

**Analysis of bud-development  
theories based on long-term  
phenological and air temperature  
time series: application to  
*Betula* sp. leaves**

Risto Häkkinen





Metsäntutkimuslaitoksen tiedonantoja 754, 1999  
Finnish Forest Research Institute, Research Papers 754, 1999

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Analysis of bud-development theories  
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To be presented, with the permission of the Faculty of Agriculture and  
Forestry of the University of Helsinki, for public criticism  
in Auditorium XII of the University Main Building,  
Aleksanterinkatu 5, on Friday 21 January 2000, at 12 o'clock noon.

Helsinki, 1999

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ISBN 951-40-1709-9  
ISSN 0358-4283  
Hakapaino Oy, Helsinki 1999

*To Smilla and Aapo*

**Häkkinen, R.** 1999. Analysis of bud-development theories based on long-term phenological and air temperature time series: application to *Betula* sp. leaves. Metsäntutkimuslaitoksen tiedonantoja 754. Finnish Forest Research Institute, Research Papers 754. 59 p.

A condensed history of phenological and climatic observation in Finland covering a time span of 250 years was outlined. The information from fragmentary, partly overlapping, systematically biased time series was combined into one reliable, continuous time series of bud burst of *Betula* sp. leaves in Jyväskylä (1896–1955). Systematic bias comprising 76 % of the total random variation of individual series was eliminated. The theory in which the temperature-driven ontogenetic bud development starts on a fixed date in spring predicted the timing of bud burst more precisely than the theories in which the start and rate of ontogenetic development depended on the stage of dormancy. Methods of statistical inference based on resampling were applied to analyse the properties and to test the differences of the models. The values of model parameters were strongly inter-related and unstable. On the basis of long-term data not enough evidence was found to conclude that an on/off-type factor, like specific night length, triggers the onset of developmental phases. Bud-development models were found to be precise tools for predicting the moment of bud burst.

**Keywords:** annual cycle of trees, *Betula* sp., bootstrap, bud-burst timing, cross-validation, dormancy, ontogenetic development, phenological observation, prediction error, resampling.

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## Preface

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In 1982 Pertti Hari (Pepe), then acting professor of the Department of Mathematics at the Finnish Forest Research Institute (Metla), suggested that we should begin to study the annual cycle of trees. At the time, Metla and the Meteorological Institute were involved in a joined effort to digitize the long climatic observation series (Jyväskylä 1883–1981) gathered by the Meteorological Institute, an effort first of its kind in Finland. We were going to utilize this massive data set and the then efficient new VAX computer at Metla to apply dynamic models to frost damage risk analyses. The idea gradually grew up in my mind and I am very grateful to Pepe for his continuing and inspiring encouragement, without which the work would have remained undone. – Another fundamental innovation came from Pepe as well. Somehow he found out in the late 80s that the Finska Vetenskaps-Societeten had published fragmentary phenological time series since the 19th century. These proved valuable in the bud-development studies.

I wish to thank Tapio Linkosalo, who got interested in 1993 in our annual cycle studies and joined the team while working in the Information Systems Services at Metla. The cooperation with him has been fruitful: he is a co-author of two of the articles in this thesis.

Thanks to Jukka Nyblom for discussions on the bootstrap method, to Veikko Koski and Heikki Hänninen for answering my many questions about the annual cycle, to Carl-Gustaf Snellman, who always provided expert help when I had computer-related problems, to Aarne Reunala, who kindly translated the article of de Reaumur from French, to Marko Kaakinen, whose programming expertise speeded up the research process, and to Seppo Oja and Tommi Salonen for assistance in preparing the manuscript for printers.

I thank members of the ‘gang of four’ (Pepe, Timo Tuomivaara, Hannu Rita, and me), which has been a most important source of my knowledge of philosophy of science and of scientific research process in general during the last ten years.

I should like to extend my very special thanks to Jaakko Heinonen and Timo Pekkonen, my colleagues and friends since the 70s. We have studied, as a never-ending task, both statistics and life together.

Finally, I would like to express my warmest thanks to Ritva Seppi, whose emotional and practical support during the writing process was essential.

# Contents

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<b>1</b>	<b>Introduction and aims of the study</b> .....	
<b>2</b>	<b>Observational versus experimental research</b> .....	
<b>3</b>	<b>Long-term phenological and air temperature time series</b> .....	
3.1	Phenological time series .....	
3.1.1	Phenological observation in Finland .....	
3.1.2	Plant phenological observations published by Finska Vetenskaps-Societeten .....	
3.1.3	Birch species problems in the observations of Finska Vetenskaps-Societeten .....	
3.1.4	Observations on the bud burst of <i>Betula</i> sp. leaves in Saarijärvi (1907–50) recorded by Mrs. Nordenstreng .....	
3.1.5	The 19 observation series of the bud burst of <i>Betula</i> sp. leaves in Central Finland (1896–1955) used to construct a combined time series .....	
3.2	Air temperature time series .....	
3.2.1	History of air temperature measurement .....	
3.2.2	Air temperature observations in Jyväskylä (1883–1981) .....	
<b>4</b>	<b>Construction of the combined time series of the bud burst of <i>Betula</i> sp. leaves in Jyväskylä (1896–1955)</b> .....	
4.1	Estimation of the combined time series .....	
4.2	Quality of the individual and combined time series .....	
<b>5</b>	<b>Analysis of bud-development theories based on the combined phenological time series of <i>Betula</i> sp. leaves and the air temperature observations in Jyväskylä (1896–1955)</b> .....	
5.1	Fundamental ideas of bud-development theories .....	
5.2	Mathematical model of bud-development theories .....	
5.2.1	Estimation of the values of model parameters .....	
5.2.2	Specification of the mathematical models of the bud-development theories to be evaluated .....	
5.3	Evaluation of the submodels of ontogenetic bud development based on conditional distribution of spring minimum temperatures in Jyväskylä (1883–1981) .....	
5.4	Evaluation of the bud-development theories of <i>Betula</i> sp. leaves based on air temperature observations in Jyväskylä and (i) the bud-burst time series in Saarijärvi (1907–50) and (ii) the combined bud-burst time series in Jyväskylä (1896–1955) .....	
5.5	Statistical evaluation of bud-development theories of <i>Betula</i> sp. leaves based on resampling methods .....	
5.5.1	Resampling methods .....	

5.5.2	Test of equality of the mean square errors of the models based on bootstrap percentile confidence intervals .....
5.5.3	Properties of the model parameters .....
5.5.4	Prediction error of the models .....
<b>6</b>	<b>Discussion and conclusions</b> .....
6.1	The combined phenological time series of bud burst of <i>Betula</i> sp. ....
6.2	Analysis of bud-development theories of <i>Betula</i> sp. leaves .....
6.2.1	Submodels of the ontogenetic bud development .....
6.2.2	Bud-development theories from the beginning of dormancy to bud burst .....
6.3	Statistical analysis .....
6.4	Conclusions in brief .....
	<b>References</b> .....
	<b>Appendix:</b> Chronological list of the publications of phenological observations by Finska Vetenskaps-Societeten (Suomen Tiedeseura, The Finnish Society of Sciences and Letters) .....

## Articles I–V

## List of original articles

This thesis is based on the following original articles, which are referred to in the text by their Roman numerals I–V. In addition, some unpublished results are presented.

- I** Häkkinen, R. & Hari, P. 1988. The efficiency of time and temperature driven regulation principles in plants at the beginning of active period. *Silva Fennica* 22(2): 163–170.
- II** Hari, P. & Häkkinen, R. 1991. The utilization of old phenological time series of budburst to compare models describing annual cycle of plants. *Tree Physiology* 8: 281–287.
- III** Häkkinen, R., Linkosalo, T. & Hari, P. 1995. Methods for combining phenological time series: application to bud burst in birch (*Betula pendula*) in Central Finland for the period 1896–1955. *Tree Physiology* 15: 721–726.
- IV** Häkkinen, R., Linkosalo, T. & Hari, P. 1998. Effects of dormancy and environmental factors on timing of bud burst in *Betula pendula*. *Tree Physiology* 18: 707–712.
- V** Häkkinen, R. 1999. Statistical evaluation of bud development theories: application to bud burst of *Betula pendula* leaves. *Tree Physiology* 19: 613–618.



# 1 Introduction and aims of the study

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Conifers have existed for about 250–300 million years (Sarvas 1964, Eronen 1991). After the last Ice Age, birch (*Betula*) invaded southern Finland 10 000–9000 years ago, Scots pine (*Pinus sylvestris*) 9000–8000 years ago, and Norway spruce (*Picea abies*) 5000–3500 years ago (Alho 1990). In cool and temperate zones, the warm summer with a long daylight period is favorable for the growth of plants, but the winter is dark and cold. During evolution perennial plants and trees have developed regulatory systems to overcome the alternating cycle of seasons that threatens their survival.

Trees have adapted to the annual climatic variations, and regulate the timing of bud-burst and flowering during spring and the timing of growth cessation and dormancy development during late summer and fall. Frost damage is not common on pine and birch in Finland, but frost damage to the new shoots of spruce does occur in some years in early June. Thus in the present climate, the regulation system for the timing of bud-burst in spruce results in a higher risk of frost damage than that for birch and pine. Regulation of the timing of flowering in rowan (*Sorbus aucuparia*) fails in some years, and the flower buds open already in the autumn, e.g. in Helsinki in 1995 (Figure 1).



**Figure 1.** Flower-bud regulation fails in autumn: rowan (*Sorbus aucuparia*) blooming at Käpylä, Helsinki, October 1995 (Photo: R. Häkkinen).

The cultivation of fruit trees began in small scale in Finland in the beginning of the 16<sup>th</sup> century. Young plants were imported and frost damage was common. Some of the damage has been documented, such as the extensive damage during the very long cold winter in 1709–10. According to Count Bonde, the owner of a large fruit orchard on the shores of Lake Mälaren in Sweden, the winter began already on September 29 and the fruit trees became frozen before shedding their leaves in autumn. Stems were split down to the pith from the base to top during winter. A very large number of deciduous trees growing in the forests, such as aspen, rowan, ash and oak, were killed (Collan 1929).

The predicted climate change has increased our need for reliable theories and models to predict the timing of bud burst and the risk of frost damage. From the forestry point of view, it is essential to ensure wood production through the breeding and proper selection of tree species. The timing of bud-burst in hardwoods, and the onset of the active growth period in conifers, also has major implications for the global atmospheric water balance and, consequently, for climate warming itself (Sellers et al. 1997).

In biology the time dimension does not have the same meaning as in physics, in which time is defined by means of physical events (Suntola 1998). In biology, on the other hand, seasonal and diurnal rhythms occurring in a specific order, rather than the time dimension, describe the progression of phenomena (Leikola 1999). The biological age is not an unambiguous concept and the scale on which it should be measured is not obvious. For instance, in the biological sense trees of the same species of the same age are not at all identical. However, in early phenological research in the 19<sup>th</sup> century the timing of phenological events was examined on a time scale only. The variation in the timing of events between years was studied, and tables with the mean times of the occurrence of phenological events in different geographical locations were constructed (Moberg 1857b, Johansson 1911 and 1946). This work is still going on (Terhivuo 1988, Lappalainen and Heikinheimo 1992). In Sweden Hamberg (1899) linked the timing of phenological events with air temperature, snow melt, and the break-up of ice on the rivers and lakes. He found that the time curves of phenological events coincided with the isotherms of daily mean temperatures drawn on maps. However, these findings were interpreted as cross-sectional events on a time scale, not as dynamic processes taking place over time.

The mathematical and statistical methodology used in the early stages of phenological research in Finland was very advanced. Hällström determined the dependence of the timing of phenological phenomena on latitude using linear regression analysis in 1844 (16 species of fauna and 55 of flora), and examined the dependence of the rate of advance of phenological events on day length (Johansson 1911). The first studies on climate change in Finland were also carried out in the 19<sup>th</sup> century when Moberg (1865, 1868) studied possible trends in the timing of phenological events over the years by means of linear regression analysis.

The genetical and biochemical regulation system of bud development, and its responses to environmental signals, are under intensive study, but the exact nature of these processes still remains unknown (Rinne et al. 1994a, Rinne et al. 1994b, Hänninen 1995). The current theories are not biochemical, but describe bud development from the onset of dormancy to bud burst as a response to environmental factors. The theoretical concepts used have not been fully accepted (Hän-

ninen 1986, 1990, 1995). Selection of scale or dimension on which phenomena can be presented quantitatively has been miscellaneous. The dependences of bud development on environmental factors have often been presented in verbal or graphical form without any well-defined dimension for development.

The history of interpreting phenological processes on a scale other than the time dimension dates back as far as to de Reaumur, who invented the concept of temperature sum (de Reaumur 1735). The problem he wanted to solve was why the harvest in 1735 was nearly one month later than that in 1734. To explain this he summed the daily mean temperatures in April, May and June. He noticed that the temperature sum in every month in 1734 was higher than those in 1735 and thus solved the problem. Linsser (1867) found that the temperature sums required, e.g. for flowering, are proportional to the annual temperature sum of the region, i.e. plants have adapted to the local conditions.

According to the Finnish text book on silviculture written by Cajander (1916), plants need a specific amount of accumulated temperature, i.e. the temperature sum to achieve a given phase of development. Huikari and Paarlahti (1967) analysed the timing of the beginning of growth and flowering on time and temperature-sum scales experimentally. Sarvas (1967) studied the occurrence of the phenological phases of flower buds on temperature-sum scale instead of a time scale, and compared different threshold values for the effective temperature, and later on ontogenetic bud development on a period-unit-sum scale (Sarvas 1972), and dormancy-development on a chilling-unit-sum scale (Sarvas 1974). Hari (1968) introduced the concepts of rate of biological maturation and relative age, later called the physiological stage of development (Hari 1972). A number of the physiological processes of plants can be described mathematically and analyzed by quantitative methods on the basis of these concepts (Hari et al. 1970, Pohjonen and Hari 1973, Pohjonen 1975, Sarvas 1977, Pelkonen and Hari 1980). Hänninen (1995) reviewed the various bud-development theories presented in the literature in a unifying manner by applying and improving these concepts and formalism.

The main features of the prevailing theories on the annual cycle of trees are as follows. In the boreal and temperate zones, trees have adapted to the alternating cycle of seasons. After growth cessation in the autumn the trees enter an inactive state, called dormancy, in which ontogenetic development, i.e. morphological changes, is inhibited by a biochemical regulation system even if the environmental conditions are favorable. This prevents frost damage caused by premature bud development during late autumn and early winter. Dormancy is completed when the buds have been exposed for a sufficiently long period to chilling temperatures ranging from  $-3$  to  $+10$  °C. After dormancy the trees enter an active period in which the buds are capable of ontogenetic development in response to temperatures over 0 °C (Sarvas 1972, 1974). According to some theories, ontogenetic development begins already during dormancy but at a restrained rate that depends on the magnitude of the accumulated chilling temperatures (Landsberg 1974, Cannell and Smith 1983, Hänninen 1990). The growing season of hardwoods and conifers starts at bud burst. The theories involve theoretical concepts that are cumbersome to operationalise, e.g. the start of bud ontogenesis. Neither is the operationalisation of state variables representing stages of bud development unambiguous. There are additional problems with the theoretical concepts of the theories (Hänninen 1986 and 1990). According to one theory, ontogenetic bud

development is inhibited during dormancy and, according to another, ontogenetic bud development starts already during dormancy but at a restrained rate. This indicates that clarification of the concepts of theories and the experimental testing of the theories concerning bud development of trees are needed.

Several theories assume that bud development depends only on the prevailing temperature (Reaumur 1735, Linsser 1867, Sarvas 1972 and 1974, Landsberg 1974, Richardson et al. 1974, Fuchigami et al. 1982, Cannell and Smith 1983). Another paradigm considers that time or light signal is the environmental factor affecting bud development (Wareing 1956, Bünning 1963, Nizinski and Saugier 1988, Partanen et al. 1998). Experimental work on the effects of a light signal began at the beginning of the 20<sup>th</sup> century, when the introduction of electric lighting permitted such experimental arrangements (Koski and Selkäinaho 1982). Koski and Selkäinaho (1982) and Koski and Sievänen (1985) studied the joint effect of temperature sum and photoperiod on the growth cessation of *Betula pendula*. Temperature is the most important factor in biological processes, but the light climate is also a potential source of environmental information when plants are regulating their functioning during the annual cycle. However, neither temperature nor light alone appear to be sufficient to explain the regulation of plants, and the interactions between temperature, light and other factors have to be considered when improving bud-development theories.

Testing the theories of bud development has mainly been based on relatively short-term experiments with saplings. When trees have been observed in natural conditions the time series have been fairly short (Cannell and Smith 1983, Nizinski and Saugier 1988). Experiments carried out in artificial conditions have advantages, but the inference would be more convincing if the results would also be tested in natural conditions with mature trees. Fortunately, long-term phenological and climatic observation series covering very long time-periods are available. In Finland the collection and publishing of phenological observations was organized by the Finska Vetenskaps-Societeten (Suomen Tiedeseura, The Finnish Society of Sciences and Letters). The observations include a comprehensive range of phenological events and cover a time span of 250 years. However, the observations have so far not been properly utilized. The observation series are fragmentary, partly overlapping, and the observations were made by visual assessment without any measuring instrument. Thus, in addition to the random measuring noise, the measurements almost probably include systematic errors. To improve the quality of the raw data for research purposes the information from separate time series first has to be combined. The most extensive tree phenological time series in the records of the Finska Vetenskaps-Societeten is that for the bud burst of *Betula* sp. leaves.

Bud development is a continuous, time-dependent process and its rate depends on environmental factors. The development rates at any moment of time can be described mathematically using time derivatives that are functions of environmental factors. The stages of development are determined using integrals of the rates over a period of time (Hari 1968 and 1972, Hänninen 1995). Such dynamic models are often approximated with step functions such as the widely used temperature sum. Statistical analysis of the models has been cumbersome because no standard statistical methods have been available for analyzing dynamic models based on bud-development theories. Thus use of statistical inference has in fact

been rather limited in bud-development studies. Evaluation of the models has been based only on numerical comparison of the residual errors of the models. However, the high efficiency of modern computers has enabled us to take advantage of statistical resampling methods, which can also be utilized in analyzing bud-development theories. Resampling techniques are a new and expanding field of statistical inference (Efron 1979, Efron and Tibshirani 1993). In resampling methods the normal assumptions like the normality of errors are not needed, but the sampling distributions of the statistics required in statistical analysis are generated by computer intensive simulation methods.

## **Aims**

The results of this thesis are partly based on the five articles included. However, many results presented have not been published before. In addition, some of the numerical results slightly differ from those in the articles because analysis and computer programs written have improved during the research project.

The aims of this study were *(i)* to outline a condensed history of phenological and climatic observation in Finland, *(ii)* to construct a long, reliable phenological time series of the bud burst of *Betula* sp. leaves during 1896–1955 from separate, biased, short, fragmentary, but partly overlapping historical observation series, *(iii)* to analyze and test alternative theories of bud development from the onset of dormancy to bud burst using a combined time series of the bud burst of *Betula* sp. leaves and temperature records, and *(iv)* to apply novel statistical methods based on resampling in order to evaluate the bud-development theories.

## 2 Observational versus experimental research

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Observation is a much older method than experimentation in the history of science although simple experiments were carried out already in ancient times, e.g. light refraction experiments to explain the rainbow phenomenon. However, up until the late Middle Ages or modern times, when the natural sciences were born, the distinction between observation and experimentation to gain experience was not recognized (Niiniluoto 1980). Immanuel Kant (1787) stated in the preface to his well-known book, *Kritik der reinen Vernunft*, that a man has to force nature to answer the questions he is interested in, i.e. he has to perform experiments in which the conditions of the research object are manipulated. On the other hand, it is not possible to carry out experiments on many scientific problems, and systematic and controlled observation is the only possible way to obtain knowledge through experience. For instance, in astronomy we are forced to use controlled observations, in paleontology we have to draw conclusions on the basis of remains, and in climatology historical time series, e.g. dendrochronological time series of tree rings, are needed to study the past climate. The strength of observational methods lies in testing research hypotheses in natural conditions.

The power of experimental research lies in its ability to exclude known disturbing factors or to adjust them to a constant level, and to handle the effect of unknown disturbing factors by means of replication and randomization (Cochran and Cox 1957). In addition, the main and interaction effects of factors on a phenomenon can be studied in artificially generated extreme conditions. Finally, quantitative estimates of the effects of individual factors can be calculated and tested through the use of statistical methods for the design of experiments (Niiniluoto 1983). Experimental methods are efficient in analyzing causal relationships. However, in spite of the many advantages of experimental research, in many cases there are also inferential problems. How can we know that the factors we have excluded from the experiment do not, in reality, have interactions with the factors being studied in the experiment? Do artificially generated factors in the experiment act in the same way in natural conditions? For instance, the quality of artificial light hardly corresponds to that of natural light. In ecological research on problems involving complicated inter-dependences between factors, the area over which the conclusions are valid has to be considered carefully if the results are based on experiments in the field or in the laboratory (Tuomivaara et al. 1994).

The observational and experimental methods used to obtain knowledge through experience are not incompatible. In fact they complement each other, e.g. laboratory findings can be corroborated under natural conditions and vice versa. In analyzing the regulation of the annual cycle of plants both observational time series and experiments are useful.

## 3 Long-term phenological and air temperature time series

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### 3.1 Phenological time series

#### 3.1.1 Phenological observation in Finland

Phenology is defined as the field of research which studies the relationship between biological phenomena, like the bud burst and flowering of plants and the migration of birds, and climatic factors such as temperature and the intensity of light, and which investigates the seasonal and annual rhythms and variation in the timing of these events (Tirri et al. 1993). The tradition of observing seasonal events, in addition to those connected with fauna and flora, is long. For instance the date of the break-up of the ice on the River Tornio has been recorded since 1693 (Kajander 1995).

The first recorded initiatives to gather phenological observations systematically in Finland came from the Swedish astronomer Anders Celcius and the Swedish botanist Karl von Linné. In 1740 Celcius published his first observations in *Svenska Vetenskaps-Akademins Handlingar* and encouraged others to make notes of climatic and phenological observations (Johansson 1946). In 1749 Linné published a more detailed appeal to start observation in *Lärda tidningar* (Johansson 1946). The first published Finnish observations were made by Professor J. Leche in Turku and by the Vicar N. Mathesius in Pyhäjoki in 1750 (Moberg 1857a, Leche 1889). For example, the bud burst of *Betula* was slightly visible ('löfven urslagna, fast ænnu smål') in Turku on April 15, 1750 (Leche 1889), break-up of the ice on the River Aura in Turku occurred on March 25, 1750 (Moberg 1857a), and *Cuculus Canorus* was heard to cuckoo on May 13, 1752, in Turku (Moberg 1857a).

Finska Vetenskaps-Societeten (Suomen Tiedeseura, The Finnish Society of Sciences and Letters), founded in 1838 in Helsinki in the same year as the Magnetic Observatory of the University of Helsinki, the predecessor of the Finnish Meteorological Institute, organized a systematic observation network of voluntary observers throughout Finland to gather phenological observations from 1846. The initiative came from Professor L.A.J. Quetelet, the director of the Astronomical Observatory in Brussels, who in 1841 had proposed to the British Association for the Advancement of Science the establishment of an European observation network for climatic and phenological observations (Moberg 1857a, Johansson 1946). Professor of physics Gustaf Gabriel Hällström acted as a link between Quetelet and Vetenskaps-Societeten and the physicist Johan Jacob Nervander, the first director of the Magnetic Observatory in Helsinki, finally set up the observation network (Finska Vetenskaps-Societeten 1853, p. 63 and 77). The Vetenskaps-Societeten continued to co-ordinate and collect the observations until 1965. Since then the collection of phenological observations has been managed jointly by Vetenskaps-Societeten and The Finnish Museum of Natural History (Zoological Museum) (personal communication, Docent Juhani Terhivuo).

År 184 .

Tab. I.

Tab. II.

Tab. III.

Tab. IV.

Vextnamnet enligt Linné, jemte Sveuska och Finska namn.	Lof- eller blad-bildning.			Blomning.			Frukt- eller löf-bildning.			Luf- eller blad-fällning.		
	Böjjan.	Milt.	Sitt.	Böjjan.	Milt.	Sitt.	Böjjan.	Milt.	Sitt.	Böjjan.	Milt.	Sitt.
<i>Orobus vernus</i> . . . . .												
Vår-Gökmat.												
<i>Vicia cracca</i> . . . . .				Y. 78								
Kräk-Vicker, Hirenberne.												
<i>Hypericum quadrangulum</i> . . . . .												
Mansblod, Kiraruoho.												
<i>Leontodon Taraxacum</i> . . . . .				Y. 10								
Smörblomma.												
<i>Tanacetum vulgare</i> . . . . .												
Benfana.												
<i>Cnaphalium dioicum</i> . . . . .				Y. 20								
Kattfot.												
<i>Tussilago Farfara</i> . . . . .												
Fälfot, Leskelehti.												
<i>Solidago virgaurea</i> . . . . .												
Gullris.												
<i>Centaurea cyanus</i> . . . . .												
Bläkiut.												
<i>Viola palustris</i> . . . . .				Y. 2								
Kärr-Viol.												
<i>Betula Alnus</i> . . . . .												
Al.												
<i>Betula alba</i> . . . . .	Y. 2			Y. 3								
Björk.												

6

Kirjan nimilehdelle pannaan vuosiluku, havaintopaikka, (kaupunki tahi pitäjä, kylä ja talo) — suotava olisi myöskin että maaseuduilla kaukaisuus ja ilmasuunta lähimmäisestä kirkosta ilmoitettaisiin — sekä tekijän nimi. Seuraavan vuoden alussa lähetetään kirja lähimmän postiteimiston kautta Tiedeseuralle päällekirjoituksella: *Suomen Tiedeseura Helsingissä. — Yöpaakirje. . . . .* n (nimi) lähettämä, jonkalmiset kirjeet maksutta tulevat perille.

7

## I. Kasvuja.

## A) Lehdittyminen.

Tuomi, Hägg ( <i>Prunus padus</i> ) . . . . .
Puna siestar, Röda vinbär ( <i>Ribes rubrum</i> ) . . . . .
Kaivu, Björk ( <i>Betula alba et verrucosa</i> ) . . . . .
Pihlaja, Rönn ( <i>Sorbus aucuparia</i> ) . . . . .
Harmas leppä, Grå al ( <i>Alnus incana</i> ) . . . . .
Tervas-leppä, Klibbal ( <i>Alnus glutinosa</i> ) . . . . .
Salava paju, Pii ( <i>Salix fragilis</i> ) . . . . .
Syreeni, Syren ( <i>Syringa vulgaris</i> ) . . . . .
Pähkinäpuu, Hassel ( <i>Corylus avellana</i> ) . . . . .
Kastanjapuu, Kastanje ( <i>Aesculus hippocastanum</i> ) . . . . .
Jalava, Alm ( <i>Ulmus montana et effusa</i> ) . . . . .
Vahteri, Lönn ( <i>Acer platanoides</i> ) . . . . .
Kirsipuu, Körbärsträd ( <i>Prunus cerasus</i> ) . . . . .
Omenapuu, Äpleträd ( <i>Pyrus malus</i> ) . . . . .
Niipuu, Lehmus, Lind ( <i>Tilia ulmifolia</i> ) . . . . .
Haapa, Asp ( <i>Populus tremula</i> ) . . . . .
Tammi, Ek ( <i>Quercus robur</i> ) . . . . .
Saarni, Ask ( <i>Fraginus excelsior</i> ) . . . . .

