

# ACTA FORESTALIA FENNICA

237

ALPO LUOMAJOKI

CLIMATIC ADAPTATION OF SCOTS PINE (*PINUS  
SYLVESTRIS* L.) IN FINLAND BASED ON MALE  
FLOWERING PHENOLOGY

MÄNNYN SOPEUTUMINEN SUOMEN ILMASTOON  
HEDEKUKKIMISAIKOJEN VALOSSA

THE SOCIETY OF FORESTRY IN FINLAND  
THE FINNISH FOREST RESEARCH INSTITUTE

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## ACTA FORESTALIA FENNICA 237

### CLIMATIC ADAPTATION OF SCOTS PINE (*PINUS SYLVESTRIS* L.) IN FINLAND BASED ON MALE FLOWERING PHENOLOGY

Männyn sopeutuminen Suomen ilmastoon  
hedekukkimisaikojen valossa

Alpo Luomajoki

*Approved on 11.2.1993*

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Timing of anthesis in 21 Scots pine stands from 14 localities in Finland was studied at the canopy level 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 characterized in calendar days, in degree days (>5 °C) and in period units. The count of each unit began on March 19 (included).

The period unit was found to be the most accurate delineator of development both in a single year and also in the majority of cases as stand averages over several years. Locally, calendar days were a more accurate parameter for stand average. Anthesis in northern Finland occurred at a later date than in the south as was expected, but at a lower heat sum. The variation in the timing of anthesis and the variation of pollen catches increased northwards. The geographical correlations calculated against distances measured along simulated post-glacial migration routes were stronger than purely latitudinal correlations. Effects of the reinvasion of Scots pine into Finland are thus still visible in pine populations.

The proportion of the average annual heat sum needed for anthesis grew rapidly above a latitude of 63° even though the heat sum needed for anthesis decreased towards the timberline. In light of flowering phenology it seems probable that the northern populations of Scots pine in Finland have still not completely adapted to the prevailing cold climate at these latitudes. A moderate warming of the climate would therefore be beneficial for Scots pine.

Keywords: anthesis, flowering phenology, pollen recording, heat sum, adaptation, reinvasion, *Pinus*.  
FDC 174.7 *Pinus sylvestris* + 181.2

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Männyn siitepölyn leviämisen eli anteesin ajoittumista tutkittiin 1963–1974 puiden latvustasolla 21 metsikössä 14 paikkakunnalla. Siitepölyn takertumien perusteella saatuja jakaumia verrattiin normaali-jakaumaan. Ajoittumisen perusteeksi otettiin jakauman 50 % kohta ja sitä mitattiin päiväasteikolla, tehoisalla lämpösommalla (>5 °C) ja period unit -yksiköllä.

Period unit osoittautui keskimäärin tarkimmaksi yksiköksi, mutta paikallisesti päiväasteikko oli toisinaan tarkin. Etelä-Suomeen verrattuna anteesi oli odotetusti Pohjois-Suomessa myöhemmin, mutta vaati pienemmän lämpösomman. Ajoittumisen samoin kuin siitepölykertymän hajonta kasvoivat pohjoiseen päin mentäessä. Jääkauden jälkeistä leviämistä pitkin mitatut maantieteelliset korrelaatiokertoimet olivat suuremmat kuin puhtaasti latitudinaaliset kertoimet. Männyn leviämisen jäljet näkyvät siis yhä mäntypopulaatioissa.

Anteesin vaatiman suhteellisen lämpösomman (Linslerin osuus) valossa sopeutuminen ilmastoon heikkenee jyrkästi 63. leveysasteen pohjoispuolella, vaikka anteesiin tarvittava lämpösomma pieneneekin aina metsänrajalle asti. Kukkimisaikojen perusteella voidaan havaita, että pohjoisen puolisko Suomen mäntymetsistä on tällä hetkellä vaillinaisesti sopeutunut vallitsevaan ilmastoon ja että ilmaston lämpeneminen parantaisi männyn elinmahdollisuuksia Pohjois-Suomessa.

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## 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; 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 adapted, so the d.d. sum grows daily by  $(\bar{t} - 5)$  d.d.'s.

**Ecological latitude.** Altitude can be simulated at sea level by a shift towards north if suitable climatological data is available for calculations. 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.** 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. Not exactly true for long periods (cf. Wang 1960). Relatively long periods of more or less homogeneous development can be

found in generative development rather than in vegetative growth.

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

**Number of antheses (n).** Number of antheses studied (years/stands). For 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. The period unit in this study is considered as a heat sum unit, even if Sarvas (1972 p. 67) did not consider it so. He pointed out that no threshold is used in p.u.'s as in conventional heat sums.

