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Dependence of the flower bud burst of some plant taxa in Finland on effective temperature sum: implications for climate warming

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The connection between the effective temperature sum and the occurrence of the flower bud burst on eleven plant taxa was analyzed using historical, regionally-distributed phenological observations in Finland from the period 1918–1955. Local estimates of effective temperature sum were optimised by temporal and spatial interpolation of the temperature data that was available from a relatively sparse network of stations. During the extremely warm spring of 1921 flowering on many taxa occurred nearly one month earlier than in an average year, corresponding to the about 5°C warmer-than-average temperatures. The year-to-year fluctuation of spring-time mean temperature had a standard deviation of about 2°C. This corresponded to a fluctuation range of 18 days in flower bud burst. In the warmer climate anticipated for the near future by most climate scenarios, the occurrence of bud burst would be expected to advance correspondingly, i.e. by about 4 days per 1°C of warming, if the temperature rise remains within the present range of climate variation. Phenological maps based on the ETS indicated that the progress of flowering with latitude was regionally highly variable, with a latitudinal gradient of about 200–300 km/10 days on average. A 2°C mean climate warming would thus correspond to a latitudinal shift of about 700 km in the average date of flowering.

Key words: climatic change, effective temperature sum, flowering, phenology

INTRODUCTION

Climate variation from year to year is known to cause large interannual fluctuations in the timing of flowering, an observation that has led to numerous studies on the relationship between plant phenology and climate. Due to this response, both the anticipated climate warming and the changed occurrence of climatologically extreme seasons would produce adjustment pressures on plants under natural conditions, especially for species growing in their marginal distribution areas such

This article is also available in pdf format at http://sekj.pc.helsinki.fi/Journals as Finland. A survey of the long-term phenological dataset collected by the Finnish Society of Science and Letters showed that the average interannual range for the onset of leafing and flowering is of the order of one month for several plant species in Finland (Lappalainen & Heikinheimo 1992). This spring-time variation of phenological events is regulated by environmental factors, primarily by air temperature and photoperiod (Cannell 1990), of which temperature seems to be the major forcing factor in boreal regions (Hänninen 1987).

Experimental data for many species suggest that after the release from winter dormancy there is a linear dependence between the rate of development and temperature. This has been particularly noted for agricultural crops (Angus *et al*. 1981, Van Keulen & Seligman 1987), but supporting evidence is also available for perennial trees and shrubs (Arnold 1959, Wang 1967). Year-to-year variation in the timing of flowering and budburst has been satisfactorily accounted for by yearly differences in effective temperature sum alone (e.g. Anstley 1966, Eisensmith *et al.* 1980). However, the questions then raised are whether the effective temperature sum concept is valid, how the starting dates and base temperatures should be analyzed, and how the effective temperature sum should be calculated from the meteorological records (Cannell 1989). Sarvas (1972) pointed out that even though the regression between temperature and the active period of a tree is non-linear, the heat sum method based on the 5°C threshold value will in many cases be more expedient than the more accurate models. According to Lappalainen (1994), the effective temperature sum calculated from 1 January, using 0 or 5°C as a base temperature, provided a valid tool for predicting the average timing of flowering and its regional variations for several species in Finland.

In this study, the connection between the spring-time thermal conditions and the timing of flowering of eleven plant taxa was analyzed using the effective temperature sum method. In previous studies (Lappalainen 1993, 1994), the method was initially tested and used in regional estimations of the onset of flowering in Finland. Another backgound for this study was that due to the inhomogeneity of the phenological data, spatial analysis could not be performed directly by using observed dates of flowering. Instead, the effective temperature sum method was used, and specified interpolation methods were needed to make estimates of temperature data at the phenological sites. The climate sensitivity of the timing of flowering was demonstrated by comparing the flowering phenology for the extremely warm test year 1921 with the climatologically normal period 1961–1990. The phenological maps of the extreme spring of 1921 offered a valid analogue to the possible future effects of climate warming on flowering phenology. Maps presenting isochrones on the long-term average occurrence of flowering highlighted the regional differences within southern and central Finland.

MATERIAL AND METHODS

Phenological observations

Phenological records co-ordinated by the Finnish Society of Science and Letters (Pipping 1927ab, Reuter 1928, 1935, 1936, 1937, 1941, 1942, 1948, 1952, 1957, Lönnqvist 1974) and standard climatological data co-ordinated by the Finnish Meteorological Institute were used as the study material. The onset dates for flowering were digitalized from these published records (Lappalainen & Heikinheimo 1992). The onset of flowering was defined as the date when 50% of flower buds had fully opened (Finnish Society of Science and Letters 1894, 1928). Eleven plant taxa were selected for the study, based on their geographical distribution, quality and abundance of observations (Table 1).

The phenological data from the period 1918 to 1955 were used. The years 1918–1955 were chosen because during that period phenological routines were well-established and 30–60 sites were available to keep continuous year-to-year records (Lappalainen & Heikinheimo 1992).

Estimation of daily temperature and the effective temperature sum (ETS) at the phenological sites

During the studied period 1918–1955 the number of climatological stations varied between 44 and 77. Most climate data available for the study took the form of monthly mean values. Daily temperature data, required for an accurate determination of the effective temperature sum, were available for Helsinki–Kaisaniemi (60°10´N, 24°57´E), Maarianhamina (60°07´N, 19°54´E), Jyväskylä (62°12´N, 25°43´E), Vaasa (63°03´N, 21°46´E), Joensuu (62°36´N, 29°46´E), Kajaani (64°17´N, 27°41´E) and Sodankylä (67°22´N, 26°39´E) for the period preceding the year 1955.

To obtain estimates of the ETS at the locations of the phenological sites, the available climate data was processed as follows. First, mean monthly temperatures, available from the climatological stations, were first interpolated spatially onto a 10 km × 10 km grid network by using the kriging method (Henttonen 1991). This grid resolution was considered adequate to characterise local climate conditions. The spatial interpolation scheme accounted for the possible conservative climate anomalies near lakes and sea coasts and at greater altitudes (as observed by the climatological station network) through an optimizing statistical procedure. Information on the areal coverage of the sea or lake surface and the altitude above sea level was available for each 10 km × 10 km grid. After obtaining the gridded values, the monthly mean temperatures at the location of each phenological site were estimated by taking a distance-weighted average of the nearest four grid squares.

