Regularities and Patterns in the Spring Phenology of Some Boreal Trees

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Phenological time series of flowering and bud burst of *Populus tremula* (L.) and *Betula* sp., and the flowering of *Pinus sylvestris* (L.), *Alnus glutinosa* (L.) and *Alnus incana* (L.) were constructed from data collected in Finland during the period 1896–1955. The resulting combined time series were examined with two aims in mind: first, to determine the phenological regularities between different species and, second, to detect patterns of spring advancement over a geographically large area. The results indicate that the geographical pattern of spring advancement is rather uniform from year to year, and between different species. Furthermore, the mechanisms regulating the timing of phenological events in different species seem to function in a similar way, suggesting an unanimous optimal response to climatic conditions.

Keywords bud burst, flowering, phenological regulation, phenological time series, *Alnus glutinosa, Alnus incana, Betula* sp., *Pinus sylvestris*, *Populus tremula*

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1 Introduction

The ongoing climate change may have a considerable effect on the phenological timing of plants. To make reliable estimates of the consequences of the climate change, we need to know how the mechanisms driving the phenological events worked before the current climate change started. Historical phenological data provide the most obvious way to study those conditions.

Collecting phenological data to base models on is a time-consuming process, as most phenomena occur only once per year. Fortunately there are some historical phenological observation series of full-grown plants in natural conditions that can be utilised for phenological modelling (e.g. Lauscher 1978, Lauscher and Lauscher 1981, Hunter and Lechowicz 1992, Kramer 1994, Fitter et al. 1995, Sparks and Carey 1995, White 1995). Since the phenological data mostly consist of only one observation per year (one exception being the paper by Jeffree (1960), presenting the data by the British Royal Meteorological Society), they are vulnerable to observation errors, misprints and anomalies in the local microclimate of the observation site. If the time series could be constructed from several observations each year, such suspicious observations could be detected. Further, statistical descriptives of the variation in observations each year could be calculated, enabling estimation of the accuracy of each observation in the time series.

There are some useful phenological data series consisting of several contemporaneous phenological observations over a larger geographical area. One of these has been collected by the *Finska Vetenskaps-Societeten*, whose members took phenological observations of common garden and other plants, as well as about the most common forest trees in Finland. The collection was started at the end of the 19th century, and continued up until the mid 1950's. The data covers most of Finland as well as a long timespan.

The large geographical area of data collection may introduce a new problem in utilising the data: if the climatic conditions in different observation sites vary too much, it is not possible to utilise all of the data to construct a combined phenological time series. Large spatial deviation in the observations, especially in north-south direction brings in 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, data collected over such a large area makes it possible to study the progression of spring.

To utilise such collections of phenological observation series, Häkkinen et al. (1995) and Linkosalo et al. (1996) have presented methods of combining phenological observation series made over a larger geographical area, by estimating and eliminating the effect of local variation. In this study, one of the methods was used to make combined phenological observation series of flowering and bud burst of several boreal-zone trees. The method was applied to the flowering of *Alnus glutinosa* (L.), *Alnus incana* (L.), *Betula* sp., *Populus tremula* (L.) and *Pinus sylvestris* (L.), as well as the bud burst of *Betula* sp. and *Populus tremula* (Table 1). During the time of data collection the two most common species of *Betula* in Finland, *B. pendula* (Roth) and *B. pubescens* (Ehrh.), were not known to be different. The historical observation series thus do not state which species the observations were taken for. As *pendula* is the more common species on mineral soil growing sites, and unfolds its leaves earlier than *pubescens*, it is probable that the observations were made of the *pendula* species.

The aim of this study was to analyse the combined time series to determine the phenological regularities between different boreal tree species. The patterns of spring advancement, indicated by the varying times of phenological events over the geographically large observation area, were examined and compared to geographical variables, in order to determine what causes the variations in phenological timing. Finally, the observation series were analysed to see whether the method of data combination could be utilised for phenological observations collected over such a large geographical area.

2 Material and Methods

Construction of a combined time series from a set of observation series is not a straightforward task. The overall level of the observations varies between the series due to the large geographical area covered. Further, no single observation series covers the entire observation period, and the geographical distribution of the observations varies from year to year. Straightforward annual averaging of the observations would thus result in a combined time series with an unpredictable annual bias, depending on the geographical distribution of observations for each year.