**Significance levels.** The following markings were used to imply significance of correlation coefficients: almost significant,  $p < 0.05$ : \*; significant,  $p < 0.01$ : \*\*; highly significant,  $p < 0.001$ : \*\*\*

**Standard deviation (SD).**

**Sunhours.** The length of day 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.

**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

Acknowledgements are extended to the former Department of Silviculture of the Finnish Forest Research Institute where the material was collected, and to Mr. Pentti Manninen who was mainly responsible for the microscopy. Mr. Teijo Sirviö, M.Sc., assisted with the computer techniques involved. Professor Risto Sarvas of the Finnish Forest Research Institute initiated extensive studies on the flowering of forest trees. In 1974, following the death of Prof. Risto Sarvas, designer, leader and supporter of this study, col-

lection of further data ceased. This was unfortunate as the material was already regarded as unique in terms of geographical coverage and duration.

The English text was revised by Dr. Robin Sen. Ms. Anni Harju, Lic.Ph., Professor Veikko Koski and Mr. Seppo Ruotsalainen, M.For., made valuable suggestions on earlier drafts of the manuscript. I extend my sincere thanks to them all.

## 1 Introduction

Phenological research serves several practical purposes including determining crop timing in agriculture (Ottonson 1958) and host-pest relationships in plant protection (Blum 1988, Lysyk & Nealis 1988, Mitchell & Sower 1988, Wickman 1988). Studies of flowering frequency and phenology in conifer seed orchards are important as they may reveal contributions of different tree clones to the genetic composition of seed (Eriksson et al. 1973, Jonsson et al. 1976). Phenological research is also useful in dealing with problems related to adaptation of the annual developmental cycle of species, e.g. seasonal survival of trees. In adaptation studies, frost tolerance, chilling requirements during dormancy, adaptation to continental or maritime climates, success of flowering and seed production are all parameters frequently assessed. Survival of marginal populations under severe environmental conditions, and the genetic consequences of such extreme adaptation are also important considerations.

Methods for phenological studies have continually improved from the simple observations of the onset and completion of flowering to continuous investigations of whole flowering sequences (Sarvas 1972). Special dedicated pollen monitoring and continuous temperature measurement equipment for the study site have long been available.

In northern latitudes, temperature is regarded as a major limiting factor of forest reproduction.

The northernmost stand in this study is a separate island of forest growth north of the pine timber line. Yearly variation in the annual cumulative temperature sums are also generally much greater in the north than in the south (see Fig. 2 based on data by Ojansuu and Henttonen 1983). The climatological reasons for this were analyzed by Pohjola (1980).

Temperatures in Finland varied in such a way 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), the 1 per cent probabilities for single years being close to 1000 and 1700 d.d. respectively. In northernmost stands the average was 640 d.d., the 1 per cent probabilities for single years being at ca. 300 and 1000 d.d., respectively, as calculated from computer data of Ojansuu and Henttonen (1983).

This study concentrates on details of male flowering at anthesis in 21 Finnish Scots pine stands at 14 localities (Fig. 1) in 1963–1974. The material was collected at the Department of Silviculture (now a part of the Department of Forest Production) of the Finnish Forest Research Institute. Early studies on anthesis were made already in the 50's (Sarvas 1962) and early 60's (see Koski 1991). By 1963 an improved and more reliable model of pollen registering equipment was available and the measurement of temperatures at each stand had begun.

The aim of this study was to further analyse

the geographical variation found in the timing of anthesis in Scots pine. In the adaptation of the generative cycle to local climatic conditions, the geographical adaptability weighted with the so called Linsser's law (Linsser 1867, see Chapter 4.6) is a particularly interesting point. Is the measurable adaptation in phenological terms in agreement with Linsser's law? Can we still trace the route of reinvasion of Scots pine into Finland after the last glaciation from the pattern of phe-

nological characteristics of anthesis? How great is the phenological variability in the northern marginal stands? How large are the effects of temperatures in the two preceding years on the timing of male flowering and on amount of pollen production?

What is the efficacy of the two temperature sum systems, i.e. linear (d.d.) as compared to the curvilinear (p.u.) systems? Is simple calendar time a better delineator of development? Is there any benefit in using the mean of the idealized pollen distribution curve mean as a reference as against simple observations of the day of peak pollen catch? The effect of a possible change in climate in future on Scots pine forests will also be evaluated.

