Analyses of the spring phenology of boreal trees and its response to climate change

Tapio Linkosalo

Academic dissertation

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Summary

Linkosalo, Tapio 2000. Analyses of the spring phenology of boreal trees and its response to climate change. University of Helsinki Department of Forest Ecology Publications 22. ISBN 951-45-9362-6, ISSN 1235-4449.

The study developed methods for combining phenological observation series into one solid time series, as well as detecting and removing outliers. One of the methods was utilised to combine the time series of the flowering of *Alnus glutinosa*, *Alnus incana*, *Populus tremula*, *Betula* sp. and *Pinus sylvestris*, as well as the leaf bud burst of *Populus tremula* and *Betula* sp. from phenological data collected in Finland in the years 1896-1955. The combined time series were utilised to determine the progress of spring, and a clear trend from south to north was detected. No trends in the east-west direction were observed, nor trends due to the altitude of the observation site. Further, regularities in the phenological timing between species were investigated, and it was found that either the plants utilise similar mechanisms, or at least use the same features of the weather to regulate their phenological events.

The work used two phenological models, the first (Sarvas 1972, 1974) initiating ontogenetic development from the fulfilment of the chilling requirement in autumn, the second making an assumption that once the chilling requirement is completed, there is another signal, derived from the light climate, that triggers ontogenetic development in spring. Both models were utilised to predict the phenological events in all the 7 phenological time series. The second model performed better, especially in predicting the leaf bud burst.

The two phenological models were utilised to predict the outcome of climate change. The results differed radically for the bud burst events, indicating that the model selection dictates the results achieved. On the basis of the observed phenological data, it cannot be determined which of the models (if any) describes the phenological regulation mechanisms of the trees more realistically, even though the model based on the signal from the light climate seems better for most species. Thus phenological data does not permit reliable estimates of the effect of climate change on the spring phenology of boreal trees. Deeper understanding of the regulatory mechanisms involved is required.

The two models, however, gave rather similar results for the frost damage risk of early flowering species (*Alnus* and *Populus*), indicating a considerable increase in frost damage risk at an average annual temperature increase of a few degrees, which is likely to occur within a century. This may indicate drastic changes in the tree populations of boreal forests in the future.

Yhteenveto

Tutkimuksessa kehitettiin metodeja hajanaisten fenologisten havaintosarjojen koostamiseksi yhtenäiseksi aikasarjaksi, sekä virheellisten vierashavaintojen poistamiseksi. Yhden metodin avulla koostettiin aikasarjat vuosina 1896-1955 Suomesta kerätyistä fenologisista havaintosarjoista: harmaa- ja tervalepän, koivun, haavan ja männyn kukinta, sekä koivun ja haavan lehtisilmun puhkeaminen. Aikasarjojen avulla tutkittiin kevään etenemistä yli havaintoalueen, ja havaittiin selvä trendi etelästä pohjoiseen. Itä-länsi -suunnassa, tai havaintopaikan korkeuden mukaan ei trendiä havaittu. Samoin tutkittiin kevään fenologisten ilmiöiden säännönmukaisuutta eri lajien välillä, ja havaittiin selkeä yhteys. Joko eri kasvilajit käyttävät samanlaisia säätömekanismeja, tai ainakin hyödyntävät samoja sääilmiöitä fenologisten ilmiöiden ajoituksen ohjauksessa.

Työssä käytettiin kahta kevätfenologiaa selittävää mallia, joista ensimmäinen (Sarvas 1972, 1974) aloittaa ontogeneettisen kehityksen syksyisen kylmäaltistuksen ohjaamana, ja toinen olettaa, että kylmäaltistuksen lisäksi tarvitaan vielä signaali valoilmastosta ontogeneettisen kehityksen käynnistymiseen. Molempia malleja käytettiin em. fenologisten havaintosarjojen mallittamiseen. Jälkimmäinen tuotti tarkempia ennusteita, erityisesti lehdenpuhkeamista mallitettaessa.

Fenologisia malleja käytettiin myös ilmastonmuutoksen seurausten arvioimiseen. Lehtisilmujen puhkeamisen ajoittumista mallitettaessa tulokset erosivat merkittävästi, ja osoittivat että valittu malli määrää saadut tulokset. Fenologisen aineiston perusteella ei voitu pitävästi päätellä, kumpi malleista (vai eikö kumpikaan) kuvaa paremmin puiden fenologisia säätömekanismeja, joskin valoilmastosta signaalinsa ottava malli toimi paremmin useimpia fenologisia ilmiöitä selitettäessä. Niinpä johtopäätöksenä todettiin nykyisiin fenologisiin malleihin liittyvän vielä liiaksi epävarmuutta, jotta luotettavia ennusteita ilmastonmuutoksen vaikutuksista voitaisiin niiden pohjalta laatia. Ennusteita varten tarvitaan malli, joka pohjautuu tarkempiin havaintoihin fenologisista säätömekanismeista tai niiden biokemiasta.

Aikaisin keväällä tapahtuvia kukkimisia (leppä ja haapa) mallitettaessa molemmat mallit antoivat samansuuntaisia tuloksia, joiden mukaan jo muutaman asteen keskilämpötilan nousu lisää kukkien pakkasvaurioriskiä huomattavasti. Siten ilmaston lämpeneminen saattaa merkittävästi heikentää varhain keväällä kukkivien lajien kukinnan onnistumista, ja vaikuttaa sitä kautta lajien väliseen kilpailuun.

List of original articles

This thesis is based on the following articles, which are referred to in the text by the word 'Study' and roman numerals I-V. Some previously unpublished results are also presented.

Study I	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.
Study II	Linkosalo T, Häkkinen R, Hari P (1996) Improving the reliability of a combined phenological time series by analyzing observation quality. *Tree Physiology* **16**, 661-664.
Study III	Linkosalo T (1999) Regularities and patterns in the spring phenology of some boreal trees. *Silva Fennica* **33**(4), 237-245.
Study IV	Linkosalo T (2000) Mutual dependency and patterns of spring phenology of boreal trees. *Canadian Journal of Forest Research*. In print.
Study V	Linkosalo T, Carter TR, Häkkinen R and Hari P (subm.) Predicting spring phenology and frost damage risk of *Betula sp*. under climatic warming: a comparison of two models. Submitted to *Tree Physiology* in October 1999.

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List of symbols

symbol	unit	description
A_{crit}	days	Starting date of dormancy
b_j	days	average deviation of the observation series *j* from the reference series
c_j	days	average deviation of the observation series *j* from the combined time series
d_j	days	random block effect of observation seriesj
D_{crit}	arbitrary	dormancy (chilling) release threshold value
ε_{ij}	days	random residual error
f_D	arbitrary	rate of dormancy development
f_O	arbitrary	rate of ontogenetic development
m	days	constant (average level of all observations)
n		number of years
n_i		number of observations in year i
n_j		number of observations in seriesj
t_{crit}	days	threshold value of signal from the light climate
O_{crit}	arbitrary	phenological event threshold value
O^*_{crit}	arbitrary	phenological event threshold value
s	days^2	square sum of deviations of observation series from the combined time series
S_D	arbitrary	stage of dormancy development
S_O	arbitrary*	stage of ontogenetic development
S^*_O	arbitrary	stage of ontogenetic development
t	days	time
t_{dr}	days	starting point of ontogenetic development
τ_i	days	fixed effect of year i
T_i	days	test statistic of the outlier detection procedure
χ_{ij}	days	observation in seriesj* in year i .
χ'_{ij}	days	adjusted observation in seriesj in year i
χ_{ir}	days	observation in year i in the reference series r
z_i	days	value of combined time series in year i
$\check{z}_{\text{i}}$	days	model predicted moment of phenological event in year i

1 Introduction

1.1 The annual rhythm of boreal plants

Towards the end of the active photosynthetic and growth period in summer, perennial plants prepare themselves for the coming winter and the next growing season. New leaf and flower buds are produced. At the end of the active period the buds fall into a state of inhibited growth called dormancy (Fig. 1)[1] . The origins of the mechanisms underlying dormancy are unclear, but at present they serve the obvious purpose of keeping the buds in an inert stage during the autumn, when conditions would otherwise be favourable for growth, but when any development would expose the plants to frost damage due to extended periods of freezing temperatures during the coming winter (Levins 1969, Woolhouse 1969).

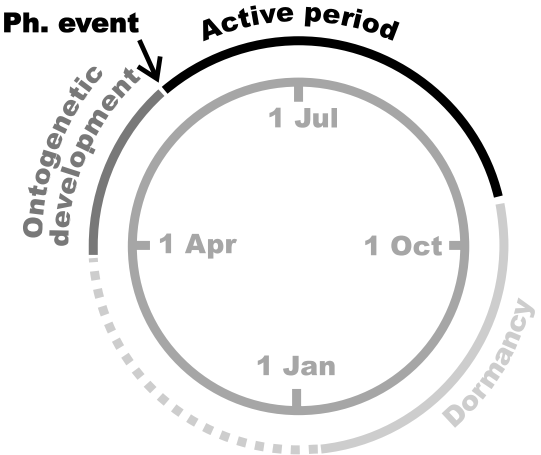

Figure 1. The annual cycle of boreal trees, with the timing of the bud burst of *Betula* sp. as an example. The dotted line of dormancy indicates that the timing of dormancy release and start of ontogenetic development is unclear.

Later in spring, after the dormancy is released, the ontogenetic, i.e. vegetative development of leaf, flower and shoot buds starts. This development is driven mostly by feasible temperatures (e.g. Sarvas 1972), and it eventually leads to leaf bud burst, flowering and the start of shoot elongation. The timing of these events is far from trivial from the survival point of view. The burst of leaf buds should take place as early as possible, to maximise the potential for photosynthetic production, while care needs to be taken to avoid exposing the leaves to spring frost, which might damage them, resulting in severe loss of photosynthetic capacity. The same applies to the shoot growth. For flowering, the case may be slightly different, as frost damage to the flowers does not harm

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[1] See chapter 6.2 for terminology of the annual rhythm.

the mature plants much, but repeated loss of seed crop will eventually effect the competitive state of the species.

1.2 Studies of phenology

The ontogenetic development of plants has long been studied. In 1735 French biologist de Reaumur tried to find out why cereal crops ripened at different times in different years (Sarvas 1974). He totalled daily average temperatures over the growing season, and in fact laid the basis for a phenological model that is still widely used, the temperature sum model. Another basic study was carried out in the 1960s by Sarvas, who extensively studied the phases of ontogenetic development of boreal broad-leaved trees. Based on his experiments with *Betula pubescens, B. verrucosa* and *Populus tremula* (1972), he presented an experimental model of ontogenetic development applicable to all plant species.

The mechanism of ontogenetic development alone is not sufficient to describe the spring phenological events. The mechanism starting the ontogenetic development in spring needs to be known as well. This has been widely studied, but the results are still unclear and contradictory. Sarvas (1974) suggested that once dormancy (he called it autumn dormancy) is released, the plants react to feasible temperatures with ontogenetic development. Romberger (1963) also found the dormancy release and the start of ontogenetic development to be a temperature-driven processes, as did Falusi and Calamassi (1990). Worrall and Mergen (1967) found in laboratory experiments that day length has an effect on dormancy release, but claimed that this does not occur in natural conditions.

Some other studies suggest that the light conditions (typically day or night length) might affect the phenological timing of plants. This seems reasonable, as light conditions have a high information content about the phase of the season (Lewins 1969). Wareing (1956, 1969), Nitch (1957) and Vegis (1964) emphasised the importance of day length in the control of dormancy release, and Farmer (1968) suggested that photoperiod has an impact on the whole cycle of dormancy. Heide (1993a, 1993b) found that the photoperiod effected the start of ontogenetic development, which also depends on the dormancy release. Yet another interpretation of the combined effect of temperature and photoperiod was presented by Murray et al. (1989), and later tested by Cannell and Smith (1983), who suggested that the photoperiod affects the bud burst threshold of ontogenetic event to occur. Vegis (1964) gives one explanation of these contradictory results in pointing out that the photoperiod has no effect on ontogenetic development immediately when the dormancy is released, but does so later.

