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ALPO LUOMAJOKI

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(*PICEA ABIES* (L.) KARSTEN) IN FINLAND
BASED ON MALE FLOWERING PHENOLOGY

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HEDEKUKKIMISAIKOJEN PERUSTEELLA ARVIOITUNA

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Anthesis was studied at the canopy level in 10 Norway spruce stands from 9 localities in Finland from 1963 to 1974. Distributions of pollen catches were compared to the normal Gaussian distribution. The basis for the timing studies was the 50 per cent point of the anthesis-fitted normal distribution. Development up to this point was given in calendar days, in degree days (>5°C) and in period units. The count of each parameter began on March 19 (included). Male flowering in Norway spruce stands was found to have more annual variation in quantity than in Scots pine stands studied earlier.

Anthesis in northern Finland occurred at a later date than in the south. The heat sums needed for anthesis varied latitudinally less in spruce than in pine. The variation of pollen catches in spruce increased towards north-west as in the case of Scots pine. In the unprocessed data, calendar days were found to be the most accurate forecast of anthesis in Norway spruce both for a single year and for the majority of cases of stand averages over several years. Locally, the period unit could be a more accurate parameter for the stand average. However, on a calendar day basis, when annual deviations between expected and measured heat sums were converted to days, period units were narrowly superior to days.

The geographical correlations respect to timing of flowering, calculated against distances measured along simulated post-glacial migration routes, were stronger than purely latitudinal correlations. Effects of the reinvasion of Norway spruce into Finland are thus still visible in spruce populations just as they were in Scots pine populations.

The proportion of the average annual heat sum needed for spruce anthesis grew rapidly north of a latitude of ca. 63° and the heat sum needed for anthesis decreased only slighty towards the timberline. In light of flowering phenology, it seems probable that the northwesterly third of Finnish Norway spruce populations are incompletely adapted to the prevailing cold climate. A moderate warming of the climate would therefore be beneficial for Norway spruce. This accords roughly with the adaptive situation in Scots pine.

Kuusen siitepölyn irtoamisen eli anteesin ajoittumista tutkittiin vuosina 1963–1974 puiden latvustasolla 10 metsikössä 9 paikkakunnalla. Kuusen kukinnan vuosien välinen vaihtelu osoittautui suuremmaksi kuin aiemmin tutkitun männyn. Siitepölyn takertumien perusteella saatuja jakaumia verrattiin normaalijakaumaan.

Ajoittumisen perusteeksi otettiin jakauman 50 % kohta ja sitä mitattiin päiväasteikolla, tehoisalla lämpösummalla (>5°C) ja period unit -yksiköllä. Etelä-Suomeen verrattuna kuusen anteesi oli odotetusti Pohjois-Suomessa myöhemmin. Anteesin vaatima lämpösumma ei kuusella vaihdellut leveysasteen mukaan yhtä paljon kuin männyllä. Siitepölykertymän hajonta kasvoi luoteeseen päin mentäessä niin kuusella kuin männylläkin. Päiväasteikko osoittautui kuuselle keskimäärin tarkimmaksi yksiköksi (toisin kuin männyllä), kun mitattuja arvoja käytettiin sellaisenaan. Paikallisesti period unit -lämpösumma oli toisinaan kuusellekin tarkin. Jos lämpösummien erot odotetun ja mitatun arvon välillä muutettiin päiviksi ja koko vertailu tehtiin päiväasteikolla, period unit oli kuitenkin tarkin parametri.

Jääkauden jälkeistä leviämisreittiä pitkin mitatut kukinnan ajoittumista koskevat maantieteelliset korrelaatiokertoimet olivat molemmilla lajeilla suuremmat kuin puhtaasti latitudinaaliset kertoimet. Kuusen aivan kuten männynkin jääkauden jälkeisen leviämisen jäljet näkyvät siis yhä puupopulaatioissa.

Anteesin vaatiman suhteellisen lämpösumman (Linsserin osuus) perusteella arviotuna kuusen niin kuin männynkin sopeutuminen ilmastoon heikkenee jyrkästi noin 63. leveyspiirin pohjoispuolella, mutta kuusen anteesiin tarvittava lämpösumma pienenee aina metsänrajalle mennessä vähemmän kuin männyllä.

Kukkimisaikojen perusteella voidaan havaita, että luoteinen kolmasosa Suomen kuusimetsistä on tällä hetkellä vaillinaisesti sopeutunut vallitsevaan ilmastoon ja että ilmaston lämpeneminen parantaisi kuusen elinmahdollisuuksia Pohjois-Suomessa.

CONTENTS

Application and abbreviation of some terms

Active period. The period when a tree is not dormant (Sarvas 1972).

Annual heat sum. The gross degree-day sum of the whole growing season.

Anther residues. Shed microstrobili sampled in funnels at the stand and dried and weighed to quantify male flowering (see Koski & Tallqvist 1978).

Anthesis. The time of dehiscence of microsporangia and pollen dispersal.

Autumn dormancy. Precedes winter dormancy; it is the period when chilling is effective. Sarvas (1974) used this term.

Biofix. Practically identical to zero point. Means simply a starting point for heat sum counting.

Coefficient of variation (CV).

Degree day (d.d.). A linear heat sum unit based on daily mean temperature minus the base temperature. A base temperature of +5°C was adopted, so the d.d. sum grows daily by (1–5) d.d.'s.

Ecological latitude. Altitude can be simulated at sea level by a shift towards the north by comparing latitudinal monthly temperature differences to the vertical temperature gradient. The ecological latitude expresses the combined effects of the latitude and the altitude in a single figure.

Growing season. The part of the year during which the daily mean temperature stays above +5°C.

Heat sum. The number of any defined units accumulated under the joint effect of time and temperature.

Homogeneity condition. A curvilinear regression can simulate thermal reactions of a physiological process as long as the reaction remains the same. This is not exactly true for long periods (cf. Wang 1960). Relatively long periods of more or less homogeneous development can more readily be found in generative development than in vegetative growth.

Linsser's law. Linsser (1867) held that the relative heat sum needed for a given stage of development should, in well-adapted populations, remain the same at any locality when weighted by the average annual heat sum of that locality.

Migration distance. In this context means the distance between two points on the earth calculated by spherical trigonometry. The true distances in reinvasion of trees were necessarily longer.

Number of antheses (n). Number of antheses studied (years/stands). For the significance tests of correlation coefficients, n–2 degrees of freedom were adopted, and for partial correlation coefficients n–3 d.f. were used.

Period unit (p.u.). Progress in development within one hour at 10°C is equivalent to 5 period units according to Sarvas (1972). This curvilinear regression is limited to the active period. In this study, the period unit is considered as a heat sum unit, even though Sarvas (1972, p. 67) did not consider it as such, as no threshold is used in p.u.'s as in conventional heat sums.

Significance levels. The following abbreviations are employed to represent the significance of correlation coefficients: almost significant, $p < 0.05 = *$; significant, $p < 0.01 = **$; highly significant, $p < 0.001 = ***$

Standard deviation (SD).

Sunhours. The day length according to the almanac, i.e. according to the upper edge of the sun. It is longer than the astronomical day length.

Temperature sum. Identical to heat sum.

Within-year variation (of anthesis). The character of the basic pollen catch distribution curve. This is visible on probability paper as the gradient of the line fitted to the accumulation pattern of daily pollen catches. It is measured by the standard deviation of the distribution.

Zero point. The onset of either the active period or winter dormancy. While this concept is somewhat theoretical, it means the relatively rapid physiological change from one major phase of the annual cycle to another. Sarvas (1974) considered the onset of winter dormancy as the zero point of the entire annual cycle.

Preface

1. Introduction

Methods for phenological studies have improved from the earliest simple observations of the onset to completion of flowering to comprehensive investigations covering the whole suite of flowering sequences (Sarvas 1972). Dedicated pollen monitoring and temperature measurement equipment for use at study sites have long been available.

For a phenological study in northern, partly marginal areas, it is essential to pay attention to the annual variations in climate. Temperatures in Finland varied such that in southernmost sample stands the average annual heat sum over the thirty year period from 1951 to 1980 was 1340 degree-days (over 5°C), with 1 per cent probability for single years being close to 1000 and 1700 d.d., respectively. In the region of the northernmost spruce stand the average was 700 d.d., with 1 per cent probability for single years being at ca. 400 and 1100 d.d., respectively, as calculated from database of Ojansuu & Henttonen (1983). Annual variation in temperature sums was also relatively greater in the north than in the south (see Luomajoki 1993).

The aim of this study is to analyze the geographical variation found in pollen catch and in the timing of anthesis in Norway spruce. The route of reinvasion of Norway spruce into Finland after the last glaciation is largely known (Aartolahti 1966, Tolonen 1983). Is the route still visible in the pattern of the phenological characteristics of anthesis? My further aim is to study the amount of phenological variability in the northern marginal stands and the effect of annual temperature sums of the previous two years on the timing of flowering and on amount of pollen production. The geographical adaptability of the generative cycle to local climate will be appraised by Linsser's law (Linsser 1867).

The efficacy of two temperature sum systems, a linear and a curvilinear one, was compared with simple calendar time as delineators of generative development. The investigation addresses the following questions: How do the phenological characteristics of flowering in Norway spruce compare to those in Scots pine? Are the geographical correlations similar in magnitude and direction? Is the amount of measurable adaptation the same?

Is there any benefit in using the idealized pollen distribution curve mean as a reference compared to simple observations of the day of peak pollen catch? The effect of a possible change in climate in future will also be evaluated.

To answer these questions, the geographical variation of pollen catches measured, the variation in the timing of anthesis and the within-year and the between-the-years variations involved were used.

2. Material and methods

2.1 Pollen registration

This study concentrates on the features of male flowering at anthesis in Norway spruce stands (Table 1, Fig. 1) in Finland from 1963 to 1974. The material was collected at the former Department of Silviculture of the Finnish Forest Research Institute. Similar studies were made in the 1950's and early 1960's, but in 1963 a more reliable model of pollen registering equipment was available.

The material consists of 85 complete registrations of antheses (years/stands) from 1963 to 1974 in 10 stands. No single stand was studied in all of the twelve years of the period from 1963 to 1974, but two stands were studied in eleven consecutive years and 7 stands from 1966 to 1969 (Table 1). The mature stands of at least a few hectares were classified as normal stands for pollination (see Sarvas 1962). They had been subjected to silvicultural thinnings in the normal way. Antheses were measured in each stand at tree-top level by 1 to 3 self-recording pollen samplers (mod. Sarvas-Vilska 1963, see Sarvas 1968). Three samplers was the ideal not always met, while two were normally used. The mean of daily pollen catches was used in calculations where more than one sampler were used. A thermograph was also placed at tree-top level in each stand, except for one occasion, stand Kittilä III in 1965. The accuracy of meters was checked two to three times a day.

The pollen catch was microscopically counted from the recording bands and the results were prepared in terms of daily catches of the recorders, catch averages, cumulative sums and cumulative percentages of the pollen catch as illustrated by Sarvas (1972). The ascending cumulative percentages were then plotted with the aid of a computer program. The ordinate scale was a Gauss integral and the abscissa scale was linear (probability paper). The abscissa showed the cumulative temperature sum at the end of each day (corresponding to the measurement of the cumulative pollen catch).

A normal distribution is represented as a straight line on probability paper. Lines of best fit within the interval from minus 2 standard deviations to plus 1.2 standard deviations over the mean (from 2.3 to 88.5 per cent) were drawn by SYSTAT/ SYGRAPH© Multivariate General Linear Hypothesis computer program. (Observe mistake by the author (Luomajoki 1993 p. 8) in this very connection in a paper on Scots pine: instead of "standard deviation", "normal distribution" was erroneously used.)