Second, a smoothed seasonal pattern of daily mean temperatures, for each year and phenological site, was established using the interpolated monthly mean temperatures over the whole year and a temporal interpolation technique by Brooks (1943). Brooks' (1943) method assumes that for a period of three calendar months covering the data required, the values of the element in question can be represented by a sine curve with an annual period. In this study an actual annual record of daily mean temperatures was also obtained in this way for the seven 'reference' climate stations that had daily temperatures available in digital form. Estimates of 'unsmoothed' daily average temperatures at a particular phenological site were finally obtained by adding the difference of the smoothed daily temperatures between the phenological site and the nearest 'reference' climate station to the observed daily average temperature at the climate station. This procedure maximized the accuracy of the daily temperature estimates for the phenological sites.

The effective temperature sum (ETS) was defined as the sum of those daily mean temperatures (T_d) (measured in a standard meteorological screen) that exceeded the threshold temperature (T_b). Below that threshold the temperature was not considered effective.

$$ETS = \sum_{d=1}^{n}\left(T_d - T_b\right), \quad \text{if} \quad T_d \geq T_b \tag{1}$$

where n is the number of days for which $T_d \geq T_b$. In practice, the ETS was accumulated (i.e. the biological activity for leaf and flower bud development was thus assumed to proceed) on each day after 1 January when the daily average temperature reached + 5°C (see Sarvas 1972). The ETS were calculated up to the observed flowering dates at phenological sites. The base temperature + 5°C (T_b) was assumed applicable for the following taxa: birch (*Betula* spp.), arctic bramble (*Rubus arcticus*), bird cherry (*Prunus padus*), cowberry (*Vaccinium vitis-idaea*), marsh marigold (*Caltha palustris*), redcurrant (*Ribes rubrum*, coll.) and rowan (*Sorbus aucuparia*). These taxa flowered on average after 1 May. For species flowering very early in April, ETS values with a base temperature set at 5°C were still near the cut-off at zero. To overcome the difficulty of interpretation of very low ETS values, a threshold temperature of 0°C was used

Table 1. List of plant taxa selected for the study. The numbers of observation (N) are for the period 1918–1955 and the characteristic distribution in Finland is according to Hämet-Ahti *et al.* (1986).

Taxa	*N*	Distribution area
Trees		
Birch (*Betula pendula/pubescens* L.)	1 070	Abundant, rare in Enontekiö and Inari, Lapland
Bird cherry (*Prunus padus* L.)	1 421	Abundant, rare in Kittilä and Sompio, Lapland not found in Enontekiö and Inari, Lapland
Goat willow (*Salix caprea* L.)	1 050	Abundant, rare in Inari, Lapland
Grey alder (*Alnus incana* (L.))	1 120	Abundant, rare north of Kainuu
Rowan (*Sorbus aucuparia* L.)	1 325	Abundant, rare in Enontekiö, Lapland
Shrubs		
Redcurrant (*Ribes rubrum/spicatum*)	1 206	Abundant across country
Dwarf shrubs		
Cowberry (*Vaccinium vitis-idaea* L.)	1 124	Abundant across country
Herbs		
Wood anemone (*Anemone nemorosa* L.)	871	Abundant, rare in: Southern-Savo, Southern-Pohjanmaa, Northen-Häme, Northen-Savo, Northen-Karjala, not found north of these areas
Arctic bramble (*Rubus arcticus* L.)	856	Moderately abundant across country
Coltsfoot (*Tussilago farfara* L.)	1 010	Abundant, rare north of Keski-Pohjanmaa and Kainuu
Marsh marigold (*Caltha palustris* L.)	1 292	Abundant, rare in Enontekiö and Inari Lapland

for such taxa, i.e. grey alder (*Alnus incana*), coltsfoot (*Tussilago farfara*), wood anemone (*Anemone nemorosa*) and goat willow (*Salix caprea*).

Phenological maps based on the ETS

The ETS's corresponding to the start of flowering were first calculated for each phenological site which had at least five operational years within the period from 1918 to 1955. The long-term average of these ETS's were called the ETS-'requirements' for the specific species at that location. The ETS requirements were interpolated onto a 100 × 100-km grid to obtain sufficiently filtered values with a smooth spatial variation within the 10 km × 10 km grid. A detailed discussion of the statistics of the ETS requirements was given in Lappalainen (1994).

Phenological maps were prepared for the extremly warm test spring of 1921 and for the baseline climatological period 1961–1990. The isochrones (isolines of dates) presented on these maps were based on the climatological data, and the plotted values were averaged from phenological observations from the period 1918–1955. For the period 1961–1990 nearly 120 climatological stations with daily data could be used to calculate the ETS, giving sufficient spatial coverage for interpolation. No attempt was made to interpolate the relatively sparsely-located phenological observations. The differences in the long-term monthly mean temperatures in April and in May for the two periods (1918–1955 and 1961–1990) were only 0.0°C and 0.7°C, respectively (Table 2). It was therefore considered justified to compare the observed phenology for the period 1918–1955 with the ETS-based phenology for the period 1961–1990.

Isochrones were produced at 10-day intervals, giving sufficient spatial resolution considering the overall accuracy of the method. The analysis based on the ETS was not extended much beyond the network of operative phenological sites. Where phenological sites clustered too closely together, only the average values of these clusters were plotted on the maps, as indicated by larger dots.

The prediction accuracy of ETS

The prediction accuracy of the ETS method was determined both for the interannual variations at a single site and for the spatial variations within the observation network in a single year. One or the other of the phenological observation sites situated at Viitasaari (63°03´N, 25°50´E) or at Padasjoki (61°26´N, 24°56´E) was selected to test the prediction accuracy of the ETS for interannual variability. Viitasaari was selected as a test site because it represented one of the most active phenological observation sites and offered long continuous phenological records. Padasjoki provided qualitative observations for wood anemone, whose distribution did not reached as far north as Viitasaari.

The completely independent dataset from the years 1961–1965 was used to test the prediction accuracy for the geographical variation of phenological dates in a single year. This independent dataset was used because there was no need for long records as at a single site test. In addition, for this period, a relatively dense network of climatological stations providing daily temperature data was available. The ETS values for the phenological sites were taken from the nearest 10 km × 10 km grid point value obtained by kriging interpolation.

When using a long-term record of phenological data for a single site, the onset of flowering could be predicted to within 3–12 days depending on the plant taxa considered (Table 3). The best agreement was achieved for goat wil-

Table 2. Monthly mean temperatures (°C) for April and May in 1921, 1924 and for the periods 1918–1955 and 1961–1990 at Helsinki–Kaisaniemi, Vaasa, Jyväskylä and Sodankylä climatological stations (Keränen & Väisälä 1926, Keränen 1928, Ilmatieteen laitos 1991).