1.3 Spring phenology and climate change

The plants in the boreal zone face a tricky problem of determining the time of growth onset in spring. To deal with this problem, the plants utilise delicate mechanisms of phenological control, which have adapted to the local environmental conditions (Weiser 1970, Sarvas 1972, 1974, Lockhart 1983, Heide 1985, Hänninen and Hari 1996). The plants in the boreal zone have slowly migrated to their current growing sites over the 10,000 years since the last ice-age. The adaptation seems to be adequate for most boreal and temperate species (Kramer 1995), which can be observed on the rare occasions of severe frost damage to harm to the native plants, although some researchers suggest that this time is still too short for the plants to have adapted to the current conditions (Lechowich 1984). The state of adaptation may vary for different species, since some broad-leaved species like *Alnus* and *Populus* tend to reproduce to a great extent by sprouting (Kellomäki 1987), which slows their adaptation.

One major problem of the spring phenological timing for plants arises from the fact that ontogenetic development seems to be driven by the complete temperature regime of favourable temperatures (throughout the day), while the frost damage risk is mostly dictated by the daily minimum temperatures. As the climate changes, so probably do the patterns of temperature on a daily and longer-term basis. The most extreme environmental changes that climatic warming may cause to the boreal plants are thus mostly due to changes in the temperature patterns during the onset and progress of ontogenetic development. Some direct and indirect effects of warming (like the lengthening of the growing season) have already been observed during recent decades (e.g. Menzel and Fabian 1999).

The bud burst of trees has a major impact on energy and mass fluxes in the atmosphere. The latent heat of water vapour 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 onset 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, itself, have considerable effects on climatic warming. The bud burst and the greening of deciduous forest canopies is increasingly recognised as a critical determinant of net primary ecosystem productivity. Myneni et al. (1997) reported that the climatic warming from

1981 to 1990 showed as an average temperature increase of more than 1°C in the higher latitudes (up to 4°C in Alaska) and lengthening of the active growing season by 12±4 days. This was reported to account for a 12% increase in net photosynthetic production in latitudes above 45°N.

1.4 Modelling the impact of climate change

There has been a number of studies on the effect of global climate change on the spring phenology of boreal trees, both theoretical and empirical, during the last couple of decades. There is some divergence in the results. A number of theoretical studies utilising models to predict the timing of bud burst under changed climatic conditions, have predicted increasing frost damage to trees. Hänninen (1991) utilised the Sarvas model with theoretical parameter values, meteorological data from Jyväskylä (62°14'N 25°20'E) and a climate change scenario for doubled atmospheric CO_2 concentration (Kettunen et al. 1987) to conclude that boreal trees will most likely suffer from extensive frost damage as climate change proceeds. Kellomäki et al. (1995) got similar results for *Pinus sylvestris* L. with the same climate change scenario and a model that uses a Sarvas-type approach to predicting the onset of growth. Kramer (1994) utilised the same phenological model as Hänninen, together with a uniform climate change scenario, and a non-uniform one (Bach 1988) to evaluate the phenological timing and frost damage risk to *Fagus sylvatica* in the Netherlands and Germany. He also made a hypothetical provenance transfer by fitting the parameter values achieved by Hänninen (1991) to the central-European climate data, to confirm the results of Hänninen for boreal trees, but pointing out that the frost damage risk will not increase in the temperate growing zone. Leinonen (1996a) used the Sarvas model to describe the onset of ontogenetic activity together with hardening-dehardening model of Repo et al. (1990), finding an increase in the probability of needle frost damage to *Pinus sylvestris*. The climate change scenario he utilised was similar to that of Hänninen (1991).

Some studies suggest that the consequences of climate change may not be so alarming. Murray et al. (1989) tested the effect of elevated temperature on the bud burst timing of 15 species in the temperate zone, finding out that majority of them showed no increase in the frost damage risk under these conditions. Hänninen (1995) collected a large framework of phenological models and fitted these to experimental results at Mekrijärvi (62°47'N 30°58'E), finding that although the models predict phenological events rather well in natural conditions, they perform less satisfactorily in conditions emulating the predicted climate change. He thus concluded that the risk of frost damage may not be as large as anticipated, and that phenological data consisting of only bud burst or flowering dates may not be sufficient to evaluate the ability of the models to estimate the outcome of climate change. Repo et al. (1996) continued with the same experimental setup at Mekrijärvi, concluding that an increase in the frost damage risk to *Pinus* was possible, but that it greatly depends on how the temperature variation in winter changes.

1.5 Phenological data sets

Since the annual nature of the events makes phenological time series slow to collect, and the climatic variation between the years is large, long time series are required to cover the whole range of climatic variation. The relatively rapid change of climatic conditions may bring in new error sources to the phenological data, which will be difficult to account for. The climate change has already increased the annual average temperatures (Johannesson et al. 1995) and thus affected the timing of phenological events (Keeling et al. 1996, Myneni et al. 1997, Menzel and Fabian 1999). The current rate of climate change may be too rapid for the plants to adapt (Billington and Pelham 1991). Thus historical data turns out to be an invaluable basis for research, as it shows the phenological timing mechanisms of plants in a steady state climate.

There are some useful phenological data series consisting of several contemporaneous phenological observations over a larger geographical area. One of these was collected by the *Finska Vetenskaps-Societeten*, whose members took phenological observations of wild and garden plants, including the most common forest trees in Finland. The collection was started in the 1830s, although the data was published in print only from 1896 onwards. The data publication continued uninterrupted until the mid 1950s. The data covers most of Finland as well as a long timespan (Table 1, Fig. 2).

There are two problems associated with using the old data. First, the data-generating process (Tuomivaara et al. 1994) cannot be reproduced to examine the error sources and their effects on the data, its reliability is not known, although large discrepancies in the data are often obvious. Second, further observations cannot be obtained to improve its reliability.

The historical time series consist of a fair number of observations by a large number of observers. Unfortunately the data is somewhat sporadic, as none of the observation series cover the whole timespan of the data collection. To fully utilise the data, the observation series thus need to be combined. The overlapping of the observations each year enables estimating the reliability of the data and further improving its reliability by discarding outliers.

The large geographical area of data collection may introduce a new problem: if the climatic conditions in different observation sites vary too much, the extreme data series are observed under climatic conditions too different from the rest. In this case it would not be possible to utilise all data to construct a combined phenological time series, as adding the extreme observations would reduce the reliability of the combined time series by introducing too much disturbing variation. Large spatial deviation in the observations, especially in north-south direction introduces a large variation in timing of the events, as in the northern hemisphere the spring phenomena generally advance from south to north. On the other hand, the systematic variation in the phenological data collected over such a large area enables studying the progression of spring and some other spatial features of phenology.

1.6 Aims

The aim of this work was to analyse the spring phenological events based on the historical phenological data on several boreal tree species to improve our understanding of the effects of climate change on the timing of these events and the corresponding frost damage risk. The work was divided into five tasks:

(1) Methods for combining sporadic observation series into a single combined time series were developed, as well as methods for improving the reliability of the time series by discarding outliers.

(2) The methods were applied to seven sets of phenological observations of the flowering and bud burst of boreal trees in Finland. The geographically large area of collection of these phenological observations and the information on average timing of phenological events at each observation site was utilised to study spatial features in the phenological timing and the progress of spring over Finland.

(3) The combined time series of the seven phenological events were compared to study mutual patterns of phenological timing between species.

(4) Two models of phenology were fitted to the time series in order to compare their performance in describing the phenological events.

(5) The two phenological models were utilised under simulated climatic warming to find out why previous studies of the consequences of climate change for the boreal trees gave such different results, and to what extent the outcome of climate change for boreal forests can be estimated with these models.

2 The data sets

2.1 phenological data

The collection of phenological observations in Finland during 1896-1955 was organised by *Finska Vetenskaps-Societeten* and the results published in (Brotherus 1905, 1906, 1907, 1908, 1910, 1914*a*, 1914*b*, 1919*a*, 1919*b*, 1920, 1921*a*, 1921*b*, 1925*a*, 1925*b*, Pipping 1927*a*, 1927*b*, Reuter 1928, 1935*a*, 1935*b*, 1936, 1937, 1941, 1942, 1948, 1952, 1957). The data collection was continued during 1960-1965, but this data was sporadic, and was not included in the analysis. The observations covered most of Finland (Table 1, Fig. 2), and several phenological events were observed, but many of the observation series span only a few years.

Two sets of phenological data were used in the study. For the studies I and II, in which the data combination process was developed, a subset of the phenological observation series for the bud burst of *Betula* sp. was selected by picking all observation series collected within a circle of 180 km in radius around the city of Jyväskylä (62°14'N 25°20'E), and consisting of at least 15 observations (Fig. 2). For the rest of the studies, the observation series from all available observation locations in Finland consisting of at least 15 observations of the following phenological events were included: the flowering of *Alnus glutinosa* L., *Alnus incana* L., *Betula* sp., *Populus tremula* L. and *Pinus sylvestris*, as well as the bud burst of *Betula* sp. and *Populus tremula*. An exception to this was made in discarding three phenological observation series from the process. These were the bud burst of *Populus tremula* observed in Maarianhamina (60°06'N 19°57'E) and the bud burst of *Betula* observed in Inari (69°06'N 27°12'E) and Kemijärvi (66°43'N 27°27'E). Since all these three sites were geographically extreme and had observations of only one phenological event, including them would have made the comparison of the events in studies III and IV difficult.

During the early phases of the data collection, only one species from the *Betula* genus, namely *B. alba* L., was included. This old species description comprises the two most common species of *Betula* in Finland, *B. pendula* Roth and *B. pubescens* Ehrn. Later the two species were distinguished, and the observations were recorded as an unspecified species *Betula* sp. The historical observation series thus do not state which species the observations were taken for. As *B. pendula* is the more common species on mineral soil growing sites, and unfolds its leaves earlier than *B. pubescens*, it is probable that the observations were made of the *B. pendula* species.

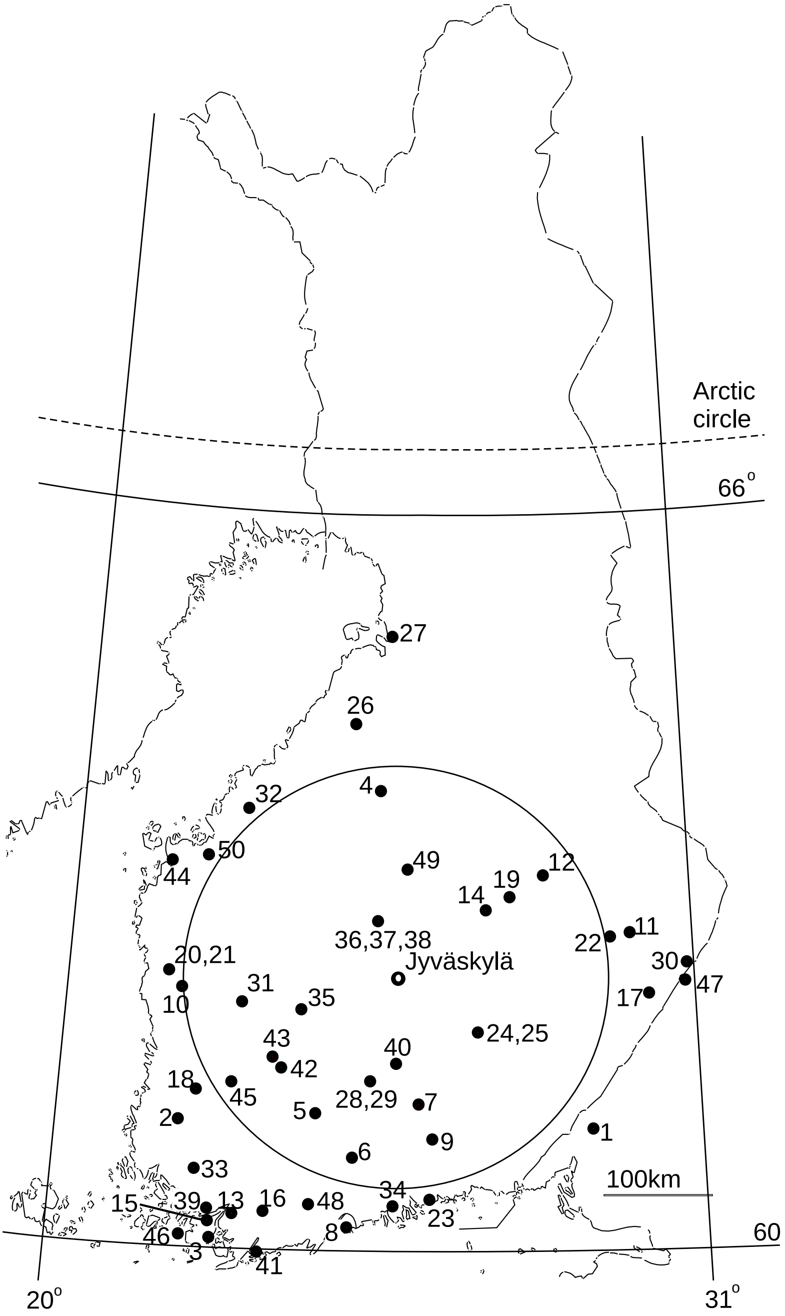


Figure 2. The sites of the phenological observations. The temperature data utilised was collected at the city of Jyväskylä. The numbers refer to Table 1.