The cumulative daily catches, considered as percentages of the total catch, approximately lie (on probability paper) on a single line, indicating
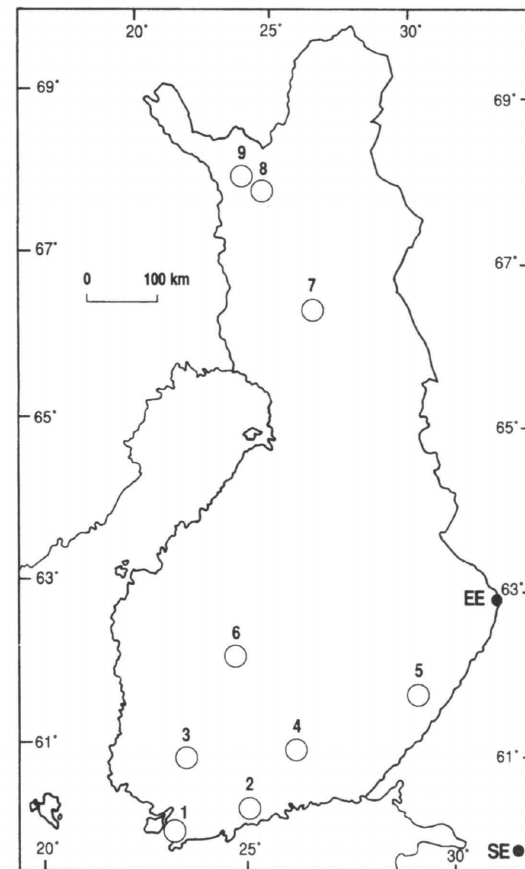

Fig. 1. Localities of the anthesis materials studied. One to two experimental stands (see Table 1) were studied at each locality which were in latitudinal order: 1. Bromarv (annexed in 1977 to Tenhola parish and later to Tammisaari in 1993), 2. Tuusula, 3. Jokioinen, 4. Heinola, 5. Punkaharju, 6. Kuorevesi, 7. Rovaniemi, 8. and 9. Kittilä. The distance between localities 1. and 9. is ca. 890 km. EE and SE are reference points for calculations of migration distances.

Table 1. Stand characteristics and years of study.

Stand	Locality	Latitude	Longitude	Elevation, m	Age, years in 1970	Years of study	Years of min. pollen catch	Remarks on stand
Bromarv I	1	60°02'	23°05'	27	126	1963–73	1963, 68	Clear cut in 1976
Heinola 566	4	61°08'	26°02'	113	120	1966–71		
Jokioinen I	3	60°50'	23°30'	106	51	1966–73		
Kittilä III	8	67°44'	24°50'	230	84	1965, 67–69, 71	1968	No temperature measurement in 1965
Kittilä, Pallas IV	9	68°02'	24°09'	275	172	1963, 65–73	1963, 66, 69	
Kuorevesi XXXV	6	62°01'	24°48'	110	110	1965–71		
Punkaharju LII	5	61°49'	29°20'	92	96	1964–74	1972, 74	Origin Finland, Lammi. Clear cut in 1975–76
Rovaniemi XVIII	7	66°21'	26°40'	182	127	1963–73	1963, 66, 68, 72	
Tuusula XXX	2	60°21'	25°02'	53	91	1964–73	1968, 72	
Tuusula XXXIV	2	60°22'	24°59'	50	67	1967–73		400 kg urea/ha given in winter 1967–68

Plot numbers come from the former Dept. of Silviculture, part of Dept. of Forest Production from 1992. All origins are local except for Punkaharju LII.

a nearly normal distribution. However, the early and the late observations usually deviate from normality, so that the first percentages are slightly larger than expected while the last ones are smaller than expected (Fig. 2).

Omitting the tails of the distribution that deviate from normality seemed justifiable because a line with a closer fit using central points (percentages) near the mean was achieved, thus eliminating the effects of secondary pollen. The standard deviation was apparent from the computed line of best fit, so a measure for the variation within a single anthesis was obtained. The mean (the 50 per cent point of the theoretical distribution) itself was unaffected by the dispersion; it was unbiased.

2.2 Temperature data

The matching temperature data from thermographs located at tree-top level in the stands were processed to give two kinds of temperature sums used as phenological parameters. The first was a daily degree-day sum (over +5°C) and the other a more specialized hourly temperature sum that obeys a curvilinear regression. That regression was developed by Sarvas (1972) by the means of generative plant material forced at various temperatures. He named the new unit a "period unit".

The mean of each anthesis was initially determined as a period unit sum. The daily accumulation of p.u.s was computer-tabulated at intervals of two hours for all the stands and years of study, and the relevant degree-day heat sums and dates were also read from the computer sheet. Three interchangeable measures (phenological parameters) of the mean of each anthesis were thereby generated. The parameters can be compared in Table 2a and 2b: each coefficient of variation is a measure of the between-years variation. Lack of stand-specific temperature measurements caused the rejection of one observation cycle from timing data (Kittilä III in 1965). The most extreme onset and termination dates of antheses are also presented standwise in this table.

A rather arbitrary zero point (biofix) was chosen for this study in order to match (and include) the first day with a 12 hour photoperiod (sun-hours measured from the upper edge of the sun), i.e. the 19th of March, close to the (mathematical) vernal equinox. Earlier starting dates were impossible owing to shortcomings of early temperature data. The data in certain cases had to be supplemented with the temperature recordings taken from near-by stands. With regard to the timing of anthesis, all dates after March 19th produce larger variations in the temperature sum data.

The zero point chosen did not affect the degree-day data (i.e. the biofix was not effective), but it did reduce the period unit sums in southern Finland in certain years when the onset of spring was early.

The date for the 50 per cent point of the theoretical pollen distribution can be compared with the peak pollen catch day. The relative value of
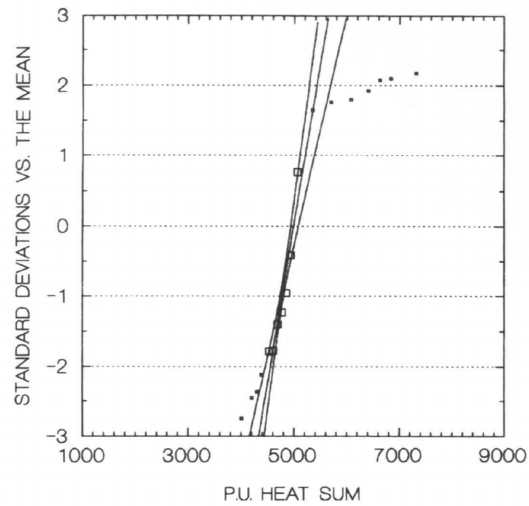
Fig. 2. The cumulative distribution of daily pollen catches at Bromarv stand I in 1972, with confidence limits at a probability level of 95 per cent. The central larger squares are used to position the line and the smaller ones are excluded beyond the limits of −2 and +1.2 standard deviations (see Chapter 2.1).
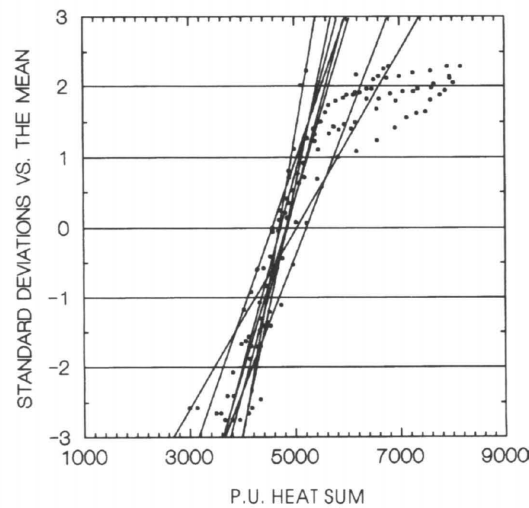

Fig. 4. The cumulative pollen catches at Jokioinen in 1966–1973. Points between −2 to +1.2 standard deviations were used to position the lines. Catches beyond these limits are also shown. The effects of refloated pollen in the upper region (beyond the +1.2 SD limit) are conspicuous.

Fig. 3. Pollen catches at Jokioinen in 1966–1973. The daily catches per mm² are divided by the period unit heat sum of each day (the ordinate). Compare to Fig. 4.

these reference points can so be assessed in terms of variability.

Diagrams showing the progress of anthesis were drawn up from daily average catches divided by the p.u. temperature sum accumulated each day. Seven of the total of 85 antheses under study were
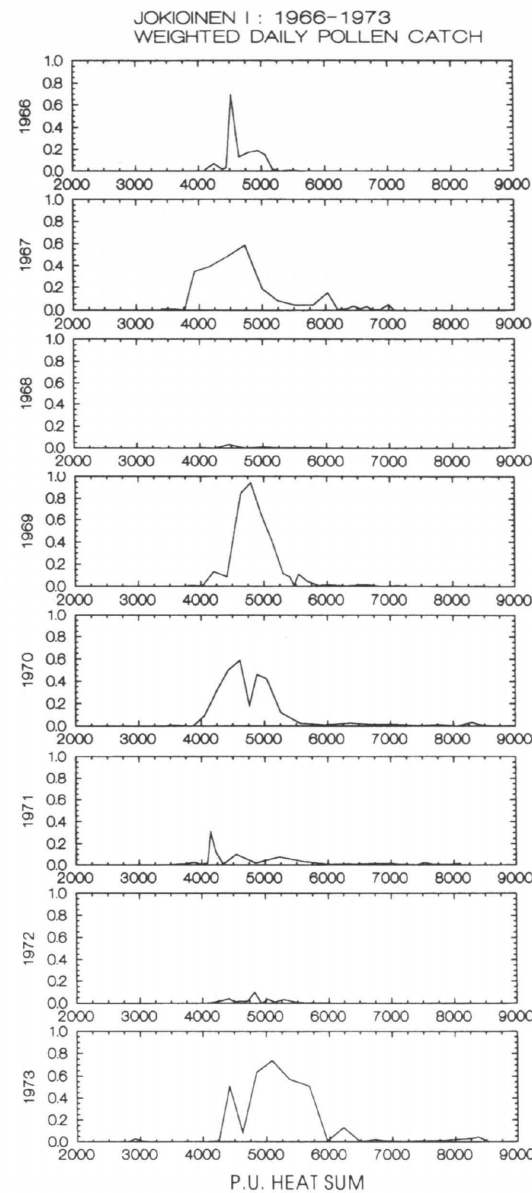
published by Sarvas (1972) as such pictures. The bulk of the data has not been used earlier in any other manner. Further examples of the diagrams are shown in Fig. 3. Compare this form of presentation to Fig. 4 in which the same years of the same site (Jokioinen I) are shown on probability paper.

2.3 Other variables

Latitudes and longitudes were used in calculating correlations to expose the usual geographical trends. The combining of latitudes and the effect of stand altitudes was possible by using climatological data by Laaksonen (1976) whose study gave the rates of monthly mean temperature change both latitudinally and with respect to altitude. Values from March to May were used to calculate the transformation for southern Finland up to Kajaani (64°15' N.lat.) while values from April to June were used for northern Finland. In the present study the combination of latitude and altitude is called the ecological latitude. Finland is quite flat, the highest altitudes occurring in the north. To consider an increase in altitude as equivalent to an increase in latitude thus stretches the latitudinal scale in an uncomplicated manner from the south to the north. The sample stands lie at altitudes from 27 to 275 meters.

A new co-ordinate system was created to help geographical conclusions. Accordingly, two geographical locations were chosen as reference points for calculating migration distances. One called the EE-point is the easternmost point of Finland (62°54'N.lat. and 31°35'E.long.) and the other was located at the point of intersection of the latitude of the southernmost point and the meridian of the easternmost point of Finland (59°48'N.lat. and 31°35'E.long.). The latter point (called the SE-point) is on the Karelian Isthmus in Russia (see Fig. 1).

Anther residues and seed crop data by Koski & Tallqvist (1978) were used for the calculations presented in Table 6.

3. Results

3.1 Flowering characteristics

Norway spruce flowered quite regularly, and at least minimal male flowering occurred every year. However, flowering varied considerably in terms of quantity. All the completed observation series enabled quantification of the pollen catch. For timing purposes only antheses with pollen catch total sums from the whole pollen period of 15 pollen grains/mm² (a purely technical value) or larger were used to determine the required point of 50 per cent completion of anthesis. While the range of pollen catches in the 85 cases was as large as 0.8–1779.4 grains/mm² (CV = 1.124), fourteen antheses had to be excluded from calculations as they were below the limit. The restriction regarding a minimal total pollen catch, for the timing of the 50 per cent point of anthesis, was necessary to prevent background pollen from giving spurious timing data. Background pollen can still inflate readings given for duration of anthesis. The more variable pollen crops in Norway spruce caused more exclusions than that was necessary in the case of Scots pine.