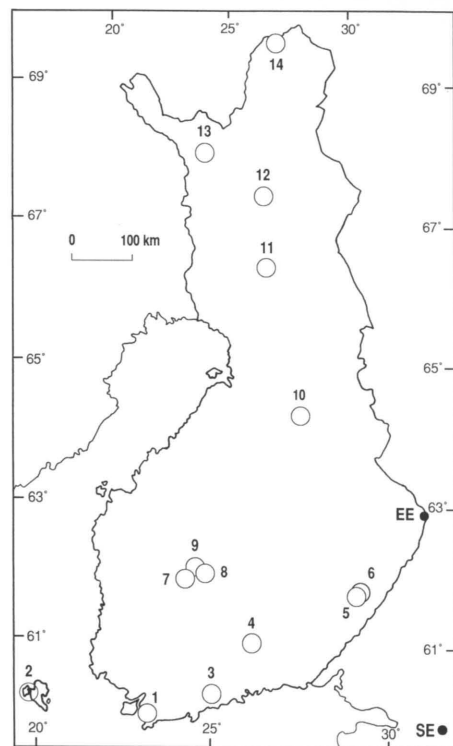


Fig. 1. Localities where anthesis materials were collected. One to three experimental stands (see Table 1) were studied at each locality which were in latitudinal order: 1. Bromarv (annexed in 1977 to Tenhola parish and further to Tammisaari in 1993), 2. Eckerö, 3. Tuusula, 4. Heinola, 5. Punkaharju, 6. Kerimäki, 7. Ruovesi, 8. Kuorevesi, 9. Vilppula, 10. Kajaani, 11. Rovaniemi, 12. Sodankylä, 13. Kittilä and 14. Utsjoki. The distance between localities 1 and 14 is ca. 1090 km. EE and SE are reference points for calculations of migratory distances.

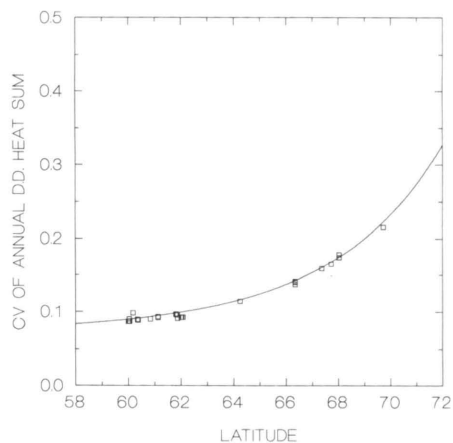


Fig. 2. The coefficient of variation of annual degree-day heat sums at the study sites. On the vertical scale 0.1 is equivalent to 10 per cent. Based on data by Ojanusu & Henttonen (1983).

## 2 Material and methods

### 2.1 Pollen registration

The material consisted of 156 complete registrations of antheses (years/stands) from 1963 to 1974 in 21 stands. A single stand was studied in all consecutive years of the full study period, but as many as 19 stands from 1966 to 1969 were studied (Table 1). The mature stands chosen covering an area of a few ha, were classified as pollination normal stands (see Sarvas 1962). These stands of local origin were subjected to normal silvicultural practises. The antheses were measured with self-recording pollen samplers (mod. Sarvas-Vilksa 1963, see Sarvas 1968), 1 to 3 samplers at each stand at tree-top level. The ideal of three samplers was met in certain stands although two were most often used. The mean of daily pollen catches was used in calculations where more than one sampler was used. A

thermograph was also placed at tree-top level in each stand. The function of meters was checked two to three times a day.

The beginning of the anthesis was not completely covered in 5 out of a total of 156 measurements taken. In these cases the daily Scots pine pollen catches from neighbouring Norway spruce stands were compared under parallel measurement periods, and a correction factor was calculated to allow for different position of meters. The few missing and corrected daily Scots pine pollen catches (read from the spruce stands) were then included in the Scots pine data. The supplements ranged from 3.3 to 16.6 per cent of total pollen catch of the particular stand.

The pollen catch was microscopically counted from the recording bands and the results prepared in terms of daily catches, catch averages, cumulative sums and cumulative percentages of

Table 1. Stand characteristics and years of study.