Figure 2. Examples of the tables for phenological observations from booklets distributed to voluntary observers by Finska Vetenskaps-Societeten (Suomen Tiedeseura, The Finnish Society of Sciences and Letters) in 1846 and 1878.

The Finnish Forest Research Institute began to record the plant phenological observations on about 50 phenological events made by trained staff at about 40 localities in 1995 (Poikolainen et al. 1996, Kubin et al. 1998).

### 3.1.2 Plant phenological observations published by *Finska Vetenskaps-Societeten*

Finska Vetenskaps-Societeten (Suomen Tiedeseura, The Finnish Society of Sciences and Letters, Societas Scientarium Fennica) is the most important publisher of plant phenological observations recorded in Finland. All the observations have been made by laymen. Up until 1846 the observation work was scattered and fragmentary and the observation instructions are not known. From 1846 the observation was organized by Vetenskaps-Societeten and the instructions to observers are known. The first observation booklet including instructions (17 pages) and tables for observations comprised 70 pages (Finska Vetenskaps-Societeten 1846). The booklet was soon after simplified, and in 1878 it contained 17 pages (four pages of instructions) (Finska Vetenskaps-Societeten 1878). Since 1895 the observation instructions have remained unchanged. Figure 2 shows examples of the tables used for phenological observations from the 1846 and 1878 booklets.

The observers were advised to choose a site normal for the observed species with several individuals growing there. In addition, the observations were to be made every year at the same place if possible. For example bud burst was defined as the date when the trees started to turn green and the largest leaves were fully open (“lehdittymis-ajaksi merkitään se, jolloin puut alkavat helakammin vihanoida ja suurimpien lehtien lapa on auvennut”) (Finska Vetenskaps-Societeten 1895).

Phenological observations with uniform observation instructions were published for the years 1896–1955 and 1960–65. The observations on the leaf bud burst of *Betula* sp. for the above period were used as the phenological material of this study.

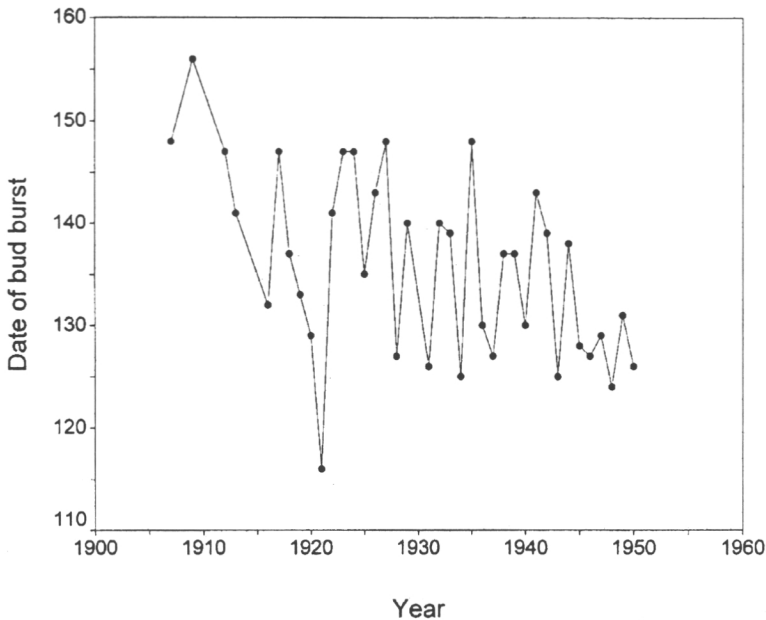
The publications of phenological observations by Finska Vetenskaps-Societeten are listed from 1750 to 1965 in the Appendix (Johansson 1946)(III).

### 3.1.3 Birch species problems in the observations of *Finska Vetenskaps-Societeten*

In the published records of Finska Vetenskaps-Societeten the bud burst of birch was labeled as the bud burst of *Betula alba*, *Betula*, or *Betula* sp. depending on the year of publication. Consequently it is not known with any certainty whether the observations were made on *Betula pendula* or *Betula pubescens*. However, it is likely that *Betula pendula* was the species observed mainly because its leaves unfold one or two weeks earlier than those of *Betula pubescens*, and because the observations were presumably made in inhabited areas, villages and courtyards of farmhouses, where the soil is dry and compact and more suitable for *Betula pendula*.

### 3.1.4 Observations on the bud burst of *Betula* sp. leaves in Saarijärvi (1907–50) recorded by Mrs. Nordenstreng

In the early phase of the research project when a number of regulation principles for the rate of ontogenetic bud development were being analyzed, only one phenological observation series of Finska Vetenskaps-Societeten was utilized (II). The criteria applied in choosing the observation series were (1) the length of the time series, and (2) the geographical distance of the observation site from the site where the Jyväskylä temperature observations were made. The time series on the bud burst of *Betula* sp. recorded by Mrs. Alma Nordenstreng in Rahkola village in Saarijärvi (62°42'N, 25°20'E) was considered the best (Figure 3, Series No. 13 in Table 1). Bud burst was observed in 1907, 1909, 1912–13, 1916–29, and 1931–50, in a total of 38 years. The observation site was about 60 km from Jyväskylä. One additional reason for choosing this series was the fact that it was made carefully by one person, Mrs. Nordenstreng, as confirmed in a conversation between the daughter of the observer, Mrs. Helka Karvonen, and the author of this study in 1989. The visit to the observation site (in the vicinity of a farm yard located on a NW slope facing a lake) strengthened the belief that the series was most probably made on *Betula pendula*. The variation between the years in the timing of birch bud burst was considerable (Figure 3). The median bud-burst date was May 17, the earliest bud burst taking place on April 26, 1921, and the latest on June 5, 1909. The range of the dates was 40 days.



**Figure 3.** Time series of the dates of bud burst of *Betula* sp. leaves observed by Mrs. Nordenstreng in Rahkola village, Saarijärvi. The dates are depicted as the number of days from the beginning of the year.

### 3.1.5 *The 19 observation series of the bud burst of Betula sp. leaves in Central Finland (1896–1955) used to construct a combined time series*

The records of Finska Vetenskaps-Societeten were used to construct a combined time series of birch bud-burst dates in Jyväskylä (= location of temperature records) from partly overlapping, individual observation series (III). Selection of the phenological time series to be used was based on the following two criteria: (1) distance of the observation point from the City of Jyväskylä to be less than 185 km, and (2) duration of the time series to be at least 15 years. The location of the sea coast determined the maximum radius of the area. Sustained observation (15 years) was considered to ensure reliable observation. Nineteen time series fulfilling the above criteria were found for the period 1896–1955 (Figure 4). The length of the time series varied from 15 to 57 years (Table 1), and comprised a total of 465 observations. 10 outlying observations were removed (Linkosalo et al. 1996) using a discordancy test (King 1953, Barnett 1978).

The bud-burst observations were made by educated, enlightened laymen as can be concluded from their professions (Table 1). The longest record, 57 years, was observed by Miss Ingeborg Ehnberg (1870–1958), a schoolteacher in Mikkeli. Her series covered the whole time period used in this analysis, only three years being lacking. The most highly qualified of the observers was Dr. Phil. (botany), Professor Hj. Hjelt (1851–1925) who observed phenology on his family estate in Karkku close to the west coast (Hjelt 1903).

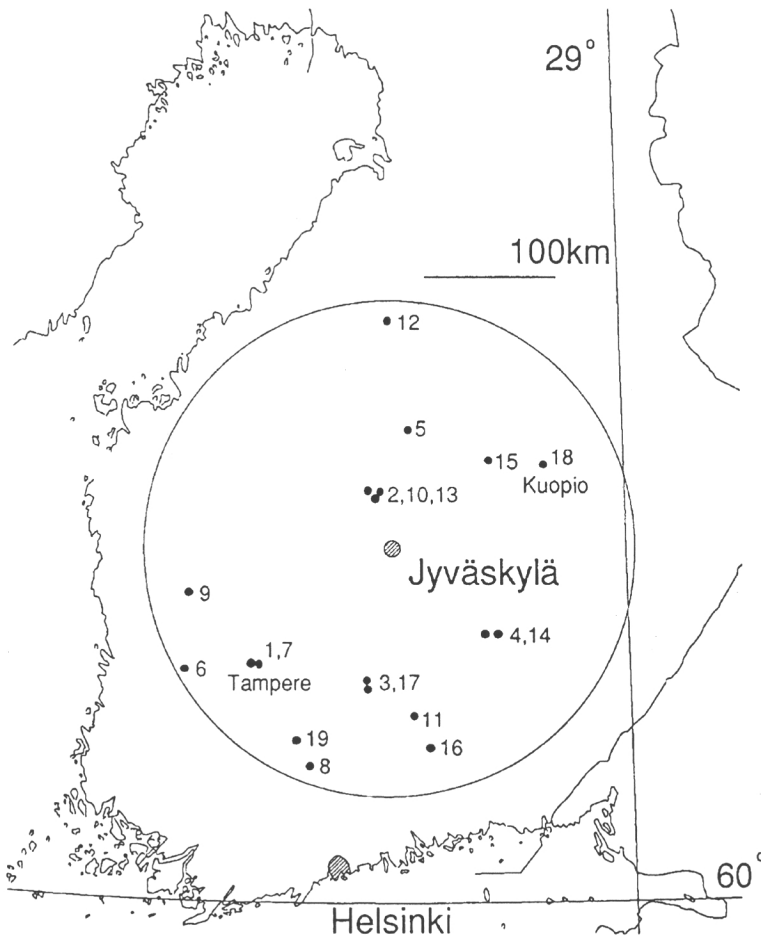
## 3.2 Air temperature time series

### 3.2.1 *History of air temperature measurement*

#### Thermometer

The first primitive thermometer (Figure 5) was probably constructed by Galileo in 1597 (Middleton 1966). Galileo's thermometer, called a thermoscope, was based on the fact that a gas (air in this case) will expand when heated and contract when cooled. When the lower end of a narrow glass tube, with the upper end sealed, is put into a bowl of water the level of the water in the tube goes up and down depending on the air temperature inside the tube. During the 17<sup>th</sup> century air thermometers were scaled, and the liquid-in-glass thermometers familiar to us, which are also suitable for measuring the temperature of objects other than air, were invented after the middle of the 17<sup>th</sup> century.

However, the scales of thermometers had no universal standards until the beginning of 18<sup>th</sup> century, and thus the air temperature measurements made in the 17<sup>th</sup> century were not comparable with each other. The liquid-in-glass thermometer with two universal fiducial points (the melting point of ice and the boiling point of water) was first constructed in 1701 by the famous Danish astronomer Olaus Rømer (1644–1710). However, Rømer never published any information about his alcohol thermometer. Fahrenheit visited Rømer in Copenhagen in 1708



**Figure 4.** Nineteen observation sites of the bud burst of *Betula* sp. leaves. Numbers are the same as in Table I.



**Figure 5.** The first published drawing of a thermometer (Biancani 1620 cit. Middleton 1966).

**Table 1.** Observation sites, observers, and statistics of nineteen time series of the bud burst dates of *Betula* sp. leaves. Numbers are the same as in Figure 4.

Location	Observer	Profession (in Germany)	Number of observations (in paren- thesis outliers included)	Period of observations	Adjustment to level of combined series, $\tau_j$ (day)	Root mean square deviation from combined series	Correlation with combined series
1 Tampere	Blomqvist	Oberförster	17	1937–55	2.7	2.3	.96
2 Saarijärvi	Brander	Förster	15	1908–23	-2.0	1.6	.99
3 Padasjoki	Böök	Lektor	16	1926–42	3.5	2.1	.96
4 Mikkeli	Ehnberg	Lehrerin	57	1896–1955	0.9	3.1	.93
5 Viitasaari	Halmesmäki	Pfarrer	25(26)	1927–55	-14.9	4.4	.88
6 Karkku	Hjelt	Professor	19(20)	1899–1925	0.8	2.8	.97
7 Tampere	Karsten	Stadtgärtner	40	1898–1943	2.5	2.3	.96
8 Janakkala	Kerkkonen	Landwirt	14(15)	1937–51	3.6	5.0	.70
9 Parkano	Koivukoski	Pfarrer	14(15)	1941–55	-7.0	3.8	.85
10 Saarijärvi	Lilius	Disponent	17	1896–1914	-2.2	2.2	.97
11 Heinola	Luotola	Lektor	17	1919–37	5.9	1.9	.98
12 Haapajärvi	Mäntyvaara	Förster	31	1920–52	-2.4	4.2	.91
13 Saarijärvi	Nordenstreng	Frau	38	1907–50	3.0	3.1	.94
14 Mikkeli	Nordström	Mag.Phil.	20	1896–1917	3.6	2.2	.97
15 Karttula	Saastamoinen	Dorfschullehrer	19(24)	1908–48	-14.7	4.9	.90
16 Iitti	Salo	Bäckerin	15	1941–55	2.9	4.9	.85
17 Padasjoki	Schildt	Gutsbesitzer	19(20)	1923–43	5.7	1.6	.98
18 Kuopio	Ståhlberg	Mag. Phil.	16	1900–15	2.5	1.7	.98
19 Hattula	Wegelius	Fräulein	46	1910–55	5.7	2.2	.96

and learnt how to graduate thermometers. Fahrenheit then developed his own temperature scale and used mercury instead of alcohol and published a description of it. He is therefore commonly, but incorrectly, known as the inventor of the modern thermometer (Middleton 1966, Gough 1971).

### Historical air temperature records

The oldest continuous instrumental records of air temperature are from Central England and begin in 1659 (Jones and Bradley 1992). Comparable temperature observations originate from the first half of the 18<sup>th</sup> century, soon after the modern thermometer was invented. The longest temperature time series from neighbouring countries are those from Uppsala (beginning in 1722), from St. Petersburg (1751), and from Stockholm (1756) (Heino 1994, Moberg and Bergström 1997). The oldest instrumental observations known in Finland are from Turku, where Professor H.D. Spöring initiated temperature observations in 1730 (Seppinen 1988). Instrumental temperature observations were also made in Tornio during 1737–49 by Dean Abraham Johannes Foug (Johansson 1913). The motivation to start these observations came from Celsius. Celsius participated in the expedition, arranged by the French Royal Academy of Sciences and led by Moreau de

Maupertuis, to the River Tornio in 1736–37. The expedition was to prove the flattening of the Earth and to verify the theoretical calculations of Newton (the other expedition went to Mitad del Mundo in Peru). Fougat put up the members of the expedition and became familiar with how to measure temperature. The measurements of Fougat were made with a Reaumur-scale thermometer (Celsius published his paper on the Celsius temperature scale in 1742).

However, most of the records from the 1700s and beginning of the 1800s in Finland cannot be used for climatological studies because the observation periods were short and the measurement practices unknown (Heino 1994). Reliable climatological observations were started by Prof. G.G. Hällström in Helsinki on October 4, 1828 (Johansson 1906). Following relocation of the station and short interruptions, temperature measurements have been made continuously in Helsinki since July 1, 1844 by the Magnetic Observatory, founded in 1838 as a unit of the Imperial Alexander University in Helsinki. Since 1846 temperature measurements, in addition to those in Helsinki, were also made in Sortavala, Kuopio, Viitasaari, Kajaani and Oulu (Finska Vetenskaps-Societeten 1853, p. 85). In 1881 the Magnetic Observatory was incorporated into Finska Vetenskaps-Societeten and was renamed the Meteorological Central Office.

### *3.2.2. Air Temperature observations in Jyväskylä (1883–1981)*

The meteorological time series collected by The Finnish Meteorological Institute (FMI) in the city of Jyväskylä (62°12'N, 25°43'E, 137 m asl), used in this study, begins in 1883 (Heino 1994). The massive data set was digitized by punch card machines from paper publications as a joint effort by the Finnish Forest Research Institute (Department of Mathematics) and FMI (Department of Climatology) according to an agreement drawn up in 1982. The Jyväskylä and Helsinki temperature time series were the first long-term records to be digitized for computers. Four daily temperature measurements (morning, early afternoon, evening, and the daily minimum temperature) were utilized in analyzing bud-burst timing. The missing minimum temperatures for the period 1883–1901 were estimated using monthly linear regressions on the morning temperatures. Owing to missing temperature observations, the years 1912–16 were omitted from the analysis. The observation times and sites varied somewhat during the different time periods (Linkosalo et al. submitted).

## 4 Construction of the combined time series of the bud burst of *Betula* sp. leaves in Jyväskylä (1896–1955)

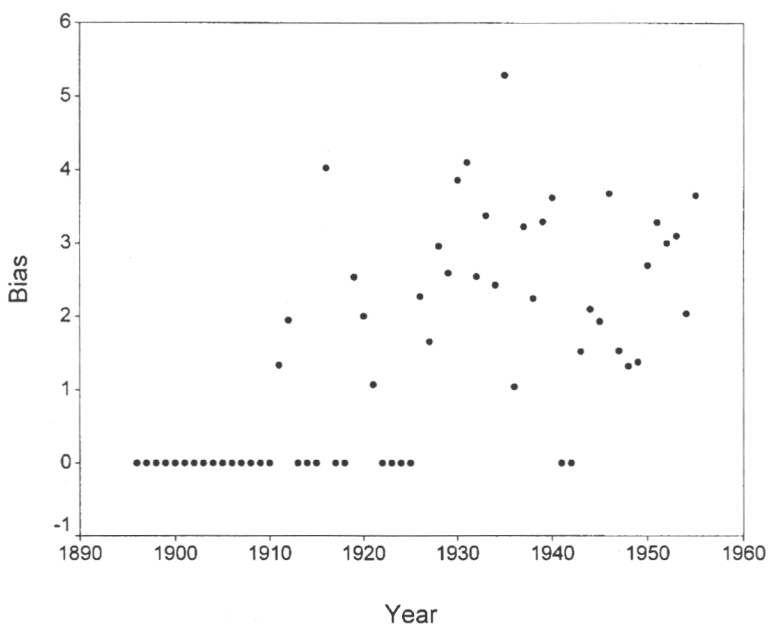
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The collection of phenological time series takes years. The single series published by Finska Vetenskaps-Societen were often short and fragmentary, and the quality of the observations was not known. Fortunately, old time series of several phenological events were available for many locations. Separate, partly overlapping series can be combined into one long continuous series using statistical methods, and its reliability can be evaluated. 19 individual time series of the bud burst of *Betula* sp. were combined (Table 1, Figure 4) (III). The resulting combined time series was used as the material in analyzing alternative theories of bud development (IV, V).

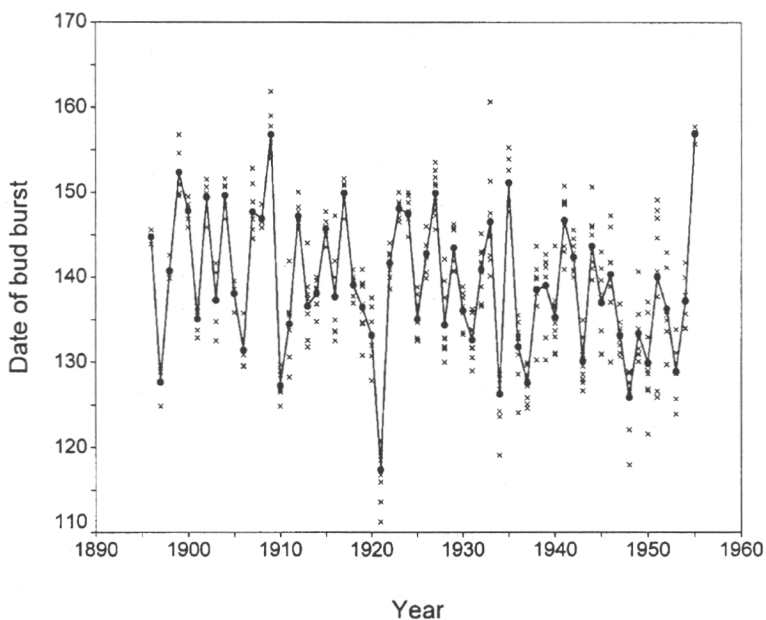
### 4.1 Estimation of the combined time series

Simple annual arithmetic means of the bud-burst dates of overlapping observation series cannot be used as an estimator for the moment of bud burst because of the locations specific systematic errors. For example, in two of the nineteen individual series the bud burst took place over two weeks later than that in the combined series ( $\hat{\tau}_5 = -14.9$  and  $\hat{\tau}_{15} = -14.7$  days, Table 1); if the annual simple arithmetic means of the observations had been used as an estimator of the bud-burst dates, we would have obtained upwards-biased estimates for the years when these two late series were included. The annual bias, i.e. the effect of two late series, can be measured as the difference between the annual arithmetic means in which two late series are included and the annual means in which the late series are excluded. The mean bias was 2.7 days and the maximum bias 5.3 days in 1935 (Figure 6).

Analysis of the data-generating process (Tuomivaara et al. 1994) revealed various potential sources of systematic measuring errors, e.g. differences in the genotypes of the observed trees, different geography of the observation sites, warmer climate in the south than in the north, different personal interpretations of the instructions about how to make bud-burst observations etc. Several systematic error components were confounded with individual series (i.e. observers, sites) and their effects on the timing of bud burst can therefore not be estimated separately (Hicks 1973). However, various systematic error components of the individual series can be treated as a whole, i.e. as one factor in which the error components are pooled. The disturbing effect of this error factor on the timing of bud burst can then be eliminated by treating the individual series (i.e. observers, sites) as blocks. If nineteen observation sites are considered as random blocks, and the years as fixed treatments, then the data-generating process is analogous to an experiment of randomized block design, and the linear mixed model of the analysis of variance can be used in estimating the combined time series of birch bud burst,



**Figure 6.** The bias (days), i.e. the disturbing effect of the two late series (Nos. 5 and 15 in Table 1 and in Figure 4) on the annual arithmetic means of the dates of bud burst of *Betula* sp. In years with a zero bias there were no observations in series Nos. 5 and 15.



**Figure 7.** Combined time series of the bud-burst date of *Betula* sp. leaves (•) in Jyväskylä, 1896–1955, and the original observations (×) adjusted to the level of Jyväskylä as the number of days from the beginning of the year (Table 2).

$$y_{ij} = m + c_i + \tau_j + \varepsilon_{ij} \quad (1)$$

where  $y_{ij}$  is the observed date of bud burst,  $m$  a constant,  $c_i$  the fixed effect of year  $i$ ,  $\tau_j$  the random block effect of series  $j$ , and  $\varepsilon_{ij}$  the residual error (III).

Because the data are unbalanced and contain empty cells, i.e. there are no observations for each observer in each year, Equation 1 cannot be solved using the ordinary least squares method. The parameter values were estimated by the method of maximum likelihood. By assumption,  $E(\tau_j) = E(\varepsilon_{ij}) = 0$ . The combined bud-burst time series,  $\hat{y}_i$ , is estimated using the expected value of Equation 1,

$$\hat{y}_i = E(y_{ij}) = \hat{m} + \hat{c}_i \quad (2)$$

where  $\hat{m}$  and  $\hat{c}_i$  are estimated values of the fixed parameters. The estimated values,  $\hat{y}_i$ , of the combined time series of the annual moment of bud burst are shown in Table 2. The combined time series and all the original observations adjusted to the level of Jyväskylä,  $y_{ij}^a$ , are presented in Figure 7,

$$y_{ij}^a = y_{ij} + \hat{\tau}_j \quad (3)$$

According to the combined time series, the median bud-burst date of *Betula* sp. was May 19, the earliest bud burst taking place on April 28, 1921, and the latest on June 6, 1955. The range of the dates was 39.5 days.

## 4.2 Quality of the individual and combined time series

### Individual time series

In evaluating the quality of the individual observation series of birch bud burst the root mean square deviation of the adjusted individual series (Equation 3) from the combined series (Equation 2), and the correlations between the individual and combined series, were used as measure of concordance of the individual and combined series. The root mean square deviation,  $RMSD_j$ , for series  $j$  was defined as,

$$RMSD_j = \sqrt{\frac{\sum_i (y_{ij}^a - \hat{y}_i)^2}{n_j}} \quad (4)$$

where  $y_{ij}^a$  is the observed value of series  $j$  adjusted to the level of the combined time series in year  $i$ ,  $\hat{y}_i$  the estimated value of the combined time series, and  $n_j$  the number of observations in series  $j$ . The summation goes over the years  $i$  present in series  $j$ . The smallest correlation between the individual and combined time series was 0.7, but fifteen of the nineteen correlation coefficients exceeded 0.9. This indicates high concordance, i.e. quality of individual series (Table 1). The Saarijärvi series recorded by Mrs. Nordenstreng was, in earlier study, considered to be the most reliable observation series (II). However, the root mean square deviation and correlation coefficient with the combined series showed that the quality of the

**Table 2.** The combined time series of the bud-burst dates of *Betula* sp. in Jyväskylä, during 1896–1955 (Figure 7).

Year	Moment of bud burst (number of days from beginning of year)	Number of observations	Standard deviation of observations adjusted to the level of Jyväskylä
1896	144.7	3	0.86
1897	127.7	3	2.53
1898	140.7	4	1.27
1899	152.3	5	3.20
1900	147.8	5	1.47
1901	135.1	6	1.52
1902	149.4	5	2.15
1903	137.3	4	4.38
1904	149.6	5	1.93
1905	138.1	4	1.57
1906	131.4	4	2.97
1907	147.7	7	3.25
1908	146.9	6	0.92
1909	156.8	7	2.91
1910	127.3	8	1.58
1911	134.5	7	4.34
1912	147.2	9	1.34
1913	136.6	9	3.94
1914	138.1	8	1.65
1915	145.7	5	1.60
1916	137.7	7	5.49
1917	149.9	6	1.67
1918	139.1	6	1.47
1919	136.5	8	3.23
1920	133.2	8	3.14
1921	117.4	9	3.31
1922	141.6	8	1.75
1923	148.1	8	1.13
1924	147.5	8	2.01
1925	135.1	8	2.49
1926	142.7	8	1.92
1927	149.9	9	2.64
1928	134.4	9	4.22
1929	143.4	8	2.28
1930	136.1	9	1.91
1931	132.6	10	2.37
1932	140.8	9	2.86
1933	146.5	10	5.86
1934	126.3	10	3.14
1935	151.1	8	2.69
1936	131.8	9	3.52
1937	127.6	10	1.94
1938	138.5	11	3.27
1939	139.0	8	4.69
1940	135.3	9	3.91
1941	146.7	11	3.07
1942	142.3	10	1.84
1943	130.1	11	2.40
1944	143.6	9	3.61
1945	137.0	9	4.24
1946	140.3	10	4.79
1947	133.2	9	1.92
1948	125.9	9	3.58
1949	133.4	9	3.26
1950	129.9	9	4.84
1951	140.0	8	9.23
1952	136.3	7	4.45
1953	128.9	6	3.62
1954	137.2	6	3.17
1955	156.9	5	0.74

Nordenstreng series was of medium standard only (Table 1). This demonstrates the importance of combining the information from individual observation series in order to improve and evaluate the quality of the data, instead of relying on single series. A more detailed investigation revealed that the residual of the adjusted Nordenstreng series from the combined series was 10.3 days in 1946, thus indicating that the observation recorded in that year was probably a mistake or a misprint. Nevertheless, the deviation was not large enough to be considered an outlier in the outlier-analysis (Linkosalo et al. 1996).