3.2 Timing of anthesis

Male flowering in Norway spruce was found to begin as early as May 15 in southern Finland and it could extend to as late as July 5 in northern

Finland (Table 2a). The onset and the termination of flowering were judged on the basis of the first and last pollen catches on the registering band. The relative level of air temperatures during spring and early summer influenced the timing in an individual year. However, the occurrence of anthesis over several years in the individual stands remained surprisingly constant in calendar time.

The average duration of anthesis in the different stands varied between 11.8 days to 20.4 days as judged from the recorded pollen catches (i.e. with some secondary pollen). High coefficients of variation (expressing variation between years in particular stands) were found: from 22.4 to 54.1 per cent (Table 2a).

The performance of the three parameters was evaluated in two ways: using coefficients of variation of the unprocessed stand data, and subsequently on a day basis, when the annual deviations in heat sums had been converted to days.

3.2.1 Simple heat sum basis

In the basic data, the period from March 19th to the 50 per cent completion point of anthesis varied from 4702 to 5133 period units in stand means (Table 2a). The respective coefficients of variation ranged from 3.2 to 7.9 per cent. During the same period heat sums varied from 127.7 to

Table 2a. Variation in timing and duration of anthesis (stand means).

Stand	Locality	Time range of anthesis (earliest first day to latest last day)	Years of study*	Duration anthesis In days	CV%	Period March 19th to 50 per cent anthesis completion						Period March 19th to peak pollen catch day	
						In period units	CV%	In degree days> 5°C	CV%	In days	CV%	In days	CV%
Bromarv I	1	May 17–June 20	9(11)	19.6	34.4	4735	4.6	134.8	7.1	76.1	3.5	75.8	5.1
Heinola 565	4	May 18–June 12	6(6)	14.3	22.4	4940	3.2	145.2	5.4	74.7	2.8	74.7	2.8
Jokioinen I	3	May 18–June 26	8(8)	20.4	37.0	4847	4.2	134.8	11.5	74.0	1.6	73.5	1.0
Kittilä III	8	June 9–29	3(5)	11.8	54.1	4702	4.1	127.7	18.6	92.7	5.4	95.4	4.3
Kittilä, Pallas IV	9	May 26–July 5	6(9)	13.0	39.0	4746	5.9	137.2	12.3	97.2	3.6	94.1	8.6
Kuorevesi XXXV	6	May 19–June 15	7(7)	15.9	27.8	5016	4.3	134.0	14.1	77.1	3.3	77.4	3.9
Punkaharju LII	5	May 23–June 19	9(11)	17.0	33.7	5133	4.0	155.7	6.4	77.3	4.3	77.6	5.1
Rovaniemi XVIII	7	May 26–June 27	7(11)	12.5	43.3	4778	3.7	136.7	11.5	87.3	6.0	86.4	8.3
Tuusula XXX	2	May 15–June 27	8(10)	18.5	27.8	4913	4.2	141.1	7.6	74.1	4.6	73.6	5.1
Tuusula XXXIV	2	May 17–June 23	7(7)	20.0	22.7	5095	7.9	153.1	10.3	74.9	3.5	73.4	5.3

* Fifteen yearly antheses were excluded from timing studies (n=70), see Table 1.
The values in brackets refer to the number of years in which the duration of anthesis and peak pollen catch day were studied (n=85).

Table 2b. Comparison of timing parameters on a day basis (stand means).

Period March 19th to 50 per cent anthesis completion (n=70).

Stand	Locality	Period units converted to days			Degree days > 5°C converted to days			Days		
		Mean (hypothetical)	Mean of annual deviations	CV%	Mean (hypothetical)	Mean of annual deviations	CV%	Mean (true)	Mean of annual deviations	CV%
Bromarv I	1	75.9	2.12	3.6	76.3	2.44	4.0	76.1	2.32	3.5
Heinola 565	4	74.7	1.44	2.5	75.3	1.67	3.1	74.7	1.67	2.8
Jokioinen I	3	74.0	1.25	2.2	74.4	1.22	2.4	74.0	0.75	1.6
Kittilä III	8	93.0	3.33	4.7	93.7	3.56	5.0	92.7	3.56	5.4
Kittilä, Pallas IV	9	97.3	3.11	4.0	98.7	4.22	5.7	97.2	2.89	3.6
Kuorevesi XXXV	6	77.3	1.76	3.3	77.6	2.65	4.5	77.1	2.12	3.3
Punkaharju LII	5	77.1	2.35	4.0	77.9	2.35	4.0	77.3	2.81	4.3
Rovaniemi XVIII	7	87.9	2.73	4.4	88.4	2.61	4.5	87.3	3.96	6.0
Tuusula XXX	2	74.1	2.63	4.4	74.5	2.25	4.5	74.1	2.63	4.6
Tuusula XXXIV	2	74.7	1.76	2.9	75.3	1.47	2.6	74.9	2.16	3.5

Pattern of accumulation of various units in measuring the timing of anthesis.
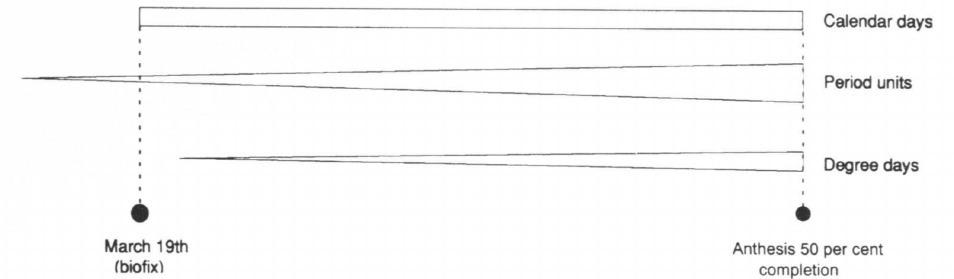
Fig. 5. A schematic pattern of accumulation of various units for measuring the timing of anthesis. The calendar day scale is an uniform variable that runs unchanged from day to day. Period units usually start to accumulate before biofix (March 19th) while degree days usually start to accumulate after the biofix. Both heat sum types accumulate at an increasing rate so that larger daily heat sums occur near the end of the period of study. Neither the onset of the accumulation of period units nor that of degree days is a useful point to place the biofix.

155.7 degree days. The respective coefficients of variation were from 5.4 to 18.6 per cent. In calendar time, the period under study ranged from 74.0 to 97.2 days. The coefficients of variation for days were from 1.6 to 6.0 per cent. In the basic data (Table 2a), calendar days were the least variable measure of timing in seven of the stands. Period units varied least in three stands, whilst degree days were always more variable than the two other measures.

The occurence of peak pollen catches in Norway spruce were, on average, 0.27 days earlier than the reference point for the timing the 50 per cent completion of anthesis. This was the outcome of a pairwise comparison of the timing data (n = 70). (The peak pollen catch day data in Table 2a are calculated from the full material of n = 85.) Using the day of the peak pollen catch as a reference point instead of anthesis 50 per cent completion clearly decreases the consistency of results in terms of calendar time. The day of 50 per cent completion was a more reliable reference point in seven out of ten cases, while the peak pollen catch day was better in two stands and there was also one case when both methods gave an equal variation coefficient of 2.8 per cent. However, the peak pollen catch day as related to calendar time was a less variable measure for the timing of anthesis than degree days (at 50 per cent anthesis completion) of the basic data in all of the ten cases. Further, the peak pollen catch day was nearly equal in constancy to period units, as period units scored six and the peak pollen catch day four wins out of ten.

3.2.2 Heat sums converted to a day basis

A comparison of parameters was also made on the basis of days (Table 2b). In this comparison, the observations made in calendar days remained as they were, but for heat sums the expected heat sum (stand mean) and each observed annual value were compared. For each year of study, the stand average heat sum was traced on the particular annual heat sum scale either forward (to higher heat sums) or backward (to lower heat sums); the day on which the sought heat sum fell was then determined. This method compensates for the fact that the daily heat sums increase towards the end of the period under study (see Fig. 5).

The annual deviations of heat sums proved smaller on a day basis, as was expected. The results of this comparison are shown in Table 2b. On a day basis, period units were the least variable measure of timing in four of the stands. Further, period units were equal in accuracy to calendar days in one stand and to degree days in another (Table 2b). Calendar days also performed well, being the least variable in three stands and, as noted above, producing the same coefficient of variation (3.3 per cent) in one stand. Degree days performed best in one stand and were equal with period units in another, as already observed.

In a few cases, each of the three parameters of the converted data gave the same forecast, i.e. the same day. This means that in a particular year, the values of all parameters for the timing of 50 per cent completion of anthesis fell close to the stand mean. In most years, this coincidence
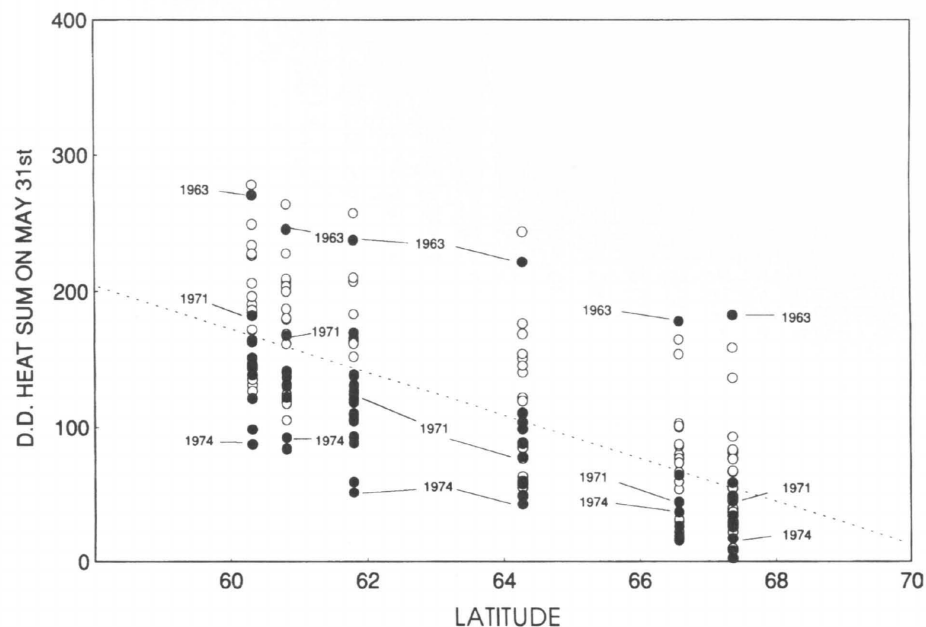
Fig. 6. Accumulated degree-day heat sums by May 31st of six locations during the period 1963–1974 (marked with black dots) are compared to other years of a thirty-year reference period 1959–1988 (open circles). The weather stations of the Finnish Meteorological Institute chosen were in latitudinal order: Helsinki–Vantaa (60°19'N.lat., 24°58'E.long; the observations of 1986 were made at Tuusula/Hyrylä at 60°25'N.lat., 25°02'E.long.), Jokioinen (60°49'N.lat., 23°30'E.long.), Punkaharju (61°48'N.lat., 29°20'E.long.), Kajaani (64°17'N.lat., 27°41'E.long.), Rovaniemi/Apukka (66°35'N.lat., 26°01'E.long.) and Sodankylä (67°22'N.lat., 26°39'E.long.). The regression line is Y = 1128.4 − 15.93 X (R² = 0.476).