	1921	1924	1961–1990	1918–1955
April				
Helsinki–Kaisaniemi	6.8	0.4	3.1	2.9
Vaasa	5.3	– 0.9	1.7	1.4
Jyväskylä	7.1	0.0	1.6	2.1
Sodankylä	2.2	– 3.6	– 2.1	– 2.1
Average difference	6.4		0.0	
May				
Helsinki–Kaisaniemi	12.0	8.3	10.7	9.2
Vaasa	10.9	6.1	8.3	7.6
Jyväskylä	13.3	8.3	9.0	8.8
Sodankylä	8.1	4.2	5.0	4.9
Average difference	4.4		0.7	

low (*S.D.* = 3 days). The poorest predictability (12 days), was found for coltsfoot, flowering very early in March.

In the regional tests of ETS with station networks and for the years 1961–1965, the ETS concept worked best for bird cherry and rowan, providing an accuracy within 10 days in most cases (Table 4). Again, the flowering of coltsfoot could not be well predicted by using ETS (base 0°C). In conclusion, the ETS concept as used here had the same order of accuracy for a single site and for a network of sites. This prediction accuracy should be compared with the long-term inter-annual and spatial variability (see Fig. 3).

RESULTS

Sensitivity of flowering to variation in spring-time mean temperature

Results for the extremely warm spring of 1921 and the moderately cool spring of 1924 were analyzed to prepare the ground for conclusions with regard to the anticipated future. In 1921 the monthly mean temperatures in April were on average 6.4°C and in May 4.4°C higher than for the corresponding months in 1924. At Jyväskylä, chosen here to represent southern and central areas, the corresponding differences were 7.1 and 5°C (Table 2, Fig. 1). Since the start of the record in 1880, the April of 1921 was the warmest and the May the second warmest of all years. The year 1924 could be characterised as only moderately cool, ranking as the 13th coldest and the 41st coldest in terms of monthly mean temperatures for April and May, respectively. In terms of probability, the chances, in the climate of the present century, of having temperatures as high as those in spring 1921 are one in a hundred, while conditions such as those in spring 1924 would occur at least once a decade. The standard deviation of monthly mean temperatures for April within the

Table 3. The prediction accuracy of the ETS method tested against a single site, Viitasaari (36°03´N, 25°50´E) for the period 1930–1955. The records of Padasjoki (61°26´N, 24°56´E) for the period 1923–1943 were used for wood anemone. *N* = number of years, *R* = correlation coefficient, *S.D.* = standard deviation between observed and predicted dates in days.

Taxa	1930–1955		
	N	*R*	*S.D*
Marsh marigold	20	0.80	4
Bird Cherry	21	0.88	4
Redcurrant	20	0.74	6
Arctic bramble	20	0.66	6
Goat willow	20	0.85	3
Rowan	20	0.74	5
Coltsfoot	18	0.30	12
Grey alder	20	0.90	4
Cowberry	20	0.72	7
Wood anemone	20	0.79	5
Birch	18	0.80	7

* = the variation in *N* is related to missing years during the observation period.

Table 4. Prediction accuracy of the ETS method tested against single-year, multi-site phenological data sets. The test years 1961–1965 represented an independent period with respect to the average ETS requirements calculated for the period 1918–1955 (*N* = number of sites, *R* = correlation coefficient, *S.D.* = standard deviation between observed and predicted date).

Taxa	1961			1962			1963			1964			1965		
	N	*R*	*S.D.*	*N*	*R*	*S.D.*	*N*	*R*	*S.D.*	*N*	*R*	*S.D.*	*N*	*R*	*S.D.*
Marsh marigold	17	0.77	5	21	0.87	5	19	0.47	8	21	0.83	3	20	0.67	6
Bird Cherry	18	0.53	5	20	0.76	5	19	0.74	2	21	0.92	3	20	0.81	3
Redcurrant	15	0.60	6	17	0.74	6	17	0.55	3	19	0.86	4	17	0.59	7
Arctic bramble	13	0.87	3	15	0.81	7	17	0.41	3	14	0.12	7	16	0.50	5
Goat willow	13	0.69	7	15	0.68	9	16	0.75	3	17	0.60	6	15	0.55	6
Rowan	17	0.85	3	19	0.60	6	19	0.88	3	20	0.76	4	17	0.56	3
Coltsfoot	14	0.41	16	18	0.69	9	14	0.82	6	17	0.60	9	17	0.10	10
Grey alder	10	0.03	18	19	0.67	9	16	0.85	3	18	0.64	5	12	0.67	5
Cowberry	17	0.90	3	15	0.69	7	19	0.89	4	16	0.52	7	18	0.78	5
Wood anemone	13	0.79	6	14	0.70	7	11	0.72	7	10	0.64	5	10	0.63	9
Birch	30	0.61	5	15	0.73	7	12	0.56	5	20	0.46	5	13	0.27	11

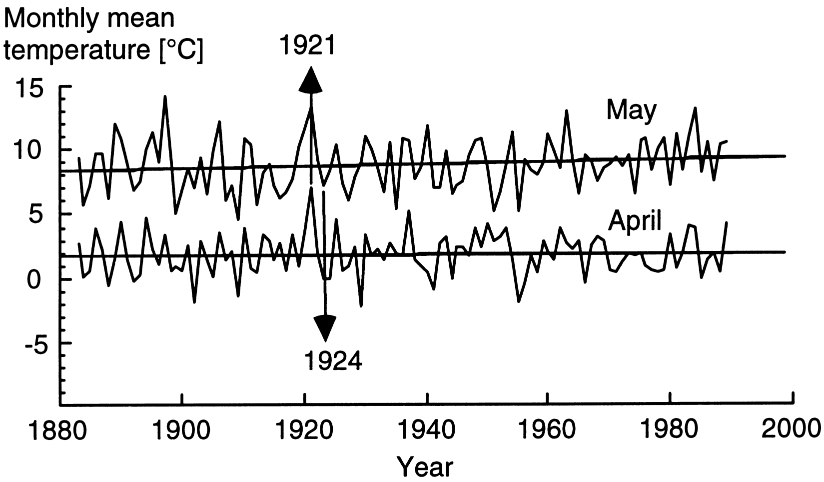


Fig. 1. Year-to-year variation in monthly mean temperatures in April and in May at Jyväskylä, representing southern and Central Finland.

period 1880–1990 was 1.6°C, and for May 2.0°C, i.e. the climatic variability for May can be quantified as *S.D.* = ± 2.0°C. The difference in monthly mean temperatures between 1921 and 1924 was (≈ 5°C) of the same order of magnitude as twice the *S.D.* of monthly mean temperatures. Scenarios for the future climate in Northern Europe indicate a warming of 1 ± 0.5 degree per decade (see Carter *et al.* 1995).

