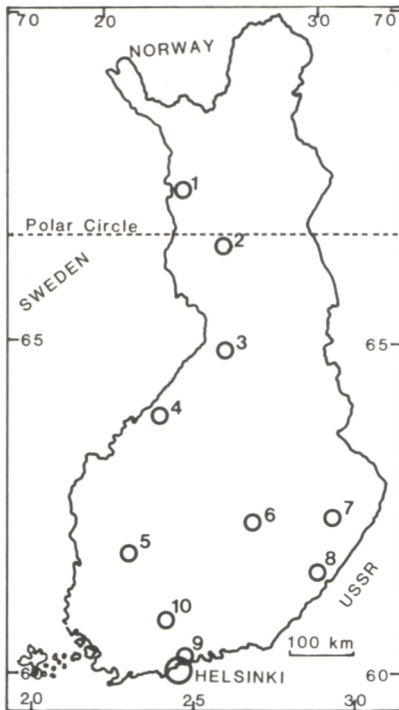


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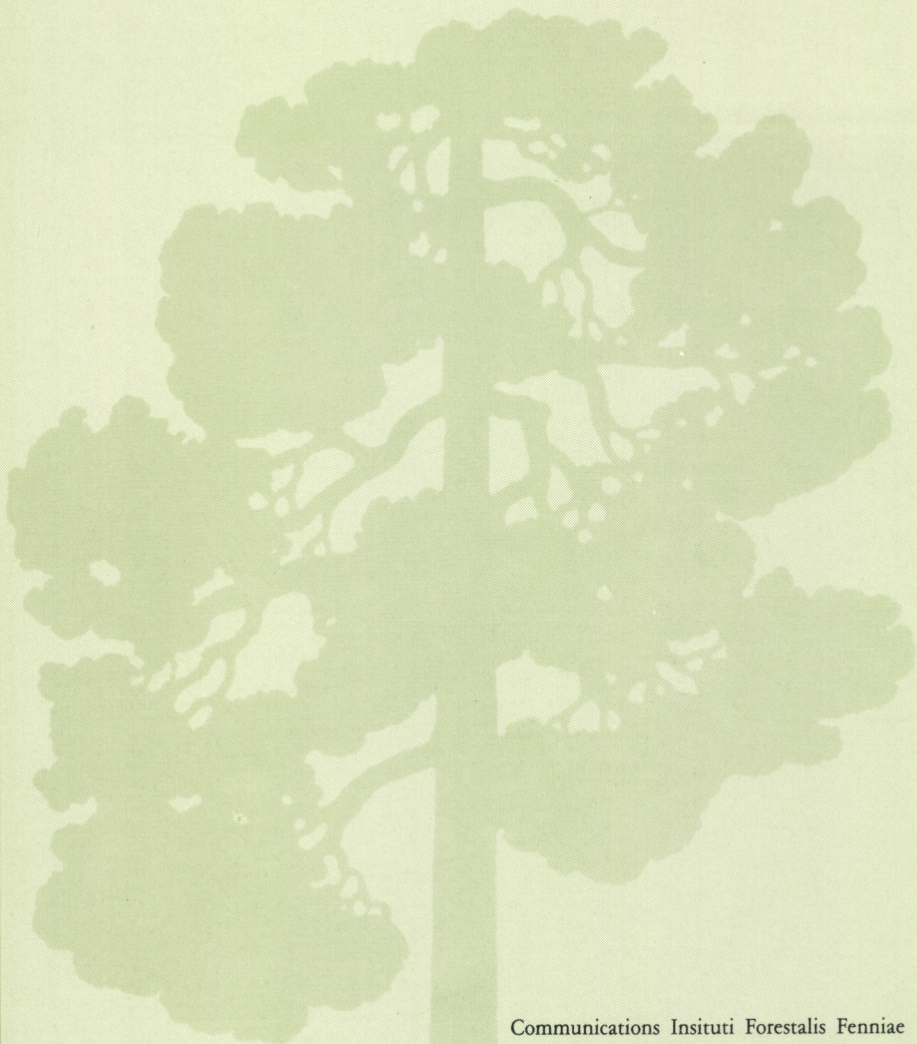
FACTS ABOUT FINLAND

Total land area: 304 642 km² of which 60–70 per cent is forest land.

Mean temperature, °C:	Helsinki	Joensuu	Rovaniemi
January	-6,8	-10,2	-11,0
July	17,1	17,1	15,3
annual	4,4	2,9	0,8

Thermal winter
 (mean temp. < 0°C): 20.11.–4.4. 5.11.–10.4. 18.10.–21.4.

Most common tree species: *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Betula pubescens*



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