Table 3a. Correlations of heat sums and durations involved in anthesis (n=70).

| | Period from March 19th to 50 per cent anthesis completion | | | Length of anthesis | |
	In period units	In degree days > 5°C	In days	In period units	In days
Latitude	−0.245*	−0.172	+0.900***	−0.431***	−0.376**
Ecological latitude	−0.246*	−0.176	+0.900***	−0.437***	−0.383***
Longitude	+0.351**	+0.378**	+0.012	−0.047	−0.106
Distance from EE	−0.464***	−0.322**	+0.463***	−0.124	−0.046
Distance from SE	−0.410***	−0.322**	+0.859***	−0.367**	−0.282**
Years since reinvasion[1]	+0.423***	+0.335***	−0.374***	+0.055	−0.016
Degree days of previous year	+0.386***	+0.299*	−0.856***	+0.450***	+0.394***
Degree days of 2 years earlier	+0.323**	+0.212	−0.738***	+0.420***	+0.322**
Age of stand	−0.212	−0.088	+0.597***	−0.351**	−0.276*

[1]   According to Tolonen (1983)
*   P < 0.05 almost significant
**   P < 0.01 significant
***   P < 0.001 highly significant

Table 3b. Partial correlations of heat sums and durations involved in anthesis: effects of latitude removed (n=70).

| | Period from March 19th to 50 per cent anthesis completion | | | Length of anthesis | |
	In period units	In degree days > 5°C	In days	In period units	In days
Longitude	+0.397***	+0.409***	−0.236*	+0.009	−0.064
Distance from EE	−0.414***	−0.337**	+0.305**	+0.047	+0.112
Distance from SE	−0.441***	−0.382***	+0.278*	+0.047	+0.132
Years since reinvasion	+0.385***	+0.306**	−0.343**	−0.063	−0.125
Degree days of previous year	+0.395***	+0.339**	−0.231	+0.158	+0.135
Degree days of 2 years earlier	+0.248	+0.134	+0.440***	+0.075	−0.053
Age of stand	−0.094	+0.010	+0.261*	−0.148	−0.085

occurred only in single stands. However, in 1971 this phenomenon occurred in as many as five stands. 1971 was an average year in terms of d.d. heat sums (Fig. 6). Further, the maximum distribution of values was recorded in 1967 (stand Rovaniemi XVIII) when the range between forecasts was nine days. In 1965 (stand Kittilä IV) the range was eight days.

Mean deviations in days between the expected and the observed days are also given in Table 2b. These mean deviations do not correlate fully with the coefficient of variation used as the principal measure. The reason for this is that coefficient of variation involves squared annual deviations, while the mean of annual deviations involves only simple (unsquared) values. Using the mean of annual deviations, rather than coefficient of variation, would make degree days the second best parameter and better than calendar days.

When reading Table 2b it should be noted that the day column (on the right) gives the original day data based on observations, while the period unit and degree day converted scales (the two leftmost columns) are hypothetical.

3.3 Geographical trends

Finnish conifer forests are young owing to the relatively recent deglaciation of our country. Norway spruce invaded Finland from the east and southeast after Scots pine. Two rather arbitrary reference points, the EE-point and the SE-point (Fig. 1) were used to calculate simulated migration distances. For simplicity, seas and other waterways were not considered in this scheme. Using stand distances from these points (rather than latitudes and longitudes) in the calculations allows a rough assessment of migration route effects on adaptative characteristics.

3.3.1 Correlations on an individual anthesis basis (n = 70)

Both kinds of heat sums relevant to the timing of anthesis were correlated with longitude. The correlations were significant, while the correlations between duration in days and both latitudes were highly significant (Table 3a). Conversely, corre-

lations between heat sums and both latitudes and respectively, calendar days and the longitude were not significant, but almost significant between both latitudes and period unit heat sum.

Interestingly, heat sum correlations with respect to migration distances from EE and SE were considerably higher than those with the latitudes, the distance to the EE-point giving with period units the highest value (Table 3a), a correlation coefficient of r = −0.464***. Generally speaking, period units produced higher correlations than degree days, but the highest correlations occurred with duration in days. Approximate reinvasion years at an accuracy of 100 years can actually be interpolated from a map presented by Tolonen (1983). Correlations calculated according to Tolonen's map (Fig. 7) agree quite well with correlations calculated against distances to point EE (Table 3a, Fig. 8).

Calendar days differed from the other measures of timing (p.u. and d.d. heat sums) by having the highest correlations with latitudes, rather than with distances to the EE or SE-points (Table 3a). The highest correlation coefficients were

the correlations between days and both latitudes (both r = 0.900***, Fig. 9), while the correlation coefficient between days and the distance to the SE-point was r = 0.859***.

The duration of anthesis in days (apart from days as a timing measure) was correlated latitudinally at a significant level (r = −0.376***, see Table 3a), and it also correlated with the cumulative pollen catch (r = 0.370**, see Table 6). In terms of the length of anthesis in period unit heat sums, there was also a highly significant latitudinal correlation, antheses being shorter in the north (r = −0.431***, see Table 3a).

From Tables 3a, and 4a it is evident that there are no noteworthy differences between latitude and ecological latitude. Altitudinal effects were not prominent in this material.

Many of the factors involved are evidently naturally correlated with latitude. This is true for the simulated migration distances, the average heat sums at any given locality, the age of a stand and the dominant height of a stand (not included in the data). Partial correlations in which the effects of latitude are removed were therefore
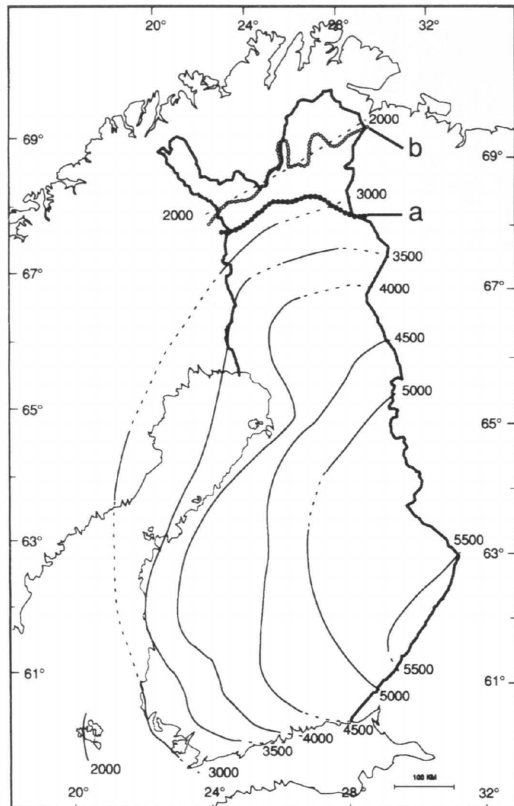
Fig. 7. The post-glacial reinvasion of Norway spruce into Finland (after Tolonen 1983). Isochrones (years B.P.) imply years elapsed since arrival of spruce. Black dotted chain (a) = northern timberline of Norway spruce, open dotted chain (b) = northern timberline of Scots pine.
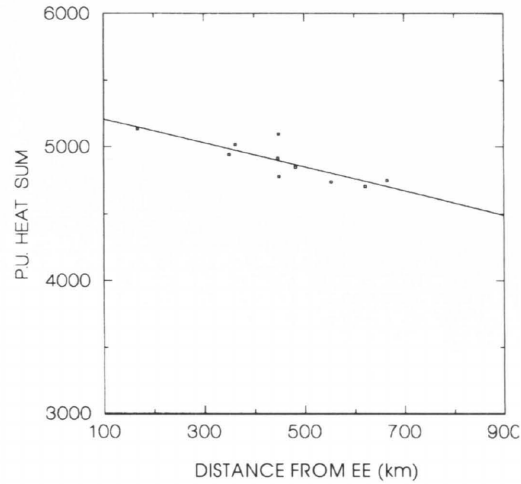

Fig. 8. The dependence of the required period unit sum for 50 per cent anthesis completion on the distance from the EE-point. Stand means are used. The regression line is Y = 5298.5 – 0.898 X (R² = 0.692).

Fig. 9. The number of days since March 19 needed for 50 per cent anthesis completion with reference to latitude. Year 1969 (stars) and year 1967 (circles) and other yearly values (dots) are shown. The regression line is Y = –81.846 + 2.584 X (R² = 0.810).

Fig. 10. The period unit sums required for 50 per cent completion of anthesis with reference to latitude. Year 1969 is shown by stars and year 1967 by circles. Other years are indicated with dots. The regression line is Y = 6356.1 – 23.272 X (R² = 0.060).

Fig. 11. These stand averages of d.d. heat sums for attaining 50 per cent anthesis completion were used together with average annual heat sums (similar to Scots pine data shown in Fig. 12) to calculate Linsser's quotient (Fig. 13). The regression line is Y = 219.59 – 1.266 X (R² = 0.208).
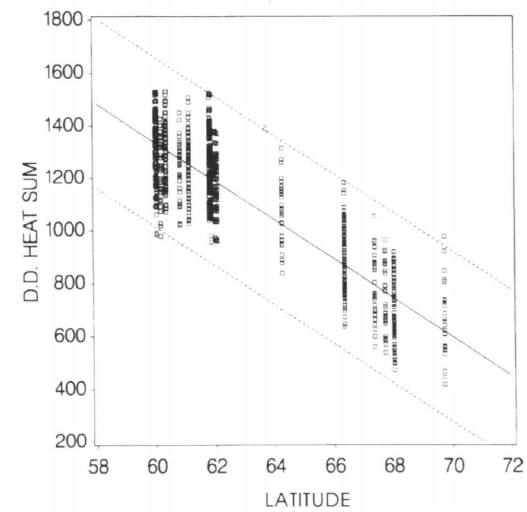
Fig. 12. Annual heat sums in 1951–1980 in Scots pine stand localities (Luomajoki 1993). A simulation program (Ojansuu and Henttonen 1983) based on temperatures measured at 80 (in 1951) to 157 (in 1979) stations was used. The regression line is Y = 5764.5 – 73.8 X, with confidence limits of 99 per cent level.

helpful. Considering distances to EE and SE-points, partial correlations with period units relevant to timing were highly significant and, respectively, also with degree days in the case of the distance to SE-point (Table 3b).

On the basis of the partial correlations in Table 3b, it was concluded that the age of the stand had no effect on the timing of anthesis in this material. In all cases the trees were of sufficient age to avoid any youth-bound effects in timing, although the northern stands are generally older than the southern stands. A warm summer seems to increase the heat sums needed for flowering in the following year, which would usually indicate later flowering. The partial correlations for period units and degree days are highly significant and significant, respectively (Table 3b).

3.3.2 Correlations on a stand basis (n = 10)

The correlations shown in Tables 3a and 3b were also calculated on a stand basis (n = 10), but are not shown as a separate table for the sake of clarity. This extra calculation was strictly a safe-ty measure. The observations originating from different years but in the same stand are not as independent as the theory of correlation analysis actually demands. However, using stand averages instead of values of individual years (n =

70) in the calculations did not result in equally significant correlation coefficients as those in Tables 3a and 3b. Following calculations based on stand means, the only geographical correlations from Table 3a that remained significant were those of period units against distances from EE and SE and years since reinvasion, while the correlations between timing in days and both latitudes and, respectively, the correlation between days and the distance from the SE-point were all highly significant. The correlation between calendar days and the annual degree day sum of the previous year retained its highly significant level. The fewer significant correlations can be attributed to the low number of degrees of freedom available (eight). Partial correlations also fared poorly, but the correlation between period units and the distance to the SE-point remained significant. The correlation between degree days and the annual degree-day heat sum of the previous year also remained significant in the stand-wise calculation process.

3.4 Stability of correlations: differences between years

Table 4a presents a comparison between the years 1966 to 1969. With yearly material from 6 to 10 stands, the statistical significance criteria are

Table 4a. Differences between years in correlations of heat sums and durations (1966: n=6, 1967: n=10, 1968: n=6, 1969: n=9). Period March 19th to 50 per cent anthesis completion.

	In period units				In degree days > 5°C				In days			
	1966	1967	1968	1969	1966	1967	1968	1969	1966	1967	1968	1969
Latitude	+0.922**	−0.393	−0.231	−0.384	+0.558	−0.534	+0.072	−0.421	−0.355	+0.934***	+0.976***	+0.971***
Ecological latitude	+0.910**	−0.384	−0.252	−0.377	+0.543	−0.518	+0.052	−0.435	−0.487	+0.945***	+0.975***	+0.958***
Longitude	+0.800*	+0.605*	+0.013	+0.625	+0.949**	+0.548	+0.254	+0.611	−0.096	−0.117	−0.226	+0.230
Distance from EE	−0.914**	−0.852**	+0.092	−0.915***	−0.907**	−0.837**	+0.093	−0.689*	+0.205	+0.639*	+0.694*	+0.349
Distance from SE	−0.701	−0.651*	−0.143	−0.725*	−0.971***	−0.753**	−0.032	−0.674*	+0.173	+0.922***	+0.930**	+0.891**
Years since reinvasion	+0.929***	+0.813**	−0.152	+0.871**	+0.889***	+0.770**	−0.142	+0.598	−0.263	−0.566	−0.691	−0.179
Degree days of previous yr	−0.780*	+0.448	+0.248	+0.452	−0.335	+0.580	+0.013	+0.481	+0.652	−0.947***	−0.955***	−0.968***
Degree days of 2 yrs earlier	−0.564	+0.455	+0.214	+0.512	−0.010	+0.584	−0.058	+0.558	+0.501	−0.949***	−0.977***	−0.943***

*   P < 0.05 almost significant
**   P < 0.01 significant
*** P < 0.001 highly significant

Table 4b. Heat sums and durations: differences between years in partial correlations removing effects of latitude (1966: n=6, 1967: n=10, 1968: n=6, 1969: n=9). Period March 19th to 50 per cent anthesis completion.