The question was then examined as to how years similar to the two test years would rate in terms of their anomaly with respect to, e.g., a 2°C warmer base-line climate. With the 2°C warming, expected to occur during the first half of the 21st century, the present (1880–1990) mean temperature at Jyväskylä in May would change from 8.8°C to 10.8°C. Providing that the climate variability remains unchanged, i.e. the 2.0°C standard deviation for mean monthly temperatures also holding for the warmer climate, moderately cool years such as 1924 would become less frequent cold years, while years similar to the extremely warm year 1921 in the present climate would become more frequent warm years in the warmer climate. In consequence, plant species adjusted to the present climate would need to readjust to more frequently-occurring extremely warm years and less frequently-occurring cool years.

In terms of the occurrence of flowering, the calculated mean difference in calendar dates between the years 1921 and 1924 for obtaining an arbitrarily-chosen 100 day degrees (d°) ETS requirement at the Jyväskylä station was 27 days (Fig. 2). The corresponding difference based on the phenological observations of many species and at many sites gave a difference of 25–30 days. Estimates of sensitivity based on ETS are therefore in agreement with observations, considering the overall accuracy of not better than about ± 3 days (Table 3) to which the start of flowering could be determined.

In light of the above, it was reasonable to evaluate the consequences of a 2°C warming (with preservation of a ± 2°C in monthly mean temperatures) on the phenology of flowering as demonstrated in Fig. 2. Taking the ETS requirement for the onset of flowering to be of the order of 100 d°, a mean warming of 2°C would enhance development on average by 9 days, while the year-to-year fluctuation range would remain at about 18 days (Fig. 2).

Regional variation

Maps presenting isochrones of the date were used to demonstrate the progress of flowering geographically (Fig. 3). For many species the spatial coverage of the observation sites was insufficient to allow analysis over the whole distribution area and to demonstrate local features. Isolines were therefore based on ETS rather than on observed dates. For comparison, isolines based on the ETS and on observed flowering dates at phenological sites for the corresponding year and period were plotted on the same map.

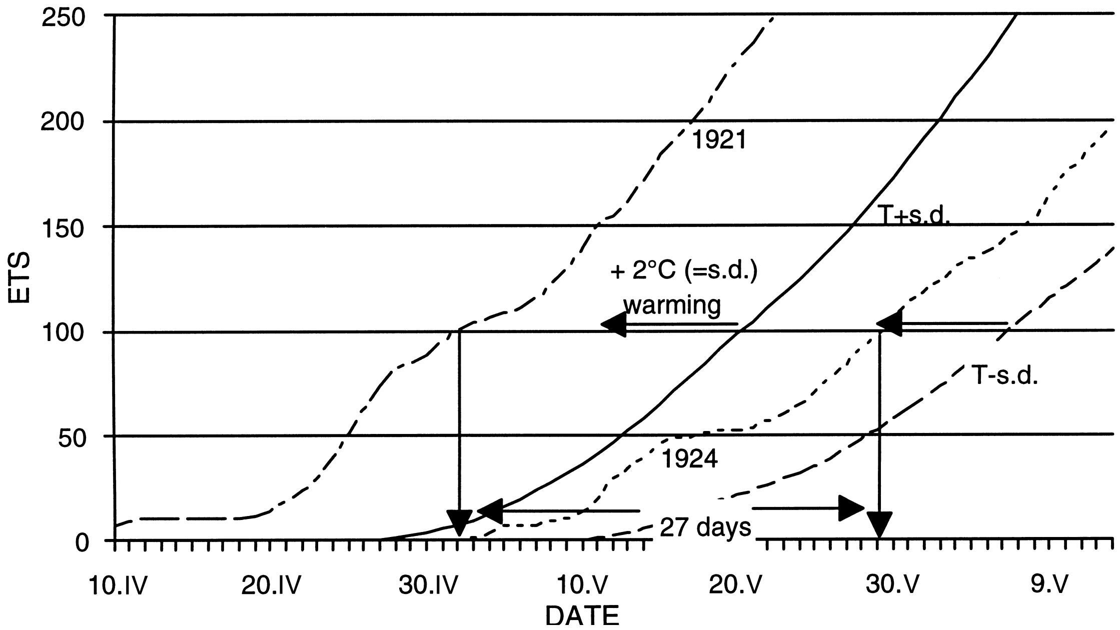


Fig. 2. Development of ETS during 1921 and 1924 and during years which are on average one *S.D.* unit (+ 2°C) warmer or one *S.D.* unit (– 2°C) colder than the average climatological year, where *S.D.* is the standard deviation of monthly mean temperatures. The curves are based on climatological data for the Jyväskylä Airport in Central Finland. Mean climatological data were taken from the period 1961–1990. As an example, the 100 ETS limit is reached within 18 days for a ± 2°C *S.D.* variation in temperature, while the corresponding difference in predicted phenological dates between 1921 and 1924 is 27 days.

In spring 1921, which was the warmest during the period of climate data considered, flowering occurred nearly one month earlier than average for the base-line periods 1961–1990 or 1918–1955. Flowering normally proceeded from south to north or from south-west to north-east, with a delay observed for most species along the coast of the Baltic Sea. The progress of flowering with latitude was highly variable, but was estimated at about 200–300 km/10 days on average.

The phenological observations and the ETS-based estimates of phenological dates were generally in agreement. The agreement was better for the test in which ETS-based dates for the base-line period 1961–1990 were compared with the phenological observations from the period 1918–1955 than for a corresponding test for the anomalous year 1921.

Herbs which grow near the ground, such as wood anemone, arctic bramble, coltsfoot and marsh marigold, formed their own group in this study. They were strongly affected by microclimatological conditions. This was demonstrated by comparing flowering patterns and actually observed dates. For instance, for coltsfoot the observed dates between closely adjacent sites varied by several days.