Stand	Locality	Latitude	Longitude	Elevation	Age, years in 1970	Years of study	Remarks on stand
Bromarv II	1	60°02'	23°03'	41	84	1964-69	
Bromarv III	1	60°03'	23°03'	35	63	1965-73	
Bromarv 559	1	60°00'	23°05'	32	110	1964	
Eckerö I	2	60°11'	19°34'	33	140	1966-69	
Heinola 566	4	61°07'	26°01'	133	127	1964-71	Clear cut in 1985
Kajaani 546	10	64°15'	27°41'	132	139	1966-73	Clear cut in 1979-80
Kerimäki XX	6	61°51'	29°23'	99	102	1965-73	Clear cut in 1985
Kerimäki XXII	6	61°51'	29°23'	102	98	1965,67-73	400 kg urea/ha given in winter 1967-68, Clear cut in 1985
Kerimäki XXXIII	6	61°50'	29°23'	92	155	1965-73	
Kittilä I	13	68°02'	24°09'	280	220	1963,65-69, 71-73	Too scant pollen catch for timing in 1963
Kittilä II	13	68°02'	24°08'	330	190	1965-69, 71-73	
Kuorevesi XXIII	8	62°00'	24°47'	110	102	1963-71	
Punkaharju I	5	61°48'	29°19'	91	147	1963-74	
Punkaharju XLV	5	61°48'	29°19'	106	119	1964-74	
Rovaniemi XXVII	11	66°21'	26°44'	118	112	1963-73	
Rovaniemi XXIX	11	66°21'	26°38'	165	106	1965-73	
Ruovesi 394	7	61°52'	24°10'	105	125	1966-69	Clear cut in 1980
Sodankylä 552	12	67°22'	26°28'	180	134	1966-69	
Tuusula XXXII	3	60°21'	25°01'	70	144	1964-69	
Utsjoki I	14	69°44'	27°01'	94	165	1964-69	No pollen catch in 1966, too scant for timing in 1969
Vilppula 2a	9	62°04'	24°29'	130	190	1965-69	

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

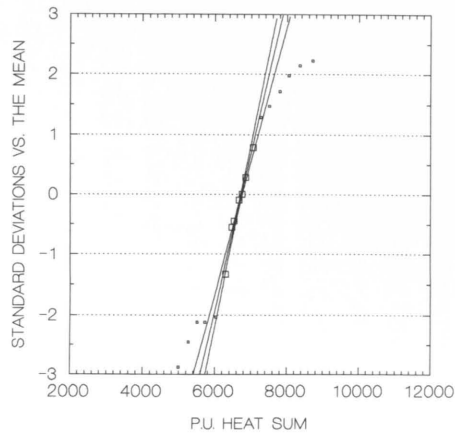


Fig. 3. Cumulative distribution of pollen catch at Rovaniemi stand XXIX in 1971 with confidence limits at a probability level of 95 per cent. The central larger squares were used to position the line while the smaller ones beyond the limits of  $-2$  and  $+1.2$  standard deviations were excluded (see chapter 4.2.). Period unit heat sum (see Application and abbreviation of some terms) was used.

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 normal distributions to plus 1.2 normal distributions over mean (from 2.3 to 88.5 per cent) were drawn by SYSTAT/SYGRAPH© Multivariate General Linear Hypothesis computer program. See Fig. 3 for an example.

The cumulative daily catches considered as percentages of the total catch approximately lie, on probability paper, on a single one line indicating a nearly normal distribution. However, in an

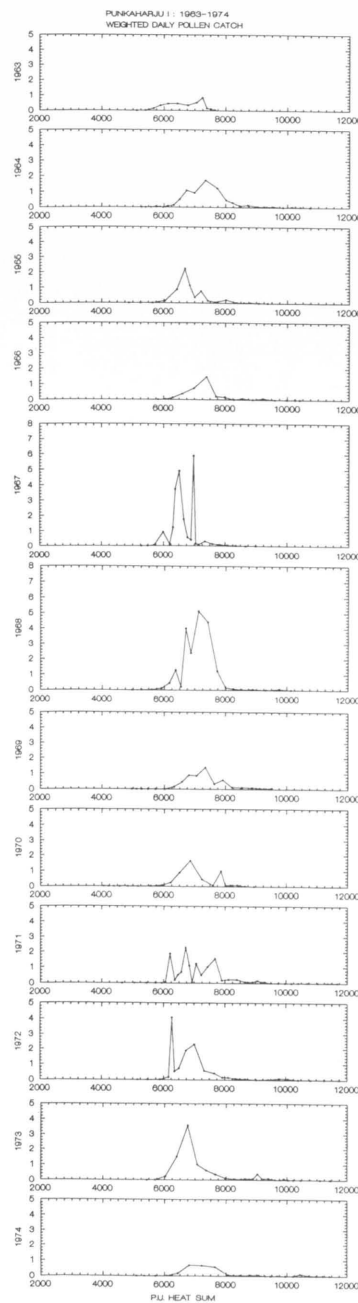


Fig. 4. Pollen catches at Punkaharju (Stand I) in 1963-1974. The daily catches per  $\text{mm}^2$  were divided by the period unit heat sum of each day (the ordinate). Compare to Fig. 5.

thesis study the early and the late observations of a series usually deviate from normality so that the first percentages are slightly larger than expected while the last ones are increasingly smaller than expected (Fig. 3).