Table 1. The geographical location and number of observations for each observation site and species in the data utilised in the study

Site number	Site	Latitude	Longitude	Elevation (m asl)	Flowering of *Alnus incana*	Flowering of *Alnus glutinosa*	Flowering of *Populus tremula*	Bud burst of *Betula* sp.	Flowering of *Betula* sp.	Bud burst of *Populus tremula*	Flowering of *Pinus sylvestris*
1	ANTREA	60´58´´	29´7´´	20	27		20	27	27	27	19
2	EURA	61´11´´	21´38´´	15				15			
3	FINBY	60´6´´	22´57´´	15		19	24	22	22	21	21
4	HAAPAJÄRVI	63´53´´	25´34´´	120	26		32	33	23	33	32
5	HATTULA	61´5´´	24´27´´	90	49		44	55	30	51	42
6	HAUSJÄRVI	60´48´´	24´50´´	70	18		17	17	18	19	16
7	HEINOLA	61´12´´	26´12´´	105	18	17	17	17	17	17	
8	HELSINKI	60´10´´	24´57´´	10		17	20			17	16
9	IITTI	60´56´´	26´24´´	0				15			
10	ISOJOKI	62´11´´	21´48´´	0	22		21	22	18	20	
11	JOENSUU	62´40´´	27´35´´	90	35		34	32	36	31	21
12	JUVANKOSKI	63´4´´	28´20´´	110	16		27	17	15		
13	KARKKU	60´23´´	22´59´´	60				20	18	22	24
14	KARTTULA	62´54´´	27´0´´	115	18			22			18
15	KIMITO	60´10´´	22´45´´	20				17		17	
16	KISKO	60´16´´	23´29´´	50	15			15		15	
17	KITEE	62´6´´	30´7´´	0	16		15	16	16		
18	KOKEMÄKI	61´15´´	22´21´´	50	20		22	20	19		15
19	KUOPIO	62´54´´	27´40´´	100	16		16	16	16	16	16
20	LAPPFJÄED	62´14´´	21´36´´	5	25		27	32			23
21	LAPPFJÄRD	62´14´´	21´36´´	5					42		
22	LIPERI	62´20´´	29´20´´	85	31	34	32	37	23	30	34
23	LOVIISA	60´27´´	26´13´´	5			23				
24	MIKKELI	61´41´´	27´15´´	90	45	15	34	57	51		
25	MIKKELI	61´41´´	27´15´´	90			18	19	19	18	
26	OULAINEN	64´16´´	24´48´´	75				15			
27	OULU	65´1´´	25´27´´	5	37		40	48	43	46	45
28	PADASJOKI	61´26´´	24´56´´	125		16	16	16	16	17	
29	PADASJOKI	61´26´´	24´56´´	85				20			
30	PÄLKJÄRVI	62´3´´	30´42´´	80	16		16	16	17	16	
31	PARKANO	62´2´´	23´1´´	110			15	15		15	
32	PEDERSÖRE	63´40´´	22´42´´	10	27		28	31	31	31	31
33	PIIKKIÖ	60´23´´	22´33´´	0				15		15	15
34	PORVOO	60´24´´	25´44´´	5	18	16	15		15		15
35	RUOVESI	61´56´´	24´3´´	100				17			
36	SAARIJÄRVI	62´42´´	25´20´´	120	32	23	26	21	31	20	
37	SAARIJÄRVI	62´42´´	25´20´´	120				38		16	17
38	SAARIJÄRVI	62´42´´	25´16´´	120				20			
39	SAUVO	60´21´´	22´35´´	5	28	20	22	24	21	24	20
40	SYSMÄ	61´27´´	25´51´´	95	16						
41	TAMMISAARI	59´58´´	23´27´´	5		28	27	28	26	27	20
42	TAMPERE	61´32´´	23´46´´	90	40		38	40	35	35	36
43	TEISKO	61´43´´	23´35´´	0				15			
44	VAASA	63´5´´	21´32´´	10	17	15					
45	VAMMALA	61´20´´	23´0´´	60	24	24	28	26	26	16	33
46	VÅRDÖ	60´15´´	22´2´´	0		19	17	17		15	
47	VÄRTSILÄ	62´10´´	30´39´´	85	40		40	40	37	39	27
48	VIHTI	60´22´´	24´26´´	55	16		16	16	16	16	
49	VIITASAARI	63´4´´	25´50´´	100	27	25	32	33	28	26	25
50	VÖRÅ	63´20´´	22´15´´	10	15			16	16	15	15
	# of observations				750	288	819	1070	768	743	596
	# of observation series				30	14	33	44	31	32	25

2.2 Temperature records

Since the city of Jyväskylä (62°14'N 25°20'E) lies quite close to centre of the data collection area (Fig. 2), a long continuous record of daily temperature observations recorded there for the period July 1883-June 1981 was obtained from the Finnish Meteorological Institute. Four temperature measurements per day were utilised, for morning, early afternoon, evening, and the daily minimum. Observation times varied somewhat during the various time periods (Table 2). Missing daily minimum temperature values were estimated for the period 1883-1901 from the morning observations using regression analysis. Gaps in the temperature data meant that the period 1912-1916 had to be omitted from the analyses involving temperature data.

Table 2. Times of temperature observations in Jyväskylä (local times)

Time period	Morning	Afternoon	Evening	Minimum
1883 - 1901	7:00	14:00	21:00	Estimated
1902 - 1926	7:00	14:00	21:00	Measured
1927 - 1946	7:00	15:00	21:00	Measured
1947 - 1952	8:00	14:00	20:00	Measured
1953 - 1981	6:00	12:00	18:00	Measured

3 The data combination methods

3.1 Straight averaging

There are several ways to combine sporadic phenological observation series into a single combined time series, covered in study I. The most obvious one is to calculate the annual averages of the observations. The method would work well provided that A) the observations were collected from an area where there are no systematic differences in the level of observations, or B) all the phenological observation series covered the same (i.e. the whole) time span. If neither of these applies, there is a risk of the combined time series becoming severely biased. The observations may be concentrated into some extreme parts of the observation area in some years, with a similar deviation from the general level, and the average for that year would thus be biased. For example, if the set of observations for one year were towards the north of the observation area, the average would be delayed compared to the “correct” level (in the northern hemisphere).

3.2 Using a reference observation series

To avoid such errors the observation series can be brought to the same overall level before combining them into one time series. This can be done utilising one long, reliable observation series as a reference for the general level of observations. The series should preferably be located near the centre of the observation area. This is the core of the second method. Each observation series is brought to the level of the reference series by calculating the average deviation of the specific observation series from the reference series, i.e.

$$E_j = \frac{\sum_i \left(x_{ij} - x_{ir}\right)}{n_j} \tag{1}$$

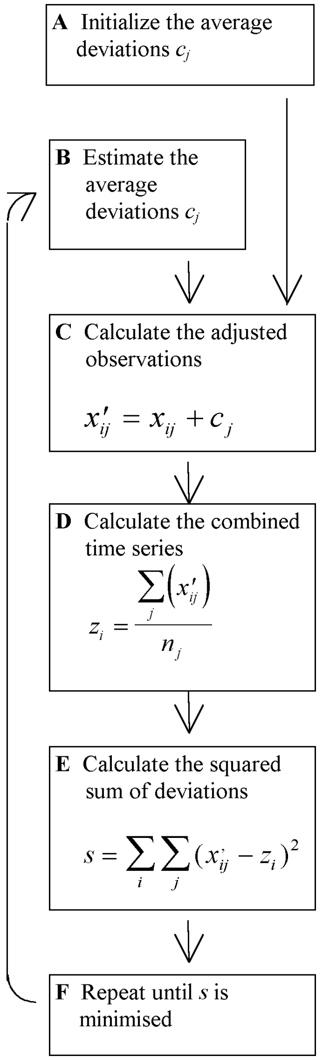
where b_j is the average deviation of the observation series j from the reference series, x_{ij} the observation in series j in year i, x_{ir} the observation in year i in reference series r, and n_j the number of observations in the series j. This difference is then subtracted from each observation in the specific series before calculating the combined time series. The problem with this method is that such a series does not necessarily exist in the data.

3.3 Iterative method

If one long, reliable observation series is not available, the combination becomes more problematic. The third method overcomes this problem: instead of using one observation series, it uses the combined time series itself as a reference. As the latter depends on the levelling process, the combination method needs to be iterative. For each step of the iteration, a temporary combined time series is calculated as the annual average of the levelled observations. The observations are brought to the level of the temporary combined time series, and the process is repeated until an optimal set of deviation constants is found. The method is quite similar to the least-squares method of parameter fitting, except that the target function (i.e. the combined time series) is changing. Despite this, an optimisation algorithm makes the task easy.

The method is best expressed by a flow chart (Fig. 3). First, the average deviations of each observation series, c_j, were initialised to zero (A). The initial adjusted observations, x'_{ij}, were thus equal to the original observations, x_{ij} (C). The values of the combined time series, z_i, were calculated as an annual average of adjusted observations (D), and the fit of the adjusted observation series to the combined time series was estimated by calculating the sum of squared deviations (E). The minimising algorithm then chose a new set of average deviations, c_j, in an attempt to minimise the squared sum of deviations (B). When the observations were re-adjusted, the fit of the observation series to the combined time series was no longer optimal, so the process choosing average deviations, adjusting the observations and calculating the combined time series was repeated until a set of average deviations c_j which minimises the squared deviation was found.

Figure 3. The flow chart of the data combination process. The symbols are: x_{ij} the original and the adjusted observation at site j in year i, c_j the average deviation of observations at site j from the combined time series, t_i the spatially averaged moment of phenological event in year i, and n_j the number of observations (sites) in year i.



3.4 The mixed model of randomised block effects

The problem of adjusting the observations to a common average (i.e. the combined time series) is rather similar to the statistical method of the linear mixed model of a randomised block design. In this approach each observation in the original observation series can be written as:

$$x_{ij} = P + \tau_i + d_j + \varepsilon_{ij} \qquad (2)$$

where x_{ij} is the observation in the series j in year i, m is constant (average level of all observations), τ_i the fixed effect of year i, d_j the random block effect of observation series j, and e_{ij} the random residual error. The random terms of the model are by assumption normally distributed with a zero mean. As the data are unbalanced and contain empty cells, the design cannot be solved by the ordinary least squares method, statistical packages being required to estimate the parameter values using the method of maximum likelihood. Once the parameters have been determined, the combined time series can be totalled from the constant m and the fixed year effects τ_i.

The last two methods result in combined time series that are almost identical both in annual values and annual variation. In studies III - V the combined phenological time series were constructed utilising the iterative method.