DISCUSSION

Effective temperature sum (ETS) was used here as the single environmental factor to explain spatial and temporal variation in the timing of the flower bud burst on some selected deciduous trees, shrubs and herbs flowering in spring. With the ETS, the date of flowering could be estimated to within 3–7 days for species flowering in May. For very early flowering species, the accuracy of estimated flowering dates was somewhat poorer, but within 7–14 days in most cases. This accuracy is, however, quite satisfactory when compared with the even larger temporal and spatial variation of phenology over a wide latitude range and with

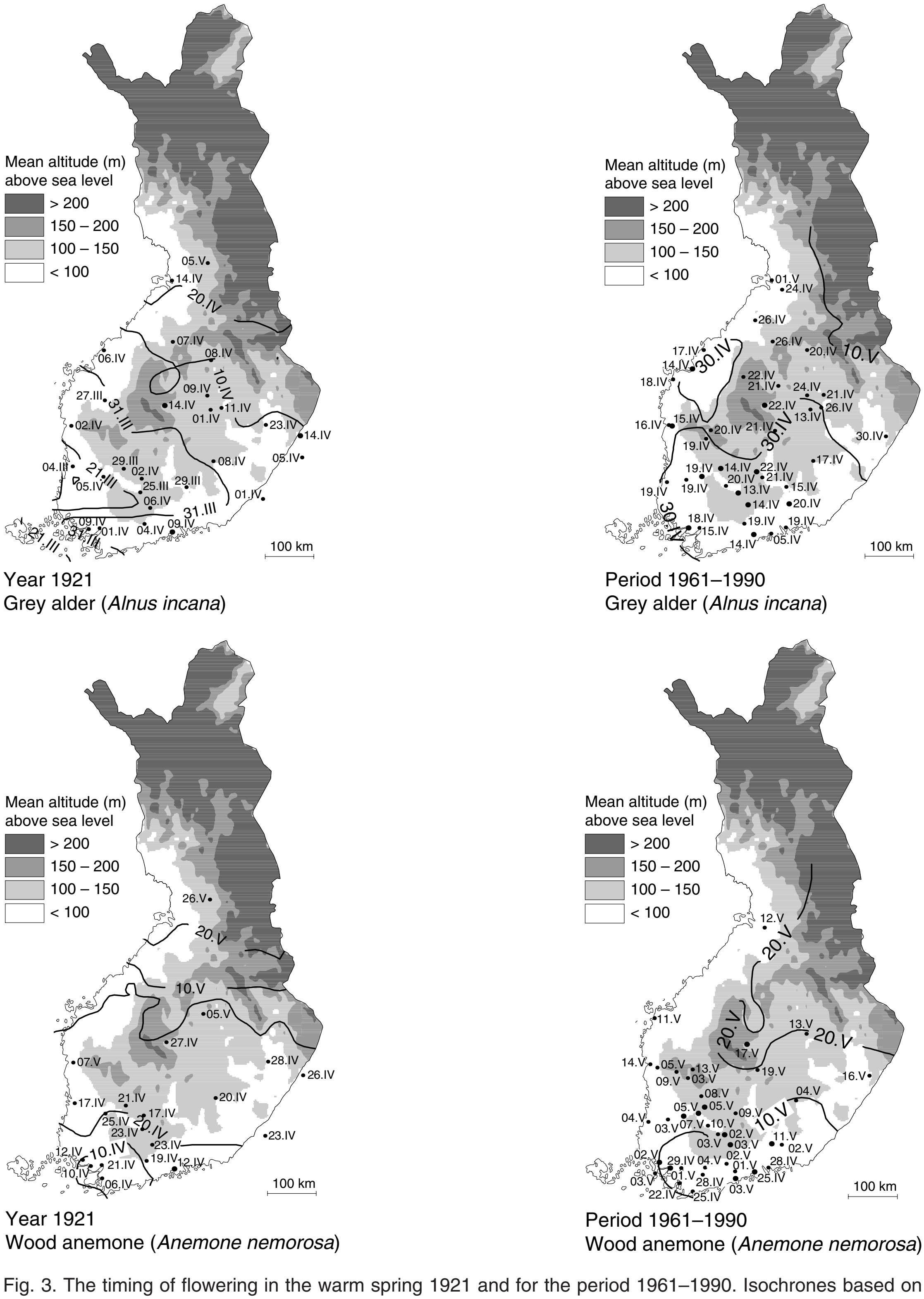
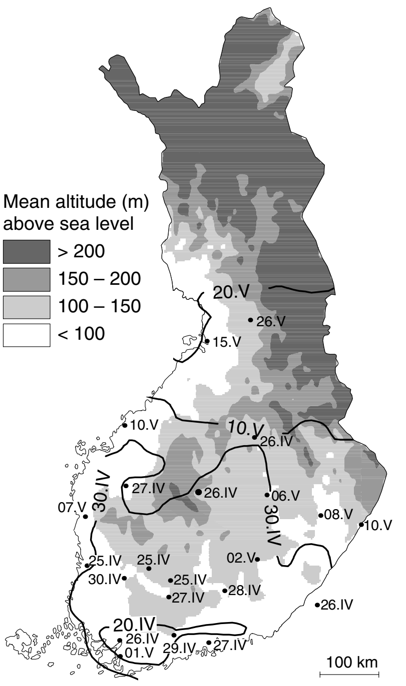
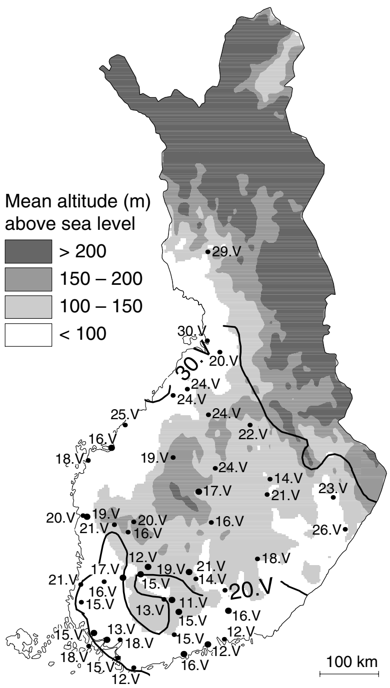


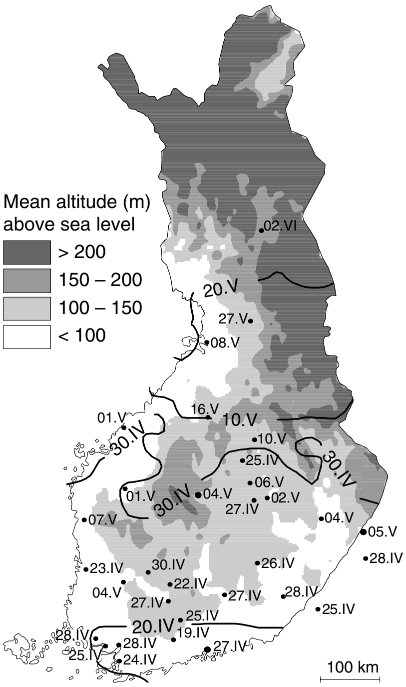
Fig. 3. The timing of flowering in the warm spring 1921 and for the period 1961–1990. Isochrones based on taxa-spesific effective temperature sum requirements and plotted values were averaged from phenological observations for the year 1921 and for the period 1918–1955.