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, i.e. a measure for the variation within a single anthesis was obtained in period units (cf. Table 5). The mean (the 50 per cent point of the theoretical distribution) itself was unaffected by the dispersion; it was unbiased.

## 2.2 Temperature measurements

The matching temperature data from thermographs located at tree-top level in the stands were processed to give two kinds of temperature sums. The first was a daily degree-day sum (over  $+5^\circ\text{C}$ ) and the other a more specialised 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 "period unit".

The mean was initially determined as a period unit (p.u.) sum. The daily accumulation of p.u. were computer-tabulated at intervals of two hours for all the stands under study, and the relevant daily degree-day heat sums and dates were also read from the computer sheet. As such three interchangeable measures of the mean of each anthesis were generated.

Parameters can be compared in Table 2; each coefficient of variation is a measure of the between-the-years variation. The most extreme onset and termination dates of antheses are also given on a standwise basis in this table.

The peak pollen catch day can be compared with the date for the 50 per cent point of the theoretical pollen distribution. The relative value of these reference points can so be assessed.

Diagrams showing the progress of anthesis were drawn up from daily average catches divided by the temperature sum accumulated each day. Eight of the total of 156 antheses now 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

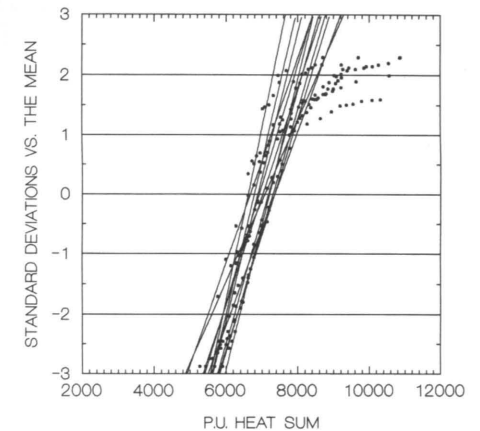


Fig. 5. Cumulative pollen catches at Punkaharju (Stand I) in 1963-1974. Points between  $-2$  to  $+1.2$  standard deviations were used to position the lines. Also catches beyond these limits are shown. The effects of re-floated pollen in the upper region (beyond the  $+1.2$  SD limit) are conspicuous.

diagrams are shown in Fig. 4. This way of presentation can be compared to Fig. 5 in which the same years of the same plot (Punkaharju I) are shown on probability paper.

A rather arbitrary zero point (biofix) was chosen for this study in order to match (and include) the first day with a 12 hour photo period (actual sunhours 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 temperature recordings taken from near-by stands. With regard to timing of anthesis all dates after March 19th produce larger variations in the temperature sum data.

March represents a metabolically active time for the microsporangiate strobilus primordia of Scots pine (Kupila-Ahvenniemi et al. 1978, Hohola et al. 1984, H. Häggman 1987, J. Häggman 1991). This supports placement of the biofix in mid-March. 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 certain years in southern Finland when the onset of spring was early. Latitudes and longitudes were used in calculating correlations to expose usual geographical trends.

Table 2. Variation in timing and duration of anthesis.