4 Removing outliers

No data is free of errors, the sources of them being numerous. Mistakes are made in the recording process (by the observers), or misprints occur, just to name two. With historical data, such as the phenological data utilised in this study, the problem of mistakes in the data is even more troublesome, as the data-generating process cannot be reproduced to assess the error sources (Tuomivaara et al. 1994), and more data cannot be produced to improve the data reliability.

To overcome these problems, two methods of data reliability estimation and improvement were developed in the study II. The first method was based on the initial assumption that the accuracy of data collection varied between observers. On this basis the reliability of each whole observation series was estimated, and observation series with larger variation in the relation to the combined time series were discarded until a global minimum in the mean of annual confidence intervals of the combined time series was achieved.

The second method assumed that the errors causing the outliers were rather random than observer-specific. After the data was adjusted to a common level (previous chapter), each observation was examined by comparing it to the other observations of the same year. The discordancy test for extreme observations according to King (1953) was utilised to detect outliers. This test calculates a test statistic, T_i, to determine the reliability of each observation:

$$T_i = \max\left[\frac{x_{(i,n)} - x_{(i,n-1)}}{x_{(i,n)} - x_{(i,1)}}, \frac{x_{(i,2)} - x_{(i,1)}}{x_{(i,n)} - x_{(i,1)}}\right] \tag{3}$$

where the adjusted observations in year i, $(x_{(i,1)},\ldots,x_{(i,n)})$ are in ascending order. The test compares the excess of the extreme observations from the closest observation to the total range of annual observations. The extreme observation is considered an outlier if the test statistic exceeds a critical value, as tabulated in Barnett and Lewis (1978). If this was the case, the process was repeated until no outliers were detected. After discarding the outliers, the data combining process was repeated.

The latter method proved to be far more efficient than the former with the original data set of *Betula* sp. collected from a circle around the city of Jyväskylä as removing only 10 outliers reduced the average annual confidence intervals of the data twice as much as removing two observation series consisting of 39 observations. This also indicated that the initial assumption behind the first method, that there is difference in the observation reliability between observers, was unjustified.

Incidentally, the number of outlying observations seemed to be relatively constant: when the method was applied to all phenological observation series in the larger geographical area, the number of outliers remained fairly steady, from 10 to 15, while the number of observations in the data sets varied from 288 to 1070 and the number of observation series from 14 to 44 (Table 1). There was a fair number of observation series less than 20 years long, while the longest observation series for bud burst of *Betula*, collected by Mrs. Alma Nordenstreng in Mikkeli, spanned 57 years.

5 Comparison of the phenological time series

5.1 Spatial comparison

The combination process was based on the hypothesis that the variation in the timing of phenological events at different observation sites can be divided into two additive components, the annual and site-specific effect (Eq. 2). The annual component varies from year to year, but is the same within the year for all observation sites. The site-specific effect is unique to each observation site, but remains the same from year to year. The annual effect was considered to be due to the large-scale climatic conditions, and thus to be the same for all sites. The site-specific effect was considered to be due to the climatic variation between the sites (latitude, longitude, elevation and microclimatic conditions), as well as the adaptation and acclimation of the plants to the site. The climatic conditions of the site were considered to remain unchanged during the observation period, as well as the acclimation of the plants, i.e. their response to the climatic conditions.[1]

To analyse the dependence of the site-specific component on the spatial variables, linear regression models between the average deviations c_j and spatial features (latitude, longitude, elevation) were fitted to the data in study III. No relationship was found between the average deviations, and the longitude or elevation ($|r^2|$ of the regression models was less than 0.4). The regressions between the deviations and latitude were similar for both flowering and bud burst of all the species, even though the change in the timing of the events as a function of latitude was somewhat larger (Fig. 4) for the events occurring early in the spring (the flowering of *Alnus glutinosa*, *Alnus incana* and *Populus*

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[1] The underlying assumptions of data combination methods were poorly formulated in study III

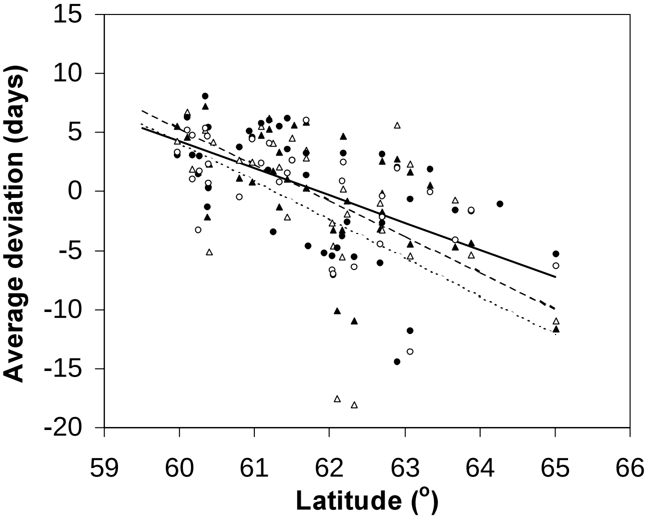

Figure 4. The deviation of average date of phenological events at a specific site and of different species as a function of latitude. All observations of flowering and bud burst of *Betula sp.* (black triangles and circles respectively) and *Populus tremula* (white triangles and circles respectively) are presented. The majority of regressions were similar (solid line), with flowering of *Populus tremula* (broken line) and *Alnus incana* (dotted line) deviating most.

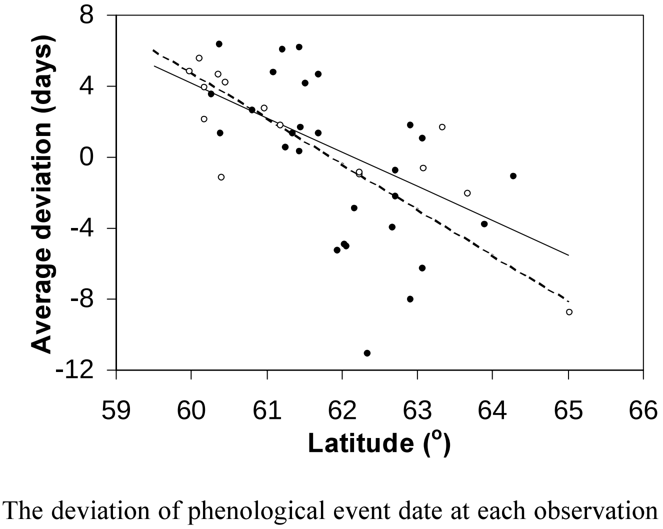

Figure 5. The deviation of phenological event date at each observation site from that of the combined time series, averaged over years and species, as a function of latitude. The white circles show sites with elevation of less than 20m ASL, the black ones those above. The lines show the linear regression between the average deviations and the latitude (solid and dotted respectively).

tremula). The average deviations between the observation sites varied at most from -20 to 10 days for the flowering of *Populus tremula*, while they were typically from -11 to 8 days. The site-specific deviations were regular between species, which implies that the hypothesis that the observation site location causes most of the variation in timing between the observation series was well founded.

The altitude can be utilised in examining the effect of maritime climate. The observations were divided into two groups, those that are £ 20 metres ASL, and those that are above. The lower sites lie on the southern or western cost of Finland, while the rest are inland sites. Since there are slight climatic differences between the coastal and inland areas of Finland, the two groups of observation sites were separated and compared to find the effect of proximity to the sea on phenological timing. The average timing of events, represented by the average deviations did not differ. However, when a regression model predicting the average deviations with latitude was fitted to the two groups separately, some difference emerged. In the inland group, the effect of latitude on the average deviations was more[2] pronounced than that for the rest. In other words, the effect of the geographical location in the north-south direction was more profound for the inland group of observation sites. This agreed well with the notion that the proximity of the sea tends to even out climatic variations, so that on the south coast the spring events took place later than at the inland sites at similar latitudes, and in the north the phenological events took place somewhat earlier than at the inland sites (Fig. 5). The overall effect of the proximity of the sea was minor, but the difference in the regression model coefficients was statistically significant (p=0.026).

All the combined phenological time series showed a quite similar annual pattern of response to the weather, when compared to the bud burst of *Betula* sp. The time deviation for events that took place later was about the same from year to year (Fig. 6). The events that occurred earlier than bud burst of *Betula*, i.e. the flowering of *Populus tremula* and the two species of *Alnus*, showed a larger variation in timing. The reason for this is probably that the species that flower early in the spring require only brief episodes of favourable environmental conditions for the event to take place, so that these events are driven by environmental factors that have little in common with the weather that drives the timing of events occurring later in spring.

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[2] Note that there is a misprint in study III (p.242, bottom left) here

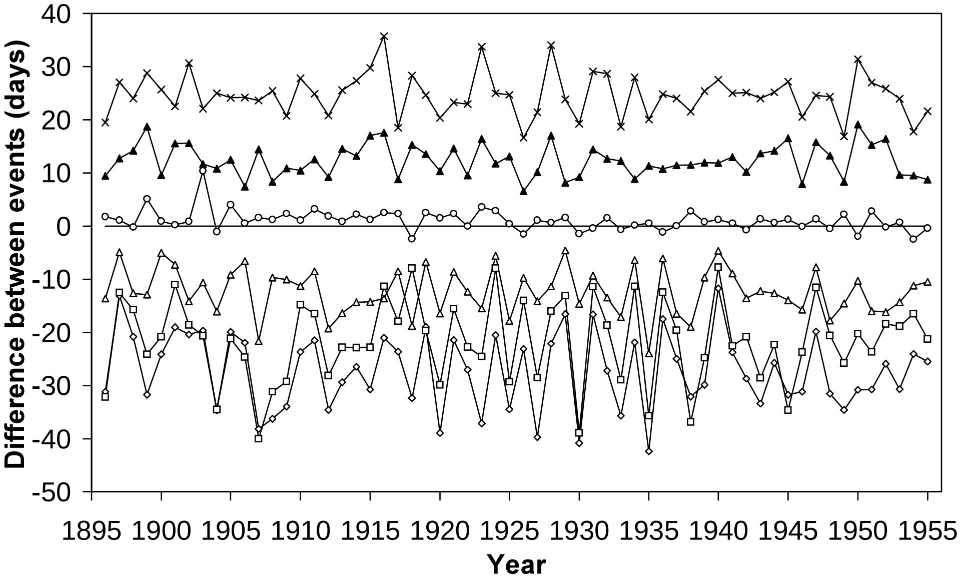
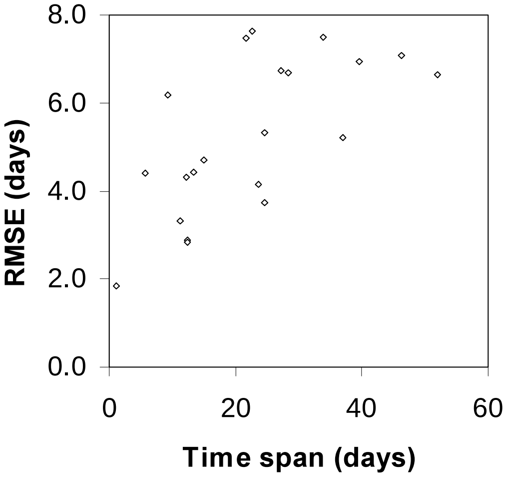


Figure 6. The annual average deviation of the phenological events from the bud burst of *Betula sp.* (shown as the zero-level). The events are: flowering of *Alnus glutinosa*, *Alnus incana*, *Populus tremula, Betula sp.* and *Pinus sylvestris* (white diamonds, white squares, white triangles, white circles and crosses respectively), and bud burst of *Populus tremula* (black triangles).

Figure 7. The root mean square error (RMSE) of the regression model between two phenological time series, as a function of the average temporal distance between the two. Note that the lower limit of RMSE increases with the time difference.