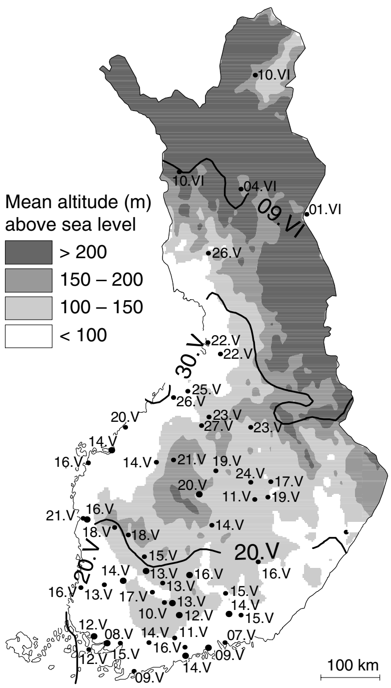
Year 1921
Birch (*Betula pendula/pubescens*)



Period 1961–1990
Birch (*Betula pendula/pubescens*)



Year 1921
Marsh marigold (*Caltha palustris*)



Period 1961–1990
Marsh marigold (*Caltha palustris*)

Fig. 3. Continued.

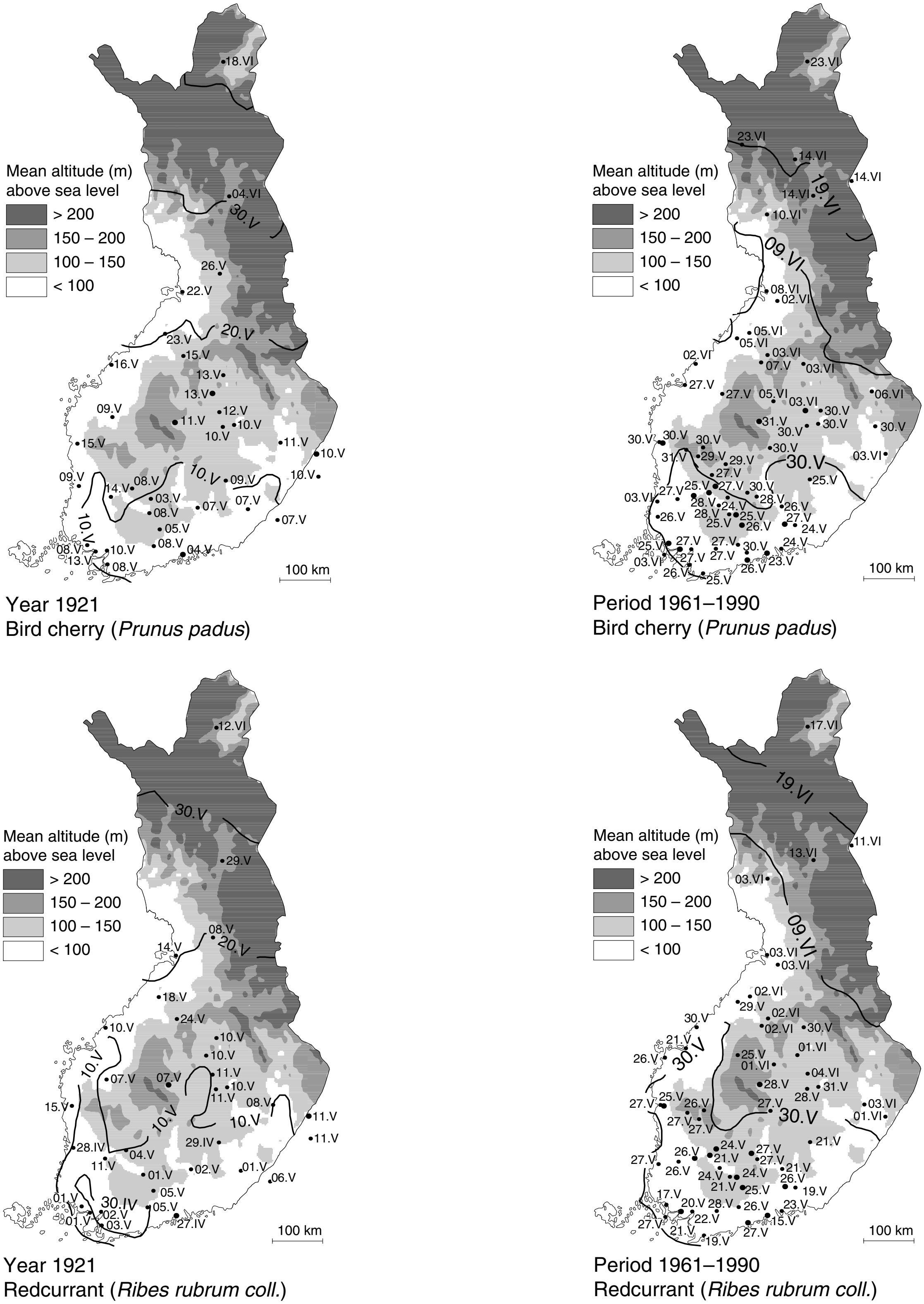
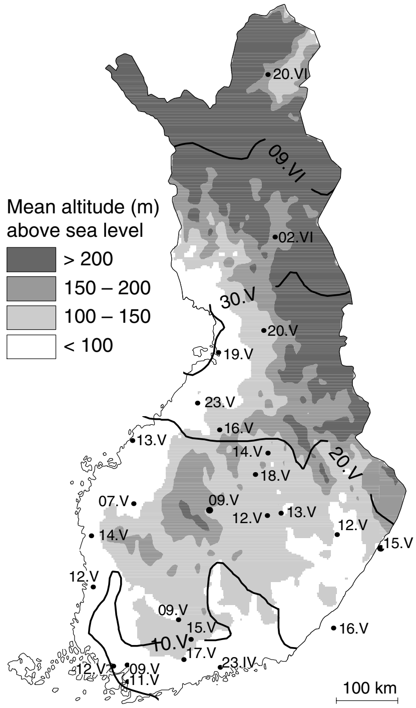
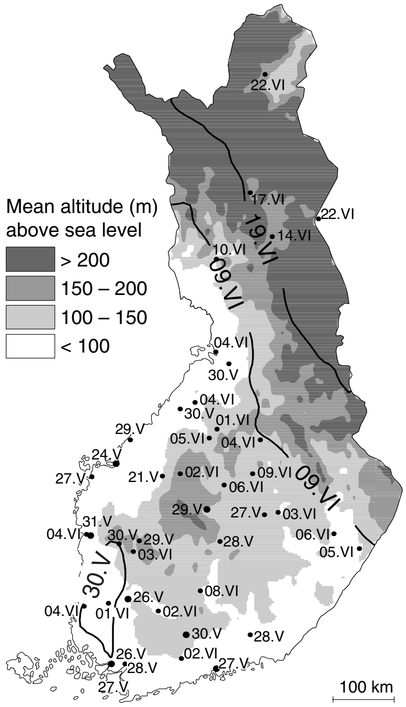