Stand	Local- Time range of anthesis (earliest first day to latest last day)	Years of study*	Duration of anthesis		Period March 19th to anthesis 50 % completed			Period March 19th to peak pollen catch day				
			In days	CV %	In days	CV %	In days	CV %	In days	CV %		
Bromarv II	May 30–June 30	6	20.2	31.3	6854	3.2	216.3	7.0	86.8	1.3	87.0	1.6
Bromarv III	May 31–July 3	9	23.9	31.2	6848	3.3	214.2	7.4	84.9	3.2	84.6	4.1
Bromarv 559	June 4–23	1	20.0	-	7167	-	236.0	-	88.0	-	89.0	-
Eckerö I	June 4–July 7	4	25.0	29.4	6468	3.5	196.3	4.8	90.0	1.8	90.8	1.9
Heinola 566	May 31–June 27	8	17.4	17.1	7041	3.3	231.6	7.5	84.8	4.0	84.3	4.4
Kajaani 546	June 2–July 4	8	21.3	22.9	6824	4.6	221.9	8.4	91.5	3.5	90.8	3.9
Kerimäki XX	May 29–July 5	9	21.7	31.2	7078	3.5	232.0	7.3	85.7	4.0	85.1	4.0
Kerimäki XXI	May 30–July 5	8	22.6	27.3	7106	4.6	233.3	8.0	85.8	3.9	85.4	4.8
Kerimäki XXXIII	May 30–July 5	9	21.3	33.5	7125	3.2	233.7	6.8	85.8	3.6	84.3	4.1
Kittilä I	June 5–July 24	8	17.8	33.7	6366	6.1	198.8	10.1	104.9	7.0	102.4	11.1
Kittilä II	June 16–July 25	8	19.5	31.8	6313	6.8	198.6	9.4	105.4	7.2	105.4	7.3
Kuorevesi XXIII	May 23–June 24	9	15.8	21.4	7038	5.0	218.7	7.4	85.0	6.4	85.1	6.6
Punkaharju I	May 24–July 6	12	21.0	29.5	7027	3.7	232.0	6.7	85.3	6.5	85.3	7.0
Punkaharju XLV	June 1–July 5	11	20.9	29.8	7154	4.1	236.0	7.3	86.6	4.6	85.6	4.9
Rovaniemi XXVII	May 30–July 8	11	18.2	28.7	6686	2.5	210.8	5.4	95.2	6.7	94.7	6.4
Rovaniemi XXIX	June 10–July 10	9	18.0	22.7	6557	3.3	208.1	6.8	96.6	4.0	96.4	4.2
Ruovesi 394	June 3–June 26	4	18.8	18.7	7034	6.1	224.8	7.9	87.8	1.9	87.0	1.6
Sodankylä 552	June 16–July 14	4	16.8	20.3	6547	3.3	203.5	8.6	99.5	6.3	99.0	6.4
Tuusula XXXII	May 24–June 30	6	19.5	20.7	7012	3.7	224.8	8.6	85.2	3.3	84.7	4.2
Utsjoki I	June 16–August 8	4	22.8	40.1	5953	14.9	169.3	20.1	113.5	10.3	114.0	10.2
Vilppula 2a	June 4–24	5	14.8	27.6	7048	4.5	222.0	6.5	87.2	1.5	86.8	1.5

\* Three yearly antheses were excluded from timing studies, see Table 1.

### 2.3 Other variables

Combination of latitudes and effect of stand altitudes was possible by using the climatological data of Laaksonen (1976a). The study gave rates of mean temperature change both latitudinally and with respect to altitude on a monthly basis. 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 this study the combination of latitude and altitude was termed 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 only resulted in a stretching of the latitudinal scale in an uncomplicated manner from the south to the north. The

sample stands lie at altitudes from 32 to 330 meters.

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

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

## 3 Results

### 3.1 Flowering characteristics

Regular flowering of Scots pine was observed, and male flowering occurred annually except for during a few exceptional years in the northernmost Lapland north of 67° N.lat. All the completed observation series enabled quantification of the pollen catch, but for timing purposes only antheses with total pollen catches of 15 pollen grains/mm<sup>2</sup> (a purely technical value) or larger were used to determine the required value representing 50 per cent completion of anthesis. While the range of pollen catches in the 156 cases studied was 0–4862.9 grains/mm<sup>2</sup> (CV = 0.707), three antheses had to be excluded from timing calculations owing to minimal pollen catch. On a single occasion, in 1966, the northernmost stand at Utsjoki did not produce any pollen. The restriction regarding a minimal total pollen catch, for timing of anthesis, was necessary in order to prevent background pollen from giving spurious timing data. This kind of error is not such a problem with Scots pine as it is with some other conifers having smaller and more variable pollen crops.

### 3.2 Timing of anthesis

Male flowering in Scots pine was found to begin

as early as May 23 in southern Finland and it could extend as late as August 8 in northernmost Finland (Table 2). The onset and the termination of flowering were judged on the basis of the first and last pollen catches on the registering band. In an individual year air temperatures during spring and early summer had a considerable influence on the timing of flowering. However, long-term stand averages of timing in individual stands remained surprisingly constant in calendar time.

The average duration of anthesis varied between 14.8 days to 25.0 days as judged from pollen catch (i.e. also some background pollen included) although the coefficient of variation (expressing variation between years) was high: from 17.1 to 40.1 per cent (Table 2).

Owing to considerably greater variation the Utsjoki plot has to be viewed separately when comparing the efficacy of the three parameters for the timing of antheses (Table 2, see also Fig. 11). The shortcomings of temperature measurements in 1964 at Utsjoki can partly explain the variation in the period unit sums, but a high variation also occurred in days which are not affected by temperature. Lack of early temperature data, due to temperatures being lower than +5 °C, had no real effect on degree-day sums but the variation was still high.