To avoid this bias, the combined time series was constructed with an iterative process described by Häkkinen et al. (1995) and Linkosalo et al. (1996). The method utilised a Hooke-Jeeves (Hooke and Jeeves 1961) minimising algorithm to bring all observation series to a common level. This was done by estimating the average deviation of each observation series from the overall average level of observations, and bringing the observation series to this level before constructing the combined time series. A flow chart of the algorithm is presented in Fig 1.

First, average deviations of each observation series, c_j, were initialised to zero (A), thus the initial adjusted observations, x'_{ij}, were equal to original observations, x_{ij} (C). The values of the

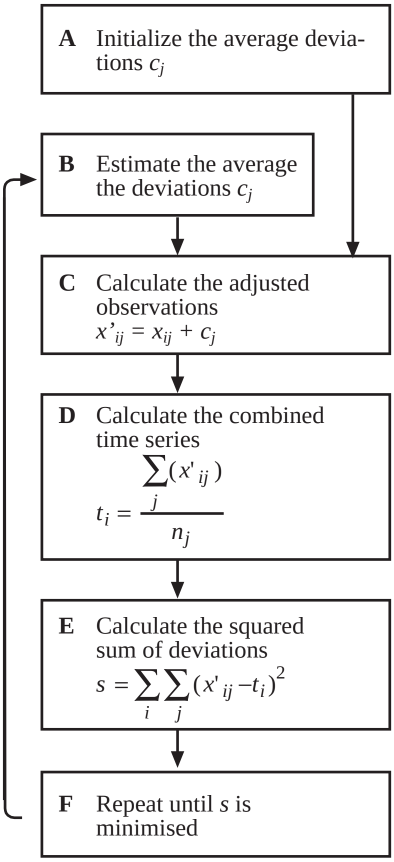

Fig. 1. The flow chart of the data combination process. The symbols are: x_{ij} the original and x'_{ij} the adjusted observation at site j in year i, c_j the average deviation of observations at site j from the combined time series, t_i the spatially averaged moment of phenological event in year i, and n_j the number of observations (sites) in year i.

combined time series, t_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 of the two (E). The minimising algorithm then chose a new set of average deviations, c_j (B). The process of choosing average deviations, adjusting the observations and calculating the combined time series was (automatically) repeated until a set of average deviations c_j that minimises the squared sum of deviations was found.

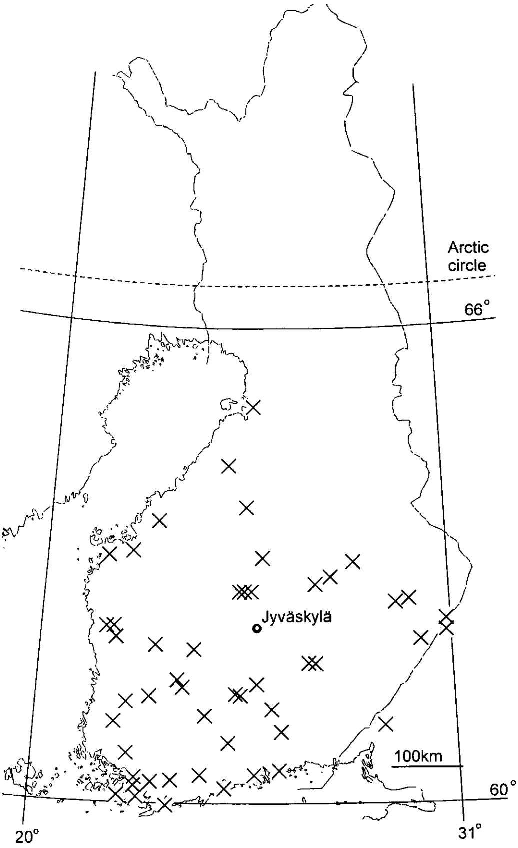

Fig. 2. The sites of the phenological observations.

The resulting average deviations, c_j, present the average deviation of the unadjusted observation series from the combined time series. These were later utilised to study the spatial variation of phenological timing.