#### The combined time series

The estimated random (block) effects  $\hat{\tau}_j$  for each of the nineteen individual observation series  $j$  describe the average deviation of the bud burst dates from the combined time series (Table 1). For example, bud burst in Saarijärvi (Series No. 13) took place on the average 3.0 days earlier than in the combined time series at the level of Jyväskylä. Further adjustment of the combined time series to the level of Jyväskylä was not needed because the value of parameter  $\hat{\tau}_j$  at the latitude of Jyväskylä was zero (cf. Figure 4 in III).

The number of observations and standard deviations of the adjusted observations per year can be used as a measure of the annual quality of the estimated combined time series when weighting or selecting subset of years for further analysis (Table 2). The variance component of the disturbing variation,  $\tau_j$ , between the series was 37.3 and the variance component of the residual error variation,  $\varepsilon_{ij}$ , was 11.7. Thus 76 % of the total random variation was induced by the disturbing variation between the series.

## 5 Analysis of bud-development theories based on the combined phenological time series of *Betula* sp. leaves and the air temperature observations in Jyväskylä (1896–1955)

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### 5.1 Fundamental ideas of bud-development theories

At the end of the growing season in autumn trees enter an inactive state called dormancy, during which ontogenetic bud development, i.e. morphological changes in buds are inhibited by biochemical regulation. The theoretical concepts used in bud-development theories have not been fully accepted (Hänninen 1986, 1990, 1995). For example, for the concept of dormancy Sarvas (1974) used the term ‘dormancy I’ or ‘autumn dormancy’, and Hänninen (1990, 1995) the term ‘rest’. The growing season of trees begins at bud burst, which is a visible point event in time. According to most simple theory the bud burst occurs on a specific date and the regulation of the bud development is based on a biological clock (Bünning 1963). This theory, however, does not explain the great year-to-year variation in the timing of bud burst. According to slightly modified theory of Sarvas (1972, 1974) temperature driven ontogenetic bud development starts spontaneously at the moment when dormancy, driven by low chilling temperatures, has completed. According to other common type of theories, ontogenetic bud development begins at a slow rate during dormancy (Landsberg 1974, Cannell and Smith 1983, Hänninen 1990 and 1995). Finally there are theories in which light signal, e.g. photoperiod, is considered to affect the start of temperature driven ontogenetic development (Wareing 1956). The theories involve problematic theoretical concepts that are not directly observable, like the start of ontogenetic bud development and the stages of the development of dormancy and ontogenesis of bud. However, the different ideas above can be condensed into the following four main types of alternative theories (cf. Hunter and Lechowicz 1992, Kramer 1994, Hänninen 1995):

Theory 0: Bud burst takes place on a fixed date.

Theory 1: Ontogenetic development starts at the end of dormancy.

Theory 2: Ontogenetic development starts during dormancy.

Theory 3: Ontogenetic development starts on a fixed date.

As an example, the progression of the ontogenetic bud development in a specific year according to Theories 1–3 is shown in Figure 11 (Chapter 5.2.2). All the alternatives can be treated within the framework of the mathematical model presented.

## 5.2 Mathematical model of bud-development theories

The mathematical model of bud development from the onset of dormancy to bud burst has been based on the concepts of stage of bud dormancy, stage of bud ontogenesis (Hari 1972, Sarvas 1974), and the growth competence (Hänninen 1990, 1995). Three scalar valued state functions, the stage of dormancy,  $S_D(t)$ , the stage of ontogenesis,  $S_O(t)$ , and the growth competence,  $C(t)$ , describe the developmental stage of a bud at moment  $t$ . The rate of dormancy development was defined as the time derivative of the stage of dormancy,  $f_D(t) = dS_D(t)/dt$ . Dormancy is completed when the stage of dormancy reaches the threshold value,  $D_{crit}$ . Analogously, the rate of bud ontogenesis was defined as the time derivative of the stage of bud ontogenesis,  $g_O(t) = dS_O(t)/dt$ . Bud burst takes place when the stage of ontogenesis exceeds the threshold value  $O_{crit}$ . Alternative theories specify different dependences of the rate of dormancy development on environmental factors,  $f_D(t) = f_D(u(t))$ , and of the rate of ontogenetic development on environmental factors and, possibly, on the stages themselves,  $g_O(t) = g_O(v(t), S_D(t), S_O(t))$ , where  $u(t)$  and  $v(t)$  are sets of environmental factors. The restraining effect of the stage of dormancy on the ontogenetic development rate can be modelled with the multiplier,  $C(t) = C(S_D(t)) \in [0, 1]$ , called growth competence by Hänninen (1990, 1995). Thus  $g_O(t) = C(S_D(t)) g'_O(v(t), S_O(t))$ .

The stage of dormancy and the stage of ontogenesis at moment  $t$  depend on the history of environmental factors. Thus they can be obtained by integrating the corresponding rates over time from the start of dormancy,  $t_0$ , and from the start of ontogenetic development,  $t_1$ ,

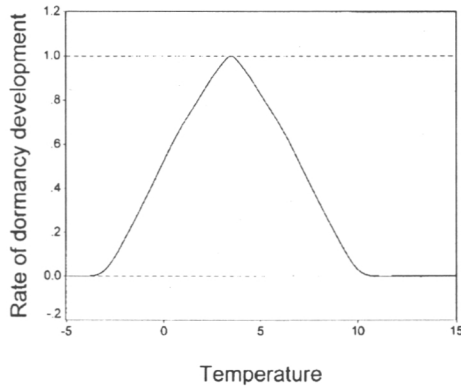
$$S_D(t) = \int_{t_0}^t f_D(t) dt = \int_{t_0}^t f_D(u(t)) dt \quad (5)$$

$$S_O(t) = \int_{t_1}^t g_O(t) dt = \int_{t_1}^t C(t) g'_O(t) dt = \int_{t_1}^t C(S_D(t)) g'_O(v(t), S_O(t)) dt \quad (6)$$

The bud burst takes place at the moment,  $t_b$ , when the stage of ontogenetic development,  $S_O$ , increases to the threshold value  $O_{crit}$ . I.e. the predicted moment of bud burst,  $t_b$ , for each year is obtained as the solution of the following equation:

$$S_O(t_b) = \int_{t_1}^{t_b} g_O(t) dt = O_{crit} \quad (7)$$

The different functions for the rate of dormancy development,  $f_D(t)$ , the rate of ontogenetic development,  $g_O(t)$ , and the growth competence,  $C(t)$ , presented in literature, have been collated in Hänninen (1995) as graphs and mathematical equations.



**Figure 8.** Dependence of the rate of dormancy development (chilling-units/hour) on temperature ( $^{\circ}\text{C}$ ) according to Sarvas (1974).

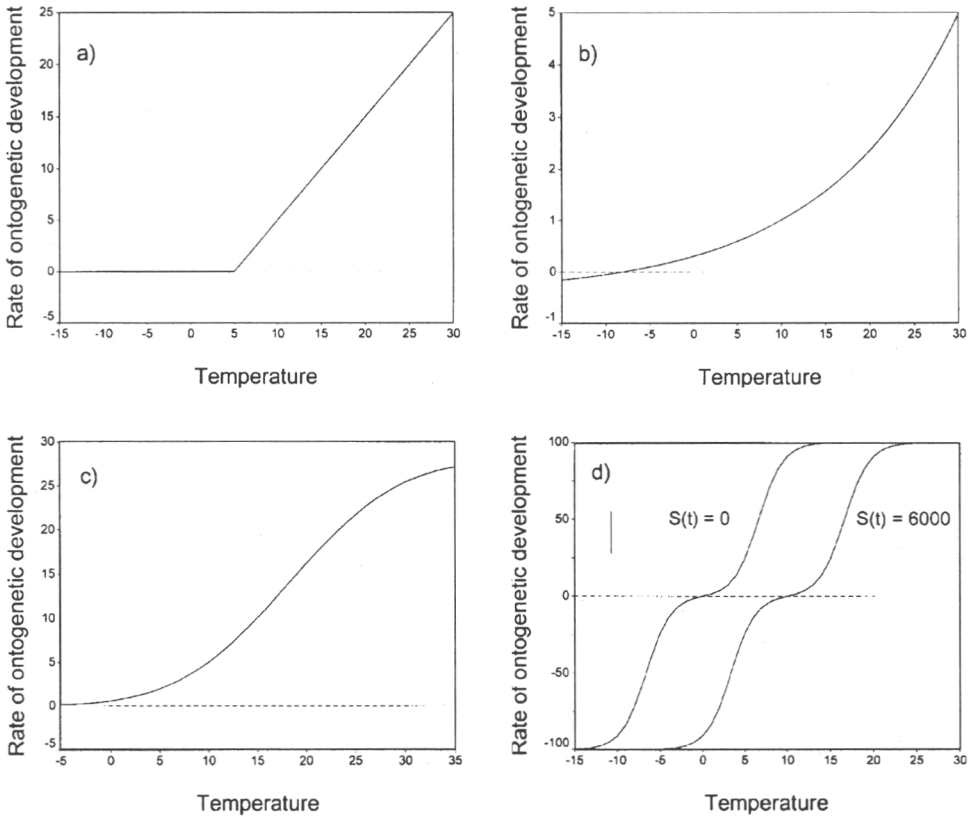
### 5.2.1 Estimation of the values of model parameters

The integrals in Equations 5–7 were approximated by summing over a 6-hour time interval. The least square estimates of the model parameters, i.e. the beginning of dormancy  $t_0$ , the threshold value of dormancy release  $D_{\text{crit}}$ , and the beginning of ontogenetic development  $t_1$ , were determined by minimizing the mean square error (Equation 9),  $MSE$ , of the predicted bud-burst dates by iterative procedure. The value of the parameter  $O_{\text{crit}}$ , the threshold value of bud burst, was estimated as the average of the annual values of the stage of ontogenesis,  $S_0$ , at the observed moment of bud burst over the years 1896–1955 (IV).

### 5.2.2 Specification of the mathematical models of the bud-development theories to be evaluated

Theories 0–3 (cf. Chapter 5.1) to be analysed resulted in four corresponding mathematical models of bud development, later called Model 0–Model 3, i.e. in different specifications of Equations 5–7 (IV).

Furthermore, the specifications of the submodels of Models 0–3 were needed. Some of the submodels of ontogenetic development analysed in this study have been developed to describe other processes and tree species than the bud development of birch (I, II). However, they made it possible to analyse the fitness of different model families for bud-development modelling. As representatives of various alternatives, the following submodels for the rate of dormancy development, the rate of ontogenetic development and the growth competence were selected from Hänninen (1995). In Theory 0 the submodels for dormancy development and ontogenesis are not needed because, according to Bünning (1963), the biological clock determines the fixed bud-burst day. In Models 1 and 2, the dependence of the rate of dormancy development on the prevailing temperature,  $f_D(T(t))$  according to the chilling-unit-sum submodel of Sarvas (1974) was used (Figure 8). In Models 1–3, four different submodels (a–d) for the dependence of the rate of ontogenesis on temperature,  $g_O(T(t), S(t))$ , were applied (Figure 9):



**Figure 9.** Dependence of the rate of ontogenetic development on temperature ( $^{\circ}\text{C}$ ): a) temperature-sum submodel ( $^{\circ}\text{C}$ ) (Reaumur 1735), b) respiration submodel (arbitrary units) (Hari et al. 1970), c) period-unit-sum submodel (period units) (Sarvas 1972), and d) feedback submodel (arbitrary units) (Pelkonen and Hari 1980).

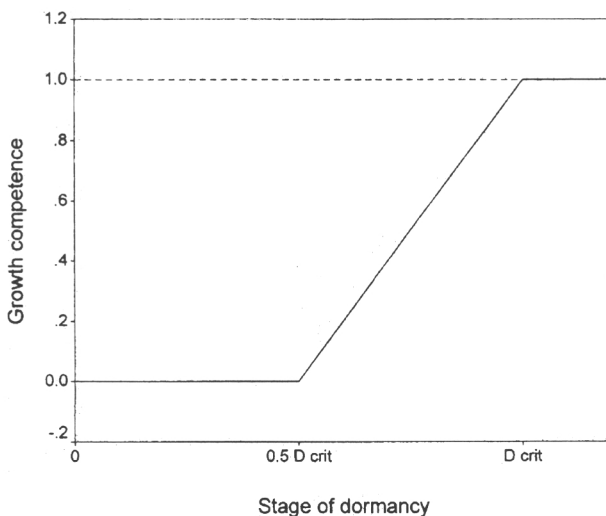
- a) Temperature-sum submodel of Reaumur (1735)
- b) Respiration submodel, based on the dependence of respiration on temperature, of Hari et al. (1970)
- c) Period-unit-sum submodel of Sarvas (1972)
- d) Feedback submodel, based on the recovery of photosynthesis in spring, of Pelkonen and Hari (1980)

The mathematical equations of submodels a–d are as follows (I,II),

$$g(T(t)) = \begin{cases} 0, & \text{if } T(t) \leq 5^{\circ}\text{C} \\ T(t) - 5, & \text{if } T(t) > 5^{\circ}\text{C} \end{cases} \quad (8a)$$

$$g(T(t)) = a + be^{cT(t)}, \text{ where } a = -0.4207, b = 0.727 \text{ and } c = 0.067 \quad (8b)$$

$$g(T(t), S(t)) = \frac{100}{1 + 100a^{-\frac{(T(t) - S(t))}{c}}} + \frac{100}{1 + 100a^{\frac{(T(t) - S(t))}{c}}}, \text{ where } a = 2 \text{ and } c = 600 \quad (8d)$$



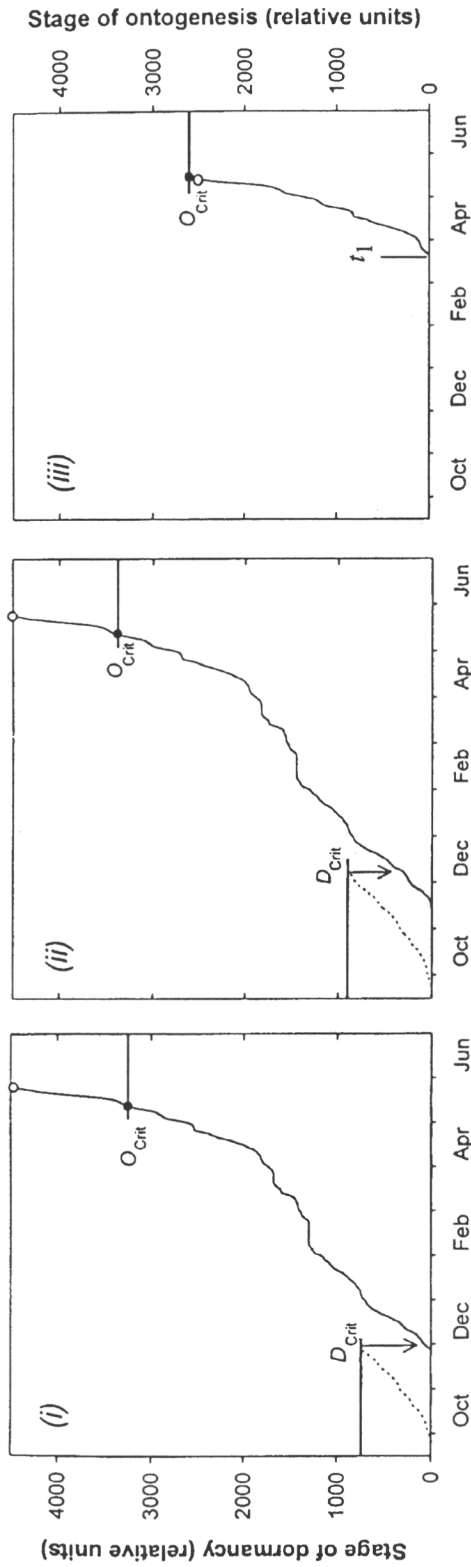
**Figure 10.** The dependence of the growth competence,  $C(t)$ , restraining the rate of ontogenesis during dormancy, on the stage of dormancy,  $S_D(t)$  (chilling units);  $D_{crit}$  denotes the threshold value for dormancy completion.

The chilling-unit-sum submodel of dormancy development (Sarvas 1974)(Figure 8) and the period-unit-sum submodel of ontogenesis (Sarvas 1972) (Figure 9c) were used in tabular form.

The chilling-unit-sum, temperature-sum, and period-unit-sum submodels are all positive functions of temperature, following the idea that the stages of dormancy and ontogenesis are irreversible. The respiration submodel is mainly a positive function of temperature, but also attains negative values at low temperatures, ( $T < -9$  °C), resulting in reversal of the stage of development (Figure 9b). Extrapolation of this model to low negative temperatures is not justified from the point of view of respiration, but it represents a submodel in which ontogenetic progression may also be reversed. According to the feedback submodel, the progression of stage of development depends, in addition to temperature, also on the stage itself and its values are positive or negative following that the stage can also be reversed. The values of the stage of ontogenesis based on the feedback submodel at specific moment depend only on the temperature during the preceding two weeks (Figure 9d).

In Theory 2, the dependence of ontogenetic development on the stage of dormancy, i.e. the growth competence,  $C(t)$ , according to Hänninen (1990) was utilized (Figure 10).

The theories describe the progression of bud ontogenesis in a different way. Especially if late autumn and winter are warm, the ontogenesis according to Theories 1–3 differs considerably, as shown in Figure 11 where bud development in 1929–30 was used as an example.



**Figure 11.** Progression of the stage of bud dormancy (.....) and stage of bud ontogenesis (—) in *Betula* sp. leaves according to models of Theories 1–3 in 1929–30. The chilling-unit-sum submodel of Sarvas (1974) and the period-unit-sum submodel of Sarvas (1972) were applied. The arrows show the end of dormancy, i.e. the moment when threshold value  $D_{crit}$  has been reached. (i) In Model 1 ontogenetic bud development starts at the end of dormancy, (ii) in Model 2 ontogenetic development starts at a slow rate during dormancy, and (iii) in Model 3 ontogenetic development starts at a fixed calendar date  $t_1$ .  $O_{crit}$  denotes the threshold value of the stage of ontogenetic development at bud burst,  $\circ$  denotes observed, and  $\bullet$  predicted date of bud burst.

**Table 3.** Mean values and ranges of the standard deviations of the twelve conditional distributions of spring minimum temperatures after simulated date of bud-burst for each of five different regulation principles of ontogenetic development

Regulation based on	Mean of standard deviations (°C)	Range of standard deviations (°C)
Biological clock	2.4	1.7–3.6
Temperature sum	2.4	2.0–3.3
Respiration rate	2.2	1.6–3.0
Period-unit sum	2.3	1.8–3.2
Feedback principle	1.6	1.4–1.8

### 5.3 Evaluation of the submodels of ontogenetic bud development based on conditional distribution of spring minimum temperatures in Jyväskylä (1883–1981)

A analysis of the regulation principles of ontogenetic development can be based on theoretical argumentation and on long-term temperature observations only. According to theoretical argument, during evolution trees have developed regulation system of ontogenetic development that maximises the length of the growing season and minimises the risk of frost injury. Thus regulation is based on the principle that predicts most precisely the risk of frost damage. In this case the analysis can be based on the precision of the distribution of minimum temperatures during spring after the occurrence of bud burst. The standard deviation of the conditional minimum temperature distribution was used as a measure of precision; a small standard deviation indicates high precision (I).

The five regulation principles of ontogenetic bud development were compared. In one it was assumed that bud burst takes place on a fixed calendar date (Theory 0), and in four it was assumed that ontogenetic development starts on April 1 (Theory 3) according to the submodels presented in Figure 9 and in Equation 8. The period of temperature observation was 1883–1981. The conditional minimum temperature distribution was estimated using the frequency distribution of 96 minimum temperature observations, one for each year. For each of the five regulation principles of ontogenetic development, twelve conditional minimum temperature distributions were calculated according to twelve threshold values of bud burst,  $O_{crit}$ . The mean values and ranges of the twelve standard deviations of the minimum temperature distributions for each regulation principle were calculated. The mean and range of the standard deviation of the feedback submodel, developed to describe the recovery of photosynthesis in spring, were found to be the smallest (Table 3) (I).

**5.4 Evaluation of the bud-development theories of *Betula* sp. leaves based on air temperature observations in Jyväskylä and (i) the bud-burst time series in Saarijärvi (1907–50) and (ii) the combined bud-burst time series in Jyväskylä (1896–1955)**

Evaluation of the theories of the timing of bud burst has been traditionally based on comparison of the numerical magnitude of the mean square errors, *MSE*, of models only,

$$MSE = \frac{1}{n} \sum (y_j - \hat{y}_j)^2 \quad (9)$$

where  $y_j$  is the observed, and  $\hat{y}_j$  the predicted moment of bud-burst, and  $j$  runs over  $n$  observation years.

Sometimes the coefficient of determination,  $R^2$ , has also been used,

$$R^2 = 1 - \frac{\sum (y_j - \hat{y}_j)^2}{\sum (y_j - \bar{y})^2} \quad (10)$$

where  $\bar{y}$  is the mean of the observed bud-burst dates (Draper and Smith 1981, Weisberg 1985).

The four Theories 0–3 (cf. Chapter 5.1.) of the bud development of *Betula* sp. leaves from the onset of dormancy to bud burst were evaluated using four different submodels (a–d) of ontogenetic development (Figure 9 and Equation 8), and calculating the corresponding values of *MSE* and  $R^2$ .

The calculations were made using (i) the 38-year-long observation series of Mrs. Nordenstreng in Saarijärvi (1907–50), and (ii) the 55-year-long combined time series in Jyväskylä (1896–1955) constructed from nineteen individual observation series. The results are shown in Table 4. Theory 3, in which ontogenetic bud-development starts on a fixed date when applying the period-unit-sum submodel of ontogenetic development (Sarvas 1974) had the smallest *MSE* value (= 6.1). In addition, the fit on the basis of the *MSE*'s of all the models using the combined bud-burst time series was consistently more accurate than the fit obtained with the single observer series of Mrs. Nordenstreng.

The dates of dormancy completion were not observed but they are a fundamental concept of Theories 1 and 2. Besides the predicted date of bud burst, the predicted dates of annual dormancy completion according to Theories 1 and 2 can be calculated corresponding to the estimated values of  $t_0$  and  $D_{crit}$ . The modelled dormancy completion took place according to Model 1 as late as between February 1 and April 8 (April 27) in 4(14) out of 55 years, and according to Model 2 between February 1 and April 23 (May 23) in 11(35) years utilising the period-unit-sum submodel (the corresponding values obtained with the temperature-sum submodel are given in parentheses) (IV).

**Table 4.** The mean square error, *MSE*, root mean square error, *RMSE*, coefficient of determination,  $R^2$ , and estimated parameter values of models of the bud development of *Betula* sp. leaves from the onset of dormancy to bud burst when applying four submodels of ontogenetic development. Abbreviations:  $t_0$  = starting date of dormancy;  $D_{crit}$  = threshold value for the stage of dormancy completion;  $t_1$  = threshold date for the start of bud ontogenesis;  $O_{crit}$  = threshold value of the stage of ontogenesis for bud burst; and  $\bar{t}_{bud-burst}$  = mean date of observed bud burst; CU = chilling units; AU = arbitrary units. The calculations were based, in addition to the air temperature data, on A) the 38-year-long bud-burst time series of Mrs. Nordenstreng in Saarijärvi, and B) the 55-year-long combined bud-burst time series in Jyväskylä.

**A. Observations made by Mrs. Nordenstreng in Saarijärvi (1907–50)**

	<i>MSE</i> (day)	<i>RMSE</i> (day <sup>2</sup> )	$R^2$ (CU)	$t_0$ (AU)	$D_{crit}$ (day)	$t_1$	$O_{crit}$	$\bar{t}_{bud-burst}$
<b>Theory 0:</b> Bud burst takes place on a fixed date								
Biological clock	81.9	9.0	.0	–	–	–	–	May 16 (135.5)
<b>Theory 1:</b> Ontogenetic development starts at the end of dormancy								
Period-unit sum	31.2	5.9	.62	Sep 2	780	–	2995	–
Temperature sum	20.9	4.6	.75	Sep 22	460	–	1523	–
Respiration	95.1	9.8	–.161	Sep 2	760	–	863	–
Feedback	–	–	–	–	–	–	–	–
<b>Theory 2:</b> Ontogenetic development starts during dormancy								
Period-unit sum	32.4	5.7	.60	Sep 1	1050	–	3026	–
Temperature sum	21.2	4.6	.74	Sep 27	720	–	1486	–
Respiration	95.5	9.8	–.167	Sep 2	1200	–	786	–
Feed back	–	–	–	–	–	–	–	–
<b>Theory 3:</b> Ontogenetic development starts on a fixed date								
Period-unit sum	18.5	4.3	.78	–	–	Apr 19	1754	–
Temperature sum	19.8	4.5	.76	–	–	Apr 17	1289	–
Respiration	21.1	4.6	.74	–	–	Mar 19	620	–
Feed back	27.8	5.3	.66	–	–	Apr 25	4753	–

**B. Combined time series in Jyväskylä (1896–1955) based on 19 individual observation series**

	<i>MSE</i> (day <sup>2</sup> )	<i>RMSE</i> (day)	$R^2$ (CU)	$t_0$ (AU)	$D_{crit}$ (day)	$t_1$	$O_{crit}$	$\bar{t}_{bud-burst}$
<b>Theory 0:</b> Bud-burst takes place on a fixed date								
Biological clock	69.9	8.4	.0	–	–	–	–	May 20 (139.2)
<b>Theory 1:</b> Ontogenetic development starts at the end of dormancy								
Period-unit sum	17.6	4.2	.75	Sep 13	710	–	3339	–
Temperature sum	9.9	3.1	.86	Sep 25	810	–	1732	–
Respiration	77.0	8.8	–.102	Sep 2	940	–	821	–
Feed back	–	–	–	–	–	–	–	–
<b>Theory 2:</b> Ontogenetic development starts during dormancy								
Period-unit sum	19.0	4.4	.73	Sep 12	900	–	3447	–
Temperature sum	10.0	3.2	.86	Oct 7	890	–	1731	–
Respiration	76.5	8.7	–.094	Sep 10	1200	–	832	–
Feed back	–	–	–	–	–	–	–	–
<b>Theory 3:</b> Ontogenetic development starts on a fixed date								
Period-unit sum	6.1	2.5	.91	–	–	Mar 21	2658	–
Temperature sum	7.2	2.7	.90	–	–	Apr 19	1569	–
Respiration	9.1	3.0	.87	–	–	Mar 30	645	–
Feed back	37.8	6.1	.46	–	–	Apr 25	5106	–

## 5.5 Statistical evaluation of the bud-development theories of *Betula* sp. leaves based on resampling methods

### 5.5.1 Resampling methods

Bud development is a dynamic process in which regulation of the rate of development depends on the history of the environmental factors (Hari 1968, Sarvas 1972 and 1974). The theories include concepts that are treated with time derivatives and integrals. For instance, the stage of ontogenetic development described by the temperature sum depends on the history of the temperature conditions. No standard statistical methods are available for the analysis of these models because the sampling distributions of the parameters and of the mean square errors of dynamic models are not known. Analysis of the theories on the timing of bud burst has been based only on comparison of the numerical magnitude of the mean square errors of the models. Consequently, because of the lack of statistical tests, we do not know whether the estimated parameter values are statistically significant, and whether the models differ significantly from each other. In addition, no independent data sets have been available for analysing the predictive power of the models.