	In period units				In degree days > 5°C				In days			
	1966	1967	1968	1969	1966	1967	1968	1969	1966	1967	1968	1969
Longitude	+0.743	+0.684*	−0.036	+0.790*	+0.926**	+0.686*	+0.276	+0.797*	+0.172	−0.481	−0.123	+0.060
Distance from EE	−0.745	−0.824**	+0.315	−0.905***	−0.931**	−0.775**	+0.061	−0.645	−0.148	+0.506	+0.468	+0.169
Distance from SE	−0.857**	−0.844**	+0.191	−0.927***	−0.974***	−0.825**	−0.092	−0.735*	+0.021	+0.405	+0.328	+0.211
Years since reinvasion	+0.751	+0.779**	−0.384	+0.896***	+0.924**	+0.719*	−0.124	+0.602	+0.063	−0.596	−0.522	−0.206
Degree days of previous yr	+0.208	+0.620	+0.107	+0.904***	+0.417	+0.584	+0.385	+0.813**	+0.779	−0.489	−0.050	−0.026
Degree days of 2 yrs earlier	+0.640	+0.644*	−0.117	+0.754*	+0.818*	+0.588	+0.108	+0.822**	+0.383	−0.543	−0.323	+0.187

stricter than in larger materials. The significance of correlations suffered from the rather small number of observations, and the situation did not improve when the effects of latitude were removed in partial correlations (Table 4b). Overall, the geographical correlations, especially the partial correlations, were found to be unstable.

The correlations between timing in days and both latitudes were highly significant from 1967 to 1969, but 1966 was an exception (Table 4a). The correlation regarding the distance from the SE-point behaved similarly to the latitudinal correlations, but at a little lower numerical, significant or highly significant, level. The correlation between distance from the EE-point and period units was significant or highly significant in 1966, 1967 and 1969, with 1968 being the exception. The effects of temperatures of two previous years were only seen in the highly significant correlation coefficients for days in 1967–1969, but not in 1966.

There were also other, systematic, differences between the years. A difference can be found between the years 1967 and 1969 as well as in terms of heat sums and days (Figs. 9 and 10). In 1967, the heat sums at 50 per cent completion of

anthesis tended to be lower than the average and this reference point also occurred earlier in calendar time.

3.5 Adaptation

To measure the adaptational situation, the heat sums needed for reaching the point of 50 per cent completion of anthesis were divided by the average annual heat sum of the locality and given as a percentage. This method had been already suggested by Reaumur (cit. Robertson 1973) while Linsser (1867) gave more information on the adaptability of species at various localities. This method is only applicable to degree days (Figs. 11 and 12) owing to the need for additional material from European localities south of Finland which only have been measured in this form. With the aid of this additional reference material, it becomes evident that the adaptation of Norway spruce suffers considerably north of a latitude of ca. 63° as increasing percentages of annual heat sum are needed for anthesis (Fig. 13).

The correlations between geographical variables and the within-year variation of anthesis in terms of p.u. sums were not significant (Table 5). The variation in flowering time between the years with respect to period unit heat sums only had a minor northwards flux. The corresponding variation along the two hypothetical migration routes increased measurably but not at a significant level (Table 5). The years elapsed since reinvasion gave correlation coefficients of similar magnitude to distance from the EE-point (but with a negative sign). The Punkaharju stand LII originating from Lammi called for an alternative calculation using reinvasion year values for Lammi instead of those of the stand site. The differences were, however, small and not significant. Only the figures according to the site are shown.

3.6 Pollen catch

The total pollen catches measured were relative, rather than quantitative values due to natural effects of wind and rain. However, the catches correlated with anther residues assessed in the same years in the same stands (n = 84; figures from Koski & Tallqvist 1978) at a highly significant level r = 0.816*** (Table 6, Fig. 14). The effect of the amount of pollen catch on seed production in the following year was also highly significant (r = 0.710***). Both correlations re-

Fig. 13. The proportion (Linsser's quotient) of the average annual d.d. heat sum (1951–1980) required for 50 per cent completion of anthesis. The additional points far south of Finland are 1. Bedovice, CSSR, year 1958 (Sarvas 1967 referring to Chalupa 1964) and 2. Eberswalde, Germany, year 1936 (Sarvas 1967 referring to Scamoni 1955). The curve fitted is $Y = 9.826 + e^{-7.286 + 0.00205\, X^2}$ ($R^2 = 0.969$).

Table 5. Correlations with variation coefficients of period unit heat sums of antheses.

	Variation within each yearly anthesis in period units (n=70)		Variation of period unit sums between years at each stand (n=10)	
	Correlation	Partial correlation with effects of latitude removed	Correlation	Partial correlation with effects of latitude removed
Latitude	−0.125	–	−0.042	–
Ecological latitude	−0.123	+0.037	−0.040	−0.023
Longitude	−0.023	−0.007	−0.282	−0.280
Distance from EE	−0.083	−0.038	+0.306	+0.383
Distance from SE	−0.123	−0.025	+0.074	+0.306
Years since reinvasion	+0.050	−0.025	−0.401	−0.455

None of the correlations are significant

Table 6. Correlations with total pollen catch (n=84).

	Correlations	Partial correlations with effects of latitude removed
Latitude	−0.330**	–
Ecological latitude	−0.335**	−0.101
Longitude	−0.007	+0.031
Distance from EE	−0.134	+0.004
Distance from SE	+0.298*	+0.002
Years since reinvasion	+0.089	−0.007
Lenght of anthesis in days	+0.370**	+0.284*
Degree days of previous yr	+0.429***	+0.335**
Degree days of 2 yrs earlier	+0.167	−0.333**
Age of stand	−0.207	−0.020
Anther residues	+0.816***	+0.795***
Seeds /m²	+0.710***	+0.677***

Table 7. Variability between years (CV) in pollen catches in the stands studied (n=10).

	Correlations	Partial correlations with effects of latitude removed
Latitude	+0.927***	–
Ecological latitude	+0.925***	−0.041
Longitude	+0.112	+0.155
Distance from EE	+0.450	−0.095
Distance from SE	+0.853**	−0.068
Years since reinvasion	−0.348	+0.055

mained highly significant when the effects of latitude were removed.

Likewise, pollen catches were correlated with the annual d.d. temperature sums in the preceding year at a highly significant level (Table 6). The relevant partial correlation, free from latitudinal effects, was significant. The temperatures measured two years earlier had no positive effect on pollen catches resulting in a negative partial correlation value (r = −0.333**). The stand ages had little effect even latitudinally. When the effects of latitude were removed, the correlation approached zero (Table 6).

Of the pollen catch-related geographical correlations, only those calculated for both latitudes were significant. This means that pollen catches diminish northwards (Fig. 15). Along with diminishing pollen catches, the variability of the pollen catches increased northwards (Table 7). Variation coefficients reflecting pollen catch differences between years at each stand increased

latitudinally northwards (Fig. 16) and along the two simulated migration routes. A correlation of r = 0.927*** was calculated for latitude, and for distance from SE-point, a correlation of r = 0.853** (Table 7). Along the suggested migration route from EE, the variability of pollen catches increased less conspicuously (r = 0.450, not significant) with accordance to a low coefficient of correlation obtained against years since reinvasion.

Stand XXXIV at Tuusula differed from the other stands (including stand XXX at Tuusula) in that it had on one occasion received urea fertilization (Table 1). No large fertilization effects on flowering could be observed. The two stands at Tuusula remained comparable in flowering behaviour, but the flowering in the fertilized stand XXXIV was once somewhat more abundant (in 1968) and the anthesis was also more protracted than expected. This contributed to a higher than normal period unit value for 50 per cent completion of anthesis in 1968 and to a relatively high coefficient of variation for the mean of the period unit sums for plot XXXIV (Table 2a).
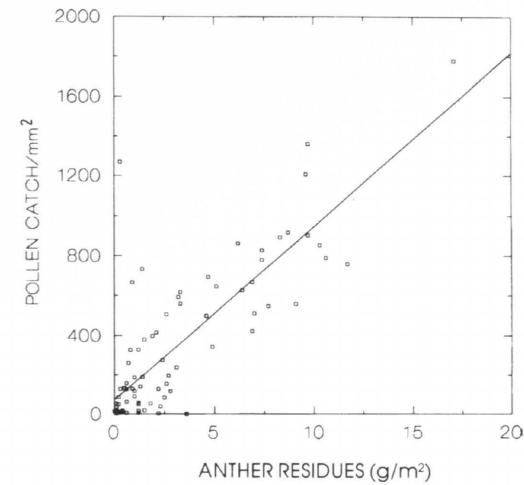

Fig. 14. The dependence of pollen catch on the amount of anther residues (residues data from Koski and Tallqvist 1978). The line fitted is Y = 72.822 + 87.389 X (R² = 0.666).
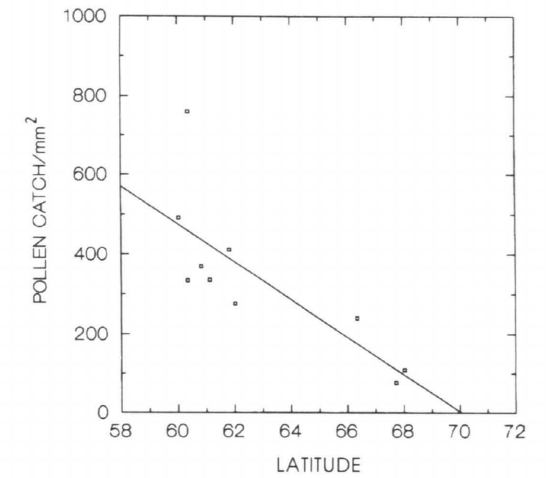

Fig. 15. The dependence of the size of pollen catch on latitude. The values used are stand averages. The regression line shown is Y = 3316.3 − 47.342 X (R² = 0.603).
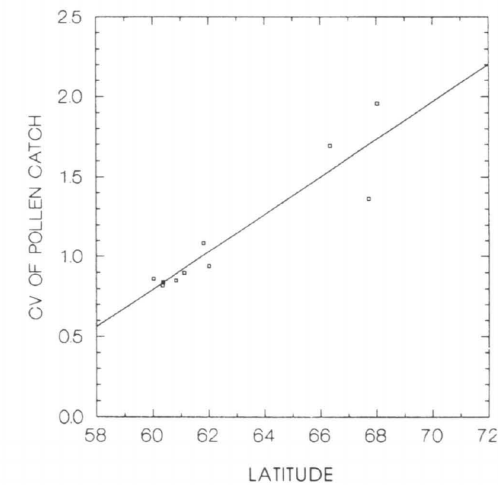

Fig. 16. The dependence of the coefficient of variation of stand average pollen catch on latitude. The regression line is Y = −6.242 + 0.11728 X (R² = 0.859).

4. Discussion

Questions related to sampling, statistical distribution and the circumstances of pollen spread were similar to those for Scots pine and have been discussed previously (Luomajoki 1993).

4.1 Flowering characteristics

One of the main differences in the male flowering between Scots pine and Norway spruce is that the production of pollen in Norway spruce is much more variable in quantity. Years of high pollen production are relatively rare in Norway spruce. The variability of the pollen catch between years increases in Norway spruce with increasing latitude still stronger than in Scots pine. Sarvas (1968) showed that small pollen crops as such mean larger variation measurable in flowering. He pointed out later (1972) that individual trees of a population differ from each other with respect to the length of their "active periods". This means there are early and late blooming trees in a population. In a year of minimal flowering only a selected part of the population (early or late blooming trees) would flower.