Previous studies carried out to develop a method for combining the observation series (Häkkinen et al. 1995, Linkosalo et al. 1996) were based on a subset of the phenological data of bud burst of *Betula* sp., collected from an area covering a 180 km radius around the city of Jyväskylä in Central Finland. For this study all the observation series collected in Finland were included (Fig. 2, Table 1), except for two observation series in the north (Inari 69°06'N 27°12'E and Kemijärvi 66°43'N 27°27'E) and one in the south-west (Maarianhamina 60°06'N 19°57'E). Since observations of only one phenomenon (bud

Table 1. The geographical locations and numbers of observations for each observation site and species in the data

Site	Latitude	Longi-tude	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*
Antrea	60°58’	29°7’	20	27		20	27	27	27	19
Eura	61°11’	21°38’	15				15			
Finby	60°6’	22°57’	15		19	24	22	22	21	21
Haapajärvi	63°53’	25°34’	120	26		32	33	23	33	32
Hattula	61°5’	24°27’	90	49		44	55	30	51	42
Hausjärvi	60°48’	24°50’	70	18		17	17	18	19	16
Heinola	61°12’	26°12’	105	18	17	17	17	17	17	
Helsinki	60°10’	24°57’	10		17	20			17	16
Iitti	60°56’	26°24’					15			
Isojoki	62°11’	21°48’		22		21	22	18	20	
Joensuu	62°40’	27°35’	90	35		34	32	36	31	21
Juvankoski	63°4’	28°20’	110	16		27	17	15		
Karkku	60°23’	22°59’	60				20	18	22	24
Karttula	62°54’	27°0’	115	18			22			18
Kimito	60°10’	22°45’	20				17		17	
Kisko	60°16’	23°29’	50	15			15		15	
Kitee	62°6’	30°7’		16		15	16	16		
Kokemäki	61°15’	22°21’	50	20		22	20	19		15
Kuopio	62°54’	27°40’	100	16		16	16	16	16	16
Lappfjärd	62°14’	21°36’	5	25		27	32			23
Lappfjärd	62°14’	21°36’	5					42		
Liperi	62°20’	29°20’	85	31	34	32	37	23	30	34
Loviisa	60°27’	26°13’	5			23				
Mikkeli	61°41’	27°15’	90	45	15	34	57	51		
Mikkeli	61°41’	27°15’	90			18	19	19	18	
Oulainen	64°16’	24°48’	75				15			
Oulu	65°1’	25°27’	5	37		40	48	43	46	45
Padasjoki	61°26’	24°56’	125		16	16	16	16	17	
Padasjoki	61°26’	24°56’	85				20			
Pälkjärvi	62°3’	30°42’	80	16		16	16	17	16	
Parkano	62°2’	23°1’	110			15	15		15	
Pedersöre	63°40’	22°42’	10	27		28	31	31	31	31
Piikkiö	60°23’	22°33’					15		15	15
Porvoo	60°24’	25°44’	5	18	16	15		15		15
Ruovesi	61°56’	24°3’	100				17			
Saarijärvi	62°42’	25°20’	120	32	23	26	21	31	20	
Saarijärvi	62°42’	25°20’	120				38		16	17
Saarijärvi	62°42’	25°16’	120				20			
Sauvo	60°21’	22°35’	5	28	20	22	24	21	24	20
Sysmä	61°27’	25°51’	95	16						
Tammisaari	59°58’	23°27’	5		28	27	28	26	27	20
Tampere	61°32’	23°46’	90	40		38	40	35	35	36
Teisko	61°43’	23°35’					15			
Vaasa	63°5’	21°32’	10	17	15					
Vammala	61°20’	23°0’	60	24	24	28	26	26	16	33
Vårdö	60°15’	22°2’			19	17	17		15	
Värtsilä	62°10’	30°39’	85	40		40	40	37	39	27
Vihti	60°22’	24°26’	55	16		16	16	16	16	
Viitasaari	63°4’	25°50’	100	27	25	32	33	28	26	25
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

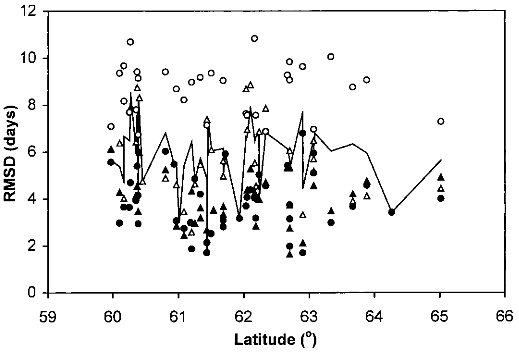

Fig. 3. The root mean square deviation (RMSD) of each adjusted observation series from to the combined time series plotted against the latitude of the observation site. Flowering and bud burst of *Betula* sp. (black triangles and circles respectively) and *Populus tremula* (white triangles and circles respectively) are shown. The solid line shows the overall average of all 7 phenological time series examined.