Resampling methods can be used in statistical inference although usual statistical assumptions, like the normality of errors, are not valid, or when statistical textbook test statistics with known sampling distributions are not available. Resampling methods are not based on new ideas, but the modern high-power computers have enabled us to apply the methods in practical research. The following resampling methods were applied in this study; (i) the bootstrap method to test the statistical significance of the differences in the mean square errors of the models, and to analyze the properties of the distributions of the model parameters; (ii) the cross-validation method to estimate the prediction error of the models, i.e. the prediction power of the models in an independent data set (Efron and Tibshirani 1993).

The underlying idea in resampling is to consider the actual sample as a population and to draw new samples from it repeatedly. In bootstrap method the new bootstrap-samples are formed by drawing items (observation years in our case including temperature time series and one phenological observation) from the 'population' (= original data) one-by-one with replacement until the original sample size (55 years) has been reached. In this procedure the same item (year) can be included in the bootstrap sample on no occasions or many times. This procedure of drawing a bootstrap sample is repeated, for instance, 2000 times. The statistics under consideration, i.g. the mean or parameter value of the model, is calculated from each sample. These 2000 values form the simulated empirical sampling distribution, i.e. the bootstrap-distribution of the statistics, which is utilised in statistical testing (V).

The word "bootstrap" comes from the phrase "to pull oneself up by one's bootstraps" which is commonly attributed to the "Adventures of Baron Munchausen" by Rudolf Erich Raspe (1737–94). The Baron had fallen into a deep lake. Just when it looked as if everything was lost, the idea occurred to him to get out of this difficult situation by pulling himself up by his own bootstraps (Efron and Tibshirani 1993) (Figure 12).



**Figure 12.** Baron von Münchhausen (Picture: Gustave Doré, 1833–83).

In cross-validation the model is fitted to a subsample (training set), which is formed by omitting observations from the original data. The omitted observations are then predicted with the estimated model, and the prediction error of the model, i.e. the prediction ability in the independent data set, is calculated (Marriot 1990).

### 5.5.2 Test of equality of the mean square errors of the models based on bootstrap percentile confidence intervals

Theories 1–3, including the period-unit-sum and temperature-sum submodels of ontogenetic development, were evaluated. The mean square errors (*MSE*) of the corresponding models, presented in Table 4, were:

		Period-unit sum submodel	Temperature sum submodel
Theory 1:	Ontogenetic development starts at the end of dormancy	17.6	9.9
Theory 2:	Ontogenetic development starts during dormancy	19.0	10.0
Theory 3:	Ontogenetic development starts at a fixed date	6.1	7.1

**Table 5.** Statistical significance levels of rejecting the hypothesis of equality of MSE's. Subscripts 1, 2 and 3 refer to Theories 1–3, and subscripts P and L to the period-unit-sum and temperature-sum submodels.

Pairwise <i>MSE</i> comparison	Significance level (%)
a) $\hat{\theta}_{1P-3P} = MSE_{1P} - MSE_{3P} = 11.5$	< 0.0
b) $\hat{\theta}_{2P-3P} = MSE_{2P} - MSE_{3P} = 12.9$	< 0.0
c) $\hat{\theta}_{2P-1P} = MSE_{2P} - MSE_{1P} = 1.4$	1.4
d) $\hat{\theta}_{1T-3P} = MSE_{1T} - MSE_{3P} = 3.8$	2.8
e) $\hat{\theta}_{3T-3P} = MSE_{3T} - MSE_{3P} = 1.0$	30.0
f) $\hat{\theta}_{1T-3T} = MSE_{1T} - MSE_{3T} = 2.8$	6.0

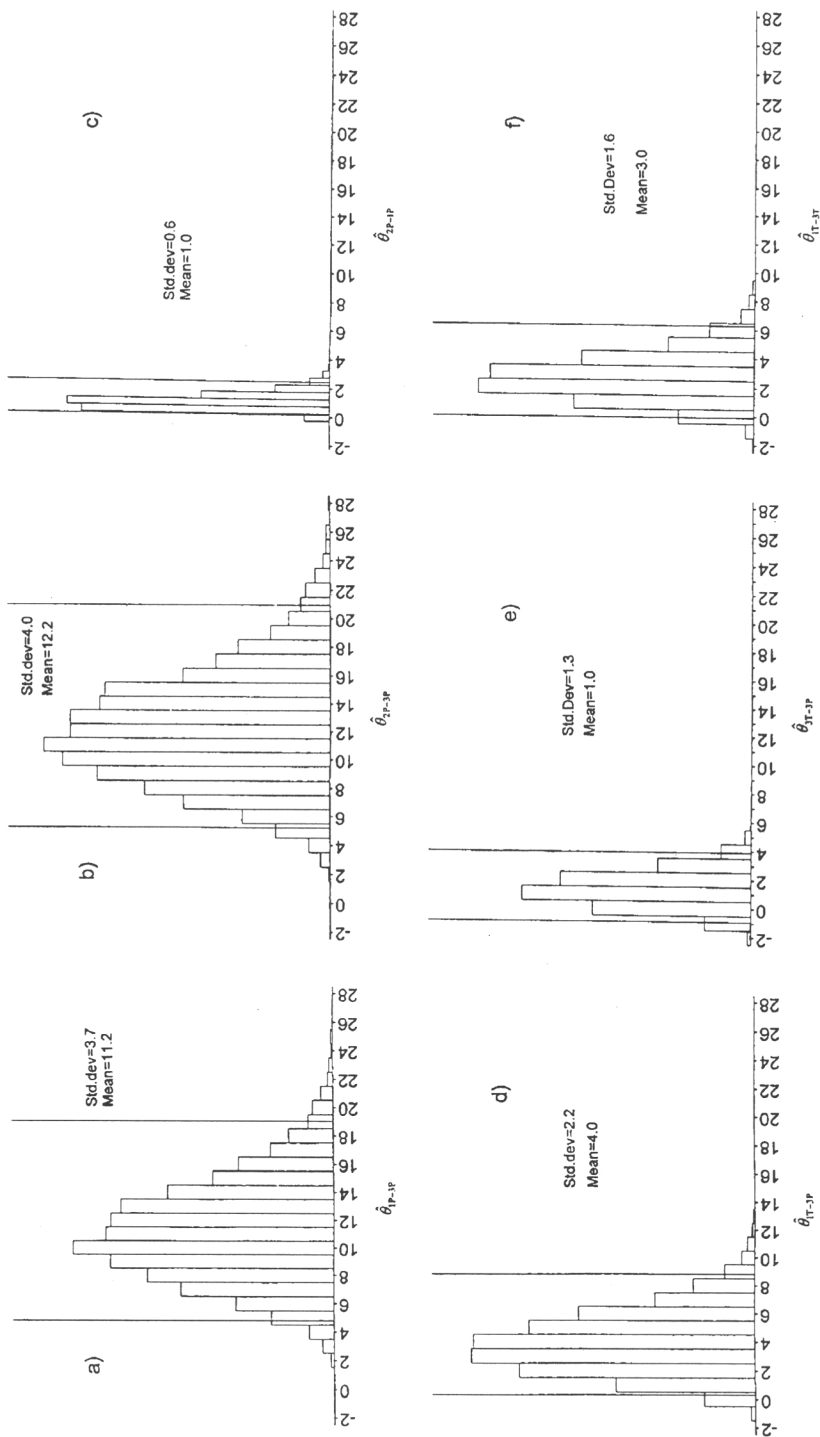
The statistical significance of pairwise equality of *MSE*'s of the models were tested (Table 5). The tests were based on the bootstrap percentile confidence intervals of each of the *MSE* differences. If the value zero was not included in the confidence interval, the difference was considered statistically significant (Efron and Tibshirani 1993). The confidence level of the confidence interval is the probability that the true *MSE* difference belongs to the interval. The complement of the confidence level, i.e. 1–(confidence level), was used as a measure of the statistical significance of the rejection of the hypothesis that the mean square errors are equal.

The bootstrap percentile confidence intervals were determined from the estimated bootstrap sampling distributions of the *MSE* differences as follows. (i) Altogether 7000 bootstrap samples of size 55 were drawn with replacement from the original 55-year-long data. (ii) Models 1–3 with the period-unit-sum and temperature-sum submodels were fitted to each sample and the *MSE* values calculated. (iii) 7000 bootstrap replicates of each *MSE* differences,  $\hat{\theta}_{1P-3P}$ ,  $\hat{\theta}_{2P-3P}$ ,  $\hat{\theta}_{2P-1P}$ ,  $\hat{\theta}_{1T-3P}$ ,  $\hat{\theta}_{3T-3P}$  and  $\hat{\theta}_{1T-3T}$ , (notation same as in Table 5) were calculated. (iv) The bootstrap confidence intervals of each  $\hat{\theta}$  were determined from the corresponding frequency distributions (i.e. empirical bootstrap sampling distributions) of the 7000 bootstrap replicates (Figure 13).

The significance levels based on bootstrap confidence intervals, in which the lower or upper limit = 0 are presented in Table 5. The model of Theory 3, in which ontogenesis starts on a fixed calendar date with the period-unit-sum submodel, differed from the dormancy-dependent Models 1 and 2 at a very small significance level (< 0.0 %) when the period-unit-sum submodel was applied, and at a significance level of = 2.8 % when the temperature-sum submodel was applied (V).

### 5.5.3 Properties of the model parameters

The high inter-correlations of the parameters of Models 1–3 when applying the period-unit-sum model of ontogenetic development calculated from 7000 bootstrap replications, indicated high multicollinearity (Weisberg 1985) (Table 6).



**Figure 13.** The frequency distributions, i.e. the bootstrap sampling distributions of the pairwise differences of the mean square errors,  $\hat{\theta}_{1P-3P}$ ,  $\hat{\theta}_{2P-3P}$ ,  $\hat{\theta}_{2P-1P}$ ,  $\hat{\theta}_{1T-3P}$  and  $\hat{\theta}_{1T-3T}$  (notation same as in Table 5) calculated from 7000 bootstrap samples drawn randomly with replacement from the original data set (= 55 years). Vertical solid lines at 2.5 % and 97.5 % percentiles give the 95 % bootstrap confidence intervals of  $\hat{\theta}$ 's.

**Table 6.** Linear correlation coefficients between parameter values of models based on 7000 bootstrap samples when applying the period-unit-sum submodel of ontogenetic development. Abbreviations as in Table 4.

Model 1		Model 2		Model 3
$t_0$	$D_{crit}$	$t_0$	$D_{crit}$	$t_1$
$D_{crit}$ -.68		$D_{crit}$ -.81		
$O_{crit}$ -.10	-.59	$O_{crit}$ -.20	-.33	$O_{crit}$ -.92

**Table 7.** Mean square errors (*MSE*) in the original data set and cross-validation prediction errors (*CV*) of Models 1–3 when applying the period-unit-sum submodel of ontogenetic development.

	<i>MSE</i> (day <sup>2</sup> )	<i>CV</i> (day <sup>2</sup> )
Model 1: Ontogenetic development starts at the end of dormancy	17.6	19.7
Model 2: Ontogenetic development starts during dormancy	19.0	20.7
Model 3: Ontogenetic development starts on a fixed date	6.1	7.5

Thus the parameter values were sensitive to changes in the data, i.e. the estimated parameter values depend on which years are included in the actual sample. Consequently, no strong inference can be drawn from the magnitude of the estimated parameter values of the models (V).

#### 5.5.4 Prediction error of the models

The classic leave-one-out cross-validation was used to estimate the prediction error of bud-development Theories 1–3 when applying the period-unit-sum submodel of ontogenetic development. The models were fitted to subsamples formed by omitting one observation (year) from the original data set in sequence. The omitted bud-burst observation was then predicted with the estimated model using temperature observations of omitted year as input data. The original data set contained 55 observations. Thus 55 models were fitted to 55 subsamples, each of size 54. The prediction error was estimated as the mean of 55 squared prediction residual errors (Efron and Tibshirani 1993).

The mean square error, *MSE*, measures how well the estimated model predicts the observations used in model estimation. The prediction error, *CV*, measures, on the same scale as *MSE*, how well the models predict new observations that are not used in model estimation. The prediction errors were 2.1, 1.7, and 1.4 units greater than the mean square errors of the original data, 17.6, 19.0, and 6.1 correspondingly (Table 7), which indicates almost as good prediction power of the models in the independent data sets than in the original data (V).

## 6 Discussion and conclusions

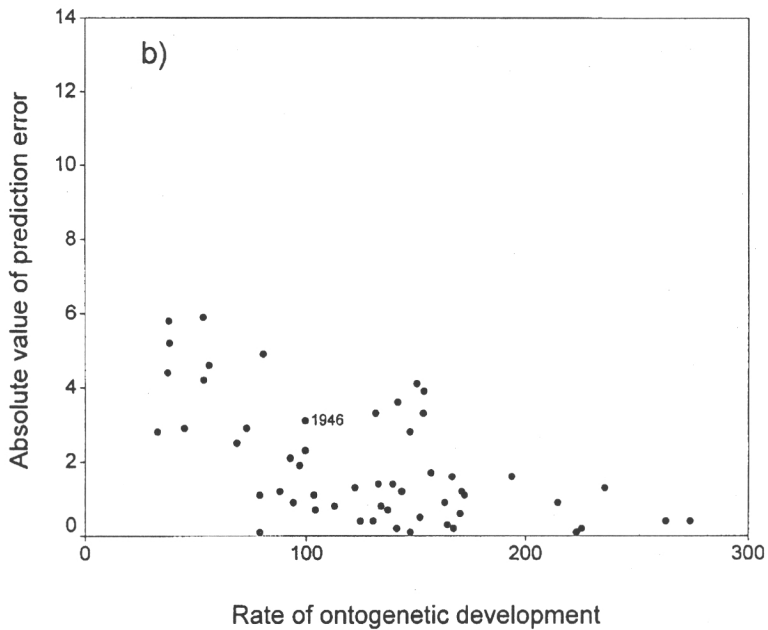
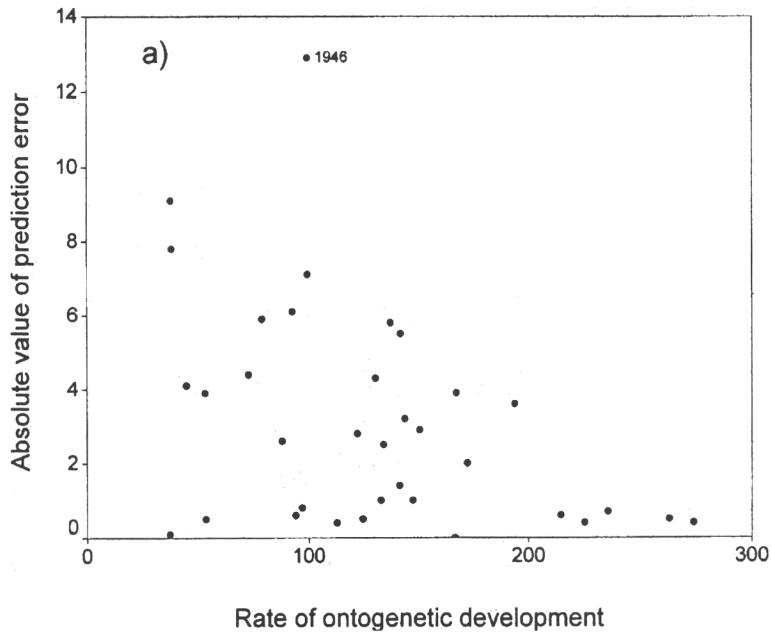
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### 6.1 The combined phenological time series of bud burst of *Betula* sp.

Historical phenological observation series can be used to evaluate phenological theories and to test whether the results obtained in laboratory or field experiments are valid in nature. This is important because we are not sure whether the artificial conditions of laboratories correspond to natural ones. For instance, it is difficult to imitate the features of natural light. In addition, laboratory results mainly concern young trees, but by utilizing old phenological time series the results can also be tested with mature trees. Unfortunately, old phenological observation series are often short, fragmentary, systematically biased, and it takes many years to produce new series because only one observation per year is available. However, the linear mixed model method (Equations 1–2) enables combination of the information from partly overlapping individual series into one long time series. The reliability of combined series is also known.

The 60-year-long time series of the bud burst of *Betula* sp. leaves for the time period 1896–1955 was constructed from 19 partly overlapping individual series from Central Finland. Use of the combination method eliminated the bias caused by the systematic measurement errors of individual series (76 % of the total random variation). The improvement in the quality of the data becomes evident when we look at the magnitudes of the mean square errors (*MSE*) of the models. The *MSE*'s of all the models and submodels decreased consistently when the combined time series of bud burst was used compared to the *MSE*'s of the single observer series of Mrs. Nordenstreng in Saarijärvi (Table 4.A and 4.B). The *MSE* of most precise Theory 3, in which ontogenetic development started on a fixed calendar date when applying the period-unit submodel of ontogenetic bud-development, decreased from 18.5 to 6.1. The fact that the fit of the model based on the combined series was better than the fit based on the single series, does not provide direct proof that the combined time series was more unbiased or precise than the single one. However, it gives substantial evidence for the advantages of a combined time series because the models are based on most comprehensive knowledge of bud development.

Besides removing bias, the combination method also reduced the disturbing effect of random-like errors of single observations caused by misprints or by exceptionally difficult observation conditions. The 'averaging' feature of a linear model, i.e. determination of the expected annual values of bud-burst dates (Equation 2), smooths the disturbing effect of single outlying observations. The observation of bud burst is especially difficult if the progression of bud development is slow before and after bud burst, i.e. if a cold period occurs around bud burst. The magnitude of the prediction error was proportional to the rate of bud development, i.e. to the rate of temperature accumulation (Figure 14). The prediction errors of the combined series as a function of the rate of bud development were consistently smaller (Figure 14b) than the prediction errors of the single observer series



**Figure 14.** Absolute value of the annual prediction residual error (days) of the bud-burst date of *Betula* sp. leaves as a function of the rate of ontogenetic development during two days before and after the observed bud burst (arbitrary units) according to Theory 3, in which ontogenetic development starts on a fixed calendar date when applying the period-unit-sum model of ontogenetic development (Sarvas 1972). a) The single-observer series of Mrs. Nordenstreng in Saarijärvi (1907–50) (38 observations). b) Combined time series in Jyväskylä (1896–1955) (55 observations). The 1946 observation in Mrs. Nordenstreng’s series was a potential outlier.

(Figure 14a). In addition, the disturbing effect of a potential outlier in 1946 in the series of a single observer was diminished (Figure 14). This corroborates the conclusion that the timing of the bud burst of *Betula* sp. was measured more accurately with a combined time series than with a single observer series.

## 6.2 Analysis of the bud-development theories of *Betula* sp. leaves

### 6.2.1 Submodels of the ontogenetic bud development

The analysis of the submodels of ontogenetic bud development was based, in the early phase of this research project, on the conditional distribution of spring minimum temperatures after bud burst (I). Only the temperature observations for 1883–1981 were used. The values of the bud burst thresholds,  $O_{crit}$ , were simulated. The feedback model of Pelkonen and Hari (1980) based on the recovery of photosynthesis in the spring was the most accurate in predicting the conditional minimum temperature distribution (Table 3). It was concluded that the feedback-principle was the most truthful model of the rate of ontogenetic development (I). However, the result was completely the opposite to the final results of this study obtained when phenological observations were also used (Table 4). The contradiction can be explained by theoretical argumentation. According to the feedback model the stage of development fluctuates which is appropriate to describe photosynthesis in which underlying biochemical states may also be reversed. However, reversal is against the fundamental assumption of theories of ontogenetic bud-development, which postulate that the division of plant cells is irreversible. In addition, the time period that affects the value of the stage of development based on the feedback submodel is about two weeks only, whereas according to the bud-development theories the stage of development depends on a longer temperature history. The conclusion that the feedback submodel most accurately predicts the conditional minimum temperature distribution was correct, but the conclusion that it was the best description of the ontogenetic bud-development rate was wrong. Consequently, for theoretical reasons the feedback model is an unrealistic description of ontogenetic bud development. This emphasizes the importance of theoretical argumentation instead of ‘data snooping’ in research and in the interpretation of measurements (Tuomivaara et al. 1994).

When the bud-burst observations were also used, the simplest Theory 0, in which bud burst does not depend on environmental factors at all but takes place at the mean of observed dates, was included in the analysis as the base-line for the mean square error comparisons ( $MSE = 69.9$ ) (Table 4.B). The submodel of ontogenesis based on the temperature dependence of respiration was included in the analysis as an example of a model of ontogenesis in which the stage of development depends on a long temperature history and in which the development is reversed at low temperatures,  $T < -9\text{ }^{\circ}\text{C}$  (Figure 10b). (The model was extrapolated to temperatures below zero and it describes respiration in an unrealistic manner because negative respiration rate is impossible). Occasional low temperatures during winter and early spring had a strong effect on the value of the stage of development. This resulted in unforeseen behavior of the respiration submodel, which was reflected in even higher mean square errors ( $MSE = 77$  and  $76.5$ ,

Table 4.B) according to the dormancy-dependent Theories 1 and 2 than the *MSE* of base Theory 0. The *MSE* according to Theory 3 when applying the respiration submodel was not as high because the exponential form of the model was very close to the period-unit-sum and temperature-sum submodels at the temperature range applied in spring (Figure 9a–c). Consequently, the theoretical arguments and the values of *MSE* corroborate the conclusion that the feedback and respiration submodels do not properly describe the progression of bud ontogenesis.

The temperature-sum and period-unit-sum submodels are not far from each other. The temperature-sum submodel is a fairly good approximation of the period-unit-sum submodel over the temperature range 5–25 °C (Figure 9a and 9c). The mean square errors of dormancy-dependent Models 1 and 2 were lower with the temperature-sum submodels (*MSE* = 9.9 and 10.0) than with the period-unit-sum submodel (*MSE* = 17.6 and 19.0). On the other hand, the mean square error of Model 3 was lower with the period-unit-sum submodel (*MSE* = 6.1) than with the temperature-sum submodel (*MSE* = 7.2) (Table 4.B). However, the period-unit-sum model can be preferred to the temperature-sum model on the basis of the following arguments: (i) the temperature-sum submodel is unrealistic at high temperatures; (ii) the period-unit-sum submodel is based on empirical measurements (Sarvas 1974); and (iii) the *MSE* of Model 3 with the period-unit-sum submodel was the lowest of all the models analyzed. Our results agree with the finding of Hänninen (1995) based on experiments with saplings of *Pinus sylvestris*, in which the 8 most accurate models (out of 96 models to be compared) included the period-unit-sum submodel for the ontogenetic development.

### 6.2.2 Bud-development theories from the beginning of dormancy to bud burst

Bud dormancy is an essential phase of the annual cycle of trees in the boreal and temperate zones in order to avoid bud damage during winter. Experiments have shown that, in the case of *Betula pendula* (Leinonen 1996) and many other tree species (cf. list in Cannell and Smith 1983), incomplete chilling during dormancy can be compensated by an increased temperature requirement for bud burst. However, our analysis based on the combined time series of the bud burst of *Betula* sp. leaves in natural conditions showed that incorporation of the dependence of ontogenetic bud development and the stage of dormancy into the models (Theories 1 and 2) resulted in a statistically significantly higher mean square error compared to the *MSE* of the model in which ontogenetic bud development starts on a fixed calendar date (Theory 3) (Table 4.B). Additional problem of Theories 1 and 2 concern parameter,  $D_{crit}$ , the threshold value of dormancy completion (estimated values 710–900 chilling units, cf. Table 4.B) which is a fundamental structural parameter of Models 1 and 2. The predicted moment of the dormancy completion of *Betula* sp. buds according to the estimated values of  $D_{crit}$  took place in late winter and spring in 9–44 % of observed years (cf. Chapter 5.4), which does not agree with the experimental results of Sarvas (1974), Heide (1993) and Leinonen (1996). Sarvas (1974) found that the dormancy completion of *Betula verrucosa* took place at 220–400 chilling units, according to Heide (1993) vegetative buds of *Betula* sp. were released from dormancy in December, and Leinonen

**Table 8.** The mean square errors (MSE) of the dormancy-dependent model (Theory I) when applying the temperature-sum submodel of ontogenetic bud development according to fixed values of parameters  $t_0$ , beginning of dormancy, and  $D_{crit}$ , the threshold value of dormancy completion (chilling units).