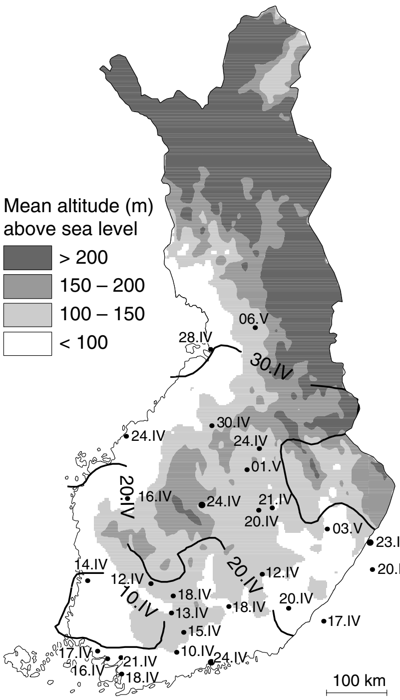
Fig. 3. Continued.



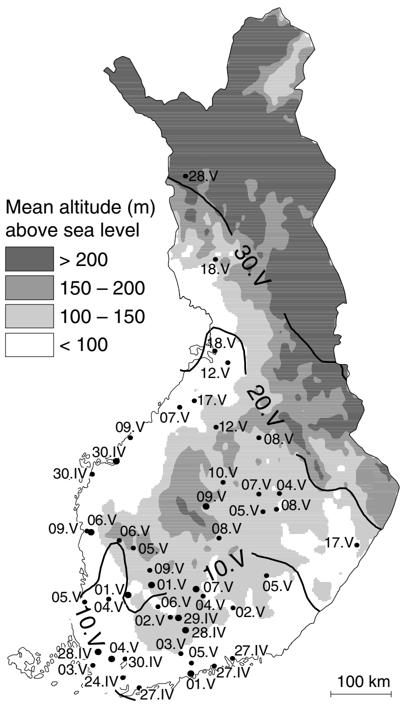
Year 1921
Arctic bramble (*Rubus arcticus*)



Period 1961–1990
Arctic bramble (*Rubus arcticus*)

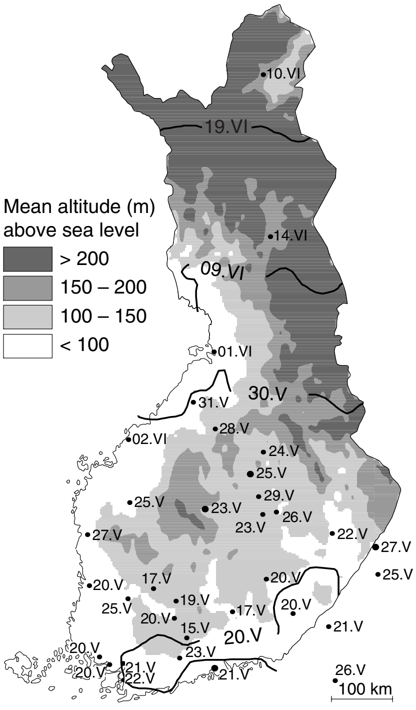


Year 1921
Goat willow (*Salix caprea*)

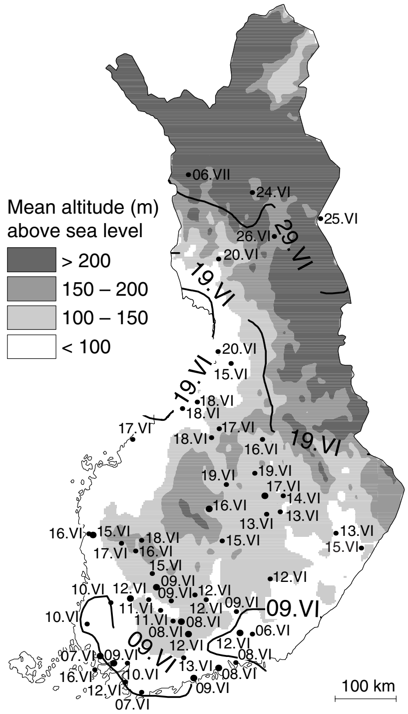


Period 1961–1990
Goat willow (*Salix caprea*)

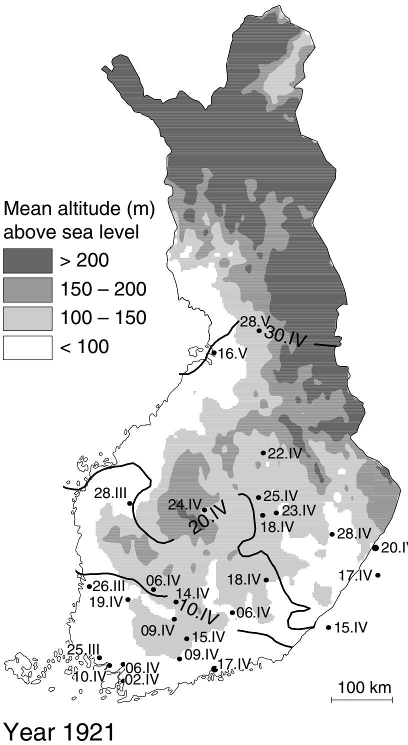
Fig. 3. Continued.