5.2 Comparison between phenological events

The range of the average occurrence of the phenological events studied was almost two months, from the flowering of the two species of *Alnus* in late April to the flowering of *Pinus sylvestris* in mid-June. The time gap between the average date of phenological events varied from 1.1 (bud burst and flowering of *Betula sp.*) to 52 days (flowering of *Alnus incana* and flowering of *Pinus sylvestris)* (Table 3 in study IV). The time span *of* the phenological events of the combined time series between the years remained fairly constant for all species and phenomena in this study (Fig 3 in study IV).

Linear regression models were fitted between the phenological time series in order to determine the predictability of one series with another. The fit of the regression models was estimated by root mean square error (RMSE) between the observed and predicted dates.

$$\mathrm{RMSE} = \sqrt{\frac{\sum_i (z_i - \breve{z}_i)^2}{n}} \tag{9}$$

where z_i is the value of the combined time series in year *i*, $\check{z}_i$ the model predicted moment of phenological event in year i, and *n* the number of years. The RMSEs of the regression models were relatively uniform in magnitude, but showed a slight tendency to increase with the increasing time span between the average date of the events. This seems natural, as the further the occurrences of the events are apart, the less similar are the climatic conditions prevailing the events. The two series of *Alnus* flowering had the largest RMSEs among the regression models when forecasting other phenological events. These two phenological phenomena take place quite early in spring, and thus are probably driven by less similar climatic conditions than the rest (Fig. 7).

The average temporal deviation of the flowering and bud burst of *Betula* sp. was 1.1 days, and the RMSEs of the regression models between the two about 1.9 days. As the correlation between the events was high (0.971), the RMSEs of these two regression models was considered to be lergely due to the inaccuracies in the phenological data, and the figure was utilised as a rough estimate of its accuracy (Fig. 10).

6 Phenological models

6.1. Definitions of dormancy

There are various definitions of the concept of dormancy in the literature. In general, buds are considered to be dormant, when no ontogenetic development in them takes place. This may be due to the internal state of the bud, some other organs of the plant keeping buds dormant, or to external conditions being unfavourable to growth. The dormancy of boreal plants starts in the autumn, and lasts until some point in time in late winter or spring.

Vegis (1964) and Wareing (1969) considered that dormancy refers to the *internal* state of the bud, i.e. a state when no ontogenetic development can take place even if the environmental conditions are favourable. Sarvas (1974) chose the same approach, as he divided the progression from growth cessation in autumn to bud burst in spring into three phases: autumn dormancy, during which the buds remain dormant despite environmental conditions, winter dormancy, during which the buds gradually achieve an ability to develop ontogenetically, and finally an active period (which, according to Sarvas, continues until the next growth cessation), during which ontogenetic development rushes, towards bud burst (and some growth events continue even after that), while the environmental conditions are favourable.

Samish (1954), Romberger (1963, p.75) and Lang et al. (1987) chose another approach, defining dormancy as a state of the bud during which no visible growth takes place, independent of the cause. Hänninen (1990) utilised the same approach in his definition of the basic concepts of bud dormancy, and it was also used by Kramer (1994). This definition means that buds are considered dormant even if they have acquired an ability to develop ontogenetically, as long as environmental conditions are unfavourable.

The definition above is somewhat problematic. The concept is a state of bud that is solely the result of environmental conditions. A change in weather conditions will change the state of the bud, even though its internal state remains the same. Another shortcoming of this definition is that dormancy is considered to end at bud burst, which means that no visible changes in the bud should occur before that. This is not so, as bud burst is the result of a complicated process of cell divisions and growth, which can also been visually observed at least several days before the bud burst itself occurs (e.g. Sarvas 1974).

In my work I have chosen to use the internal state of the bud development as the definition of dormancy, i.e. buds are dormant when no ontogenetic development takes place even though the environmental conditions are favourable, but dormancy is released when the ability for ontogenetic development is attained.

6.2 A few words about terminology

Because of the different types of dormancy, and their somewhat inaccurate definitions, there seems to be no consensus on the terminology of the phases of phenological development, even though the phases themselves are quite similar in the majority of the phenological models presented in the literature.

Sarvas (1974) calls the phase of dormancy caused by inhibition within the buds themselves *autumn dormancy* or *dormancy I*, while many others use the term *dormancy* alone. There is less consensus on the name of the process leading to the release of dormancy. Sarvas calls this the *progress of dormancy*, while many others (like Cannell and Smith 1983, Hänninen 1990, 1991 and Kramer 1994, 1995, 1996) use the term *chilling*.

Dormancy due to the internal inhibition of the plant ends at a point event usually called *rest break* or *dormancy release* (although the latter may also refer to the bud burst), after which the trees are hypothesised to be able to develop towards bud burst in spring. The trees have now reached a phase which Sarvas (1974) calls *winter dormancy* or *dormancy II*. During this phase the trees react to favourable temperatures according to an empirically determined sigmoidal function (Fig. 8). Once the winter dormancy is released, the *active period* leading to bud burst is achieved (Sarvas 1972). The dependence of development during the active period on the ambient temperature is described by another sigmoidal function. It should be noted, as Sarvas himself did (1974, p. 42), that these two sigmoidal functions are quite similar at lower temperatures (Fig. 8), and it is possible that they are actually identical. Since there are few data points in the higher temperature regime, the difference between these rate functions is somewhat speculative.

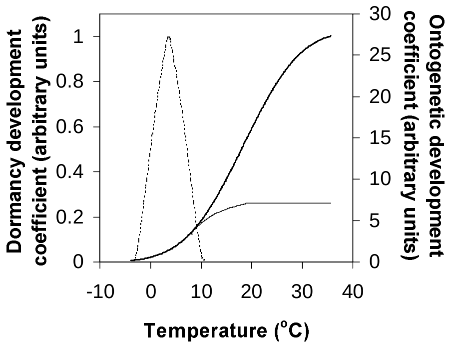


Figure 8. Rate of dormancy development (dotted line, scale to the left), rate of *dormancy II development* (Sarvas 1974, thin solid line, scale to the right) and rate of ontogenetic development (thick solid line, scale to the right) as a function of temperature.

Most implications of Sarvas’ models (Hänninen 1990, 1991, 1995, Kramer 1994, 1995, 1996, Kellomäki et al. 1995, Leinonen 1996a, Chuine et al. 1998, 1999, Häkkinen et al. 1998, Fabian and Menzel 1999, Menzel 1999) do not distinguish between the winter dormancy and the active period, grouping these together into a single phase and using the dependence of the active period for the whole phase. The names used for this phase in these studies are often different from those Sarvas (1974) used. Hänninen (1990) and Kramer (1994, 1995, 1996) call it *quiescence*, while Hänninen (1995) uses the term *state of ontogenetic development*. They both use the term *forcing* for the process driving the development forward. Both have also rejected the term Sarvas used, i.e. *active period*, which is easy to understand, as it also refers to the active growing and photosynthetic period during the summer.

In this study I have used the terms *dormancy development* and *ontogenetic development*, as well as *rate of* dormancy/ontogenetic development to describe the mechanisms present in the phenological models, and *stage of* dormancy/ontogenetic development for the state of development at a given time. The dormancy development, when expressed in function form, is temperature-dependent, like an on/off switch mechanism driven by the light climate. Whatever the mechanism, the term *dormancy* refers to the state of inhibited growth, and in some places the term *chilling requirement* is used to refer to the temperature-dependent part of dormancy. The term *dormancy release* means the event when the buds achieve an internal ability to develop ontogenetically.

6.3 The chilling triggered model

Two models of spring phenology were utilised in the studies IV and V. The first was formulated by Sarvas (1972, 1974). This model describes a chilling requirement that must be met before ontogenetic development could commence, regardless of the ambient conditions. Dormancy is released when the chilling requirement is met. Since no other requirement is present, the stage of dormancy in this model is equal to the state of chilling. The stage of dormancy is assumed to develop cumulatively, as a function of temperature, from a fixed date each year, so that the stage of dormancy, S_D, at time t was:

$$S_D(t) = \int_{A_{crit}}^{t} I_D(t)\,\mathrm{d}t \qquad (4)$$

The rate of dormancy development, f_D, was determined empirically as a function of chilling temperatures, and tabulated by Sarvas (1974). Dormancy develops when the air temperature is between -3.5 and 10.2°C, and attains its fastest rate at 3.5°C (Fig. 8). The autumn starting date for dormancy, A_{crit}, was determined by fitting the model to the phenological time series and temperature data.

Once S_{D} reaches a threshold value, D_{crit}, dormancy is released, and ontogenetic development of leaf and flower buds can proceed when the temperatures are favourable. The stage of ontogenetic development, S_{O}, at time t is described by:

$$S_O = \int_{t_{dr}}^{t} I_O(W)\mathrm{d}W \tag{5}$$

where f_{O} is the rate of ontogenetic development as a function of temperature, also empirically determined and tabulated by Sarvas (1972) and depicted in Fig. 8. The starting date of development, t_{dr}, corresponds to the dormancy release, and varies from year to year. Bud burst occurs when S_O exceeds a threshold value O_{crit} (Fig. 9).

6.4 The light climate triggered model

The evidence showing that the dormancy is released solely by the chilling requirement is far from solid. There is in fact evidence that increasing day length has to do with the onset of ontogenetic development (Myking and Heide 1995, Olsen et al. 1997, Partanen et al. 1998) for some boreal tree species.

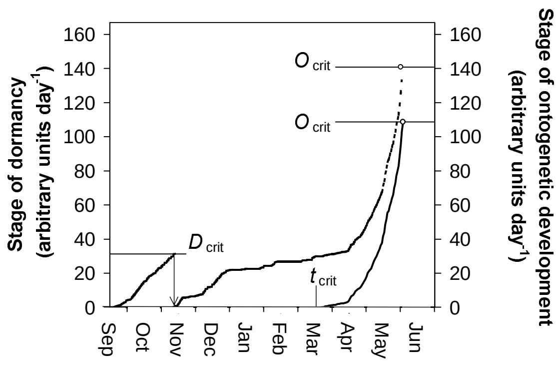


Figure 9. A comparison between the dormancy triggered model (dotted line) and the light climate triggered model (solid line) using 1955 as sample year. Dormancy accumulates until November, when the critical threshold value, D_{crit}, is reached. This triggers ontogenetic development, which proceeds somewhat during a warm spell in December, starts again in April, and finally reaches the critical threshold value for bud burst, O_{crit}, in May. Ontogenetic development according to the light climate model starts at the threshold date, t_{crit}, and also reaches the threshold value for bud burst, O^*_{crit}, in May.

Thus in this study another model, utilising the day length or some other annual feature of the light climate as the signal triggering the ontogenetic development was used. It should be noted that in the boreal climate zone the winter is long and cold, and the chilling requirement is usually met early in the winter (Sarvas 1974, Hanninen 1990, Heide 1993a, Leinonen 1996a). Assuming that the ontogenetic development is triggered by a signal from the light climate in spring does not deny the existence of the chilling requirement, but rather suggests that the chilling is a necessary, but not a sufficient condition for ontogenetic development to commence.

The second model, referred to as the *light climate triggered model*, is thus a modification of Sarvas' model. In addition to chilling requirement, a regulatory mechanism related to the light conditions is assumed to hinder ontogenetic development until spring. This mechanism is operationalised as calendar date, i.e. ontogenetic development in the model is assumed to begin at a constant, parametrised date, t_{crit}. The stage of ontogenetic development, S^{*}_{O}, is once again described with a temperature sum type model, with the rate, f_O, identical to that in the dormancy model (Fig. 8):

$$S_O^*(t) = \int_{t_{crit}}^{t} f_O(t)\mathrm{dt} \tag{6}$$

Bud burst takes place once the stage of ontogenetic development reaches a hreshold value O^{*}_{crit} (Fig. 9).