Tirén (1935) stated that two successive years of abundant flowering in spruce are not possible for organo-ontogenic reasons. If, therefore, two successive years of relatively abundant flowering have occurred, the flowering of different individual trees of the population is probable. This was in fact easily confirmed for female flowering in southern Finland in 1992–1993. Both years were good flowering years, and different branches of the same spruce trees as well as different individual trees contributed to flowering in 1993.

Eis (1973) gives another reason for variable flowering and cone production in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and grand fir (*Abies grandis* (Dougl.) Lindl.) Alternatively cool and warm summers are needed for a good cone crop. This was also found true with Norway spruce (Brøndbo 1970). In southern Finland, abundant male flowering occurs approximately every third or fourth year (Koski & Tallqvist 1978). This situation has also been regarded as an escape from the severe threat on spruce seed production from cone- and seed-damaging insects (Annila 1981, Fenner 1991). Squirrels eat generative buds of spruce in years of simultaneous bad cone crop in spruce and pine (Grönwall 1982) thus cutting back pollen production.

4.2 Timing parameters

Beyond the main aim of this study, the flowering phenology of the Norway spruce, also the value of the three phenological parameters was assessed. The first was calendar time, which was as such the best alternative for assessing the average occurrence of anthesis in Norway spruce. The time-honored degree-day system was regarding the basic data inferior to days and period units as an explanatory parameter. The third alternative, the less known period unit heat sum system, was the second best of the tree methods for the basic data. As a heat sum system, it can better predict anthesis in an exceptional year than calendar time.

On a calendar day basis (Table 2b), the annual deviations between the expected and the measured heat sums were reduced owing to the fact that daily heat sums increased strongly towards the end of period of study. Consequently, the calendar day basis resulted in the period unit becoming the best parameter, followed by days actually observed. Degree days also scored some success when judged on a calendar day basis (Table 2b).

The use of the basic heat sum data can be defended for its simplicity. On the other hand, conversion to a day basis compensates for the rapid heat sum accumulation towards the end of the period under study. Accordingly, it makes the comparison of parameters more objective, at the cost of extra calculations involved.

High correlation coefficients between the latitudes and calendar days arise the following new questions. "Were the years of study (1963–1974; for timing studies, 1964–1973) so closely average in terms of temperatures that this generated only minimal scatter into the latitudinal regression between 50 per cent completion of anthesis and calendar days?" "Is there some effective factor, e.g. photoperiodism, that synchronizes the development in spruce latitudinally?"

To study the first problem, years 1963–1974 were compared to a 30-year period (1959–1988) for d.d. heat sums recorded on May 31, June 15 and June 30, respectively. The reference period of 1959–1988 could not be centered more closely around the years of study owing to the fact that suitable computerized d.d. data were not available until 1959 onwards. (The second problem will be dealt with in Chapter 4.6.)

No timing data were available for 1963 and 1974 owing to minimal pollen catches. Those years were also found to be the most extreme years with respect to heat sums (see Fig. 6 on d.d. heat sums of May 31). Consequently, the remaining data period (1964–1973) had a restricted distribution of heat sums. Generally speaking, this period also fell somewhat below the long-term average with respect to d.d. heat sums. Later, on June 15 and June 30, 1974 acquired enough heat sums to make it almost an average year in the north by June 30th. However, in the south of Finland, 1974 was an extremely cold year whereas 1963 was a very warm year throughout Finland.

The period of timing studies, i.e. ten years of data, did not have as much variation in terms of temperatures that it could be considered ideal for an effective comparison of phenological parameters. Consequently, calendar days were somewhat favored in this study. In a thermally average year (e.g. 1971) heat sums and calendar days agree very well indeed.

4.3 Geographical trends

The p.u. and d.d. heat sums needed for 50 per cent completion of anthesis in Norway spruce varied little with latitude compared to Scots pine. Thus, the heat sums needed at Bromarv (60° 02' N.lat.) and at Kittilä (stand IV at 68° 02' N.lat.) were practically the same for spruce. Lack of latitudinal variation was also reported by Luomajoki (1984) for tetrad stage of microsporogenesis that precedes anthesis by ca. three to five weeks.

In Scots pine, the latitudinal trend was considerably stronger. At Kittilä only about 90 per cent of the two types of heat sums at Bromarv were needed. When latitude was not considered, heat sums were found to be the best single-figure estimators for timing of anthesis in Scots pine (Luomajoki 1993), and this is even more true for Norway spruce (cf. Table 3b).

In terms of calendar days, the latitudinal variation is high in both species. For Norway spruce, the slope of the regression line for calendar days by latitude is equally steep (Fig. 9) as for Scots pine. The effects of strong latitudinal adaptation would actually reduce the slope of the regression between calendar days and latitude. On the other hand, this did not happen in Scots pine; the regression of calendar days on latitude retained its slope despite considerable latitudinal adaptation in terms of heat sums (Luomajoki 1993).

The variations in heat sums, pollen catches and standard deviations of period unit sums (i.e. within-year variation) were more pronounced in approximately east-west or southeast-northwest directions (respective distances from EE and SE; cf. Fig. 8) than purely latitudinally. The reason for the deviation of geographical trends from south to north might be found in Finnish glaciation history. The history of the reinvasion of Norway spruce into Finland (Aartolahti 1966, Tolonen 1983), is better known than that of Scots pine (see Hyvärinen 1987).

The more or less arbitrarily chosen points (EE and SE) served only to reveal the strong eastern trend, not to explore the true reinvasion routes. Nevertheless, correlations calculated against reinvasion years of Norway spruce agree well with the theoretical calculations. Longitudinal rather than latitudinal variation in Norway spruce has also been observed by Krutzsch (ref. Eriksson 1982).

The duration of anthesis in days is negatively correlated at highly significant or significant levels with both latitudes and with distance from SE (Table 3a). (Nevertheless, the corresponding partial correlations in Norway spruce were not significant.) This result deviates from Scots pine which showed no significant correlations (Luomajoki 1993). The different behaviour of Norway spruce may be attributed to the smaller pollen crops found in the north and to the fact that distribution-flattening within-anthesis variation in Norway spruce is no higher in the north (Table 5). This contrasts with the increasing variation (and flatter distributions) found in Scots pine in the north.

4.4 Adaptation

Using the same method as for Scots pine (Luomajoki 1993), the adaptation in Norway spruce was appraised with proportions of local annual degree-day heat sums to evaluate geographical adaptability in Linsser's (1867) sense. As seen in Fig. 13, there is no abrupt change in adaptability. The d.d. heat sums needed for attaining 50 per

cent completion of anthesis (Fig. 11) as well as the local annual heat sums (Fig. 12) continued to decrease right up to the timberline. The pattern was, however, different from that in Scots pine (Luomajoki 1993) because the latitudinal change in d.d. sums needed for 50 per cent completion of anthesis for Norway spruce is relatively small. In fact, the regression coefficient (see Fig. 11) was not significant according to the t-test.

Linsser's quotient, consequently, did not stay within the usual 9 to 12 per cent range with regard to heat sum required for flowering (which is typical for Norway spruce in Europe) in central or northern Finland. That anomaly could in Norway spruce as well as in Scots pine (Luomajoki 1993) be taken to represent the limits of its adaptive capacity. The failure to adapt completely would lead to a progressively higher Linsser's quotient. However, the latitudinal d.d. heat sum variation in Norway spruce contributes little to Linsser's quotient. The modest geographic variation found in heat sums, was seen best versus distances from EE in terms of period units (Fig. 8); the regression coefficient was significant in this case.

There is less precise information available about the annual heat sum needed for maturation of Norway spruce seed than in the case of Scots pine. The heat sum needed by spruce is a little less (roughly by 10 per cent) than that needed by pine judged by monthly temperature averages required (see review by Skre 1988).

Achieving the limits of adaptive capacity in the marginal zone does not mean an end to variation. As reported earlier, both within-year (visible in the form of the pollen catch distribution) and between-years phenological variations actually increased in Scots pine towards the north (Luomajoki 1993). This is not the case in Norway spruce, in which the same level of (especially in within-year variation of p.u. heat sums) variation in timing was maintained (Table 5). On an isozyme basis, Tigerstedt (1973) reports for spruce in the north high variation, complete randomness in gene distribution and strong gene flow. Bergman (1978) found that the frequency of the allele group, APH–B_1/B_2, actually increases with latitudes in Finland, following a climatic gradient. On the basis of isozymes, Muona et al. (1990) also found considerable genetic variability in spruce in northern Finland.

During a warm period in the Holocene ca. 5000 to 7000 years ago the timberline of Scots pine was considerably farther in the north and at higher altitudes (Eronen 1979, Alho 1990). Nor-

way spruce had just invaded northern Finland by the end of the Holocene and this latecomer could not colonize new areas farther to the north or at higher altitudes like Scots pine (Tolonen 1983). In the 1930's, spruce invaded higher altitudes (Kullman 1991) similar to Scots pine (Hustich 1948). In the 1940's, the colonization by spruce still continued (Kullman & Engelmark 1991). In the 1980's spruce has changed trend and actually begun to suffer at high altitudes in Scandinavia (Kullman 1989, Kullman & Högberg 1989) perhaps expressing a growing extremity of climate. Scots pine has not suffered to the same extent, and there are indications of a new advance of pine at the timberline (Sirén 1993).

It has been proposed that Finnish coniferous forests are in danger owing to a global warming of the atmosphere (Hänninen 1990, 1991). However, in the light of the adaptation of the generative cycle roughly a third of Norway spruce forests in Finland are still not fully adapted to our present cold climate. A moderate warming (up to ca. 3°C in annual average temperature) would be quite beneficial rather than damaging to Finnish Norway spruce forests even though spruce forests are more common in southern Finland than in northern Finland.

Hänninen (1991) was concerned with the likelihood of increased frost damage risk in spring as a result of climatic warming. His concern is certainly well-founded for Norway spruce which is sensitive to spring frosts (Dormling 1982, Lundkvist 1987). If expectations of Hänninen (1991) prove correct, imported spruce provenances with later flushing (see Giertych 1972) may become even more valuable than they now are. Dietrichson (1980) appraised the performance of White Russian Norway spruce provenances in Sweden, recognizing the reduced risk of spring frost damage.

There is an other important adaptive difference between Norway spruce and Scots pine. Norway spruce could be called a "generalist" and Scots pine a "specialist" species (cf. Rehfeldt 1984 for these concepts). The sensitivity of response of Scots pine to climatic conditions was shown in its improved survival when the seeds were sown about one hundred km south of their origin (Mononen 1987, Koski 1989). Conversely, the adaptivity-related variation in Norway spruce seems less pronounced (Tables 3a, 3b) than in Scots pine. Norway spruce also tolerates transfers northwards (Remröd 1974, Koski 1989), as well as to higher altitudes (Remröd 1974).

The silvicultural gain from spruce can be high-

er if the seedlot sown originates from south of the plantation locality (Remröd 1974, Koski 1989). This expresses the considerable phenotypical plasticity of Norway spruce. However, the adaptability of Scots pine varies geographically so that the plasticity of Finnish pine populations seems to be relatively low compared to, e.g., Polish provenances (Oleksyn et al. 1986, Giertych 1991). There is some evidence that different species' histories during the Pleistocene could have involved strong selection pressures (Critchfield 1984, Lagercrantz & Ryman 1990). This could also contribute to the genetic composition of the present Norway spruce and Scots pine populations in Finland.

4.5 Pollen catch

The clear pattern created by high pollen catch variation in spruce also enhances the correlations with anther residues and seed production. The correlation coefficients for Norway spruce are definitively higher than those calculated for Scots pine. There is also evidence about disproportionally low pollination efficiency of small pollen crops (Fenner 1991).

In spruce, a high correlation between seed crop and temperature sums of the previous year (Table 6) was expected, e.g., from observations by Tirén (1935). This correlation was still stronger in Scots pine (Luomajoki 1993). Following Luomajoki (1993), temperature sum of two years earlier showed a negative partial correlation (effects of the latitude removed) with pollen catch of Scots pine, and this is true also with its seed crop (Pukkala 1987). In spruce, the respective partial correlation, i.e. pollen catch vs. temperature sum of two years earlier, was still stronger (r = –0.333" Table 6).

Pukkala (1987) found for spruce a negative correlation between seed crop and monthly temperatures of the summer two years earlier. This correlation was weaker in Norway spruce than in Scots pine in Pukkala's (1987) data, and on a monthly temperature basis there were further differences in correlations in comparisons with Scots pine.