$D_{crit}$	Date of start of dormancy (numbers of days from the beginning of the year)																
	227	232	237	242	247	252	257	262	267	272	277	282	287	292	297	302	307
100	114.1	110.2	91.5	135.9	77.8	48.2	42.9	42.7	55.5	27.3	22.4	18.5	15.4	12.0	11.5	10.8	10.3
150	93.7	94.6	77.4	58.5	46.6	44.1	50.6	40.7	26.8	22.8	19.2	15.7	13.4	11.8	11.2	10.4	10.2
200	60.1	60.6	51.8	53.3	48.4	56.2	39.1	30.4	22.5	19.6	16.1	13.7	12.4	11.6	10.4	10.2	10.1
250	53.2	45.4	50.9	49.4	41.2	38.3	27.5	22.8	19.5	15.9	13.8	12.0	11.7	10.8	10.3	10.1	10.1
300	49.6	43.7	43.2	39.0	29.8	23.9	22.5	19.2	16.1	14.2	12.0	11.9	11.1	10.3	10.1	10.0	10.0
350	38.3	37.1	37.9	21.8	23.2	20.3	19.0	16.8	14.0	12.6	11.8	11.4	10.3	10.2	10.0	10.0	9.9
400	22.9	22.6	22.5	21.5	18.9	18.1	15.8	13.2	12.2	11.4	11.6	10.4	10.2	10.0	10.0	9.9	9.9
450	20.8	20.0	19.7	18.3	17.1	15.7	12.8	12.5	11.3	11.5	10.4	10.2	10.1	10.0	9.9	9.9	9.9
500	17.9	16.9	17.0	16.4	14.9	13.6	12.8	12.0	11.4	11.0	10.2	10.0	10.0	9.9	9.9	9.9	9.9
550	15.4	15.4	15.2	14.2	13.6	12.6	12.1	11.3	10.5	10.3	10.2	10.0	10.0	9.9	9.9	10.0	10.1
600	14.4	14.5	14.1	13.4	12.6	12.1	11.1	10.6	10.3	10.2	10.0	10.0	9.9	10.1	10.0	10.3	10.7
650	12.4	12.4	12.4	12.4	12.2	11.5	10.5	10.2	10.1	10.0	10.0	10.0	10.1	10.1	10.2	11.2	11.1
700	12.0	12.2	12.2	12.1	11.7	10.6	10.3	10.1	10.0	10.0	9.9	10.1	10.1	10.4	11.3	11.6	12.0
750	11.4	11.5	11.4	11.1	11.0	10.3	10.1	10.0	10.0	9.9	10.1	10.2	10.8	11.7	12.8	25.2	25.2
800	10.4	10.4	10.3	10.3	10.2	10.0	10.0	10.0	9.9	10.1	10.2	10.7	11.3	13.3	25.8	29.2	33.5
850	10.2	10.2	10.2	10.2	10.1	10.0	9.9	9.9	10.1	10.1	10.2	11.6	13.4	26.9	28.9	112.0	129.9
900	10.1	10.1	10.1	10.1	10.0	9.9	9.9	10.1	10.3	11.4	21.7	28.5	30.3	29.4	131.8	319.6	349.6
950	10.0	10.0	10.0	10.0	10.0	9.9	10.0	10.1	10.2	11.1	12.4	28.5	30.3	142.8	324.0	383.4	437.5
1000	10.0	10.0	10.0	10.0	9.9	10.1	10.1	10.2	11.5	12.2	27.7	35.3	230.6	322.2	368.4	442.5	780.5
1050	9.9	9.9	9.9	9.9	10.1	10.1	10.3	11.5	12.1	26.3	30.0	234.5	339.2	353.3	435.3	759.0	1229.9
1100	10.1	10.1	10.1	10.1	10.1	10.3	11.4	12.3	25.6	29.4	231.4	343.6	364.9	424.2	246.4	943.1	1689.7

(1996) reported that the dormancy of *Betula pendula* seedlings was completed in natural conditions in December after 80 days chilling. This suggests that Theories 1 and 2 result in over-estimated values of the parameter of dormancy completion,  $D_{crit}$ , when  $MSE$  is minimized, or that the ontogenetic development starts later than at the end of dormancy, which takes place according to experimental results before the end of the year. It follows that the evidence against the truthfulness of Models 1 and 2 is even stronger than in the inference based on the results of Table 4. As an example, the relationship between  $MSE$  and the fixed values of parameters  $t_0$ , beginning of dormancy, and  $D_{crit}$ , the threshold for dormancy completion, are presented in Table 8 according to Theory 1 when applying the temperature-sum submodel. If, for instance, dormancy starts on August 30<sup>th</sup> and is completed at  $D_{crit} = 400$  chilling units, then  $MSE = 21.5$  instead of optimum value (= 9.9).

Consequently, dormancy-dependent Theories 1 and 2 (Sarvas 1972 and 1974, Hänninen 1990) weakly explained the timing of bud burst as measured with  $MSE$  compared to Theory 3, in which ontogenesis begins on a fixed calendar date (Table 4.B). In addition, the  $MSE$  differences were also statistically significant. These findings are along the same lines as the experimental results of Hänninen et al. (1993). In an experiment in open-top chambers they found that the onset of growth of Scots pine was not speeded up by increased winter temperature as much as the models based on dormancy development predicted, and concluded that the models need to be developed further. Our result is also corroborated by experiments on *Pinus sylvestris* saplings by Hänninen (1995). The four most accurate models ( $MSE = 16.8$ – $19.5$ ) in the study of Hänninen included the most accurate model of our study, Model 3. On the other hand, the results of our analysis of bud development of *Betula* sp. are in conflict with the results presented e.g. by Landsberg (1974) for apple tree, by Cannell and Smith (1984) for *Picea sitchensis*, and by Kramer (1994) for *Fagus sylvatica*, in which ontogenetic bud development was found to depend on the stage of dormancy. However, the contradiction between the results can partly be explained with the following arguments, (i) the regulatory systems of different tree species from different climatic zones may be based on different mechanisms; (ii) some of the results concern exotic tree species and the regulative response to the environment may differ from that in native conditions; (iii) the bud development of mature trees may differ from that of seedlings.

According to the model of Theory 3 with lowest  $MSE$  the ontogenetic development of *Betula* sp. buds was estimated to start on March 21. The factor triggering the ontogenetic bud development was represented by calendar date parameter,  $t_1$ . Which factors or their interactions are represented in model by the calendar date parameter,  $t_1$ , remains an open question. A signal from the light climate is one apparent candidate for the environmental factor to which the regulation of trees respond. The signal could, for instance, be the light intensity, night length, spectral composition of light, or certain changes in them. (The character of the signal has been further analyzed with the sensitivity analysis of the parameter  $t_1$  in the next Chapter 6.3) The phytochrome molecule is probably the receptor of the light signal (Wareing 1956, Smith 1995). The effects of time and light conditions are confounded in data generation process based on historical observations of bud burst and temperature, and cannot be distinguished without experiments in which these factors are manipulated (Hicks 1973). However, it is reasonable to assume that the mechanisms in *Betula* sp., which respond to light conditions or to the

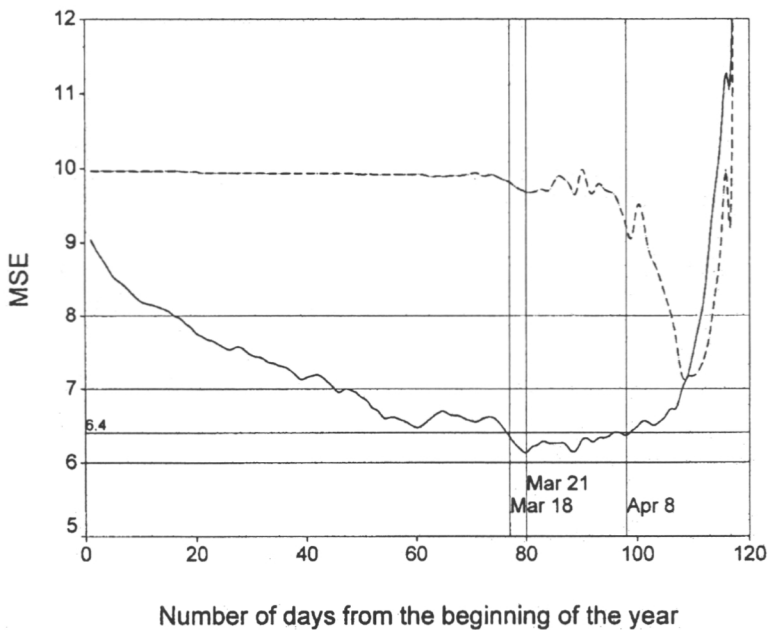
interaction of light conditions with other factors, have developed during evolution, especially in the boreal zone where the changes in light conditions are large and effectively reflect the timing of the seasons of the annual cycle. There is also evidence in the literature suggesting that trees utilize a signal from the light climate in regulating their functions during the annual cycle. The germination of birch seeds depends on the red/far-red ratio (Atkinson 1992). The growth cessation of *Betula pendula*, *Picea abies*, *Pinus sylvestris*, and *Salix* is driven by temperature and day length (Junttila 1980, Koski and Selkänaho 1982, Koski and Sievänen 1985). Campbell (1978) found that photoperiod is one of the components affecting the timing of bud burst in Douglas-fir. Myking and Heide (1995) reported that long photoperiods reduced thermal time requirement of bud burst of birch after incomplete chilling. Recent experimental results of Partanen et al. (1998) corroborate the light hypothesis. They found that a fluctuating day/night temperature and continuous lengthening of the photoperiod hastened the bud burst of *Picea abies*, and that shortening of the photoperiod delayed bud burst, indicating that no ontogenetic development takes place before winter solstice (Partanen et al. 1998). In our analyses, however, based on long-term temperature observations and bud-burst time series of *Betula* sp. leaves, the hypotheses concerning the interpretations of parameter  $t_1$ , the start of ontogenetic bud development, could not be tested. Further clarifying of the concepts and improvement of bud-development theories and experimental testing of the hypotheses concerning the effects of factors postulated in these theories are needed.

### 6.3 Statistical analysis

Evaluation of the bud-development theories has been based on numerical comparison of the mean square errors (*MSE*) of the models only, because standard statistical methods for evaluating dynamic models have not been available. It therefore follows that the risk of making an erroneous inference has not been known. However, the statistical analysis of *MSE* differences and behavior of model parameters can be carried out by applying resampling methods and the prediction power of the models analyzed. The disadvantage of resampling methods in the context of dynamic bud-development models is that they require self-written computer programs.

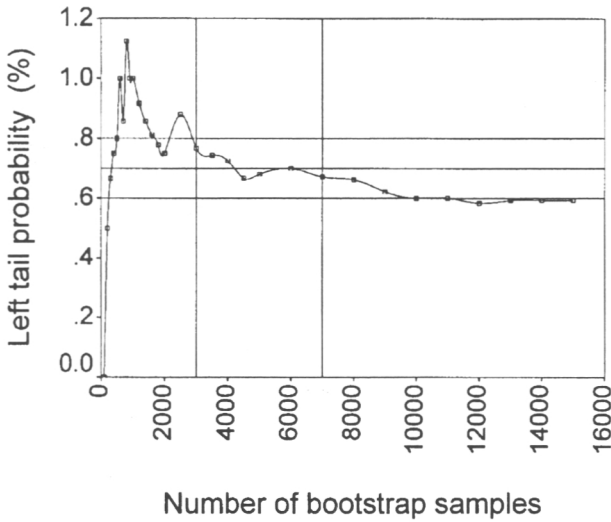
#### Sensitivity analysis

According to the model based on Theory 3 and the period-unit submodel the ontogenetic development was estimated to start on March 21, at vernal equinox. However, sensitivity analysis of parameter  $t_1$ , the starting date of ontogenetic development, as well as the bootstrap analysis of the model parameters, suggests that the character of the phenomenon operationalized as the calendar date is not of the on/off type, a specific night length for instance. The bootstrap analysis in which the period-unit-sum submodel was applied revealed high multicollinearity of parameters  $t_1$  and  $O_{crit}$ , the threshold for bud burst ( $r = -.92$ ) (Table 6), indicating that the parameter values are strongly inter-related and vary from sample to sample.



**Figure 15.** The mean square error ( $MSE$ ) as a function of  $t_1$ , the start of ontogenetic development of *Betula* sp. buds according to the model in which ontogenetic development starts on a fixed calendar date (Theory 3) when applying (i) the period-unit-sum (—) and (ii) the temperature-sum (- - -) submodel of ontogenetic development.

Thus no definite conclusions concerning the magnitude of the parameter values can be drawn. The conclusion was corroborated by sensitivity analysis, in which values of the mean square error ( $MSE$ ) were calculated from the original data by simulating the values of parameter  $t_1$  from January 1 to April 27. The  $MSE$  value did not vary very much before and after the optimum point  $t_1 = 80$  (March 21). When the start of ontogenetic development varied from March 18 to April 8, the mean square error ( $MSE$ ) was between 6.1 and 6.4 (Figure 15). It therefore follows that, instead of point estimate, the interval estimate  $t_1 \in$  (March 18, April 8) is more justified in this connection. However, when the temperature-sum submodel of ontogenetic development was applied the optimum range was rather narrow (Figure 15). The explanation for this is evidently the fact that temperatures of below  $+5^\circ\text{C}$  do not contribute to ontogenetic development according to the temperature-sum submodel, whereas according to the period-unit-sum submodel bud-development progresses at a slow rate, and modeled development therefore starts earlier. Consequently, when it was assumed that the period-unit-sum model is relevant, our analyzes based on the long-term observational data gave no strong evidence to conclude that a specific on-off signal, such as the threshold night length (or biological clock), triggers bud ontogenesis, although technically the least square analysis resulted in one optimal point estimate. Rather the result suggests that additional explanatory factors and/or more accurate and precise measurements are needed to explain to which environmental factors the regulation of the beginning of ontogenetic bud development of *Betula* sp. leaves responds.



**Figure 16.** Probability of the difference of the mean square errors (of Models 2 and 1 with Period-unit-sum submodel) being less than zero,  $P(\hat{\theta}_{2P-1P} = MSE_{2P} - MSE_{1P} \leq 0)$ , as a function of the number of bootstrap samples (notation same as in Table 5). The probabilities were estimated as the left tail probabilities of the bootstrap frequency distributions of  $\hat{\theta}_{2P-1P}$  (cf. Fig. 13c).

A similar conclusion can be drawn from the relationship between  $MSE$  and parameters  $t_0$ , the start of dormancy and  $C_{crit}$ , the threshold of dormancy completion according to dormancy-dependent Theories 1 and 2. Bootstrap analysis revealed high multicollinearity of parameters  $t_0$  and  $C_{crit}$  ( $r = -0.68$  and  $-0.81$ ) (Table 6). Sensitivity analysis of  $MSE$  to the parameter values of  $t_0$  and  $C_{crit}$  showed that there are many pairs of parameter values resulting in the same magnitude of  $MSE$  (Table 8). Consequently, instead of the point estimates of Table 4, more justified is the two-dimensional interval estimate, i.e. a set of pairs of values of parameters  $t_0$  and  $C_{crit}$  resulting in similar values of  $MSE$  denoted in Table 8 with bold numbers in ‘diagonal’ of  $MSE$  matrix.

## Resampling

The basic assumption underlying the statistical inference based on resampling methods is that the observed original sample is large enough to represent the phenomenon to be analyzed. The conclusions become stronger as the sample size increases. The combined time series of the bud burst of *Betula* sp. leaves was longer than those used in most corresponding studies. The 55-year time span can be considered to sufficiently represent the year-to-year-variation in temperature and timing of bud burst to draw valid conclusions.

The nature of statistical inference based on the resampling method is asymptotic, i.e. the accuracy of the estimates increases as the number of bootstrap

samples increases. The analysis was based on 7000 bootstrap samples from the original data. The effect of the number of bootstrap samples on the reliability of statistical inference was analyzed by means of a simulation experiment in which the number of bootstrap samples varied from 200 to 15 000, and the left tail probabilities of the test statistic  $\hat{\theta}_{2P-1P} = MSE_{2P} - MSE_{1P}$  being less than zero,  $P(\hat{\theta}_{2P-1P} \leq 0)$ , were determined (notation same as in Table 5). It was found that, even with a sample size of 3000, which is less than half the sample size used in our analysis, the inference is fairly accurate (Figure 16).

The estimated numerical parameter values of the bud-development models were not accurate, but were related to each other and varied from one data set to another. However, the bud-development models were very precise (lowest  $MSE = 6.1$ ). In addition, the prediction errors of the models in independent data sets estimated with the cross-validation method were not much above the  $MSE$ 's of the models (Table 7). This indicates that the bud-development models are precise tools for applications in which the timing of the bud burst of *Betula* sp. need to be predicted.

Statistical methods are not an end in itself, but they are an important tool for scientific inference when unexplained disturbing variation is included in the data-generation process (Tuomivaara et al. 1994). The statistical methods enables us to measure the uncertainty caused by this disturbing variation. In the case of bud-development models, the bootstrap method was appropriate for model comparison. In addition, the knowledge of the properties of the distributions of parameters analyzed by resampling methods and sensitivity analysis helped us to understand how well the theories are able to catch the real nature of bud development.

## 6.4 Conclusions in brief

- 1.1 The old phenological observations published by the Finska Vetenskaps-Societeten (Suomen Tiedeseura, The Finnish Society of Sciences and Letters) and climatic time series have not been utilized extensively in analysing phenological theories. Especially when studying tree phenology they can be exploited to test whether the results based on experiments are valid in natural conditions with mature trees.
- 1.2 The quality of fragmentary, systematically biased, but partly overlapping raw data observed by single persons can be improved for research purposes by combining the information into one long reliable time series by utilizing linear mixed model. 76 % of the total random variation caused by the bias of 19 individual series was eliminated when the 60-year-long time series of the bud burst of *Betula* sp. leaves was constructed.
- 2.1 The model of bud-development theory, in which the ontogenetic development starts on a fixed calendar date with the period-unit-sum submodel of Sarvas (1972), had the lowest mean square error ( $MSE = 6.1$ ) of all the models analyzed.
- 2.2 When the dependence between the ontogenetic bud development and the stage of dormancy of *Betula* sp. was incorporated into the models, the  $MSE$ 's were statistically significantly higher compared to the  $MSE$  of the model in which the ontogenetic bud development starts on a fixed calendar date.

- 2.3 The *MSE* of the model in which ontogenetic development starts on a fixed calendar date with the period-unit-sum submodel, did not differ statistically significantly from the *MSE* when the temperature-sum submodel was applied. The submodels based on the respiration and recovery of photosynthesis were not appropriate for describing bud development.
- 3.1 The statistical resampling methods were useful as an additional inferential tool in analysing dynamic models of various bud-development theories. Increasing the number of bootstrap samples from 3000 did not markedly increase the accuracy of the statistical inference in testing the equality of the *MSE*'s of the models.
- 3.2 Bud-development models are precise tools for predicting the moment of bud burst.
- 3.3 The model parameters were strongly inter-related. The interval estimates were more justified than point-estimates to describe the beginning of dormancy, the threshold of dormancy completion, the beginning of ontogenetic development, and the threshold of bud burst. Analysis based on long-term data did not enable us to conclude that an on-off type factor (e.g. specific night length) triggers the developmental phases.
- 3.4 Further conceptual development of bud-development theory and experimental testing of the hypotheses based on it are needed. Additional explanatory factors and/or more accurate and precise measurements of phenological events are necessary to explain to which environmental factors and how the regulation of the start and rate of ontogenetic development of *Betula* sp. buds responds.

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**Appendix: Chronological List of Publications of Phenological Observations by Finska Vetenskaps-Societeten (Suomen Tiedeseura, The Finnish Society of Sciences and Letters)**

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

Risto Häkkinen & Pertti Hari

*TIIVISTELMÄ: KASVIEN AIKAAN JA LÄMPÖTILAAN PERUSTUVIEN SÄÄTÖPERIAATTEIDEN TEHOKKUUDESTA KASVUKAUDEN ALUSSA*

Häkkinen, R. & Hari, P. 1988. The efficiency of time and temperature driven regulation principles in plants at the beginning of the active period. Tiivistelmä: Kasvien aikaan ja lämpötilaan perustuvien säätöperiaatteiden tehokkuudesta kasvukauden alussa. *Silva Fennica* 22(2): 163–170.

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

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

Keywords: annual cycle, regulation, spring frost, temperature  
ODC 161 + 181.22

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Accepted April 20, 1988

## 1. Introduction

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

monthly or daily means of temperature.

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

The phenological development of plants in the spring is strikingly regular in the temper-

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

Several regulation principles have been

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

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

## 2. The activation of plants in the spring

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

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

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

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

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

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

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

1. The time principle (Bünning 1963)

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

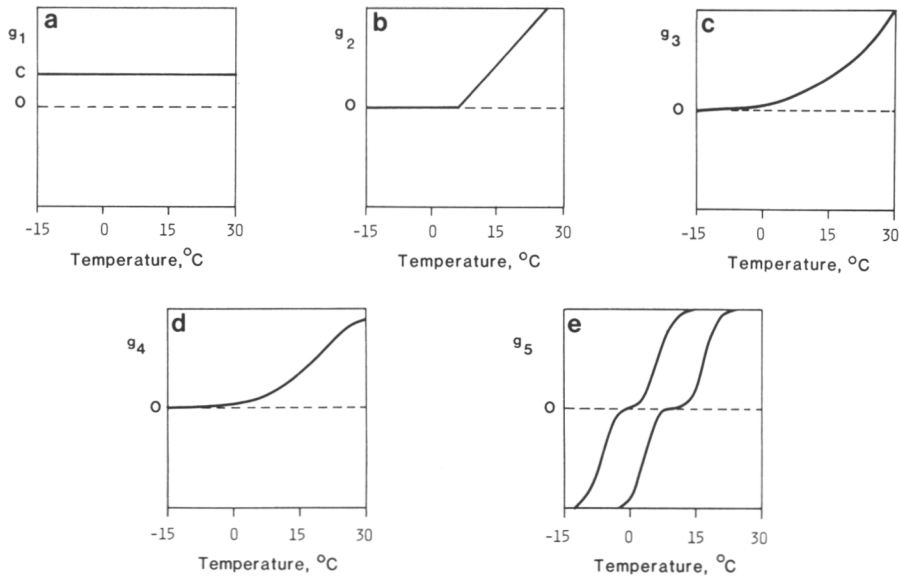


Fig. 1. The rate of change,  $g_i$ , of the stage of the development as a function of temperature: a) The regulation is based on time, b) on temperature sum, c) on respiration, d) on period units, e) on feedback principle. The function  $g_5$  depends on temperature as well as on the stage of development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

2. The temperature sum principle (de Reaumur 1735)

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

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

$$g_3(T(t)) = a + be^{cT(t)},$$

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

4. The period unit principle (Sarvas 1972)

$$g_4 = \text{tabulated values (Fig.1d).}$$

5. The feedback principle (Pelkonen & Hari 1980)

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

where  $a = 2$  and  $c = 600$ .

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

### 3. Meteorological data

The study is based on official weather statistics collected by the Finnish Meteorological Institute in the city of Jyväskylä in Central Finland (62°14' N, 25°44' E, 86 m asl) during the period 1883–1980. Temperatures recorded 2 m above the

ground at 8 am, 2 pm and 8 pm each day, and the daily minimum temperature, were utilised.

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

The most important ones were: missing data during 1912 and 1913; missing minimum temperatures for the period 1883–1901; missing observations at the beginning of April in 1914 and 1915; and some variation in the timing of measurements during the period. Consequently, the data for 1912 and 1913 were excluded from the analysis; the missing

minimum temperature values were approximated by using an empirical regression function from the temperature measurements made at 8 am; and the missing observations in early April 1914 and 1915 were replaced with corresponding average temperatures for the data set. The number of observations utilised totaled 34944.

## 4. Results

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

### 4.1. Reliability of the regulation principles

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

Let  $t$  denote time counted from the beginning of the year,  $T(t)$  temperature at the moment  $t$ , and  $T_{\min}$  the minimum of the temperatures  $T(t)$  of the year before 1 July. The conditional frequency distribution of the minimum temperatures,  $f(T_{\min} | t \geq t^\circ)$ , after the fixed time,  $t^\circ$ , is determined using weather statistics for years 1883–1980. Thus, the frequency distribution is based on 96 minimum

temperature observations, one for each year. Changing the condition time  $t^\circ$  different conditional distributions are formed (Lindgren 1976). The increase in temperature during the spring can clearly be seen in a shift in the location of the empirical histograms (Fig. 2a).

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

$$S_i(t) = \int_0^t g_i(T(t) | S(t)) dt, \quad (2)$$

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

The reliability of the regulation principles was measured by means of the standard deviation of the conditional frequency distribution. The smaller the standard deviation the more precise is the information about the coming minimum temperatures, thus small standard deviation means good reliability. The conditional distributions (Fig. 2) were computed for each regulation principle with

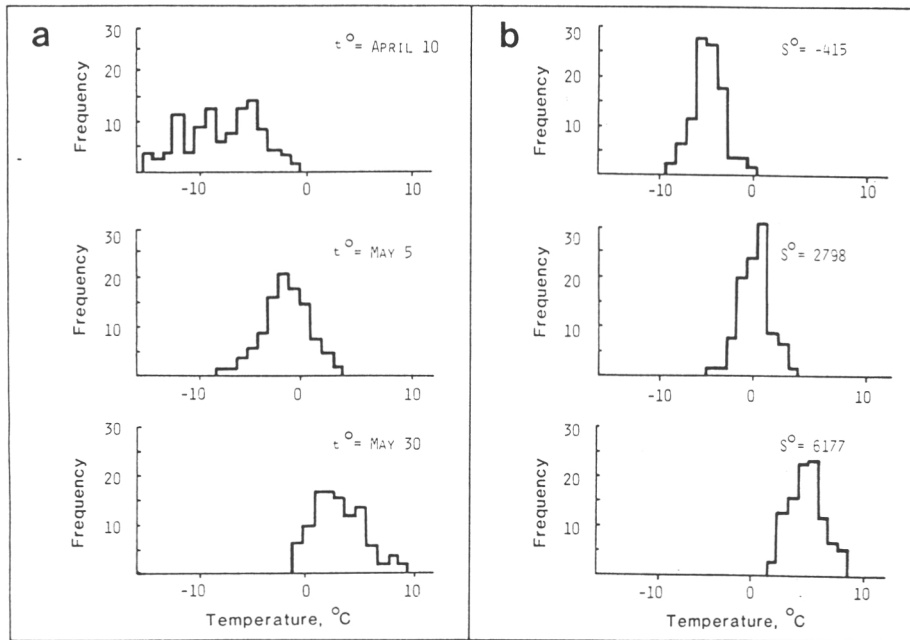


Fig. 2. Conditional distributions of minimum temperatures during spring (years 1883–1980). Examples of empirical histograms, each based on 96 temperature values, one for each year: a) Regulation is based on time (three alternative condition dates were applied). b) Regulation is based on the feedback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

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

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

varying values  $S^\circ$  of the conditional stage of the annual cycle. The number of computed distributions for each principle equaled 12. The means and the ranges of the standard deviations of the distributions for each regulation principle are shown in Table 1.

The conditional distributions based on the feedback principle had the smallest standard

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

#### 4.2. The length of the active period

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

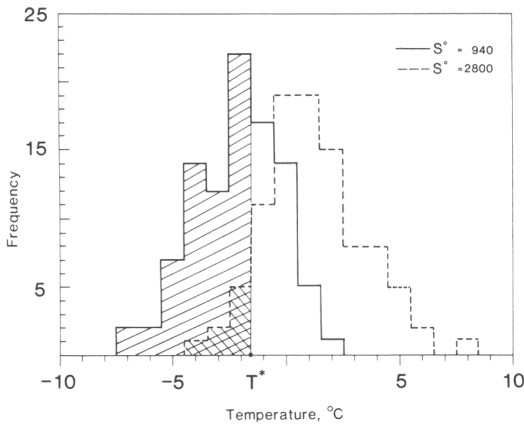


Fig. 3. Determination of the risk of injury. The conditional minimum temperature distributions in the example were generated by the period unit principle. Two empirical histograms corresponding to the stage of the development,  $S^\circ = 940$  and  $S^\circ = 2800$ , are presented. The threshold temperature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

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

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

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

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

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

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

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

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

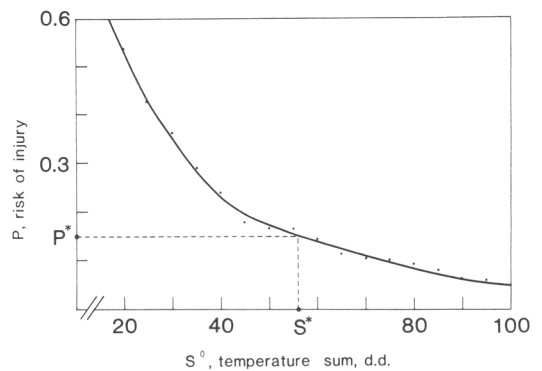


Fig. 4. The dependence of the risk of injury on the stage of the development. In this example the regulation is based on temperature sum principle. The threshold temperature of injury is  $T^* = -2^\circ\text{C}$ . The threshold state  $S^*$  corresponding to the given threshold risk of injury,  $P^*$ , is found graphically.