On a stand basis the period from March 19th to

the 50 per cent point of anthesis varied in stand means from 6313 to 7167 (Utsjoki 5953) period units (Table 2). The respective coefficients of variation varied from 2.5 to 6.8 (Utsjoki 14.9) per cent. Similarly, the period under study counted from 196.3 to 236.0 (Utsjoki 169.3) degree days. The corresponding coefficients of variation ranged from 4.8 to 10.1 (Utsjoki 20.1) per cent. In calendar time the period ranged from 84.8 to 105.4 (Utsjoki 113.5) days. The respective coefficients of variation ranged from 1.3 to 7.2 (Utsjoki 10.3) per cent (Table 2).

Period units were the least variable measure in eleven of the twenty stands comparatively. Days varied least in nine stands, whilst degree days were more variable than the two other measures with one exception (Rovaniemi XXVII). With all methods the trend to highest variation occurred in northern Finland and the lowest figures were from southern Finland.

In this material the occurrence of peak pollen catches in Scots pine were on average 0.33 days earlier than the reference point of 50 per cent completion of anthesis. Changing the reference point to the day of peak pollen catch clearly decreases the consistency in terms of calendar time. As seen from Table 2, the day of 50 per cent completion was a more reliable reference point in 15 out of twenty cases, while the peak

pollen catch day was better in three stands and there was also two cases when both methods gave equal variation coefficients of 1.5 and 4.0 per cent, respectively. 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 anthesis 50 per cent completed) in 17 out of twenty cases.

Comparison of the two best methods, period units vs. days at the 50 per cent point, revealed an interesting geographical difference. Period units were more efficient in eastern Finland and in the north except in the case of the Utsjoki stand (Table 2). Days were a more reliable measure in the southern and western parts of Finland and at Utsjoki.

### 3.3 Geographical trends

Finnish conifer forests are young owing to the relatively recent glaciation. Scots pine, and subsequently Norway spruce invaded Finland from the east and southeast. Two rather arbitrary reference points, the EE-point and 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 the possibility of a rough assessment of migration route effects on adaptive characteristics.

Heat sums and durations relevant to timing of anthesis were correlated with the latitude, the ecological latitude and the longitude (Table 3a). The correlations were all highly significant with the exception of the correlation between duration in days and the longitude, which was almost significant.

Interestingly, timing-related correlations be-

tween heat sums and migration distances from EE-point and SE-point were higher than those between heat sums and the latitude, the distance to the SE-point giving highest values. This latter reference point gave in relation to period units a correlation of  $r = -0.687^{***}$  (Table 3a). Overall, period units mostly gave higher correlations than degree days, but the highest correlations occurred with timing in days.

The numerical difference found in correlations between period units and the latitude, or respec-

Table 3a. Correlations of heat sums and durations involved with anthesis (n = 153).

	Period March 19th to anthesis 50 % completed			Length of anthesis	
	In period units	In degree days >5 °C	In days	In period units	In days
Latitude	-0.584 ***	-0.491 ***	+0.807 ***	-0.384 ***	-0.080
Ecological latitude	-0.575 ***	-0.474 ***	+0.803 ***	-0.387 ***	-0.101
Longitude	+0.321 ***	+0.391 ***	-0.191 *	-0.122	0.061
Distance from EE	-0.603 ***	-0.615 ***	+0.597 ***	-0.261 **	-0.007
Distance from SE	-0.687 ***	-0.640 ***	+0.806 ***	-0.369 ***	-0.056
Degree days of previous year	+0.649 ***	+0.512 ***	-0.732 ***	+0.426 ***	+0.193 *
Degree days of 2 years ago	+0.613 ***	+0.502 ***	-0.696 ***	+0.365 ***	-0.004
Age of stand	-0.278 **	-0.199 *	+0.478 ***	-0.205 *	-0.057

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

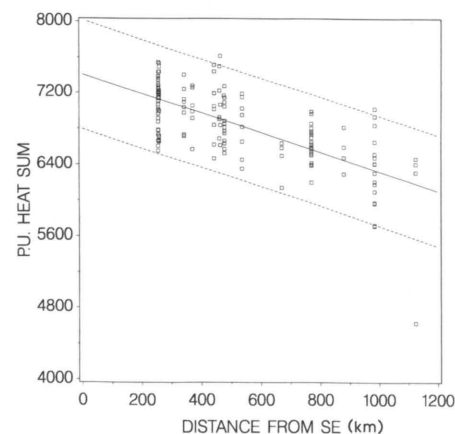


Fig. 6. The dependence of required period unit heat sum for anthesis (50 per cent completed) on the distance from SE-point with confidence limits at 95 per cent level. The regression line is  $Y = 7406.3 - 1.0849 X$  ( $R^2 = 0.472$ ).