4.6 Generative cycle

Development in spring can be affected by the temperatures of the previous late autumn. A warm autumn can shift the chilling period towards win-

ter, which in turn can lead to a later dormancy break in the spring (Sarvas 1972).

The annual temperature sum of the previous year extends its effects on the heat sums required for anthesis in the following year in Norway spruce as well as in Scots pine, even when latitudinal effects are removed (Luomajoki 1993). Previous year annual temperature sums also correlate with pollen catches of the following year in both species. Temperatures no doubt affect the cone harvest of spruce in the following year (Tirén 1935) and thus the seed crop.

Temperature sums and dates relevant to anthesis vary in spruce between years (Figs. 9 and 10) in the same manner as in Scots pine (Luomajoki 1993). This unexplained variation is caused by the mobility of the zero point (biofix) of the heat sum and calendar day scales. There is yet no good basis for routinely placing the biofix in a physiologically meaningful way. There is far less knowledge about the metabolic changes in the spring in Norway spruce than in Scots pine. This makes the biofix problem even tougher with Norway spruce. As reported earlier (Luomajoki 1993) it is doubtful that any perennial species would rely on synchronization from a single factor once in a year, i.e. chilling in the autumn, as Sarvas (1974) supposed (cf. Worral & Mergen 1967).

In Scots pine, the timing of flowering correlated rather closely with calendar time. However, both the differences between individual years and the effects of temperatures of the previous summer on the timing of anthesis in the subsequent year contradict ideas concerning direct daylength-induced synchronization (Luomajoki 1993). Nonetheless, the direction of change in daylength seems to affect dehiscence of the microsporangia in some pine species. Burdon (1977) suggests that a decreasing photoperiod inhibits pollen shedding in *Pinus radiata* D.Don.

The effects of photoperiodism have been observed in the spring in deciduous species such as beech. Beech (Fagus sylvatica L.) needs a 12 hour photoperiod for bud-break (Wareing 1953, Heide 1993). On the other hand, the possible role of light in the spring for spruce is rather speculative even though the flowering in Norway spruce correlates with calendar time even more closely than in Scots pine. If no other explanations are found, the role of light as a synchronizing factor should be reconsidered. Giertych (1972) suggests that April sunshine promotes flushing of northern provenances of Norway spruce. This arises expectations of further light-bound effects controlling the development of spruce in the

spring which may be detected in due course. The susceptibility of spruce to spring frosts might also be better understood if daylength was an effective factor contributing to onset of development together with favourable temperatures.

4.7 Concluding remarks

A study of twelve years can not possibly reveal the true range of variation in flowering of Norway spruce. This seems to be the case also in the earlier study of Scots pine flowering (Luomajoki 1993). Frequent years of minimal pollen crop make the problem with spruce more acute, however. It is not clear how much of the observed variation in period unit sums is due to error in the biofix, to the less than perfect homogeneity of development (J. Sarvas 1977), the effects of direct radiation (Luomajoki 1977, Pukacki 1980) or to the effects of sharp fluctuations of temperatures (Ryan 1941, Chung 1981). Nevertheless, in spite of its shortcomings, the period unit system

has demonstrated the superiority of curvilinear heat sum systems over linear systems that require a temperature threshold; a fact also stressed by Sarvas (1972).

The differences found between years, notably 1967 vs. 1969, were found to be similar to those in Scots pine (Luomajoki 1993). All three timing parameters used (p.u., d.d., calendar days) gave comparable results in this respect. However, the annual differences in Norway spruce were less conspicuous than in Scots pine (Luomajoki 1993) owing to the smaller spruce material.

Norway spruce and Scots pine have different histories of reinvasion into Finland in the postglacial time. Ecological factors slowed down the invasion of spruce (see review by Alho 1990). Different species' strategies in adaptation mean weak measurable variation in spruce and clearcut variation in pine for adaptation to local climates. In both species the reinvasion, different routes of migration and deviating timetables in migration are still visible in the populations.

References

Aartolahti, T. 1966. Über die Einwanderung und die Verhäufigung der Fichte in Finnland. Annales Botanici Fennici 3:368–379.

Alho, P. 1990. Suomen metsittyminen jääkauden jälkeen. Silva Fennica 24(1):9–19.

Annila, E. 1981. Kuusen käpy- ja siementuholaisten kannanvaihtelu. English summary: Fluctuations in cone and seed insect populations in Norway spruce. Communicationes Instituti Forestalis Fenniae 101. 32 p.

Bergman, F. 1978. The allelic distribution at an acid phosphatase locus in Norway spruce (Picea abies) along similar climatic gradients. Theoretical and Applied Genetics 52: 57–64.

Brøndbo, P. 1970. The effect of meteorological factors on the flowering intensity and cone crop of Picea abies in southeastern Norway. Proceedings IUFRO section 22 working group. Varparanta, Finland. I. 14 p.

Burdon, R.D. 1977. Photoperiodic effect on pollen shedding in Pinus radiata? New Zealand Journal of Forestry Science 7(2): 214–215.

Chalupa, V. 1964. Dynamika kvetení lesních drevin. English summary: The flowering of forest trees. Práce vyzkumnych ústavu lesnickych (CSSR) 28: 139–173.

Chung, M.-S. 1981. Flowering characteristics of Pinus sylvestris L. with special emphasis on the reproductive adaptation to local temperature factor. Acta Forestalia Fennica 169. 69 p.

Critchfield, W.B. 1984. Impact of the Pleistocene on the genetic structure of North American conifers. Proceedings 8th North American Forest Biology Workshop, July 30–August 1 1984, Utah State University, Logan (Ed. R.M. Lanner): 70–118.

Dietrichson, J. 1980. Skal vi ha hvitrussisk gran over hele landet? English summary: Should we use White Russian Norway spruce over the whole country? Sveriges Skogsvårdsförbunds Tidskrift 78(1–2): 24–34.

Dormling, I. 1982. Frost resistance during bud flushing and shoot elongation in Picea abies. Silva Fennica 16(2): 167–177.

Eis, S. 1973. Cone production of Douglas-fir and grand fir and its climatic requirements. Canadian Journal of Forest Research 3: 61–70.

Eriksson, G. 1982. Ecological genetics of conifers in Sweden. Silva Fennica 16: 149–156.

Eronen, M. 1979. The retreat of pine forest in Finnish Lapland since the holocene climatic optimum: a general discussion with radiocarbon evidence from subfossil pines. Fennia 157(2): 93–114. ISSN 0015-0010.

Fenner, M. 1991. Irregular seed crops in forest trees. Quarterly Journal of Forestry 85(3): 166–172.

Giertych, M. 1972. Provenance differences in the time of spruce (Picea abies (L.) Karst.) flushing in Poland. Arboretum Kornickie 17: 169–183.

— 1991. Provenance variation in growth and phenology. In: Giertych, M. & Matyas, C. (eds.) Genetics of Scots pine, Akadémiai Kiadó, Budapest: 87–101. ISBN 96305.

Grönwall, O. 1982. Aspects of the food ecology of the red squirrel (Sciurus vulgaris L.). Thesis, Department of Zoology, University of Stockholm. 131 p.

Hänninen, H. 1990. Modelling bud dormancy release in trees from cool and temperate regions. Acta Forestalia Fennica 213. 47 p. ISBN 951-651-088-4.

— 1991. Does climatic warming increase the risk of frost damage in northern trees. Plant, Cell and Environment 14: 449–454.

Heide, O.M. 1993. Dormancy release in beech buds (Fagus sylvatica) requires both chilling and long days. Physiologia Plantarum 89: 187–191.

Hustich, I. 1948. The Scotch pine in northernmost Finland and its dependence on the climate in the last decades. Acta Botanica Fennica 42. 75 p.

Hyvärinen, H. 1987. History of forests in Northern Europe since the last glaciation. Annales Academiae Scientiarum Fennicae, Series A. III. Geologia-Geographica 145: 7–18.

Koski, V. 1989. Siemensiirrot ja ilmastoon sopeutuminen. Metsäntutkimuslaitoksen tiedonantoja 328: 20–37.

— & Tallqvist, R. 1978. Tuloksia monivuotisista kukinnan ja siemensadon määrän mittauksista metsäpuilla. English summary: Results of longtime measurements of the quantity of flowering and seed crop of forest trees. Folia Forestalia 364. 60 p.

Kullman, L. 1989. Cold-induced dieback of montane spruce forests in the Swedish Scandes — a modern analogue of paleoenvironmental processes. New Phytologist 113: 377–389.

— 1991. Structural change in a subalpine birch woodland in North Sweden during the past century. Journal of Biogeography 18(1): 53–62.

— & Engelmark, O. 1991. Historical biogeography of Picea abies(L.) Karst and its subarctic limit in northern Sweden. Journal of Biogeography 18(1): 63–70.

— & Högberg, N. 1989. Rapid natural decline of upper montane forests in the Swedish Scandes. Arctic 42(3): 217–226.

Laaksonen, K. 1976. The dependence of mean air temperatures upon latitude and altitude in Fennoscandia. Academia Scientiarum Fennica 119. 19 p.

Lagercrantz, U. & Ryman, N. 1990. Genetic structure of Norway spruce (Picea abies): Concordance of morphological and allozymic variation. Evolution 44(1): 38–53.

Linsser, C. 1867. Die periodischen Erscheinungen des Pflanzenlebens in ihrem Verhältniss zu den Wärmeerscheinungen. Memoires de L'Académie Impériale des Sciences de St.-Pétersbourg, VII$_E$ Serie. Tome XI,7. 44 p.

Lundkvist, K. 1987. Earliness and growth performance in clones of Picea abies selected for late frost resistance. Scandinavian Journal of Forest Research 2: 31–43.

Luomajoki, A. 1977. Effects of temperature on spermatophyte male meiosis. Hereditas 85: 33–48.

— 1984. The tetrad phase of microsporogenesis in trees with reference to the annual cycle. Hereditas 101: 179–197.

— 1993. Climatic adaptation of Scots pine (Pinus sylvestris L.) in Finland based on male flowering phenology. Acta Forestalia Fennica 237. 27 p.

Mononen, S. 1987. Männynsiemenen siirrot Pohjois-Suomessa. Metsäntutkimuslaitoksen tiedonantoja 278: 80–91.

Muona, O., Paule, L., Szmidt, A.E. & Kärkkäinen, K. 1990. Mating system analysis in a central and northern European population of Picea abies. Scandinavian Journal of Forest Research 5: 97–102.

Ojansuu, R. & Henttonen, H. 1983. Kuukauden keskilämpötilan, lämpösumman ja sademäärän paikallisten arvojen johtaminen ilmatieteen laitoksen mittaustiedoista. English summary: Estimation of local values of monthly mean temperature, effective temperature sum and precipitation sum from the measurements made by the Finnish meteorological office. Silva Fennica 17(2): 143–160.

Oleksyn, J., Giertych, M. & Redko, G.I. 1986. Novyi vglyad na geograficheskie kultury sosny obyknovennoj V.D. Ogievskogo. Lesnoi Zhurnal 6: 20–24.

Pukacki, P. 1980. Temperature of Norway spruce and Scots pine buds. Arboretum Kórnickie 25: 277–286.

Pukkala, T. 1987. Kuusen ja männyn siemensadon ennustemalli. English summary: A modell for predicting the seed crop of Picea abies and Pinus sylvestris. Silva Fennica 21(2): 135–144.

Rehfeldt, J. 1984. Microevolution of conifers in the northern rocky mountains: a view from common gardens. Proc. 8th North Amer. For. Biol. Workshop, July 30–Aug. 1, Utah State Univ., Logan: 132–146.

Remröd, J. 1974. Resultat från granproveniensförsök i norrländska höglägen. Föreningen Skogsträdsförädlingen och Institutet för Skogsförbättring, årsbok 1974: 117–135.

Robertson, G.W. 1973. Development of simplified agroclimatic procedures for assessing temperature effects on crop development. Proceedings Uppsala Symposium, 1970, Plant response to climatic factors: 327–343.

Ryan, F.J. 1941. Temperature change and the subsequent rate of development. Journal of Experimental Zoology 88: 25–54.

Sarvas, J. 1977. Mathematical model for the physiological clock and growth. Acta Forestalia Fennica 156. 25 p.