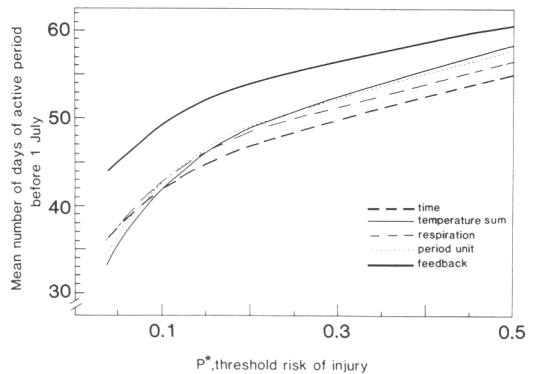


Fig. 5. The mean length of the active period before 1 July as function of threshold risk of injury,  $P^*$ , for the five regulation principles.

If the threshold risk of injury is  $P^*$  then the number of days of the active period before 1 July, when  $S(t) \geq S^*$  can be computed for each principle for each year using weather statistics. The efficiency of the regulation principles can now be evaluated by comparing the mean number of days in active period

before 1 July during the period 1883–1982 as a function of the threshold risk of injury. The results are shown in Fig. 5, when the threshold temperature  $T^*$  was assumed to be  $-2^\circ\text{C}$ . The principle based on feedback resulted a clearly longer active period than the others.

## 5. Discussion

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

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

Annual cycle of plants involves two types of phenomena, i.e. development and growth. These two are to some extent parallel but they are different. Development refers mainly to the status of the regulation system, and

growth to the formation of a new structure, especially concerning the division of cells. Perhaps the most prominent difference between the development and growth rates is that development may obtain negative values, as in the feedback principle, but the growth rate is always non-negative. This means that the stage of the annual cycle may retreat towards the winter stage during cold periods in the spring, but the disappearance of cell walls is not possible.

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

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

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## The utilization of old phenological time series of budburst to compare models describing annual cycles of plants

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Received July 17, 1990

### Summary

A phenological time series of the date of budburst of birch (*Betula pendula*) was constructed using data from the years 1907–1950. Data for the years 1908, 1910–1915 and 1930 are missing. The phenological observations were made at Saarijärvi (62°42' N, 25°44' E) in Central Finland. Different models describing the rate of development in the spring were analyzed using temperature data from the city of Jyväskylä about 60 km to the southeast of Saarijärvi. The models based on temperature sum gave more accurate predictions of the date of budburst than the model based on time. Differences between different development rates seemed to be negligible when computing the temperature sum.

### Introduction

Increases in the concentrations of atmospheric gases such as carbon dioxide and freon are evidently changing the climate of the earth. It is estimated that the global mean temperature will increase by 1.5–4.5 °C by the year 2030 (Boer et al. 1990). The increase is predicted to be greatest at high latitudes during winter. This change in climate will have major consequences for the plant kingdom. One of the crucial consequences will be disturbances in the annual cycle of plants, especially in the onset of the active period in spring.

The systematic collection of phenological observations gained increasing attention during the nineteenth century, especially in central Europe. Long time series of phenological events, such as budburst, flowering, and fruit ripening, are available. Systematic recording of the weather also started on an extensive scale during the nineteenth century, although the first series in Uppsala, Edinburgh, and St. Petersburg/Leningrad originate from the early eighteenth century.

The phenological and weather time series offer a good opportunity to study the annual cycle of plants. This challenge has not, however, yet been taken up. The aim of our paper is to describe a method for linking these two important sources of knowledge. The present climate change stresses the importance of gaining an understanding of the link between weather and the development of the annual cycle of plants.

## Theory

The process of maturation or development runs continuously in plants. The rate of the process, i.e., the rate of development, depends on environmental factors. Development is marked by annual stages such as budburst, flowering, and fruit ripening. Phenological observations consist in dates when specific stages of development have been reached.

These ecological statements can be translated into the language of systems analysis as follows. The annual stage of development is a state variable, and the rate of development is its time derivative (Hari 1972). Let  $S$  denote the stage of development and  $g$  the development rate. Then,

$$\frac{dS}{dt} = g. \quad (1)$$

Let  $u(t)$  denote the vector describing environmental factors at the moment  $t$ . The rate of development depends on environmental factors, i.e.,  $g = g(u(t))$ . When Equation 1 is integrated from the beginning of the year,  $t_0$ , to the moment  $t$ , then the stage of annual development is obtained as a function of the weather conditions preceding the moment  $t$ :

$$S(t) = \int_{t_0}^t g(u(t)) dt. \quad (2)$$

When a plant reaches a phenological event, e.g., budburst, it is always at the same stage of annual development. Thus the variable  $S$ , calculated according to Equation 2, should have the same value each year at the time when the phenological observation is made. This enables testing of different hypotheses concerning the dependence of development rate on environmental factors.

Five models describing the dependence of development rate on environmental factors were selected from the literature for further analysis.

### 1. A time or day length model (Bünnig 1963):

$$g_1 = c, \quad (3)$$

where  $c$  is a constant.

### 2. The temperature sum model (Reaumur 1735):

$$g_2(T(t)) = \begin{cases} 0, & \text{if } T(t) \leq 5 \\ T(t) - 5, & \text{if } T(t) > 5, \end{cases} \quad (4)$$

where  $T$  ( $^{\circ}\text{C}$ ) is temperature.

3. A model based on respiration as an indicator of development (Hari et al. 1970):

$$g_3(T(t)) = a + b e^{c T(t)}, \quad (5)$$

where  $a$ ,  $b$  and  $c$  are parameters,  $a = -0.42$ ,  $b = 0.73$  and  $c = 0.07$ .

4. The period unit model (Sarvas 1972):

$$g_4(T(t)) = \text{tabulated values (Figure 1)}.$$

5. A model of feedback development (Pelkonen and Hari 1980):

$$g_5(T(t), S(t)) = \frac{100}{1 + a^{-(T(t) - S(t)/c)}} - \frac{100}{1 + a^{+(T(t) - S(t)/c)}}, \quad (6)$$

where  $a$  and  $c$  are parameters,  $a = 2$  and  $c = 600$ . Thus the development rate depends on the stage of development  $S(t)$  itself.

The phenological events can be predicted for each year using the alternative functions  $g_i$ ,  $i = 1, \dots, 5$ . The function which gives the most accurate predictions of the phenological event under consideration is the best description of the dependence of the development rate on the environment.

## Data

The temperature data were collected by The Finnish Meteorological Institute in the city of Jyväskylä (62°14' N, 25°20' E) in Central Finland. The data cover the years 1883–1980. The temperature was measured three times each day, and the daily minimum temperature was also recorded.

The phenological observations of the date of budburst of birch (*Betula pendula*) in

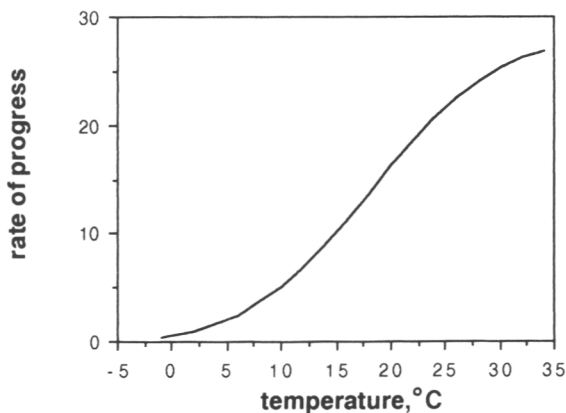


Figure 1. The rate of development as a function of temperature according to tabulated values (Sarvas 1972, p. 39).

the spring were made at the village of Saarijärvi (62°42' N, 25°44' E) about 60 km to the northwest of Jyväskylä by Mrs. Alma Nordenstreng. The variation among years in the timing of budburst was considerable (Figure 2). The range of observed dates exceeds 40 days. The phenological time series covers the years 1907–1950, the years 1908, 1910–1915 and 1930 are missing (Brotherus 1910, 1914, 1925a, 1925b, Pipping 1927a, 1927b, Reuter 1928, 1935, 1941, 1942, 1948, 1952).

**Results and discussion**

Budburst occurs when the stage of annual development  $S(t)$  reaches a certain threshold value. This threshold is, of course, specific for each development rate,  $g_i$ . Let  $B_i$  denote the threshold value of the stage of development at budburst according to the rate of development,  $g_i$ , and let  $t_b$  denote the moment of budburst. Then,

$$\int_{t_0}^{t_b} g_i(T(t)) dt = B_i . \tag{7}$$

The threshold values  $B_i$  for each function  $g_i$  were estimated using the mean of the annual values of the stage of development  $S_i(t_b)$  at the date of observed budburst (Table 1). The values for the development stages  $S_i(t_b)$  were calculated for each year by means of the Riemann sum approximations of Equation 2 using temperature and phenological observations as follows:

$$\int_{t_0}^{t_b} g_i(T(t)) dt \approx \sum_{j=1}^N g_i(T(t_0 + j \Delta t)) \Delta t , \tag{8}$$

where  $\Delta t = 0.25$  day and  $N = (t_b - t_0)/\Delta t$ .

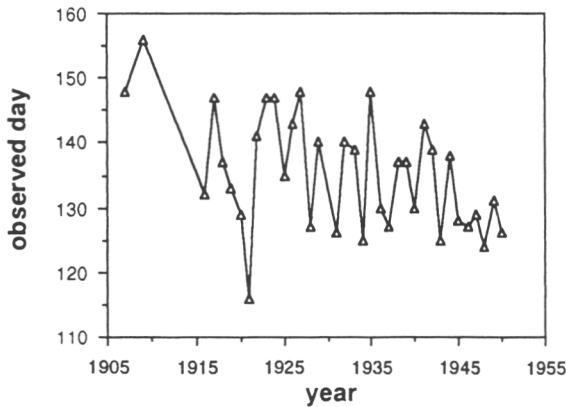


Figure 2. The number of days from the beginning of the year to the observed date of budburst of birch (*Betula pendula*) at Saarijärvi, Central Finland.

A comparison of observed dates of budburst of birch and those predicted with Equation 7 during the years 1907–1950 is depicted in Figure 3. It is evident that the date or day length model cannot predict the date of budburst. The other models tested gave satisfactory results. The differences between the fits of functions  $g_i$  are small. The correlation coefficient between the observed and predicted dates varied from 0.78 to 0.87 (Table 1). This is not surprising because the functions to be integrated

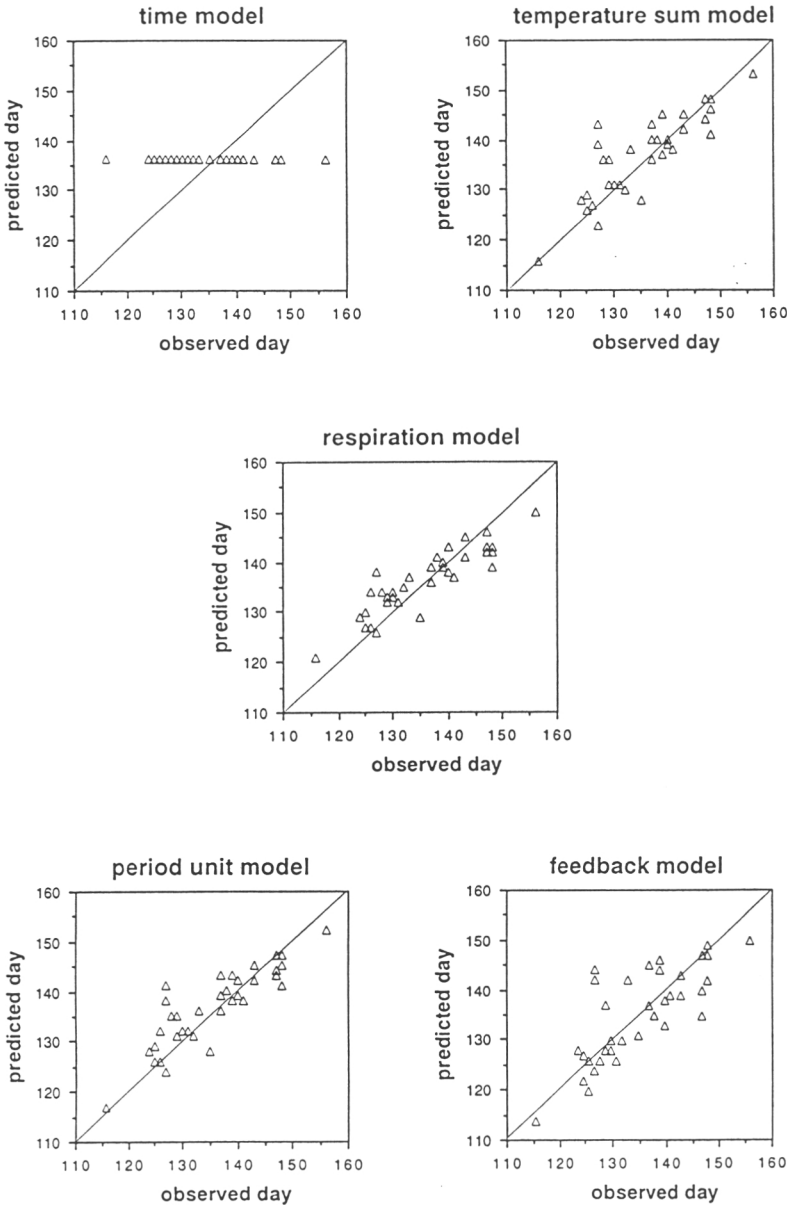


Figure 3. The observed and predicted dates of budburst of birch (*Betula pendula*) calculated from the beginning of the year using development models ( $g_i$ ) based on time and temperature.

Table 1. The estimated threshold values ( $B_i$ ) of the stage of development of budburst of birch according to maturation models ( $g_i$ ) and the corresponding correlation coefficients ( $r_i$ ) between observed and predicted dates of budburst.

Development model	Threshold of budburst $B_i$	Correlation coefficient ( $r_i$ ) between observed and predicted dates
Time or day length	135 (day)	0.00
Temperature sum	58 (°C day)	0.85
Respiration model	557	0.87
Period unit model	2150	0.87
Feedback model	4830	0.78

are rather similar.

The fit between the observed and predicted dates of budburst is so good that it is close to the limits of the data because it is often difficult to make reliable phenological observations. For example, if a cold period occurs at the moment of budburst, then determination of the proper date is very difficult. Another source of error is the distance (60 km) between the weather station and the site of the phenological observations. In addition, minor changes in the location of the weather station may cause inaccuracies.

It is evident that temperature plays a major role in the timing of budburst. A warming of the climate will generate changes in the annual cycle of plants in the spring. Dates of budburst and flowering will be earlier than those recorded in the phenological observations. In 1989, *Coryllus avellana* was flowering in early February in Helsinki, which is at least one month earlier than it should occur according to the phenological observations available. This early flowering was caused by a warm period in January and February 1989. This kind of timing of phenological events should be normal in 2030 if the predicted climate change occurs and if the models defined by Equations 4–7 give reasonable descriptions of the development rate.

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# Methods for combining phenological time series: application to bud burst in birch (*Betula pendula*) in Central Finland for the period 1896–1955

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Received August 18, 1994

**Summary** We compared four methods for combining separate fragmentary phenological time series into a single long reliable series. The systematic linear effect of differences in observers, genotypes, geography and climate at the observation points produces disturbing variation in the observations and bias in the means of some time points. The three methods based on the adjustment of individual series eliminated the disturbing variation and bias. The methods were compared based on phenological observations of bud burst in birch (*Betula pendula* Roth). The method based on a linear mixed model of analysis of variance and the maximum likelihood estimation was considered preferable to the other methods.

**Keywords:** annual cycle, combined time series, phenological observations.

## Introduction

The environment of plants in the temperate zone is characterized by the favorable light and warmth of summer and the unfavorable cold and dark of winter. Plants have developed regulatory systems for overcoming the alternating cycle of the seasons. In winter, plants are resistant to low temperatures, but during the growing season, they are vulnerable to frost damages. Thus a regulatory system for timing the onset and cessation of frost tolerance and active metabolism is necessary for the survival of perennial plants.

If plants lose their frost resistance too early in spring, frost damage normally results. On the other hand, if they start their active period at too late a stage, they will miss favorable growing conditions. Thus there is evolutionary pressure to adapt the regulatory system to the prevailing climate. The predicted global warming will change the temperature throughout the year and cause disturbances in the timing of the annual cycle resulting in damage to plants (Cannell and Smith 1986, van der Kamp and Worrall 1990). The predicted global climate change makes it crucial to gain a better understanding of the phenological development of plants.

The collection of phenological time series takes years. Fortunately, old time series of several phenological events are available for many locations. Because single series are often fragmentary and their reliability is not known, there is a need to combine separate series into long continuous series whose reliability can be evaluated. These time series can be utilized in the analysis and modeling of the regulation of the annual cycle of plants.

Four methods for combining phenological time series were analyzed, and the reliability of the resulting time series was examined. A combined time series of bud burst in birch (*Betula pendula* Roth) was constructed to illustrate the application of the methods.

## Phenological data

The collection of phenological observations in Finland during 1896–1955 was organized and the results published by Finska Vetenskaps-Societeten (Brotherus 1905, 1906, 1907, 1908, 1910, 1914a, 1914b, 1919a, 1919b, 1920, 1921a, 1921b, 1925a, 1925b, Pipping 1927a, 1927b, Reuter 1928, 1935a, 1935b, 1936, 1937, 1941, 1942, 1948, 1952, 1957). The observations covered the whole country and several phenological events were observed, but many of the time series span only a few years.

For the present study, the selection of the time series used in constructing the combined time series for the date of bud burst in *B. pendula* was based on two criteria: (1) distance between the observation point and the City of Jyväskylä to be less than 185 km, and (2) duration of the time series to be at least 15 years. Jyväskylä was chosen as the center of the observation area because weather data collected there by The Finnish Meteorological Institute date back to 1883. The sea coast determined the maximum radius of the area. The geography of the area was considered homogeneous. The landscape is hilly with many lakes, and the altitude at the observation points ranges from 60 to 140 m above sea level. The mean temperature in May in the northeastern part of the area in Kuopio, near

observation point number 18, was 7.7 °C, and in the southwest in Tampere, near observation points numbers 1 and 7, it was 8.9 °C (Figure 1).

Nineteen time series fulfilling the above criteria were found. They comprised a total of 465 observations during the period 1896–1955 (Figure 1, Table 1). The length of each time series varied from 15 to 57 years.

The observed local time series for 1896–1955 are presented in Figure 2. The number of annual observations in the data set varied from a minimum of 3 to a maximum of 12, the average number being 7.8. The range of dates of bud burst was 57 days. The earliest date of observed bud burst was April 25, 1921, and the latest date was June 21, 1955. The standard deviation of the annual dates varied from 1.0 to 14.7 days.

## Methods

Four methods were used to construct the combined time series of the annual date of bud burst in *B. pendula* at Jyväskylä. In Method 1, the annual dates were estimated from the average of the unadjusted observations. Part of the large annual variation in the individual observation series (Figure 2) was due to various systematic effects. Thus the criterion for bud burst may have varied between observers; there were systematic differences in the genotypes of the trees and in the geography at the observation points, and the climate is warmer in the south than in the north. These systematic effects produced disturbing variation in the observations and bias in the mean dates of some years. Method 1 did not take account of these effects.

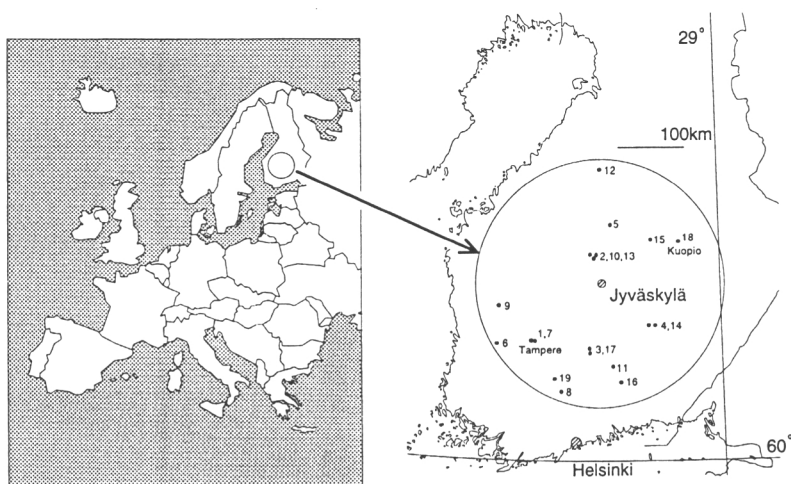


Figure 1. Location of the observation points of bud burst in birch (*Betula pendula*) fulfilling the selection criteria. The numbers refer to the observers listed in Table 1.

Table 1. Observers, duration of observation period, and geographical information about the phenological series used.

Observer	Location	Number of observations	Period of observations	Latitude	Longitude	Altitude (m a.s.l.)
1 Blomqvist	Tampere	17	1937–1955	61°32'	23°41'	120
2 Brander	Saarijärvi	15	1908–1923	62°42'	25°16'	120
3 Böök	Padasjoki	16	1926–1942	61°22'	25°17'	85
4 Ehnberg	Mikkeli	57	1896–1955	61°41'	27°15'	90
5 Halmesmäki	Viitasaari	26	1927–1955	63°03'	25°58'	100
6 Hjelt	Karkku	20	1899–1925	61°23'	22°59'	60
7 Karsten	Tampere	40	1898–1943	61°30'	23°46'	120
8 Kerkkonen	Janakkala	15	1937–1951	60°54'	24°42'	100
9 Koivukoski	Parkano	15	1941–1955	62°20'	23°01'	140
10 Liljus	Saarijärvi	17	1896–1914	62°42'	25°16'	120
11 Luotola	Heinola	17	1919–1937	61°12'	26°12'	105
12 Mäntyvaara	Haapajärvi	31	1920–1952	63°45'	25°19'	120
13 Nordenstreng	Saarijärvi	38	1907–1950	62°42'	25°20'	120
14 Nordström	Mikkeli	20	1896–1917	61°41'	27°15'	90
15 Saastamoinen	Karttula	24	1908–1948	62°54'	27°00'	115
16 Salo	Iitti	15	1941–1955	60°56'	26°24'	80
17 Schild	Padasjoki	20	1923–1943	61°26'	24°56'	125
18 Ståhlberg	Kuopio	16	1900–1915	62°54'	27°40'	100
19 Wegelius	Hattula	46	1910–1955	61°05'	24°27'	90

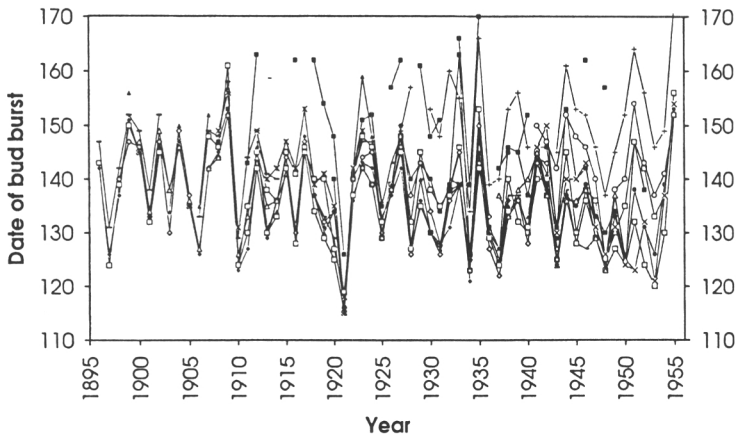


Figure 2. The observed time series of dates of bud burst in birch (*Betula pendula*) at 19 locations during 1896-1955. The dates were measured as the number of days from the beginning of the year.

However, if the observation points are considered as blocks and the years as treatments, then the data generating process is analogous to an experiment with a randomized block design. In Method 2, the disturbing block effects were eliminated by adjusting the individual series to the level of a reference series before calculating the means. In Method 3, the individual series were adjusted to the common level found by the optimization procedure. In Method 4, the estimation of the annual dates was done by the linear mixed model of analysis of variance.

#### Method 1

The annual dates of bud burst were estimated based on the mean values of the observations:

$$y_i^{(1)} = \frac{\sum_j x_{ij}}{n_i}, \quad (1)$$

where  $y_i^{(1)}$  is the value of the time series in the year  $i$  ( $i = 1896, \dots, 1955$ ) estimated by Method 1,  $x_{ij}$  is the observed date of bud burst of the local series  $j$  ( $j = 1, \dots, 19$ ) expressed as the number of days from the beginning of the year, and  $n_i$  is the number of observations in year  $i$ . The summation goes over series  $j$  present in year  $i$ .

#### Method 2

The annual dates of bud burst were estimated based on the mean values of observations adjusted to the level of a fixed reference series:

$$y_i^{(2)} = \frac{\sum_j (x_{ij} + a_j)}{n_i}, \quad (2)$$

where  $y_i^{(2)}$  is the value of the time series estimated by Method 2, and  $x_{ij}$  and  $n_i$  are as above. The parameter values  $a_j$  for each series  $j$  were calculated as the differences of the means:

$$a_j = \frac{\sum_k r_k}{K} - \frac{\sum_k x_{kj}}{K}, \quad (3)$$

where  $r_k$  is the value of the reference series in year  $k$ ,  $x_{kj}$  is the observed date of the series  $j$ , and  $K$  is the number of years in common. The summation goes over the common years  $k$ . A long, reliable series is used as the reference series. If necessary, the reference series can be augmented by a number of series covering the observed time period. Each augmenting series is first adjusted to the level of the reference series by the same method.