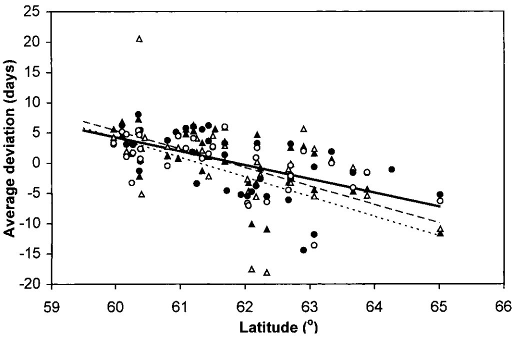

Fig. 4. The average date of phenological events of different species as a function of latitude. All observations of flowering and bud burst of *Betula* sp. (black triangles and circles respectively) and *Populus tremula* (white triangles and circles respectively) are presented. The majority of regressions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

burst of *Betula* sp. in north, and bud burst of *Populus tremula* in south-west) were made on these three sites, it was considered best to discard them from the analysis.

To evaluate the fit of a single observation series to the combined time series, the root mean square deviation (RMSD) of each adjusted observation series from the combined time series was calculated for each phenological phenomenon. With the three above-mentioned observation sites excluded, no relationship was found between the latitude of an observation site and the root mean square deviation of a observation series from the combined time series (Fig. 3). As stated below, the latitude is the only spatial variable that was found to correlate with the timing of the phenological events.

3 Results

The combination process is based on the hypothesis that the variation in the timing of phenological events at different observation sites within each year is mainly caused by the varying climatic and microclimatic conditions, primary influenced by latitude. The effect is presumed to be similar from year to year and the same for all species. To analyse this, linear regression models between the average deviations c_j and latitude were fitted to the data. For most phenomena the regression models were similar, even though the change in the timing of the events as a function of latitude was somewhat larger (Fig. 4) for the phenological events occurring early in the spring (the flowering of *Alnus glutinosa*, *Alnus incana* and *Populus tremula*). The deviations varied at most from –20 to 10 days for the flowering of *Populus tremula*, while they were typically from –11 to 8 days. This implies that the hypothesis about the cause of the variation in timing between the observation series was well founded.

The dependence of the changes in the timing of phenological events on spatial features was examined by plotting the average deviations c_j against some geographical variables. The spring advancement from south to north, which can be described by latitude, is the major factor causing variation in the phenological timing (r = –0.60) (Fig. 5). There was a small correlation (r = –0.38) between the average deviation and the longitude (Fig. 6). This was probably due to the slight trend in the locations of the observation sites from

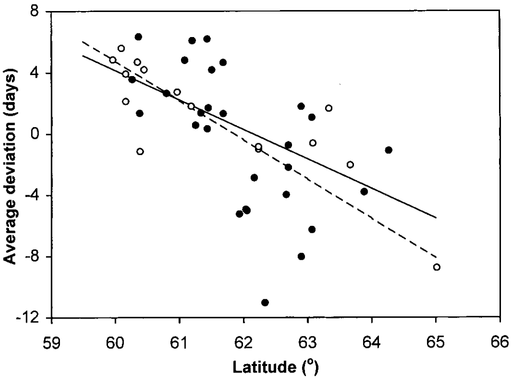

Fig. 5. The deviation of phenological event date at each observation site from that of the combined time series, averaged over years and species, as a function of latitude. The white circles show sites with elevation of less than 20 m asl, the black ones those above. The lines show the linear regression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

south-west to north-east, rather than to any climatic differences in the east-west direction. There was not much correlation between the average deviations and the elevation of the observation site (r = –0.25) (Fig. 7).

The altitude can, however, be utilised when 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, the rest are inland sites. Climatically, there are slight differences between the coastal and inland areas of Finland. Thus, 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 c_j, did not differ. However, when a regression model predicting the average deviations with latitude was fitted to the two groups, some difference emerged. In the inland group, the effect of latitude to the average deviations was less pronounced than that for the rest. In other words, the occurrence of phenological events was delayed more than with the coastal sites, when moving towards the north. 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 was delayed compared to inland sites at similar latitudes, and in the north the phenological events took place somewhat earlier compared to the inland sites (Fig. 5). The overall effect of the sea was, however, minor.