7 Model evaluation

7.1 Parameter estimation

The two phenological models (chapters 6.3 and 6.4) were fitted to all 7 combined time series (chapter 2. 1) by finding a set of model parameter values that minimise the root mean square error (RMSE) between the observed and predicted dates.

$$\mathrm{RMSE} = \sqrt{\frac{\sum_i (z_i - \breve{z}_i)^2}{n}} \tag{10}$$

where z_i is the value of the combined time series in year i, $\breve{z}_i$ the moment of a phenological event in year i predicted by the model, and n the number of years. An iterative optimisation algorithm (Hooke and Jeeves 1961) was utilised. The date parameters (starting date for dormancy and ontogenetic development) were constrained to between 1 July and 30 June, while no limits for the threshold parameters were set. Despite the loose constraints, all the parameter values of both models attained realistic values (Table 3). The timing of the release of dormancy of *Pinus sylvestris* was modelled to take place in mid-March (Fig. 12), which alone seems unrealistically late in the boreal growing zone.

In this study the value of the starting date of dormancy, A_{crit}, was not fixed to any specific phenological event. In previous studies the onset of dormancy has been linked to the first autumn frost (Landsberg 1974), negative accumulation of chilling temperatures (Richardson et al. 1974), defoliation (Walser et al 1981), fixed date (Cannell and Smith 1983, Hänninen 1990, 1991, 1995, Kramer 1994, Chuine et al. 1998, 1999) or to the growth cessation driven by temperature and photoperiod (Koski and Sievänen 1985).

The parameter value was found in the same iteration process as the rest of the model parameter values. This resulted in rather different parameter values for different species, and even a different timing of onset of flower and leaf bud dormancy of *Populus tremula*. This may seem a bit strange, but Romberger (1963 and the references therein) claims that "not all parts of plants are dormant at the same time". In any case, the precise value of the parameter A_{crit} has little effect on the results, so that I found the "optimised" value more feasible than choosing an arbitrary one.

7.2 Comparison of the two models

The chilling triggered model gave relatively accurate estimates of the bud burst dates of leaves of *Populus tremula* and *Betula* sp., but did not manage so well for the flowering events, whether they took place in early spring (*Populus tremula* and the two species of *Alnus*), or in early summer (*Pinus sylvestris*) (Fig. 10). The light climate triggered model, on the other hand, estimated the dates of most phenological events with an RMSE only slightly larger than that of a regression model between flowering and bud burst of *Betula* (Fig. 10). Since the latter was considered to give an estimate of the accuracy of the phenological data, it was concluded that there is not much room for improvement in the predictive capability of the model with the phenological data utilised. The higher RMSE of the light climate triggered model for predicting the flowering of the early species may partly be due to the lower accuracy of the phenological data, indicated by the higher pooled standard deviation (Table 3).

Häkkinen's (1999) recent study using a leave-one-out cross-validation method (Efron and Tibshirani 1993) with the smaller data set of *Betula* leaf bud burst (Fig. 2) showed that the prediction error for both phenological models

Table 3. Model parameter values and root mean square error of the model predictions

			Chilling triggered model				Light climate triggered model		
	Average date of occurrence	Pooled standard deviation	Starting date	Dormancy release threshold	Event threshold	RMSE	Starting date	Event threshold	RMSE
			A_{crit}	D_{crit}	O_{crit}		t_{crit}	O^*_{crit}	
Flowering of *Alnus incana*	22 Apr	6.3	18 Jul	29.768	76.680	10.070	11 Jan	38.895	4.112
Flowering of *Alnus glutinosa*	28 Apr	6.5	1 Aug	26.709	90.212	9.060	6 Jan	49.362	6.028
Flowering of *Populus tremula*	7 May	5.9	19 Sep	26.759	95.570	6.029	17 Feb	68.036	2.927
Bud burst of *Betula sp.*	19 May	4.1	10 Sep	33.322	140.743	3.859	10 Apr	100.767	2.485
Flowering of *Betula sp.*	20 May	4.2	10 Sep	33.347	144.702	3.769	1 Apr	113.598	2.603
Bud burst of *Populus tremula*	1 Jun	3.9	31 Aug	34.595	210.546	3.366	15 Apr	170.930	1.994
Flowering of *Pinus sylvestris*	13 Jun	4.7	23 Sep	47.154	206.595	9.579	10 Mar	279.135	2.215

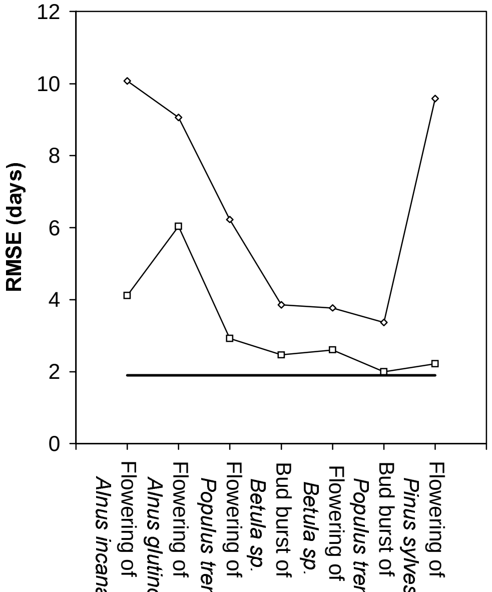


Figure 10. The root mean square error (RMSE) of the two phenological models with different phenological phenomena. Diamonds indicate the chilling triggered model, and squares the light climate triggered model. The solid line shows the regression model RMSE between flowering and bud burst of *Betula* sp., which was considered to be an estimate of the phenological data accuracy.

is largely due to the inaccuracies in the data utilised. The method enables the efficient use of a data set that the model is fitted with, to estimate the goodness of fit and data dependence of a model from the data set. In a case when the data is rare and not easily reproduced, as is often the case with phenological data, this is most useful. The data needs not to be split into two independent groups, which would drastically reduce the data size. The result he achieved should also apply to the data sets in this study, as the larger data sets show less internal deviation on an annual basis, and the fit of the models to the larger data sets is better.

7.3 Comparison of the results to other studies

The parameter values achieved with the two models are in good agreement with results from some other studies, and very different than those from still others. Table 4 presents a comparison with some of these.

Sarvas (1974) measured the dormancy release threshold for the flowering of *Alnus incana*, *Populus tremula* and *Betula pubescens*. These values, especially that of *P. tremula*, are in good agreement with those of the chilling triggered model for related species. Leinonen (1996a) estimated the dormancy release threshold value of *Pinus sylvestris* as 28, and Hänninen (1990) used values from 5 to 50 in his theoretical work. All the values in this study (Table 3) fall within those limits. The bud burst threshold values found by Sarvas (1972) are slightly smaller than the comparative values in this study, but still of the same magnitude (Table 4). Hänninen (1990) used values from 50 to 200 in his theoretical work.

In the temperate growing zone Kramer (1994) utilised Sarvas' model (he calls it the "sequential model") to predict the timing of flowering of *Fagus sylvatica* L. His results are relatively close to those in this study, taking into account that in a warmer temperature zone the thresholds should be higher (Table 4, in parenthesis). However, he pointed out that the fit of the model to the data was not satisfactory with those parameter values. He therefore re-estimated them with looser limits, and got new values, which were not quite as realistic. In another paper (1995) he estimated the parameters for bud burst of *Betula pubescens* and *Pinus sylvestris*. Once again, the dormancy release threshold values are large, and bud burst threshold values extremely small. Chuine et al. (1998) fitted the Sarvas' model (called "sequential") and a thermal time model ("spring warming") into data including *Alnus glutinosa*. The parameter values of the former model are quite close to those in this study (Table 4).

Table 4. A comparison between parameter values of phenological models. See text for the description of the models. D_{crit} is the dormancy release threshold, and O_{crit} the bud burst/ flowering threshold, independent of the symbols used in the original publications.

	Linkosalo			Sarvas[1]		Chuine et al.			Kramer		
	Chilling triggered model		Light climate triggered model			Sequential		Spring warming	Sequential		Thermal time
	D_{crit}	O_{crit}	O_{crit}	D_{crit}	O_{crit}	D_{crit}	O_{crit}	O_{crit}	D_{crit}	O_{crit}	O_{crit}
Flowering of *Alnus incana*	29.8	76.7	38.9	17.5	32						
Flowering of *Alnus glutinosa*	26.7	90.2	49.3			26.2	141.9	344.4			
Flowering of *Populus tremula*	26.8	95.6	68.0	26.3							
Flowering of *Betula* sp.	33.3	144.7	113.6								
Flowering of *Betula pubescens*				17.5	95						
Bud burst of *Betula* sp.	33.3	140.7	100.8								
Bud burst of *Betula pubescens*									99.4	5.4	
Flowering of *Pinus sylvestris*	47.2	206.6	279.1		195				85.3	2.4	
Flowering of *Facus sylvatica*									115.6 (57.4)	2.0 (262.5)	(206.4)

[1] Note that the threshold values presented are the originals divided by 24, as Sarvas calculated the units on an hourly, not a daily basis.

The results of this study compared to those in the literature are rather different for the model evaluation. Most applications, especially those in the temperate zone, find the models based on Sarvas' principles perform better than those utilising a signal from the light climate to start ontogenetic development from. There is no obvious best model, but different models perform best with different species, and in some cases, e.g. *A. glutinosa* in Chuine et al. (1999), a model utilising day length performs as well as some chilling-based ones. Some studies utilising the data from the temperate zone also report considerable problems in parameter estimation (Kramer 1994, 1995, Chuine et al. 1998). Such problems were not encountered in this study.

8 Simulation of the impact of climate change on phenology

8.1 The climate warming scenario

A strengthening of the greenhouse effect has already started to take effect on the climate in Finland (Heino 1994). To predict the climatic outcome of this change, the Finnish Research Programme on Climate Change (SILMU) (Carter et al. 1996) calculated scenarios of climatic warming, considering the uncertainties in both future greenhouse gas emissions and the climatic responses to these emissions. Of all the scenarios, the central one (assuming both average emissions of greenhouse gases in the future and average sensitivity of the climate to them) was utilised in this study to investigate the behaviour of the two phenological models under climatic warming. The scenario consists of a seasonal pattern of warming, greater in the winter half year, with temperature increases by ratios relative to the annual mean increase of 1.41 (December to February), 0.94 (March to May), 0.71 (June to August) and 0.94 (September to November).

Climatic warming was simulated by increasing the daily air temperature observations (four per day) at Jyväskylä throughout the 92-year temperature series according to the scenario pattern of temperature change for 0.5°C increments of mean annual temperature increase up to +10°C. All other features of the 92-year time series were assumed to remain unchanged (e.g. inter-annual, daily and diurnal temperature variability). It should also be noted that a mean annual warming of 10°C is well in excess of the warming described in the SILMU central scenario (about 4.7°C by 2100). The justification for the extrapolation in this study is to observe the behaviour of the two phenological models under extreme warming conditions.

In study V, another scenario of uniform climatic warming was also utilised. Since this is less realistic climatologically, and the results were rather similar to those with a more appropiate climatic warming scenario only the latter scenario was utilised in this study.

8.2 Utilisation of the phenological models

The parameter values achieved when fitting the two phenological models to the phenological data series were utilised to determine the effects of climate change (Table 3). The parameter values were fixed when the models were used with the changed climate data to predict the change in the timing of leaf bud burst or flowering. Both models were applied to the 20 different levels of mean warming (chapter 8.1). The average change in bud burst date was calculated by subtracting the average date of bud burst under a given warming scenario from the average date of bud burst achieved with the same model utilising unmodified climatic data.

The frost damage risk was estimated as the propability of damaging temperatures (i.e. below a spesific threshold) to occur between the phenological event and 30 June. Few studies of the frost damage threshold temperatures of broad-leaved boreal trees at the bud burst are available. However, in a study of an extensive case of frost damage in eastern Canada and the northeast U.S. in 1957, Braathe (1995) found the temperature was -5°C, and later verified this figure in a laboratory study (1996). This value seemed appropriate, as a minimum temperature of -4.1°C was recorded for *Betula* from the unmodified temperature records after the observed bud burst. The same threshold value was used for the bud burst of *Populus*, and a threshold of -8°C was utilised for the flowering of *Alnus*, *Populus* and *Betula* corresponding to results for the frost damage threshold of *Alnus glutinosa* and *Alnus incana* (Juhani Häggman, personal communication). A threshold of -3.5°C was utilised for the flowering of *Pinus sylvestris* (Repo 1993).