#### Method 3

The annual dates of bud burst were estimated based on the mean values of observations adjusted to the optimized level:

$$y_i^{(3)} = \frac{\sum_j (x_{ij} + b_j)}{n_i}, \quad (4)$$

where  $y_i^{(3)}$  is the value of the time series estimated by Method 3, and  $x_{ij}$  and  $n_i$  are as above. The parameter values  $b_j$  are obtained by minimizing the function of the sum of the squared differences between the adjusted observations and the annual means of the adjusted observations, i.e.:

$$\min_{b_j} \left[ \sum_i \sum_j \left( (x_{ij} + b_j) - y_i^{(3)} \right)^2 \right] = \min_{b_j} \left[ \sum_i \sum_j \left( (x_{ij} + b_j) - \frac{\sum_j (x_{ij} + b_j)}{n_i} \right)^2 \right]. \quad (5)$$

For this optimization, the Fortran subroutine UMCGF of the IMSL mathematical library was used. The subroutine uses Powell's conjugate-gradient method (Powell 1964), which is

an effective algorithm for minimizing functions with unknown gradients. The solution of  $b_j$  is unique up to an additive constant. An additional requirement, that the sum of  $b_j$  equals zero, is needed.

#### Method 4

The annual dates of bud burst were estimated using the linear mixed model of the randomized block design:

$$y_i^{(4)} = m + c_i, \quad (6)$$

where  $y_i^{(4)}$  is the value of the time series estimated by Method 4. The coefficients  $m$  and  $c_i$  were obtained as the solution of the following mixed model of the analysis of variance:

$$x_{ij} = m + c_i + \tau_j + \varepsilon_{ij}, \quad (7)$$

where  $m$  is a constant,  $c_i$  is the fixed effect of year  $i$ ,  $\tau_j$  is the random block effect of series  $j$ , and  $\varepsilon_{ij}$  is the random residual error. The random terms of the model are by assumption normally distributed with zero mean. The expected value of Equation 7 gives the estimated date in Equation 6:

$$y_i^{(4)} = E(x_{ij}) = E(m + c_i + \tau_j + \varepsilon_{ij}) = m + c_i. \quad (8)$$

Because the data are unbalanced and contain empty cells, Equation 8 cannot be solved using the ordinary least squares method. The parameter values were estimated by the method of maximum likelihood. The calculations were made using the BMDP Statistical Software Release 1990 with programs 3V and 5V.

## Results

We compared the combined time series of the date of bud burst of *B. pendula* estimated by the randomized block design model with an unadjusted local series (Figure 3). The Nordenstreng series in Saarijärvi was systematically lower than the com-

bined series estimated by Method 4. The estimated block effect was 3.2 days, which reflects the deviation of the Saarijärvi series from the common level of the data. The range of all estimated block effects was 20.2 days.

The overall means for the whole period of the combined series estimated by Methods 1, 3 and 4 were 140.0, 139.3 and 139.3 days, respectively. The overall mean of the combined series adjusted to local conditions at Saarijärvi by Method 2 was 136.4 days.

The series based on Methods 2, 3 and 4 described almost identically the year-to-year variation in time of bud burst. The maximum range of the annual differences between the combined series was only 0.7 days, indicating that Methods 2, 3 and 4 removed the systematic block effects in a similar manner. Because Method 1 did not include an adjustment for blocks, the annual means obtained by this method were biased by block effects in a nonsystematic manner depending on the location of the annual observations. For example, the annual difference between the unadjusted means from Method 1 and the series adjusted by Method 4 varied from -2.7 to 1.8 days.

The variation in annual observations was decreased by eliminating the disturbing variation due to block effects by Methods 2, 3 and 4. The annual standard deviation of unadjusted observations pooled over the years was 7.1 days, whereas the pooled standard deviation of the observations adjusted for block effects estimated by Method 4 was 3.9 days. The variance component of the block effect, estimated by the linear mixed model, was 33.7, and that of the residual error component was 15.7. Thus variation due to the block effects was 68.3% of the total random variation.

The climate of Central Finland in May is characterized by a south-north temperature trend (Helminen 1988). The coefficient of correlation between the estimated block effect and the latitude was -0.63 (Figure 4). The block effect at Jyväskylä was very close to zero (Figure 4), implying that the level of the combined series of bud burst obtained using Method 4 was appropriate for Jyväskylä. The correlation between the block effect and the distance of the observation points from the sea (0.25) was not statistically significant.

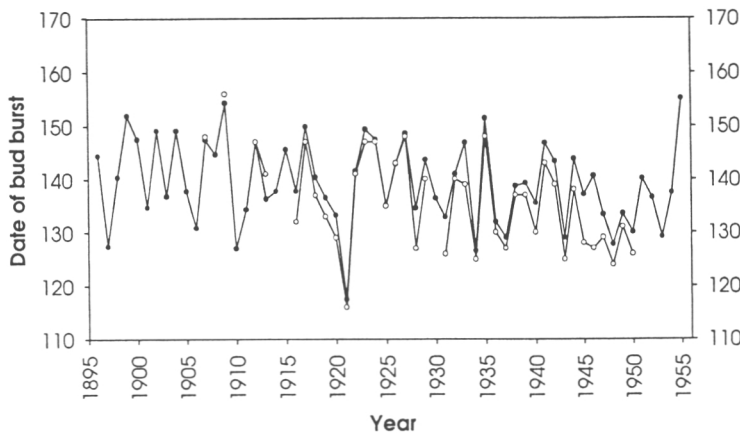


Figure 3. Combined series (●) of dates of bud burst in birch (*Betula pendula*) estimated using the mixed model of analysis of variance and the local series (○) of unadjusted observations made by Nordenstreng in Saarijärvi. The dates were measured as the number of days from the beginning of the year.

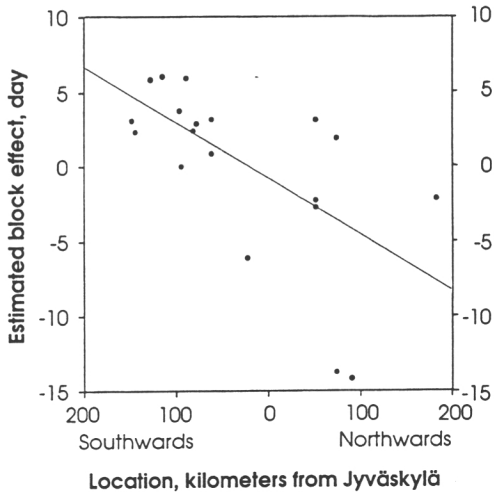


Figure 4. Linear south-north trend in block effects of observation points of bud burst.

#### Reliability of the time series

The observations were not generated by a statistical sampling procedure from a well-defined population. Instead, the data were a collection of all observations available for the area and time period that fulfilled the two criteria. It is not known how bud burst was defined in the instructions given to the observers, or whether the instructions remained the same over the decades. Further, the data did not represent the natural conditions in the whole area, but were restricted to inhabited rural areas, which were located on low-lying land close to lakes and rivers. When phenological models are tested, the data should correctly describe the relative year-to-year variation in the timing of bud burst. The time series obtained using Methods 3 and 4 reliably represented the timing of bud burst at Jyväskylä, the center of the observation area.

The Nordenstreng local series was considered reliable (Hari and Häkkinen 1991); however, there was an unusually large deviation in some of the observations, e.g., in 1946, in this series (Figure 3). Thus even the most reliable series might include some unreliable observations, misprints for example. Hence, the combined information provided by many series is needed.

Method 2, the reference series method, described the relative variation in date of bud burst similarly to Methods 3 and 4, but on a level about 3 days lower. However, the reliable reference series that is needed in Method 2 is not always available for the desired location, especially when the time span of the combined time series is long.

Method 3 is based on the estimation principle of minimizing the sum of squares. Method 4 is based on the principle of the maximum likelihood estimation and employs tools based on standard statistical theory for determining the values of the parameters. The reliability of the combined time series based on Method 4 is demonstrated in Figure 5 and includes the annual standard deviations of the adjusted observations and the 95% confidence intervals of the annual means. The width of the confidence interval was shorter than 4 days in 15 of the years (25.0%), between 4 and 8 days in 33 of the years (55.0%) and longer than 8 days in 12 of the years (20.0%). There are several possible explanations for the exceptionally large variation in the annual observations for some years. For example, if a cold period and bud burst occur simultaneously, the physiological processes take place at a slow rate, and the size of the green part of the bud may remain constant for even a week, thus making it difficult to date the observations accurately; the observers may also have interpreted the instructions differently.

The reliability of the individual observers was measured on the basis of the agreement between their observations and the combined series. Using Method 4, model-based estimation, the minimum and maximum standard deviations of the differences between the adjusted individual series and the estimated combined series were 1.7 and 5.5 days, respectively. The minimum and maximum correlation coefficients between the

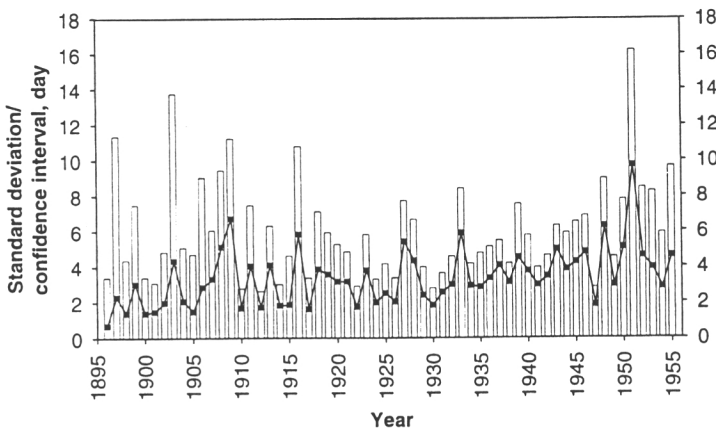


Figure 5. Annual standard deviations (■) and 95% confidence intervals (open bars) of annual means of dates of bud burst adjusted for disturbing block effects of observation points.

individual and estimated series were 0.60 and 0.98, respectively. Fourteen of the 19 correlation coefficients exceeded 0.90.

### Conclusions

A combined phenological time series can be calculated manually from annual observations by Method 1 or from observations adjusted to a reference series by Method 2. Estimation of the combined series by optimization, Method 3, requires programming, whereas the randomized block effect model, Method 4, can be solved with standard statistical software.

We found that series based on adjustment by Methods 2, 3 or 4 described the relative year-to-year variation in date of bud burst similarly. All three adjustment methods improved the reliability of the results by eliminating the disturbing block effects of the individual series. However, adjustment to the level of the reference series by Method 2 has the drawback that a reliable reference time series for the desired location and for the time span of the combined series is not always available. Method 4 is the preferred method because it provides maximum likelihood estimates.

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IV



## Effects of dormancy and environmental factors on timing of bud burst in *Betula pendula*

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Received April 30, 1997

**Summary** We tested three theories predicting the timing of bud burst in mature birch (*Betula pendula* Roth) trees utilizing a 60-year phenological time series together with meteorological temperature observations. Predictions of the timing of bud burst based on light conditions in addition to temperature were more accurate than predictions based on dormancy development and temperature (prediction standard error of 2.4 days versus 4.3 days). The signal from light conditions, represented by fixed calendar date, determined the start of bud ontogenesis rather than dormancy release. We suggest that models developed to predict the timing of bud burst be utilized in the analysis of plant responses to climate change and of climate change itself.

**Keywords:** annual cycle of development, birch, bud ontogenesis, phenology, photoperiod.

### Introduction

Trees in cool and temperate regions are assumed to be adapted to annual climatic variations that characterize these regions. To maximize growth, the trees extend the active growth period as long as possible while avoiding frost damage. To achieve this, trees regulate the timing of bud burst and flowering during the spring and the timing of growth cessation and dormancy development during late summer and fall.

Bud burst of trees has a major impact on energy and mass fluxes in the atmosphere. The latent heat of water vapor is an important component in the atmospheric energy balance (Seinfeld 1986, Sellers et al. 1997). Because bud burst in hardwoods and the onset of the active growth period in conifers determine the start of transpiration flux in spring in cool and temperate regions, the timing of the annual cycle of trees has major implications for the atmospheric water balance. Consequently, extension of the transpiration period in response to the predicted climate change may, in turn, have considerable effects on climate warming. The accurate prediction of bud burst and the greening of deciduous forest canopies is increasingly recognized as a critical determinant of ecosystem net primary productivity. Myneni et al. (1997) reported that a difference of a few days in canopy development accounted for a more than

20% interannual change in net photosynthetic production of a northeastern North American forest.

The annual cycle of trees in cool and temperate regions consists of dormant, quiescent, and active periods (Perry 1971, Sarvas 1972 and 1974, Fuchigami et al. 1982). During the dormant period, which starts at the end of the growing season, bud ontogenesis, involving morphological changes, is suspended by biochemical regulatory systems. The quiescent period starts during the winter when the trees reattain their ability for ontogenesis and can respond to environmental signals. The active period for hardwoods, which follows the quiescent period, starts at bud burst.

Several theories and models have been presented to describe the phenological development of trees from the beginning of dormancy to bud burst (Hänninen 1995). Most models are based on the prevailing temperature during autumn, winter and spring (Sarvas 1972 and 1974, Landsberg 1974, Richardson et al. 1974, Fuchigami et al. 1982, Cannell and Smith 1983), but some of them also consider time or light conditions as a factor affecting bud phenology (Bünning 1964, Campbell 1978, Nizinski and Saugier 1988). The importance of temperature for the tree's biological processes, and thus for dormancy and ontogenesis, is obvious. On the other hand, light conditions (i.e., irradiance, night length or spectral composition of light) provide a reliable reflection of seasonal variation, and so may also have a role in the timing of bud burst. Old phenological time series offer an opportunity to test theories of bud burst.

The aim of this study was to compare temperature-driven models of bud burst timing in birch with a model that incorporates light conditions as an additional factor affecting bud phenology.

### Material

The phenological time series of bud burst date of birch (*Betula pendula* Roth) in southern Finland covers the years 1896–1955 (Figure 1). Mean date of bud burst was May 19, the earliest date of bud burst occurred on April 27, 1921, and the latest on June 6, 1955. The time series was originally constructed by Häkkinen et al. (1995) and Linkosalo et al. (1996) by combining temporally overlapping observations from mature trees in their native environment.

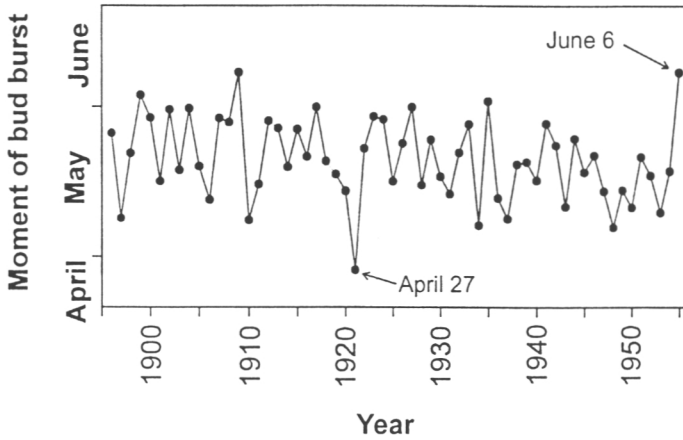


Figure 1. Combined time series of observed dates of bud burst of *B. pendula* in central Finland 1896–1955.

In addition to the phenological data, we also used temperature measurements taken four times a day in Jyväskylä (62°14' N, 25°20' E) by The Finnish Meteorological Institute. The temperature data cover the time span of the observations on bud burst in birch, except for the years 1912–1916, which were omitted from the analysis.

### Hypotheses and methods

Dormancy is considered to have a key role in the start of bud development (Hänninen 1995). We have considered three hypotheses: Hypothesis 1: bud ontogenesis begins when dormancy is complete (Sarvas 1972 and 1974, Richardson et al. 1974); Hypothesis 2: bud ontogenesis begins at the same time as dormancy, but attains its full rate only at the end of dormancy (Landsberg 1974, Fuchigami et al. 1982, Cannell and Smith 1983); and Hypothesis 3: bud ontogenesis begins when dormancy is completed and requires a light signal. We applied calendar date as an operational variable for the light signal.

### Models

Hypotheses 1–3 can be analyzed and tested using the concepts of stage of bud dormancy and stage of bud ontogenesis (Hari 1972, Sarvas 1974). During dormancy, the growth of buds is prevented, even when environmental conditions are favorable. This state can be described by a single aggregate variable,  $S_D$ , the stage of dormancy. By definition  $S_D = 0$  at the beginning of dormancy and increases slowly during autumn. The rate of dormancy development,  $f_D$ , is defined as the time derivative of the stage of dormancy,  $f_D = dS_D/dt$ . The stage of bud ontogenesis during quiescence is also described by a single aggregate variable,  $S_0$ . At the beginning of dormancy,  $S_0 = 0$  by definition. The rate of ontogenesis,  $f_0$ , is defined as the time derivative of the stage of ontogenesis,  $f_0 = dS_0/dt$ . The stage of dormancy and the stage of ontogenesis at moment  $t$  can be obtained by integrating the corresponding rates over time from the start of dormancy,  $t_0$ :

$$S_D(t) = \int_{t_0}^t f_D(t) dt, \quad (1)$$

$$S_0(t) = \int_{t_0}^t f_0(t) dt. \quad (2)$$

Dormancy is completed when the stage of dormancy,  $S_D$ , exceeds the threshold value  $D_{crit}$ , and bud burst takes place when the stage of ontogenesis,  $S_0$ , exceeds the threshold value  $O_{crit}$ . The moment of bud burst,  $b$ , for each year is obtained from Equation 3:

$$S_0(b) = O_{crit}. \quad (3)$$

If we assume that dormancy development depends on temperature,  $T$ , only:

$$f_D(t) = f_D(T(t)). \quad (4)$$

We applied the dependence of the rate of dormancy development on temperature based on experiments by Sarvas (1974) on seedlings and seeds of birch (Figure 2).

The three hypotheses result in different dependencies of  $f_0$  on temperature, light conditions and stage of dormancy. When a multiplicative model is assumed, the rate of ontogenesis,  $f_0(t)$ , is:

$$f_0(t) = w_D(S_D(t))w_L(L(t))g_0(T(t)), \quad (5)$$

where  $L(t)$  denotes the signal from light conditions,  $g_0(T(t))$  denotes the dependence of the rate of ontogenesis on temperature,  $w_D(S_D(t))$  represents the effect of the stage of dormancy, and  $w_L(L(t))$  represents the effect of the light conditions on ontogenesis. We applied the dependence of the rate of ontogenesis,  $g_0$ , on temperature based on the experiments by Sarvas (1972) on the meiotic phases of microspore mother cells of *Populus tremula* L. and *Larix sibirica* Ledeb. as well as on the

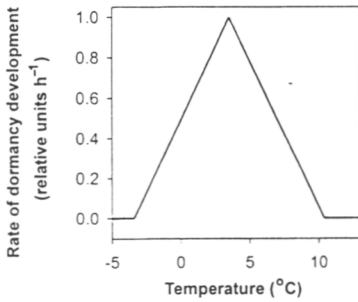


Figure 2. Dependence of rate of bud dormancy development,  $f_D$ , on temperature.

opening of male catkins of *Betula verrucosa* J.F. Ehrh. and *Betula pubescens* J.F. Ehrh. (Figure 3).

Several dependencies of the factor  $w_D$  on the state of dormancy have been proposed (Hänninen 1995). The factor  $w_D$  is often called growth competence. To test Hypothesis 2, we applied the dependency presented by Hänninen (1990) (Figure 4). We used calendar date as an operational variable for light conditions. Until threshold calendar date,  $L_{crit}$ , the factor  $w_L$  is zero, indicating halted bud ontogenesis. Thereafter,  $w_L = 1$ .

Hypotheses 1–3 can be presented using the factors  $w_D$  and  $w_L$  in Equation 5 as follows:

Hypothesis 1: bud ontogenesis begins after dormancy completion:

$$w_D(S_D(t)) = \begin{cases} 0, & S_D(t) < D_{crit} \\ 1, & S_D(t) \geq D_{crit} \end{cases}$$

$$w_L(L(t)) = 1.$$

Hypothesis 2: bud ontogenesis begins during dormancy:

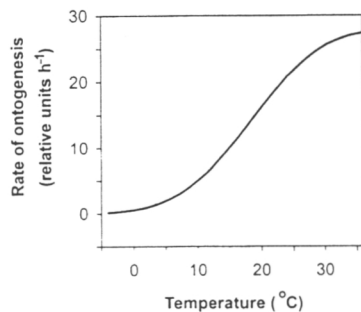


Figure 3. Dependence of rate of bud ontogenesis,  $g_0$ , on temperature.

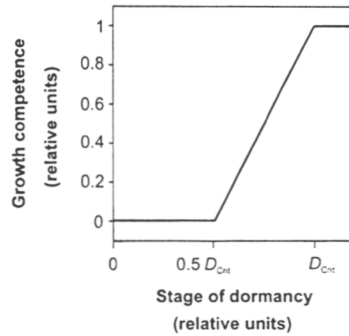


Figure 4. Dependence of growth competence factor,  $w_D$ , on stage of bud dormancy. The abbreviation  $D_{crit}$  denotes the threshold value for dormancy completion.

$$w_D(S_D(t)) = \begin{cases} 0, & S_D(t) \leq 0.5D_{crit} \\ (S_D - 0.5D_{crit}) / (0.5D_{crit}), & \text{if } 0.5D_{crit} < S_D(t) < D_{crit} \\ 1, & S_D(t) \geq D_{crit} \end{cases}$$

$$w_L(L(t)) = 1.$$

Hypothesis 3: bud ontogenesis begins when dormancy is complete and the threshold date,  $L_{crit}$ , has been attained:

$$w_D(S_D(t)) = \begin{cases} 0, & S_D(t) < D_{crit} \\ 1, & S_D(t) \geq D_{crit} \end{cases}$$

$$w_L(L(t)) = \begin{cases} 0, & L(t) < L_{crit} \\ 1, & L(t) \geq L_{crit} \end{cases}$$

#### Estimating the parameters

The integrals in Equations 1 and 2 were approximated by summing over the time intervals used. The least square estimates of model parameters  $t_0$ ,  $D_{crit}$ , and  $L_{crit}$  were determined by minimizing the residual error sum of squares of estimated bud burst dates, by an iterative procedure. The value of parameter  $O_{crit}$  was determined for each combination of the iterated values of parameters  $t_0$ ,  $D_{crit}$ , and  $L_{crit}$  as the mean of the annual values of the stage of ontogenesis,  $S_0$ , at the observed moment of bud burst over the years 1896–1955.

For Hypotheses 1 and 2, parameter values  $t_0$  and  $D_{crit}$  were simultaneously iterated,  $t_0$  from August 18 to September 19, and  $D_{crit}$  from 1 to 1200 relative units. For Hypothesis 3, parameter  $L_{crit}$  was iterated from December 21 to May 31. Dormancy completion was assumed to take place before the threshold date,  $L_{crit}$ , was attained.

#### Results

Hypothesis 3, in which the beginning of bud ontogenesis of *B. pendula* was based on calendar date, resulted in the most accurate timing of bud burst (Table 1). The model based on

Hypothesis 3, utilizing the prevailing temperatures after threshold calendar date, accounted for 92% of the variance in timing of bud burst. The standard deviation of the prediction error was 2.5 days, the maximum error was 5.8 days, and the estimated threshold date for the start of ontogenesis was March 21. Figure 5 shows the close relationship between the observed and predicted moments of bud burst and an even distribution of errors over a wide range of bud burst dates. The models based on Hypotheses 1 and 2, in which the beginning of bud ontogenesis was related to dormancy development only, resulted in an error standard deviation of 4.3 and 4.4 days, respectively, and 73% of explained variance (Table 1).

Each model describes a different progression of bud ontogenesis of *B. pendula*. If the late autumn and winter are warm, the ontogenesis according to the models differs considerably. Figure 6 demonstrates why the model based on Hypothesis 3 behaved better than the other two models, using the data from the year 1930 as an example.

According to Hypotheses 1 and 2, in which the beginning of ontogenesis was based on dormancy development only, ontogenesis had already progressed considerably in late autumn 1929 and early winter 1930 as a result of periods of warm weather after dormancy completion (Figure 6). Consequently, the predicted date of bud burst was too early. In contrast, according to Hypothesis 3, in which the beginning of bud ontogenesis was dictated by calendar date, ontogenesis started in the spring, resulting in a more accurate timing of bud burst.

Besides the poor accuracy, the models in which bud ontogenesis was dependent on dormancy development were unrealistic. This appeared in improper timing of estimated dormancy completion in some years; i.e., the date when the threshold value  $C_{crit}$  was reached. In natural conditions in southern Finland, dormancy is completed before the end of the year (Sarvas 1974, Leinonen 1996). However, dormancy completion modeled according to Hypothesis 1 occurred between February 1 and April 10 in 5 out of 55 years, and between February 1 and April 23 in 11 out of 55 years according to Hypothesis 2.

## Discussion

Several models of the regulation of bud development have been proposed for different tree species in temperate zones

Table 1. Standard deviation of the prediction error of the moment of bud burst, proportion of the variance in date of bud burst explained by the model, and estimated parameter values of the models. Abbreviations:  $t_0$  = beginning of dormancy;  $D_{crit}$  = threshold value for the stage of dormancy completion;  $L_{crit}$  = threshold date for the beginning of bud ontogenesis; and  $O_{crit}$  = threshold value of the stage of ontogenesis for bud burst; RU = relative units.

	$s_e$ (days)	$r^2$ (%)	$t_0$	$D_{crit}$ (RU)	$L_{crit}$	$O_{crit}$ (RU)
Hypothesis 1	4.3	73	Sept. 12	740	—	3250
Hypothesis 2	4.4	73	Sept. 11	900	—	3380
Hypothesis 3	2.5	92	—	—	March 21	2610

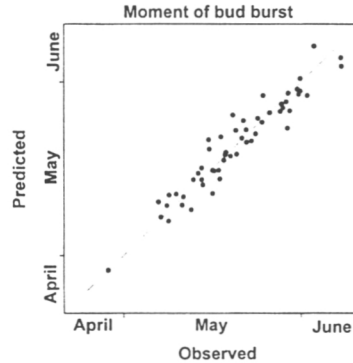


Figure 5. Comparison of observed and predicted dates of bud burst in *B. pendula* according to the model based on temperature and light conditions. The diagonal line indicates the one-to-one relationship.

(Sarvas 1972 and 1974, Landsberg 1974, Campbell 1978, Cannell and Smith 1983, Hunter and Lechowicz 1992, Kramer 1994). Our results suggest that the start of bud ontogenesis in *B. pendula* in the boreal zone is based not only on dormancy completion, but requires an additional signal from the phase of the climatic annual cycle, represented here by calendar date. In our analysis, the effects of time and light conditions on the progression of the annual cycle cannot be distinguished. However, changes in light conditions during the annual cycle, such as intensity of light, night length, and spectral composition of light, are among the most reliable sources of information reflecting the timing of seasons, especially in the boreal zone where these changes are large. Thus, it is reasonable to assume that there are mechanisms in *B. pendula*, developed during evolution, that respond to light conditions as a signal for the start of ontogenesis.

Light conditions have been observed to play an important role in several phenomena during seed development and the annual cycle of trees. For example, germination of birch seeds depends on the ratio of red to far-red light (Atkinson 1992). Photoperiod is one of the components affecting the timing of bud burst in Douglas-fir (Campbell 1978). The cessation of shoot growth in *Betula* and *Salix* is driven by temperature and daylength (Junttila 1980, Koski and Sievänen 1985). Phytochrome is probably the receptor of light signals in both herbaceous (Smith 1995) and woody (Wareing 1956) plants. Our results suggest that mechanisms based on light and temperature also control bud development in *B. pendula*.