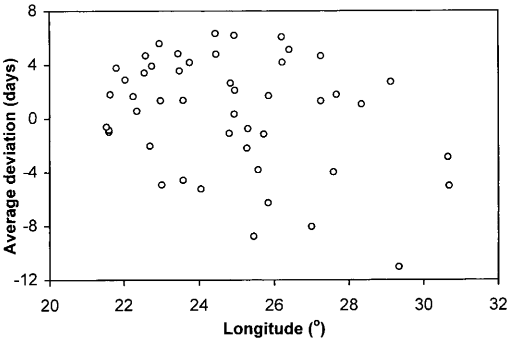

Fig. 6. The deviation of phenological event date at each observation site from that of the combined time series, averaged over years and species, as a function of longitude.

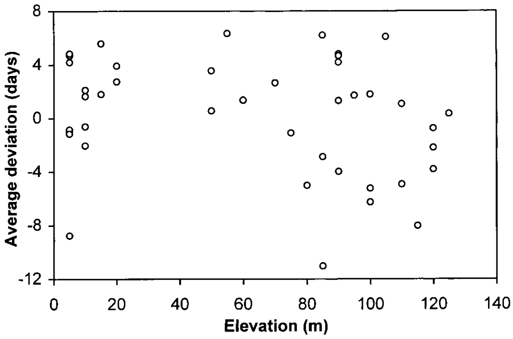

Fig. 7. The deviation of phenological event date at each observation site from that of the combined time series, averaged over years and species, as a function of elevation. The observations fall into two groups. The leftmost ones (elevation <20 m asl) lie on the southern and western coast of Finland; the rest lie inland.

All the combined phenological time series showed a rather similar annual pattern of response to the weather. All time series were 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. 8). The events that occurred earlier, i.e. the flowering of *Populus trem-*

Table 2. The differences between the annual averages of the two phenological phenomena (upper half), and the correlation between the two (lower half)

	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*
Flowering of *Alnus incana*		5.6	15.0	27.3	28.4	39.6	52.0
Flowering of *Alnus glutinosa*	0.86		9.3	21.6	22.7	34.0	46.3
Flowering of *Populus tremula*	0.83	0.73		12.3	13.4	24.6	37.0
Bud burst of *Betula* sp.	0.61	0.56	0.84		1.1	12.3	24.7
Flowering of *Betula* sp.	0.62	0.54	0.83	0.97		11.2	23.6
Bud burst of *Populus tremula*	0.58	0.56	0.75	0.93	0.91		12.4
Flowering of *Pinus sylvestris*	0.63	0.62	0.76	0.88	0.86	0.94	

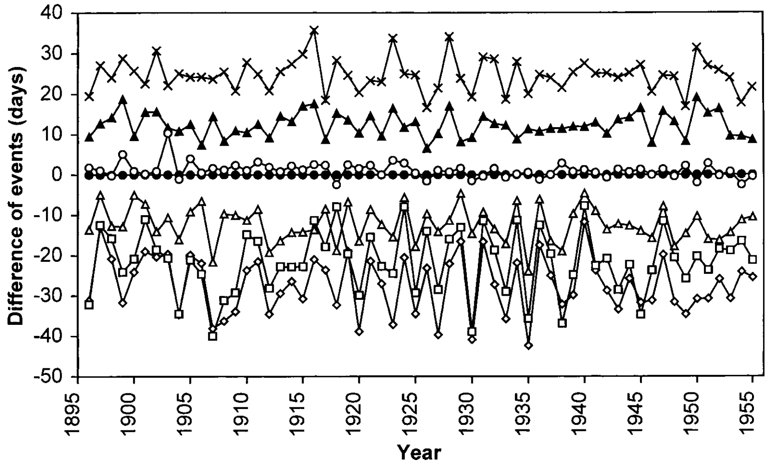

Fig. 8. The annual average deviation of the phenological events from the bud burst of *Betula* sp. (black circles). The events are: flowering of *Alnus glutinosa*, *Alnus incana*, *Populus tremula*, *Betula* sp. and *Pinus sylvestris* (white diamonds, white squares, white triangles, white circles and crosses respectively), and bud burst of *Populus tremula* (black triangles).

ula and the two species of *Alnus*, showed a larger variation in timing. The reason for this is probably that the timespan of feasible temperatures required for the flowering of the early species to take place is short, and thus the events are driven by temperature conditions that play only a minor role in the timing of the later events.