Sarvas, R. 1962. Investigations on the flowering and seed crop of Pinus silvestris. Communicationes Instituti Forestalis Fenniae 53(4). 198 p.

— 1967. The annual period of development of forest trees. Proceedings of the Finnish Academy of Science and Letters 1965: 211–231.

— 1968. Investigations on the flowering and seed crop of Picea abies. Communicationes Instituti Forestalis Fenniae 67(5). 84 p.

— 1972. Investigations on the annual cycle of development of forest trees. Active period. Communicationes Instituti Forestalis Fenniae 76(3). 110 p.

— 1974. Investigations on the annual cycle of development of forest trees II. Autumn dormancy and winter dormancy. Communicationes Instituti Forestalis Fenniae 84(1). 101 p.

Scamoni, A. 1955. Beobachtungen über den Pollenflug der Waldbäume in Eberswalde. English summary: Observations on pollen dispersal by forest trees at Eberswalde. Zeitschrift für Forstgenetik und Forstpflanzenzüchtung 4: 113–122.

Sirén, G. 1993. Biological long-term evidence of the circumpolar subarctic climate oscillation. World Resource Review 5(1): 77–83.

Skre, O. 1988. Seed ripening in forest trees: a literature review. Communications of the Norwegian Forest Research Institute 40(11). 16 p.

Tigerstedt, P.M.A. 1973. Studies on isozyme variation in marginal and central populations of Picea abies. Hereditas 75: 47–59.

Tirén, L. 1935. Om granens kottsättning, dess periodicitet och samband med temperatur och nederbörd. Meddelanden från statens Skogsforsöksanstalt 28: 414–524.

Tolonen, K. 1983. Kuusen levinneisyyshistoriaa Suomessa. English summary: The history of Norway spruce, Picea abies, in Finland. Sorbifolia 14(2): 53–59.

Wang, J. 1960. A critique of the heat unit approach to plant response studies. Ecology 41: 785–790.

Wareing, P.F. 1953. Growth studies in woody species V. Photoperiodism in dormant buds of Fagus sylvatica L. Physiologia Plantarum 6: 692–706.

Worrall, J. & Mergen, F. 1967. Environmental and genetic control of dormancy in Picea abies. Physiologia Plantarum 20: 733–745.

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Seloste

Kuusen sopeutuminen suomen ilmastoon hedekukkimisaikojen perusteella arvioituna

Kuusen hedekukinnan (anteesin) ajoittumista ja siitepölymääriä sekä niiden maantieteellisiä korrelaatioita tutkittiin 10 koealalla 9 paikkakunnalla vuosina 1963–1974. Tutkittuja anteeseja oli yhteensä 85, joista hedekukinnan ajoittumisen tutkimiseen voitiin käyttää 70 anteesia vuosilta 1964–1973. Siitepölyä mitattiin Sarvas-Vilska siitepölymittarilla puiden latvustasolta. Lämpötila kussakin tutkimusmetsikössä mitattiin niinikään puiden latvustasolta.

Tutkimuksessa määritettiin ajoittumisen selvittämiseksi tietokonetekniikkaa hyväksikäyttäen siitepölyjakauman kuvaajan muoto kunakin vuonna kussakin metsikössä, laskettiin normaalijakauman mukainen tasoitussuora frekvenssipaperilla, keskihajonta ja 50 prosentin kohta jakaumasta. Viimeksimainittua käytettiin ajoittumisen perusteena. Siitepölytakertumien perusteella piirrettiin myös siitepölydiagrammit, joissa päivittäiset siitepölytakertumat oli jaettu päivittäisellä lämpösummalla.

Ajoittumista mitattiin maaliskuun 19 päivästä alkaen (joka on ensimmäinen 12 tunnin päivä) kolmea mittayksikköä käyttäen: päivinä, tehoisina lämpösummina (d.d.> +5°C) ja Sarvaksen kurvilineaarisina period unit -lämpösummina, jotka lasketaan tunneittain mitatuista lämpötiloista.

Tutkitut metsiköt tuottivat siitepölyä joka vuosi. Kukinnan määrällinen vaihtelu oli kuusella voimakkaampaa kuin aiemmin tutkitulla männyllä. Hedekukinnan jakauman todettiin poikkeavan normaalijakaumasta siinä, että siitepölyjakauman alun arvot olivat odotettua suuremmat (tuulen tuoman taustapölyn vuoksi) ja jakauman lopun arvot odotettua pienempiä. Tästä syystä ajoituksen perusteena olevan normaalijakauman sovittaminen tehtiin ATK-ohjelmalla siitepölykertymän 2,3–88,5 % alueella. Prosenttiluvut vastaavat keskiarvoon nähden aluetta –2/+1,2 keskihajonnan yksikköä, jolla siitepölyjakauma noudattaa normaalijakaumaa.

Kun mitattuja arvoja käytettiin sellaisenaan, parhaaksi ajoittumisen kuvaajaksi osoittautui paikallisesti päiväluku, vaikka period unit -summa oli keskimäärin melkein yhtä hyvä. Tulos on päinvastainen kuin männyllä. Tehoisa lämpösumma oli keskimäärin selvästi huonoin mittari, kuten männylläkin. Yksittäisenä vuonna period unit -summa saattaa sellaisenaan olla kukkimisajan paras osoittaja, etenkin lämpöoloiltaan poikkeuksellisena vuonna. Jos lämpösummien erot odotetun ja mitatun arvon välillä muutettiin päiviksi ja koko vertailu tehtiin päiväasteikolla,

period unit oli kuitenkin tarkin parametri.

Anteesin vaatima lämpösumma ei vaihdellut kuusella maantieteellisesti läheskään yhtä paljon kuin männyllä. Kuusi ei ole siis sopeutunut maantieteellisesti lämpötekijään yhtä paljon kuin mänty. Toisaalta ajoittumista ilmaiseva päiväluku vaihteli kuusella leveysasteen mukaan yhtä jyrkästi kuin männylläkin.

Kuusi kukki pohjoisessa odotetusti myöhemmin kuin etelässä, siitepölymäärät olivat pienempiä ja siitepölymäärien hajonta suurempi aivan kuten männylläkin. Pääasiallinen vaihtelusuunta näissä korrelaatioissa ei ollut etelästä pohjoiseen vaan suurinpiirtein kaakosta luoteeseen tai jopa idästä länteen. Tähän tulokseen tultiin laskemalla etäisyyden korrelaatioita Karjalan kannaksen etelälaidalla sijaitsevasta vertailupisteestä (SE-piste) ja Suomen itäisimmästä pisteestä (EE-piste) lähtien. Itä-länsisuuntaiset korrelaatiot korostuivat kuusella suhteellisesti paljon voimakkaammin kuin männyllä. Tämä poikkeama lämpöolojen määräämästä etelästä pohjoiseen -suunnasta johtunee siitä, että kuusi levisi maahamme idästä jääkauden jälkeen (Tolonen 1983, Kuva 7).

Hedekukkimisen vaatima lämpösumma vaihteli myös vuosittain siten, että v. 1969 anteesin tarvittiin keskimääräistä korkeampi lämpösumma ja v. 1967 tavallista pienempi lämpösumma kuten männylläkin. Tämä johtuu kiinteästä nollapisteestä ajoittumisen määrittämisessä. Lämpösummien laskeminen pitäisikin aloittaa kuusen ollessa fysiologisesti samassa vaiheessa kunakin vuonna eikä tietystä kalenteripäivästä. Ei kuitenkaan tunneta keinoa, millä asteikon nollapiste määritettäisiin kullekin vuodelle ja kullekin paikkakunnalle oikeaksi. Asiaan vaikuttaa sekin, että vuosirytmin täsmäys tapahtunee vuosittain syksyisin eikä keväisin.

Linsserin lain mukaisesti hedekukkimisen vaatima suhteellinen lämpösumma (kukkimisen lämpösumma jaettuna keskimääräisellä vuotuisella kokonaislämpösummalla) pysyy vakiona Etelä-Euroopasta Etelä-Suomeen asti. Kuitenkin noin 63. leveyspiirin pohjoispuolella tarvittava suhteellinen lämpösumma nousee jyrkästi (Kuva 13) kuten männylläkin. Tämä merkitsee, ettei kuusi ole kyennyt lisääntymisessään enää juuri ollenkaan sopeutumaan ilmastoon Kaakkois-Suomen (Sisä-Suomi mukaan lukien) luoteispuolella.

Maassamme on viime aikoina keskusteltu paljon siitä, että puiden vuosirytmi saattaisi häiriintyä ilmaston lämmetessä. Kukkimisaikojen valossa luoteinen kolmannes

Suomen kuusimetsistä on kuitenkin tällä hetkellä vaillinaisesti sopeutunut kylmään ilmastoon. Ilmaston lämpeneminen parantaisi ilmeisesti myös kuusen elinmahdollisuuksia etenkin Pohjois-Suomessa. Kuusen arkuus keväthalloille tekee toisaalta vaikeaksi ilmastonmuutoksen seurausten tarkan arvionnin. Kuusi poikkeaa männystä siinä, että kuusi kestää myös siemensiirtoja pohjoiseen päin henkiinjäävien taimien osuuden romahtamatta. Kuusen ilmiasullinen joustavuus tekee siitä huonomman ilmastonmuutoksen indikaattorin kuin männystä, joka kenties muistona lämpökauden oloista menestyy parhaiten etelään päin siirrettynä.

Instructions to authors — Ohjeita kirjoittajille

Submission of manuscripts

Manuscripts should be sent to the editors of the Society of Forestry as three full, completely finished copies, including copies of all figures and tables. Original material should not be sent at this stage.

The editor-in-chief will forward the manuscript to referees for examination. The author must take into account any revision suggested by the referees or the editorial board. Revision should be made within a year from the return of the manuscript. If the author finds the suggested changes unacceptable, he can inform the editor-in-chief of his differing opinion, so that the matter may be reconsidered if necessary.

Decision whether to publish the manuscript will be made by the editorial board within three months after the editors have received the revised manuscript.

Following final acceptance, no fundamental changes may be made to manuscript without the permission of the editor-in-chief. Major changes will necessitate a new submission for acceptance.

The author is responsible for the scientific content and linguistic standard of the manuscript. The author may not have the manuscript published elsewhere without the permission of the publishers of Acta Forestalia Fennica. The series accepts only manuscripts that have not earlier been published.

The author should forward the final manuscript and original figures to the editors within two months from acceptance. The text is best submitted on a floppy disc, together with a printout. The covering letter must clearly state that the manuscript is the final version, ready for printing.

Form and style

For matters of form and style, authors are referred to the full instructions available from the editors.

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Metsäntutkimuslaitoksesta lähtöisin olevien käsikirjoitusten hyväksymismenettelystä on ohjeet Metsäntutkimuslaitoksen julkaisuohjesäännössä.

Muista käsikirjoituksista lähetetään Suomen Metsätieteellisen Seuran toimitukselle kolme täydellistä, viimeisteltyä kopiota, joihin sisältyvät myös kopiot kaikista kuvista ja taulukoista. Originaaliaineistoa ei tässä vaiheessa lähetetä.

Vastaava toimittaja lähettää käsikirjoituksen valitsemilleen ennakkotarkastajille. Tekijän on otettava huomioon ennakkotarkastajien ja toimituskunnan korjausesitykset. Korjaukset on tehtävä vuoden kuluessa siitä, kun käsikirjoitus on palautettu tekijälle. Jos tekijä ei voi hyväksyä korjausesityksiä, hänen on ilmoitettava eriävä mielipiteensä vastaavalle toimittajalle tai toimituskunnalle, joka tarvittaessa ottaa asian uudelleen käsittelyyn.

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Tekijän tulee antaa lopullinen käsikirjoitus ja kuvaoriginaalit toimitukselle kahden kuukauden kuluessa hyväksymispäätöksestä. Käsikirjoituksen saatteesta pitää selvästi ilmetä, että käsikirjoitus on lopullinen, painoon tarkoitettu kappale. Teksti otetaan mieluiten vastaan mikrotietokoneen levykkeellä, jonka lisäksi tarvitaan paperituloste.

Käsikirjoitusten ulkoasu

Käsikirjoituksen asun tulee noudattaa sarjan kirjoitusohjeita, joita saa toimituksesta.

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