Regulatory systems that utilize climatic regularities have emerged in trees during evolution. If the weather in the spring depended on temperature conditions during the preceding autumn, then trees would utilize autumn temperature information to regulate their bud development in spring. However, because weather is a chaotic phenomenon (Lorenz 1993) it is unlikely—from the evolutionary point of view—that dormancy completion in late autumn would have an effect on bud burst timing in the spring in *B. pendula*.

The regulation of the annual cycle of trees is complicated. Although laboratory and greenhouse studies of tree seedling

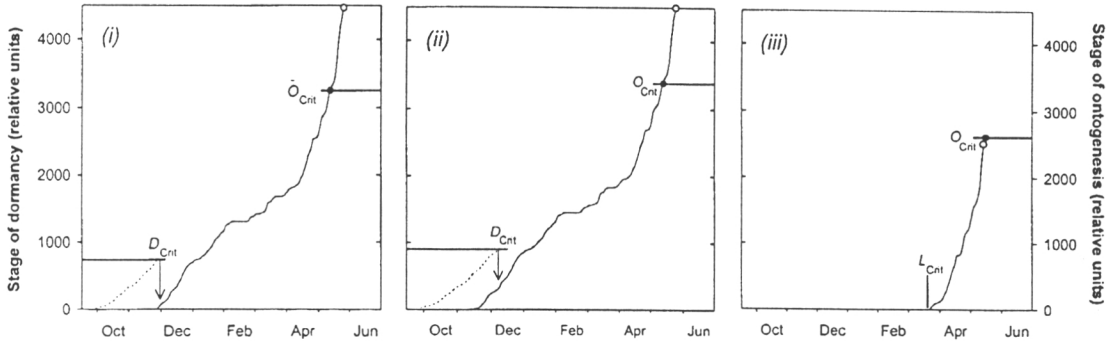


Figure 6. Progression of the stage of bud dormancy (----) and the stage of bud ontogenesis (—) in *B. pendula* according to Hypotheses 1–3 for the period 1929–1930. The arrow indicates the moment of dormancy completion when the threshold value  $D_{crit}$  has been reached. In Model 1, bud ontogenesis begins at the end of dormancy (i), in Model 2 ontogenesis begins at a slow rate during dormancy (ii), and in Model 3 ontogenesis begins at the threshold calendar date  $L_{crit}$  (iii). The abbreviation  $O_{crit}$  denotes the threshold value for bud burst; ○ and ● denote observed and predicted dates of bud burst, respectively.

physiology have provided valuable information about possible regulatory mechanisms (Sarvas 1972 and 1974, Landsberg 1974, Richardson et al. 1974, Campbell 1978, Fuchigami et al. 1982, Hänninen 1990 and 1995), it is problematic to extrapolate laboratory experiments carried out on seedlings and seeds during a few experimental years to trees growing under natural conditions. Our results show that long-term phenological series, collected extensively in the early 20th century, provide a valuable alternative that can be utilized in checking the relevance of laboratory findings.

We conclude that dormancy can be omitted in analyses of the timing of bud burst in *B. pendula* growing in boreal regions where the time span from dormancy to bud burst is long. Our results have implications for the detailed analysis of plant responses to predicted climate change, and of climate change itself, because the timing of bud burst affects both biomass production and the onset of transpiration, which influences the atmospheric water balance.

#### Acknowledgments

We thank Dr. Riitta Hari for valuable comments, and The Finnish Cultural Foundation for a scholarship to Tapio Linkosalo.

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V



## Statistical evaluation of bud development theories: application to bud burst of *Betula pendula* leaves

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Received September 18, 1998

**Summary** Resampling methods were used to evaluate models based on alternative bud development theories applied to *Betula pendula* Roth data. Statistical testing based on the bootstrap method showed that the mean square errors (MSE) of the predicted bud-burst dates of two models, in which the start of ontogenetic development depended on dormancy development only, did not differ significantly. However, the MSE of the model in which the start of ontogenesis depended on a signal from light climate, indicated by using a fixed calendar date, was significantly smaller than that of the models depending on dormancy development. Model parameters were highly multi-collinear; i.e., sensitive to changes in the data. The cross-validation method was used to determine the prediction error of the models. The predictive ability of the models was not much less for an independent data set than for the original data.

**Keywords:** annual cycle, bootstrap, bud-burst timing, cross-validation, resampling.

### Introduction

Theories on the development of leaf and flower buds from the onset of dormancy to bud burst have been published for many tree species of the cool and temperate regions (Hänninen 1995). According to these theories, bud burst takes place when bud development reaches the threshold stage. The rate of development depends on environmental factors such as temperature. Although the theories have many features in common, many of them treat the beginning of ontogenetic bud development differently. In some theories, the start and also the rate of ontogenesis depend on the state of bud dormancy as well as on temperature (Sarvas 1972 and 1974, Landsberg 1974, Richardson et al. 1974, Fuchigami et al. 1982, Cannell and Smith 1983), whereas in other theories the start of bud development depends on a biological clock or a signal from the light climate (Bünning 1964, Campbell 1978, Nizinski and Saugier 1988).

In mathematical models of bud development, the process is considered dynamic and the stage of bud development is determined by the history of environmental conditions, described, for instance, by means of the temperature sum. The mean square error; i.e., the average of the squared residuals, has usually been the only statistic used to evaluate the models.

Comparison of the models has been based on the numerical magnitude of the mean square errors of predicted bud-burst dates only. Consequently, it is not known whether the models describe the phenomenon of bud development as it appears in nature or whether they result merely from technical model fitting of mathematically complicated models to actual data sets (Hunter and Lechowicz 1992, Hänninen 1995). In addition, because of the lack of appropriate statistical tests, we do not know whether the observed differences in mean square errors of the models are statistically significant. Finally, the predictive power of the models has not been analyzed because no independent data sets have been available.

No standard statistical methods can be used to evaluate the bud-development models because the sampling distributions of the model parameters and mean square errors are not known. However, resampling methods are a recently developed technique for making a statistical inference that can be utilized when traditional sampling distributions are not available. The basic statistical ideas are not new, but these methods require much computer time. The power of modern computers has enabled us to put these old ideas into practice (Efron and Tibshirani 1993). The bootstrap method can be applied to test the statistical significance of the difference of the estimated mean square errors of the models, and to analyze the properties of the model parameters. The cross-validation method can be used to estimate the prediction error of the models.

The aim of this study was to make a statistical comparison of models based on three theories for the development of leaf buds of birch until bud burst by applying resampling methods. In two of the theories, the beginning and the rate of bud development depend on dormancy development, and in the third theory bud development begins on a fixed calendar date representing a signal from the light climate (e.g., night length or spectral composition of the light).

### Materials

The analysis was based on temperature records and phenological time series of the bud-burst date of birch (*Betula pendula* Roth) recorded on mature trees in natural conditions in Southern Finland between 1896 and 1955. Mean bud-burst date was May 19, the earliest bud burst took place on April 27, 1921.

and the latest on June 6, 1955. The bud-burst time series was originally constructed by Häkkinen et al. (1995) and by Linkosalo et al. (1996). The temperature time series (four measurements per day) was collected by the Finnish Meteorological Institute in Jyväskylä (62°14' N, 25°20' E). Because of missing temperature observations, the years 1912–1916 were omitted from the analysis.

## Methods

Bootstrap is a data-based, nonparametric simulation method for making statistical inference when standard assumptions, such as the normality of errors, are not valid, or when textbook test statistics with known distribution do not exist (Efron 1979, Efron and Tibshirani 1993). The basic idea of bootstrap is to obtain unknown sampling distributions by resampling; i.e., by drawing random samples repeatedly from the original data set. The sample units are drawn one-by-one with replacement until the original sample size has been reached, and the procedure is repeated, say 3000 times. The value of the statistic under consideration is calculated from each bootstrap sample. These bootstrap replicate values form the empirical sampling distribution that is used to determine standard deviation, bias, and confidence interval of the statistic.

The cross-validation method was utilized to estimate the prediction error of the models; i.e., a measure of how well the model predicts the response values of future observations. In classic cross-validation, the sample is divided into two subsamples. Estimation of the statistical predictor is made on one subsample (training sample), after which the prediction errors of the models are determined by applying the estimated predictor to the observations in the other subsample (Marriott 1990).

For bootstrap sampling, the pseudorandom number generator of Lüscher was utilized (James 1994, Lüscher 1994).

## Results

### Models to be evaluated

The models of bud-burst timing of *B. pendula* were based on the concepts of stage of bud dormancy and stage of bud ontogenesis (Hari 1972, Sarvas 1974, Häkkinen et al. 1998). Dormancy is completed when the stage of dormancy,  $S_D(t)$ , reaches the threshold value,  $D_{crit}$ . The rate of dormancy development is defined as the time derivative of the stage of dormancy,  $f_D(t) = dS_D(t)/dt$ . Analogously, the rate of bud ontogenesis is defined as the time derivative of the stage of bud ontogenesis,  $g_O(t) = dS_O(t)/dt$ . Bud burst takes place when the stage of ontogenesis exceeds the threshold value,  $O_{crit}$ . Alternative theories specify different dependencies of the rates on environmental factors and on the stage of dormancy.

The stage of dormancy and the stage of ontogenesis at moment  $t$  can be obtained by integrating the corresponding rates over time from the start of dormancy,  $t_0$ ,

$$S_D(t) = \int_{t_0}^t f_D(t) dt, \quad (1)$$

$$S_O(t) = \int_{t_0}^t g_O(t) dt. \quad (2)$$

In practical calculations, Equations 1 and 2 were approximated by summing over the time intervals used. The predicted moment of bud burst,  $b$ , for each year is obtained as the solution of the equation:

$$S_O(b) = \int_{t_0}^b g_O(t) dt = O_{crit}. \quad (3)$$

The main aspects of theories on bud development deal with the role of dormancy in ontogenetic bud development. Three theories were considered. In Theory 1 (Sarvas 1972, 1974, Richardson et al. 1974), bud ontogenesis started when dormancy was completed; i.e., when the threshold value  $D_{crit}$  was reached. In Theory 2 (Hänninen 1990), bud ontogenesis began during dormancy, but at a slow rate, attaining its full rate when dormancy was completed. In Theory 3, bud ontogenesis started at the threshold calendar date,  $L_{crit}$ , describing the signal from the light climate (e.g., night length or spectral composition of light) (Häkkinen et al. 1998) or from a biological clock (Bünning 1964).

These theories result in different mathematical models of bud development. In Models 1 and 2, the dependence of the rate of dormancy development on the prevailing temperature (Figure 1a) according to Sarvas (1974) was utilized. In Models 1–3, the dependence of the rate of ontogenesis on temperature (Figure 1b) according to Sarvas (1972) was utilized. In Model 2, the dependence of ontogenetic development on the stage of dormancy (Figure 1c) according to Hänninen (1990) was utilized.

The least square estimates of model parameters  $t_0$ ,  $D_{crit}$ ,  $L_{crit}$ , and  $O_{crit}$  (Table 1) were determined by minimizing the mean square error, MSE, of the models using an iterative procedure (Häkkinen et al. 1998). Parameter values  $t_0$  and  $D_{crit}$  were simultaneously iterated,  $t_0$  from September 1 to October 10, and  $D_{crit}$  from 300 to 1200 relative units. Parameter  $L_{crit}$  was iterated from January 1 to May 30.

The mean square errors of Models 1 and 2, which are based on dormancy development, differed only slightly from each other in the original *B. pendula* data set ( $MSE_1 = 17.6$  and  $MSE_2 = 19.0$ ). Model 3, which is based on light climate, had the smallest mean square error ( $MSE_3 = 6.1$ ) of the three models (Table 1). In addition, the predictions of the bud-burst day given by Models 1 and 2 were very similar (Figure 2c), whereas the predictions given by Model 3 differed from those of Models 1 and 2 (Figures 2a and 2b).

### Tests of differences in the mean square errors of models based on bootstrap percentile confidence intervals

The comparison of models has usually only been based on the magnitude of the MSE of the different models:

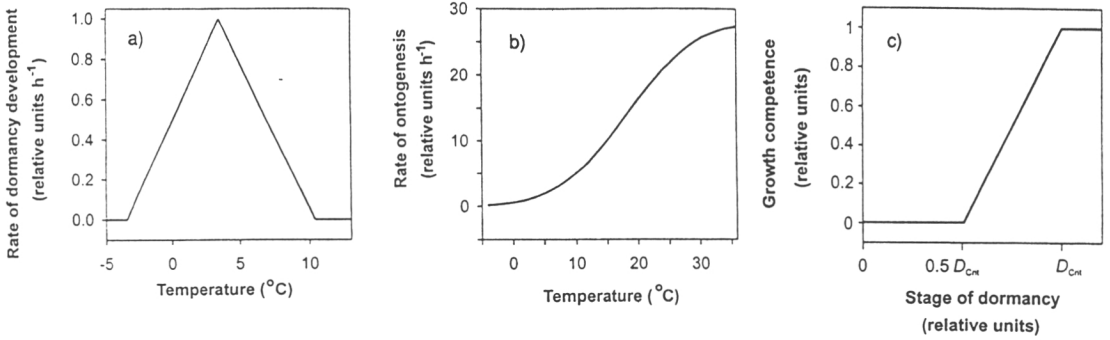


Figure 1. (a) Dependence of the rate of bud dormancy development on temperature. (b) Dependence of the rate of bud ontogenesis on temperature. (c) Dependence of growth competence multiplier, restraining the rate of ontogenesis during dormancy, on the stage of dormancy. Parameter  $D_{crit}$  denotes the threshold value for dormancy completion.

Table 1. Mean square errors, MSE, and estimated parameter values of the models. Abbreviations:  $t_0$  = beginning of dormancy;  $D_{crit}$  = threshold value for the stage of dormancy completion;  $L_{crit}$  = threshold date for the beginning of bud ontogenesis; and  $O_{crit}$  = threshold value of the stage of ontogenesis for bud burst; RU = relative units.

	MSE (days <sup>2</sup> )	$t_0$	$D_{crit}$ (RU)	$L_{crit}$	$O_{crit}$ (RU)
Model 1	17.6	Sept 13	710		3340
Model 2	19.0	Sept 12	900		3450
Model 3	6.1			March 21	2660

statistic (Efron and Tibshirani 1993, p. 192):

$$\hat{\theta}_{13} = MSE_1 - MSE_3, \tag{5}$$

$$\hat{\theta}_{23} = MSE_2 - MSE_3,$$

$$\hat{\theta}_{21} = MSE_2 - MSE_1.$$

The statistical significances of the MSE differences were tested using the bootstrap confidence intervals for the above three comparisons  $\hat{\theta}_{13}$ ,  $\hat{\theta}_{23}$  and  $\hat{\theta}_{21}$ . If the value zero was not included in the confidence interval, the difference was considered statistically significant (Efron and Tibshirani 1993, p 156). The confidence intervals were determined by bootstrap sampling distributions of  $\hat{\theta}_{13}$ ,  $\hat{\theta}_{23}$  and  $\hat{\theta}_{21}$ . Altogether 7,000 bootstrap samples of size 55 were drawn with replacement from the original 55-year time series of bud burst in birch. Models 1–3 were fitted to each sample and, using their mean square errors, altogether 7,000 bootstrap estimates for  $\hat{\theta}_{13}$ ,  $\hat{\theta}_{23}$  and  $\hat{\theta}_{21}$  were calculated. The equal-tailed  $(1-2\alpha)$  bootstrap

$$MSE = \frac{1}{n} \sum (y_j - \hat{y}_j)^2, \tag{4}$$

where  $y_j$  is the observed and  $\hat{y}_j$  the predicted moment of bud burst, and  $j$  extends over  $n$  years.

In statistical evaluation of the models, the three pairwise comparisons of the mean square errors were used as the test

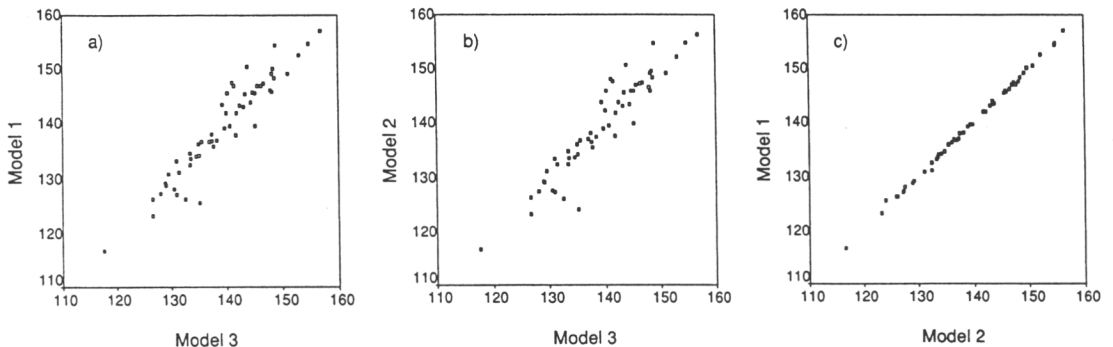


Figure 2. Relationship of predicted bud-burst dates of *B. pendula* for the years 1896–1955 as the number of days from the beginning of the year. In Models 1 and 2, the start of ontogenetic bud development was based on dormancy development only, and in Model 3 the start was based on a signal from light climate indicated by using a fixed calendar date.

confidence interval limits for  $\hat{\theta}_{13}$ ,  $\hat{\theta}_{23}$  and  $\hat{\theta}_{21}$  were determined by  $\alpha$  and  $(1 - \alpha)$  percentiles of the obtained distributions of  $\hat{\theta}_{13}$ ,  $\hat{\theta}_{23}$  and  $\hat{\theta}_{21}$ .

The frequency distributions of the 7,000 bootstrap replicates of  $\hat{\theta}_{13}$ ,  $\hat{\theta}_{23}$  and  $\hat{\theta}_{21}$ , and their 99% confidence intervals, indicated that Models 1 and 2 did not differ significantly from each other, but that Model 3 differed from Models 1 and 2 at a very small risk level (Figure 3). If the inference had been based on 95% confidence intervals, the difference between Models 1 and 2 would have been statistically significant. However, the scientific importance of this difference was negligible because the observed  $MSE_2 - MSE_1 = 1.4$  in the original data set was small compared to  $MSE_1 = 17.6$  and  $MSE_2 = 19.0$  (Table 1). In contrast, the statistically highly significant MSE differences of Model 3 compared with Models 1 and 2 were scientifically important because the observed values  $MSE_1 - MSE_3 = 11.5$  and  $MSE_2 - MSE_3 = 12.9$  were high compared to  $MSE_3 = 6.1$  (Table 1).

#### Properties of the model parameters based on bootstrap

Most of the model parameters were strongly multi-collinear, as indicated by the high linear correlations between the parameter values in 7,000 bootstrap replications (Weisberg 1985) (Table 2). In addition, the ranges of the parameter values in the bootstrap replications were nearly the same as the iteration ranges used in parameter estimation. This implies that the parameter values were sensitive to changes in data values; i.e., the parameter values depended on the collection years from which they were calculated. Consequently, no strong inference can be drawn from the magnitude of the estimated parameter values of the models.

#### Prediction error of the models

To estimate the prediction error, leave-one-out cross-validation was used, in which the training subsamples were formed by omitting one observation from the data in sequence. All three

Table 2. Linear correlation coefficients of 7,000 bootstrap parameter values of Models 1–3. Abbreviations as in Table 1.

	Model 1		Model 2		Model 3
	$t_0$	$D_{crit}$	$t_0$	$D_{crit}$	$L_{crit}$
$D_{crit}$	-0.68		-0.81		
$O_{crit}$	-0.10	-0.59	-0.20	-0.33	-0.92

models were fitted to 55 training subsamples of size 54, and the 55 outlying observations were predicted by the corresponding models to give the prediction residuals  $(y - \hat{y})$ . The cross-validation prediction error of each model was estimated as the mean of the corresponding 55 squared prediction residuals (Efron and Tibshirani 1993, p. 240).

The estimated cross-validation prediction errors were 19.7 (Model 1), 20.7 (Model 2), and 7.5 (Model 3). The prediction errors were 2.0, 1.8, and 1.4 units greater than the corresponding mean square errors of the original data set (Table 1), indicating that the models predict bud-burst dates for independent data sets with nearly the same precision as for the original data.

#### Discussion

Statistical methods are an important tool in scientific inference when the data-generating process includes disturbing variation as a result of sampling variation, measurement errors, or uncontrolled variables. This is nearly always the case in biological experiments and observations (Tuomivaara et al. 1994). Uncertainty in the conclusions caused by disturbing variation can be measured by means of statistical methods.

Standard statistical methods have not been applicable in analysis because of the dynamic nature of the models of bud development theories. The evaluation of theories has been based on numerical comparison of the mean square errors of

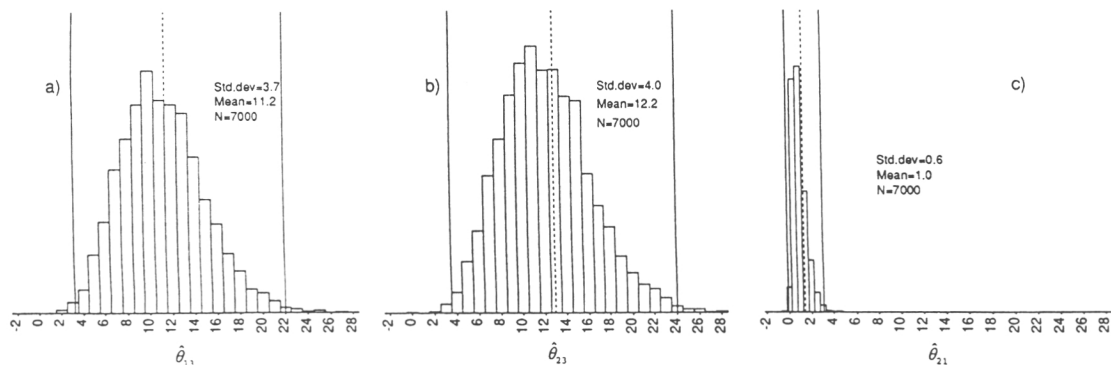


Figure 3. The frequency distributions of pairwise differences (test statistic used in model comparisons) of mean square errors, MSE, of predicted bud-burst dates of Models 1–3 calculated from 7,000 random bootstrap samples drawn with replacement from the original data set: (a)  $\hat{\theta}_{13} = MSE_1 - MSE_3$ ; (b)  $\hat{\theta}_{23} = MSE_2 - MSE_3$ ; and (c)  $\hat{\theta}_{21} = MSE_2 - MSE_1$ . Subscripts refer to Models 1, 2, and 3. Vertical solid lines at 0.5% and 99.5% percentiles give the 99% bootstrap confidence intervals of  $\hat{\theta}$ . Broken lines indicate values of  $\hat{\theta}$  in the original data set.

the models only. From the point of view of scientific inference, this is problematic because the risk of making a wrong inference is unknown. For instance, sensitivity of models to different data sets is unknown. Whether the observed differences in mean square errors are significant is also unknown (Hunter and Lechowicz 1992, Hänninen 1995). The bootstrap and cross-validation methods applied in this study enabled statistical arguments to be utilized as a part of the scientific inference of bud development theories.

The fundamental idea underlying the resampling methods is to replace the unknown population distribution with the observed sample distribution from which the bootstrap samples are drawn. The nature of the inference is asymptotic; i.e., the larger the sample size, the stronger the conclusions. The 55-year phenological and meteorological time series utilized in the analysis are longer than those used in most studies. A time span of more than half a century can be considered to represent the year-to-year-variation in the timing of bud burst and in environmental conditions sufficiently well to serve as a reasonable basis for inference.

Fast computers are necessary for the application of resampling methods. However, there are still problems in data processing. Although some computer programs are available for resampling, many problems, such as the evaluation of bud development theories, require purpose-written computer programs. In addition, many nonstandard models do not have analytic solutions and the parameter values have to be estimated by cumbersome iterative procedures, which requires much programming time.

The accuracy of bootstrap estimates increases as the number of bootstrap samples increases. But how many samples are needed? As a rule of thumb, estimation of the variance of the sampling distribution of the statistic under consideration can be made accurately with less than five hundred bootstrap samples. On the other hand, in estimating confidence intervals, based on the tails of bootstrap sampling distribution, a much larger number of samples, say 3,000, are needed (Efron and Tibshirani 1993). In order to analyze the influence of the number of bootstrap samples on the accuracy of the confidence interval estimation of this study, the number of bootstrap samples was varied from 200 to 15,000, and the left tail probabilities of test statistic  $\hat{\theta}_{21} = \text{MSE}_2 - \text{MSE}_1$  being less than zero,  $P(\hat{\theta}_{21} \leq 0)$ , were determined. Figure 4 indicates that the tail probability asymptotically approaches the value = 0.6%. With 3,000 bootstrap samples, the tail probability would have been estimated fairly accurately, the bias being less than 0.2 percent units. The results of this study were based on 7,000 bootstrap samples and the bias was less than 0.1 percent units.

We utilized resampling methods to compare three theories on the timing of bud burst in *B. pendula*. The results of statistical analyses corroborated the earlier findings (e.g., Häkkinen et al. 1998) that the models based on a fixed date for the start of ontogenetic bud development had a significantly smaller mean square error than models in which the start and rate of development depended on the stage of dormancy. New findings obtained using resampling methods showed that the predictive power of the models was not sensitive to changes in

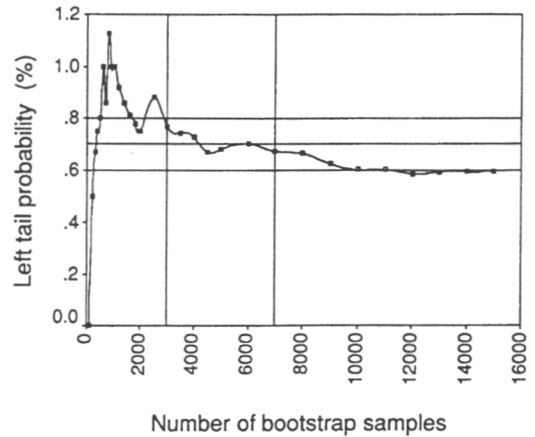


Figure 4. Probability of difference of mean square errors of Models 2 and 1 being less than zero,  $P(\hat{\theta}_{21} = \text{MSE}_2 - \text{MSE}_1 \leq 0)$ , as a function of the number of bootstrap samples. Probabilities were estimated as left tail probabilities of bootstrap frequency distributions of  $\hat{\theta}_{21}$  (cf. Figure 3c).

the data, and that the estimated parameter values were unstable because of high multi-collinearity.

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Cover photo: METLA/Erkki Oksanen

ISBN 951-40-1709-9  
ISSN 0358-4283  
Hakapaino 1999