The annual averages of the differences between two phenological events were up to 52 days (between the flowering of *Alnus incana* and the *Pinus sylvestris*) (Table 2). The correlation coefficients of the dates of occurrence of the phenological phenomena between different species were also surprisingly high, with the highest

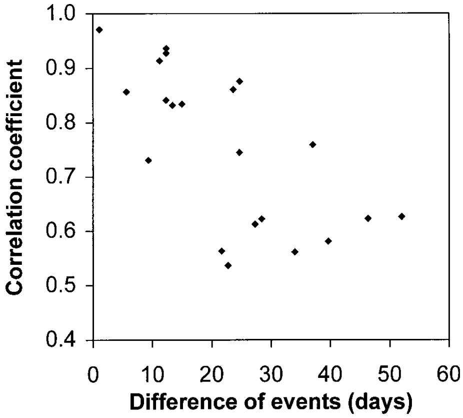

Fig. 9. The correlation coefficients between two phenological phenomena plotted against the average difference in time between them.

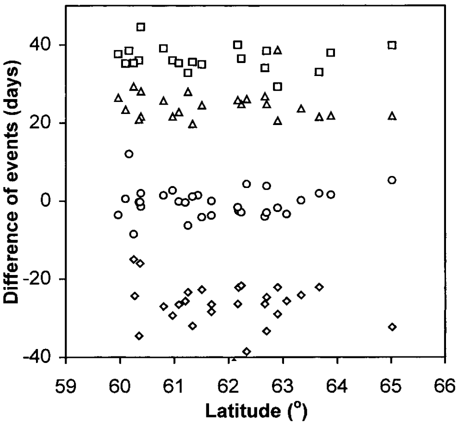

Fig. 10. The average deviations between phenological events as a function of observation site latitude. The combinations are bud burst and flowering of *Betula* sp. (circles), the flowering of *Pinus sylvestris* and the flowering of *Populus tremula* (squares), the flowering of *Pinus sylvestris* and bud burst of *Betula* sp. (triangles), and flowering of *Alnus glutinosa* and bud burst of *Betula* sp. (diamonds).

correlation coefficient being for the bud burst and flowering of *Betula* sp. (0.97). The highest correlation coefficient for phenomena of two different species was for the flowering of *Pinus sylvestris* and the bud burst of *Populus tremula* (0.94), for which the difference between the average dates was 12.3 days (Table 2). The degree of correlation for all the event pairs except one that occurred within a two-week period was above 0.83. For the remaining events, the degree of correlation was much lower. The degree of correlation decreases as the time difference between the averages of the phenological phenomena increases (Fig. 9). The time difference between two phenological phenomena also remained constant at all observation sites (Fig. 10), despite the change in latitude.

4 Discussion

The observation area is large, extending for 550 km in both the north-south and the east-west directions. The area is not too large for the combination of phenological data, as even the extreme observation series are in good agreement with the rest of the data (Fig. 3). Thus phenological data collected from an area as large as in this study can be combined, provided that the problem with the average deviations is taken care of.

The topology of the data collection area is relatively constant, with elevations from 5 to 125 metres asl. The effect of these height differences on the timing of phenological events is too small to be differentiated from the much larger effect of the observation site latitude. The latter has a much more pronounced effect, with differences of up to four weeks. These deviations need to be taken into account to avoid bias in the annual observations.

The use of several phenological observations for each year has the additional advantage that the accuracy of the combined phenological data can be estimated with statistical descriptives, and outliers can be detected (Linkosalo et al. 1996). The information of data accuracy can then be utilised when fitting phenological models to the data. The information helps to detect years with a greater variation in observations, indicating possibly inaccurate estimates of the dates of occurrence of phenological phenomena.

The phenological timing of different species is surprisingly unanimous, especially for the phenomena occurring on average in May. Our current knowledge of spring phenology suggests that the ontogenetic development leading to a phenological event occuring is a long process, heavily dependent on the prevailing temperatures. These results also indicate that the response of different plant species and different phenological events to the climatic conditions is quite similar, provided that the events occur close enough in time to each other. For events that occur further apart in time, such conclusions cannot be drawn, as the climatic conditions affecting the events are more diverse.

The similar response of adjacent events to the environment implies that either the plants utilise similar biochemical mechanisms to time their phenology, or that there is an optimal response to the environmental signals, and that evolutionary selection has adjusted the various regulation mechanisms of plant species towards similar behaviour. The high correlation coefficients between different phenological events (Table 2) imply that the phenological phenomena of different plant species are driven by the same weather phenomena.

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