8.3 Timing of bud burst

The dormancy triggered model showed an advancement in the average timing of phenological events which was larger the earlier the event took place in natural conditions (Fig. 11). For all the events, the timing was advanced linearly as a function of average temperature increase up to a warming of 6°C, at which level the advancement ceased. With warming beyond that, the advancement of timing of early events was even reversed, due to the increasing delay in the dormancy release (Fig. 12). The advancement in timing for warming of 0 to 6°C varied from 6.3 days per degree of warming for bud burst of *Populus* to 14.9 for *Alnus incana* (Fig. 11).

The advancement of timing was less pronounced when the light climate triggered model was utilised. It also continued linearly with the increasing average temperature increase. The change in timing was from 2.8 days per degree of warming for bud burst of *Populus* to 11.1 for *Alnus incana* (Fig. 13).

8.4 Frost damage risk

Basically, the phenological events could be divided into three groups: the early flowerings (*Alnus glutinosa, Alnus incana* and *Populus tremula*), the bud bursts (*Betula* sp. and *Polulus tremula*, and the flowering of *Betula* sp. also being in this group) and the late flowerings (*Pinus sylvestris).*

The frost damage risk predictions according to two models varied radically for the bud burst and flowering of *Betula*, as well as bud burst of *Populus*. The frost damage risk with these events was hardly increased when climatic warming commenced according to the light climate triggered model (Fig. 14 D, E and F), while the chilling triggered model forecast a severe increase in damage risk, even at a average temperature increase that will probably be attained within a century (Fig. 14 D, E, and F). The risks also achieved high values of up to 54% for the bud burst of *Betula* sp. at an average temperature increase of 7°C, which may be reached within a century or two, suggesting that

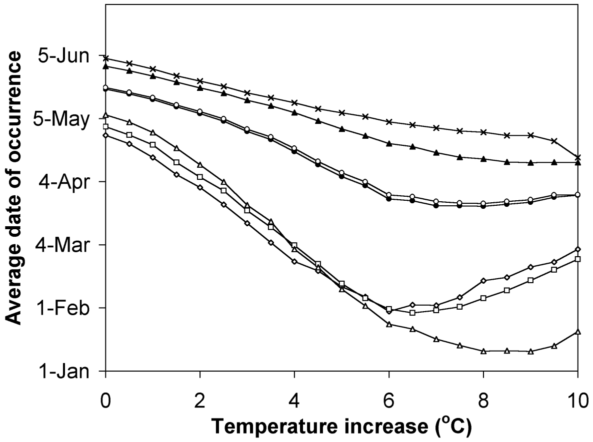


Figure 11. Dependence of the average date of a phenological event on annual temperature increase according to the chilling triggered model. Symbols: flowering of *Alnus glutinosa* (white diamonds), *Alnus incana* (white squares), *Populus tremula* (white triangles), *Betula* sp. (white circles) and *Pinus sylvestris* (crosses), and bud burst of *Populus tremula* (black triangles) and *Betula* sp. (black circles).

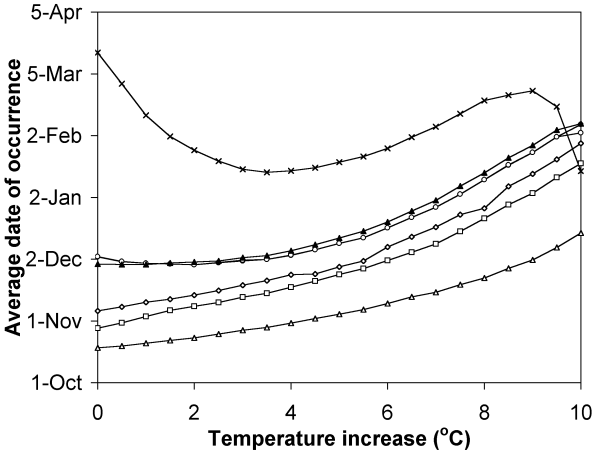


Figure 12. Dependence of dormancy completion on mean annual temperature increase according to the chilling triggered model. Symbols as in Fig. 11.

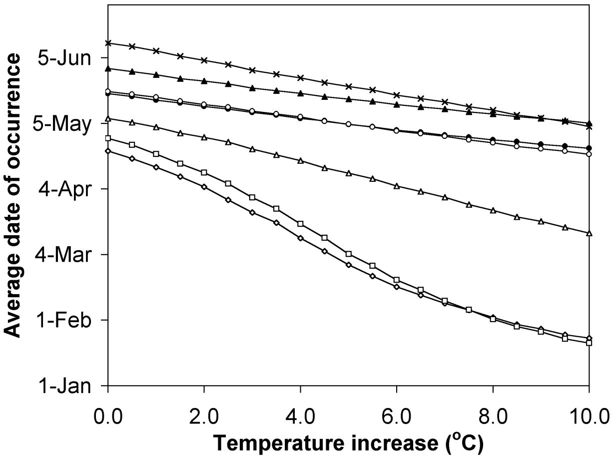


Figure 13. Dependence of the average date of a phenological event on annual temperature increase according to the light climate triggered model. Symbols as in Fig. 11.

climate change will have quite a severe impact on the boreal forests. No increase in the frost damage risk for these species was predicted by the light climate triggered model (Fig. 14 D, E and F).

With the late flowering phenomenon, the flowering of *Pinus*, the damage risk remained low for the light climate triggered model, while the chilling triggered model showed a very slight increase in frost damage risk at higher degrees of warming (Fig 14 G).

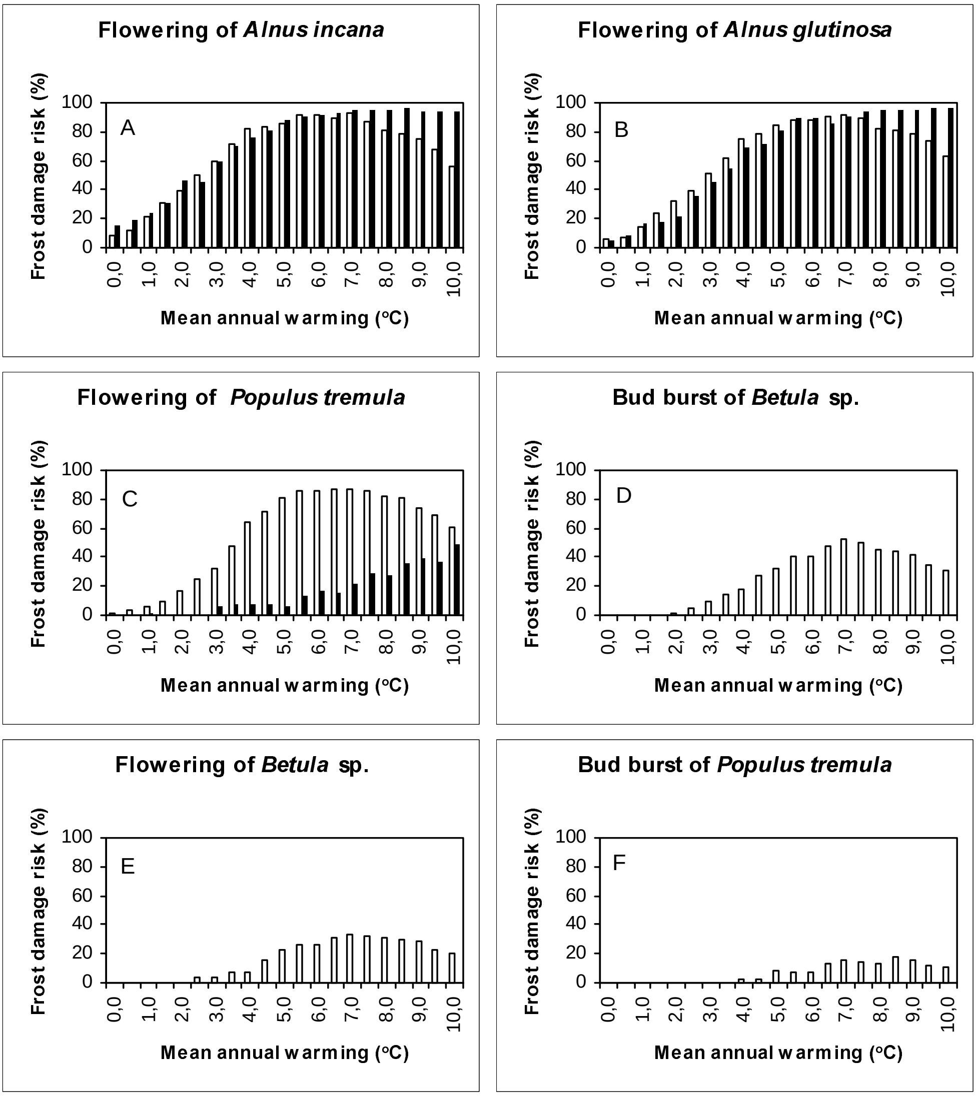
The frost damage risk for the early flowering group of two species of *Alnus* and *Populus* was quite high in both models, and was actually slightly smaller for the chilling triggered model (Fig. 14 A, B and C). This does not suggest much difference between the models, but rather reveals an interesting difference in the strategy of phenological timing between flowering and bud burst. It seems obvious that flowering in early spring poses a larger risk of frost damage to the trees even under current climatic conditions. This may however be acceptable, if the benefit from such timing is sufficient, e.g. more efficient dispersion of the pollen when the leaves do not hinder it. The possible loss of flowers and seed crop to frost is not as severe a drawback for the trees as would be a loss of leaves in spring. Both models indicate, however, that the frost damage risk reaches considerable levels, exceeding 50% at an average warming of less than 5°C. This may have a severe effect on the success rate of sexual reproduction of such early flowering species.

9 Discussion

9.1 Methods for combining the phenological data

This study is based on the use of old phenological observation data. The data has its drawbacks, since the instructions on how to collect the data have been insufficient, and the conditions in which it has been collected are not thoroughly known, and so e.g. the mechanisms possibly causing inaccuracies in the data cannot be examined in detail. Despite this, the data is plentiful, and the multiple annual observations and the overlap between the observation series can be utilised to overcome many of its shortcomings. The climate change has already started to take effect on the global climate (IPCC 1996), and it is doubtful that the plants are able to adapt to the rapidly changing conditions (Billington and Pelham 1991). Thus the historical data is valuable as it presents the phenological timing of plants in a steady-state environment.

The methods of combining the data and discarding the outliers turned out to be efficient, reducing the annual variability in the data and improving the



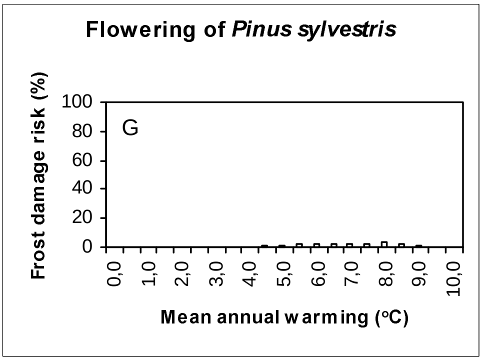


Figure 14. Frost damage risk, i.e. probability of occurrence of temperatures below a threshold value (see text) between the date of flowering/bud burst and 30 July, as a function of average annual increase in temperature. White bars refer to the chilling triggered model, black to the light climate triggered model.

predictive ability of some phenological models (Hari and Häkkinen 1991, Häkkinen et al. 1998). The methods thus permit full exploitation of the data. The method is by no means data-specific, and can therefore be utilised to combine any sets of phenological time series.

9.2 Spatial and temporal regularities of boreal phenology

The area of phenological data collection is large, extending for 550 km in both the north-south and the east-west directions. The distance in the north-south direction introduces a deviation of dates of phenological events of on average 20 and up to 30 days between observation sites within a year. Provided that these deviations are accounted for, which is possible with the combination methods developed in study I, the deviations do not reduce the reliability or usability of the historical data, as even the extreme observation series are in good agreement with the rest of the data. The deviations are also regular between species, which was expected. Spring proceeds at a regular pace from south to north in the boreal growing zone.