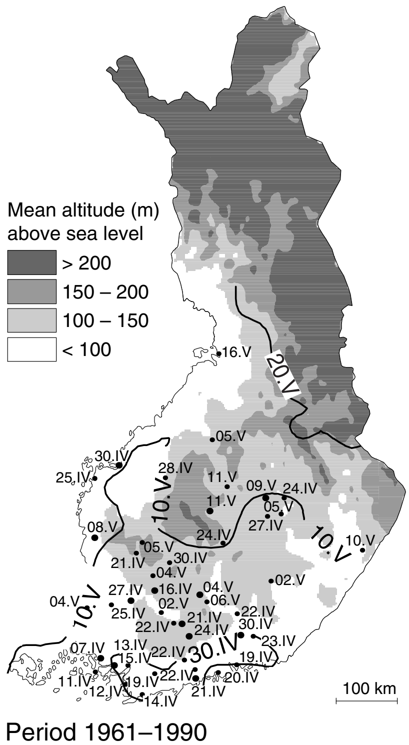
Year 1921
Rowan (*Sorbus aucuparia*)



Period 1961–1990
Rowan (*Sorbus aucuparia*)

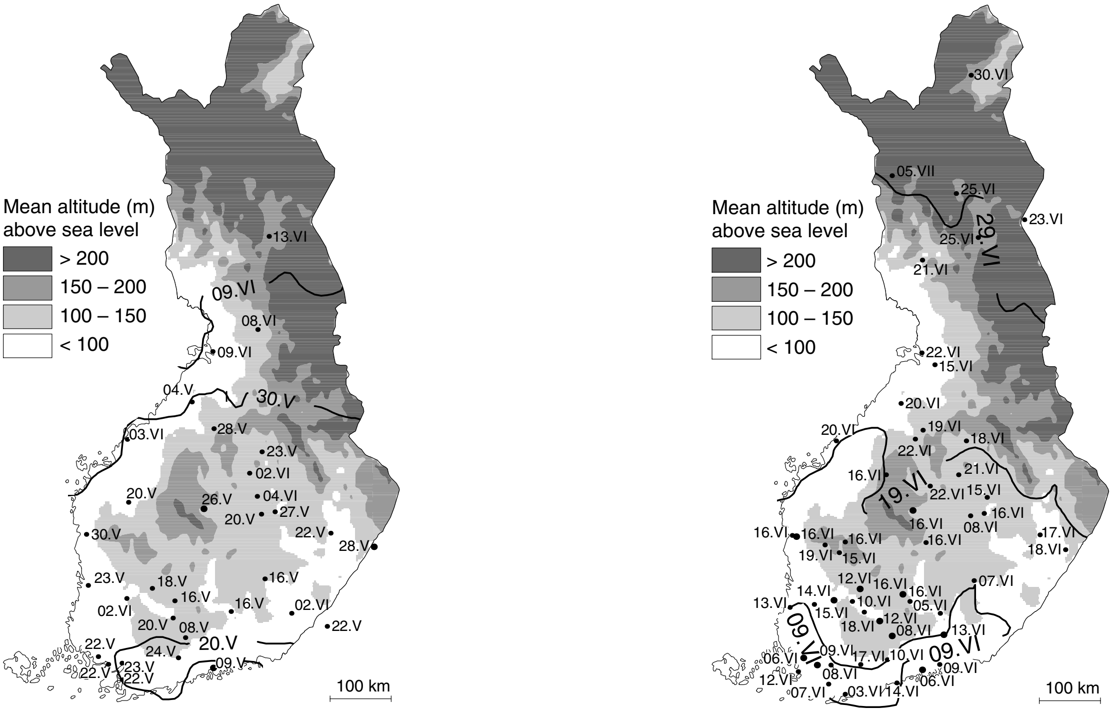


Year 1921
Coltsfoot (*Tussilago farfara*)



Period 1961–1990
Coltsfoot (*Tussilago farfara*)

Fig. 3. Continued.



Year 1921
Cowberry (*Vaccinium vitis-idaea*)

Period 1961–1990
Cowberry (*Vaccinium vitis-idaea*)

Fig. 3. Continued.

contrasting maritime and continental climates, such as is found in Finland. Phenological maps, which were in relatively good agreement with observations, could therefore be constructed using an ETS calculated from meteorological data alone. In contrast, such analyses can appear rather difficult when based solely on phenological observations, because the number of sites is often too small and there are inconsistencies due to varying observation practices.

The study showed that it was necessary to allow for the spatial variation of the ETS requirement. Earlier studies have indeed shown that the response to effective temperature sum can vary regionally; e.g. Beuker (1994) concluded from provenience experiments with Scots pine (*Pinus sylvestris*, L.) and Norway spruce (*Picea abies*, L.) that origins from higher latitudes attained needle bud burst earlier (i.e. at a lower ETS) than those from lower latitudes when the different origins had been grown at the same site over a period of many decades. There was only weak correlation between ETS requirement and mean summer temperature, when origins from low latitude and high altitude sites, and over a wide latitudinal range, where included. This suggests that the decrease in the ETS requirement towards higher latitudes implicitly accounts for the effect of day length on plant development, rather than being merely an effect of decreasing mean temperature.

In a preceding study, Lappalainen (1994) demonstrated, that coastal populations reach flower bud burst at a lower ETS than populations grown in close-by inland regions. Over such short distances the difference in ETS requirement can only be explained by the difference in local climate characteristics: during spring, coastal areas tend to be cooler and sunnier and the diurnal temperature range smaller than at locations further inland. These findings were in agreement with Sarvas (1972), who showed that development towards flowering could occur even in below-zero temperatures. Due to the sunnier conditions, vegetation attains higher surface temperatures compared with air temperature than under the more cloudy conditions typical of inland areas — all these effects resulting in an enhanced development of flower buds for a given mean air temperature.

The assumption that bud development is linearly proportional to ETS could have limited the prediction accuracy, particularly during very early springs, and could also have contributed to the lower ETS requirement found in coastal areas. For instance, Anstley (1966) reported that most errors in predictions based on ETS are caused by very warm days (mostly lacking at coasts during spring) having less effect on development than calculated.

It is appreciated that many other factors could have caused variation in the ETS requirements. These include the effects of soil moisture variation, differences in genotype, and different subjective practices by the observers; all of these are difficult to assess from the historical material used here. Nevertheless these factors were considered to cause only random variation in the observation data, mostly uncorrelated with temperature effects.

The temperature range for which the linearity assumption may be valid is also limited, depending too on the species studied; the lower threshold is known to vary from about 0°C to about 10°C for some mid-latitude and tropical crops (Arnold 1959), but is commonly taken as + 5°C (or + 6°C) by convention (Monteith 1981). In high latitudes, the use of + 5°C as a threshold for spring-time development is justified on the basis that the soil remains frozen (or even snow-covered) until the air temperature has permanently risen well above freezing.

Effects of dormancy release were excluded for simplicity and on the basis of the relatively cool climate of the region considered. Lack of winter dormancy may, however, become an important factor under warmer climate conditions (Hänninen 1990). The implications of the anticipated climate warming for spring time flowering, given here, should therefore be regarded with caution, and this problem should be further investigated with comprehensive ecological models. Nevertheless, the long-term phenological records, collected during the present century, remain a valuable source of data against which future models should be verified and/or calibrated.

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