The phenological timing of different species is surprisingly uniform, especially for the phenomena occurring on average in May. Our current knowledge of spring phenology suggests that the ontogenetic development leading a phenological event to occur is a long process, heavily dependent on prevailing temperatures. These results indicate that the responses of different plant species and different phenological events to the climatic conditions are quite similar, provided that the events occur close enough to each other in time. This seems to suggest that even if the phenological control mechanisms of the plant are different, they react to the same events in the climate in a similar manner.

9.3 Modelling dormancy and the onset of ontogenetic development

Dormancy is a phenomenon which, according to some studies, is released towards the end of the calendar year (Sarvas 1974, Hänninen 1990, Heide 1993a, Leinonen 1996a). The release of dormancy is defined as the time when the plants re-attain the ability for ontogenetic development. Several models implicitly assume that dormancy development is an entirely temperature-driven process, and that there are no other control mechanisms present.

There are, however, a number of studies of boreal trees suggesting that after the chilling requirement is met there is another mechanism related to the light conditions that plays some role in the timing of the start of ontogenetic development (Heide 1993b, Myking and Heide 1995, Olsen et al. 1997, Partanen et al. 1998). Further, with the seven phenological time series in this study the light climate triggered model performed better in estimating the observed dates of phenological events than the chilling triggered one, while having one free parameter less.

9.4 Critique of the dormancy experiments

If the start of the ontogenetic development in spring requires a signal from the light climate (in addition to the chilling requirement), how is it then possible that the end of dormancy has been defined as it has, and has also been experimentally observed? Dormancy development has usually been tested by keeping the plants in controlled temperature conditions to satisfy the chilling requirement, and then brought into another environment that should be favourable for ontogenetic development to proceed, where the occurrence of phenological phenomena have been observed and recorded. One possibility is that the experimental conditions themselves have unintentionally incorporated the additional signal required to start ontogenetic development. In his studies with *Betula pubescens*, Sarvas (1974) germinated the seeds under artificial light after the chilling treatments, so that the experiment may have incorporated the required light signal to initiate ontogenetic development. Some experiments of the control mechanisms of various phenological events, provide evidence that certain photo-receptive mechanisms, like phytochrome-A, can react to very short pulses of far-red light (Ballaré 1994), so that even if the dormancy test was conducted in darkness, the visual observation of the ontogenetic development stage may have introduced confounding elements into the experiment. Further, several studies have shown how favourable temperatures can substitute for the lack of chilling (Cannell and Smith 1983, Leinonen 1996b), so it may be possible that suitable temperature conditions could also substitute for the lack of required light signal, or *vice versa*.

9.5 Signals from the light climate

The light climate triggered model does not state what the feature in the light climate triggering the ontogenetic development in spring might be. Day or night length is of course the most obvious, but some research (Hänninen 1995) suggests that these have negligible effect on timing. There are also other possibilities. The plants utilise a mechanism that senses the red/far red ratio to control the growth cessation in autumn (Junttila 1980, Junttila and Kaurin 1990), and to detect their position in relation to the light competition in the canopy (Ballaré 1994). Another possibility is the blue light that the plants can sense by the phytochrome-B mechanism (Ballaré 1994). It should be noted that in April the amount of cloud cover rapidly increases when daily average temperatures reach melting point (Sarkkula 1987), and the evaporation of snow and ice cover from both the ground and lakes into the atmosphere increases. If the change in the cloud cover had an effect on the spectral composition of light and the plants had a mechanism for sensing such a change, this might prove to be a useful feature to investigate in terms of phenological control. As the increase in cloud cover also reduces the daily temperature range (DTR) a lot (fig. 15), this mechanism might give the plants a strong and solid signal about when the chance of night frosts is reduced so that ontogenetic development can start. Measurements of the variation in the spectral composition of the light in natural conditions so far are, however, rare.

9.6 The evolutionary argument

From the evolutionary point of view, the light climate driven approach should be superior to the dormancy triggered one. Short of annual scale regularity, the weather is a chaotic phenomenon that cannot be predicted on a time scale longer than two weeks (Lorenz 1993). In the chilling triggered model the autumn weather conditions control to some extent the start of ontogenetic development in spring which, given the chaotic nature of the weather, should not be useful. On the other hand, the light conditions have a high information value for the phase of the seasons (Levins 1969).

The plants utilise the light signals to control different features in their growth. The red/far red ratio, for instance is used to detect the position in the plant community, and to increase length growth when light competition is severe (Ballaré 1994). The same feature of light conditions is also used to control the timing of growth cessation of some boreal trees (Junttila 1980, Paus et al. 1986, Junttila and Kaurin 1990). Thus the plants have the mechanisms to detect varying light conditions throughout the year.

Can we then conclude, based on the evolutionary argument, that boreal plants utilise the light conditions to control their phenological timing? Evolutionary selection does not drive the plant population towards any specific “goal”, but rather prunes features that are less efficient in the individual survival sense. Starting ontogenetic development from dormancy release in the middle of winter may be less rational than starting it from a signal from the light climate later in spring, but in the boreal climate zone the winter is long and cold, and even if the ability for ontogenetic development were attained in the winter, no development takes place (except in rare, exceptional years only) until spring.

Thus there may not be enough evolutionary selection pressure towards the light signal driven control under current climatic conditions.

9.7 Modelling the spring phenology of boreal trees

Both models utilised in this study predict the spring phenological timing of several boreal trees under unchanged climatic conditions well. The light climate triggered model had slightly better prediction power for all the phenological events examined. A study utilising a smaller data set of bud burst of *Betula* (Häkkinen 1999) indicated that the difference was statistically significant in that case, and that the greater part of the model prediction error was due to the inaccuracies in the data.

This result is most interesting in relation to other studies. Several qualitative studies of dormancy and ontogenetic development emphasise the significance of photoperiod to the timing of spring phenological events (e.g. Myking and Heide 1995, Olsen et al. 1997, Partanen et al. 1998). However, most recent studies using models to predict the observed phenological time series (Kramer 1994, 1995, Chuine et al. 1999) have found the dormancy based model, as presented by Sarvas (1972, 1974), better than those involving photoperiod. These results are contradictory to the ones presented here.

9.8 Climate change, phenological timing and frost damage risk

Under simulated climate change the outcome of the two models varied radically. The sensitivity of phenological timing to climatic warming on the chilling triggered model was almost twice that of the light climate triggered model. The same divergence of results was encountered with the frost damage risk of the bud burst of *Populus* and *Betula*, as well as the flowering of the latter. The chilling triggered model predicted frost damage risk would reach 50%, while the light climate triggered model predicted no increase at all (Fig. 14 D, E and F). Both models, however, predicted a large increase in the frost damage risk of the flowering of early species like *Alnus* and *Populus* (Fig. 14 A, B and C). If this proves true, it might have a major impact on the sexual reproduction of the broadleaf boreal trees within the next few centuries. On the other hand, these species reproduce to a great extent vegetatively, which may diminish this effect.

The analysis assumes that the pattern of daily temperatures, e.g. the daily temperature range (Fig. 15) remains unchanged as climatic warming proceeds. This may not be the case, as the current climate change already shows a reduction in the daily temperature range due to the climate change (Heino 1994, Kaas and Frich 1995). On the other hand, the increase in the frost damage

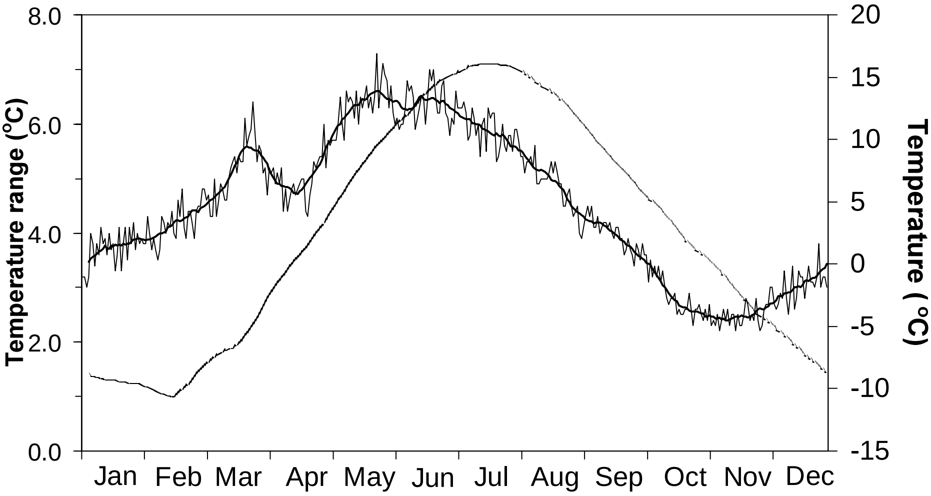


Figure 15. Diurnal temperature variation (afternoon observation minus daily minimum) and daily average temperature as a function of date (both 1883-1981 mean). The thick solid line shows the 14-day moving average with the thin line showing daily observations of the temperature variation. The smooth thin solid line shows the 14-day moving average of daily average temperature.

risk on both models is so large that even if the true effect were smaller, it may still be considerable.

9.9 The recent lengthening of the growing season

Several studies have indicated that the climate change has already started, with estimates of warming from around 1°C in latitudes higher than 45°N and up to 4°C e.g. in Alaska (Myneni et al. 1997). Such an increase should also have a noticeable effect on the phenological timing, and there have recently been some studies utilising recent phenological observations made directly from plants in phenological gardens, or indirectly with remote sensing methods or from the annual pattern of atmospheric CO_2 concentration, which suggest the climate change will advance the start of the growing season by 8 to 12 days per degree of warming (Keeling et al. 1996, Myneni et al. 1997, Menzel and Fabian 1999). These figures are in better agreement with those achieved in this study with the chilling triggered model (9.0 and 8.8 days per degree of warming for the bud burst of *Betula* sp. and *Populus tremula* respectively) than those with the light climate triggered model (2.8 and 3.1 days per degree).

9.10 Concluding remarks

The historical phenological data provides a valuable basis for studies of phenology, and the combination methods discussed here improve their usability a lot. Since a comparison between several phenological time series indicates a great regularity in the phenological events of different plants, the use of similar, even to some extent statistical models is justified. The two models tested here predict phenological events under unchanged climatic conditions well, but the results diverge considerably when extrapolated to simulated climatic conditions. To achieve more accurate results, such as accurate estimates of the consequences of climate change, we need to base our models on more detailed understanding of the mechanisms driving the control of phenological events in plants.

I see two ways of improving our understanding of the spring phenology. One is to utilise biochemical research (e.g. Wareing 1969, Rinne et al. 1994, 1997) to assess the actual phenological control mechanisms. This may be a long path, as the biochemical control mechanisms of phenology are not yet throughoutly known. The other approach would be to run extensive tests which closely control the environmental conditions of the plants examined. This approach also has its problems, as setting up an experiment that controls several features of climatic conditions, including temperature, light spectrum, etc., without manipulating others that might have an effect on the phenomenon, is difficult, if not impossible.

Before taking further steps in the latter direction, it might be worthwhile to stop for a while, and try to think what the controlling phenomena might be. This could be done by theoretical analysis of stating the optimal behaviour strategy for specific growing conditions, and analysing climatic data like historical records of temperature and cloud cover, ongoing measurements of changes in the light spectrum, or a synthesis of the two, in respect to what kind of control and strategy would lead to the best results. Such analysis could give us some clue about what environmental factors should be manipulated and concentrated on while conducting such tests and how to set up the experiments to avoid misleading secondary effects confounding the experiments.

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A few years ago Timothy Carter joined the group, bringing in useful knowledge of climate change and features related to it. Our work at the moment aims to find out the impact of climate change on the phenology of boreal forests.

I have greatly enjoyed working in the group. Our meetings vary a lot: sometimes we spend hours engaged in wild speculation about how things work in nature; at other times we focus solely on finishing some small details of a paper. The work has been fascinating, and very educational. Thank you, Pepe, Risto and Tim for an opportunity to work with you.

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