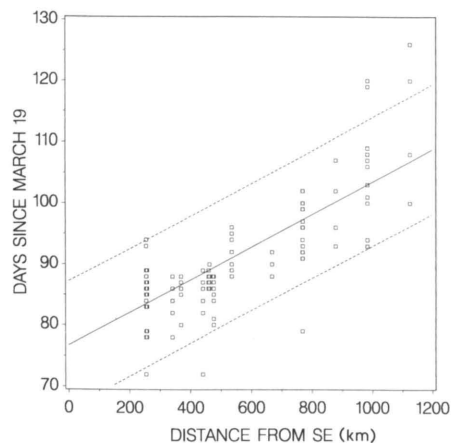


Fig. 7. The day of 50 per cent anthesis completion counted from March 19 (included). The yearly durations in days to anthesis (50 per cent completed) and 95 per cent confidence limits are shown. The regression line is  $Y = 76.73 + 0.02677 X$  ( $R^2 = 0.649$ ).

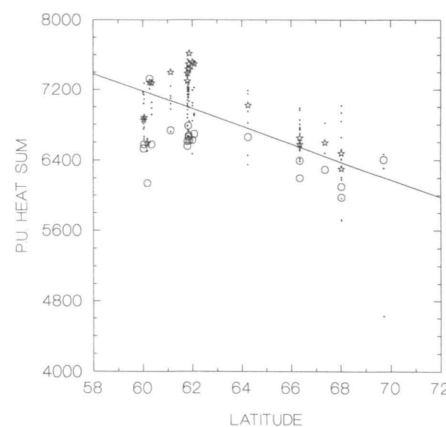


Fig. 8. The required period unit sums for 50 per cent anthesis completion with reference to the latitude. Year 1969 is shown with a star and year 1967 with a circle. All other years are indicated with dots. The regression line is  $Y = 12298.2 - 86.241 X$  ( $R^2 = 0.342$ ).

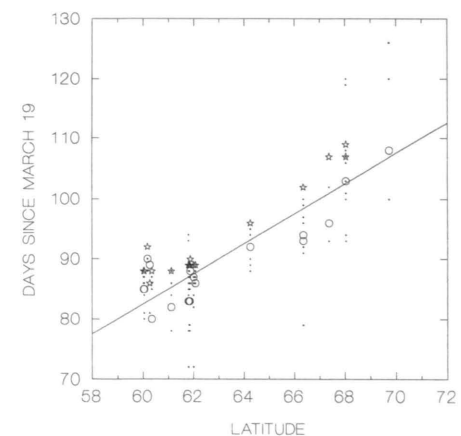


Fig. 9. The durations in days needed for 50 per cent anthesis completion with reference to the latitude. Year 1969 (star) and year 1967 (circle) and other yearly values (dot) are shown. Some of the values are identical and the respective marks actually mean double or triple observations (cf. Fig. 8). The regression line is  $Y = -68.151 + 2.51 X$  ( $R^2 = 0.652$ ).



Table 3b. Partial correlations of heat sums and durations involved with anthesis: effects of latitude removed (n = 153).

	Period from March 19th to anthesis 50% completed			Length of anthesis	
	In period units	In degree days	In days	In period units	In days
Longitude	+0.391 ***	+0.445 ***	-0.316 ***	+0.134	+0.060
Distance from EE	-0.449 ***	-0.494 ***	+0.394 ***	-0.093	+0.036
Distance from SE	-0.447 ***	-0.493 ***	+0.361 ***	-0.079	+0.027
Degree days of previous year	+0.349 ***	+0.190 *	-0.054	+0.200 *	+0.265 **
Degree days of 2 years ago	+0.253 **	+0.166 *	+0.076	+0.057	-0.164 *
Age of stand	+0.035	+0.074	+0.118	-0.007	-0.018

tively, the simulated migration distance from the SE-point is, however, hardly visible in the graphical presentation (Figs. 6 and 8). In the case of calendar days there was practically no difference between the correlation with the latitude and with the distance to the SE-point (Table 3a). The highest single figure was the correlation between days and the latitude ( $r = 0.807^{***}$ ), while the correlation between days and the distance to the SE-point was as close as  $r = 0.806^{***}$  (see also Fig. 7).

There was no geographical correlation with the duration of anthesis in days (apart from days used as a timing measure) as seen from Table 3a. Instead, it was weakly correlated with the cumulative pollen catch ( $r = 0.160^*$ , see Table 6). However, in terms of the length of anthesis in period unit heat sums there was a highly significant latitudinal correlation, anthesis being shorter in p.u.s. in the north ( $r = -0.384^{***}$ , see Table 3a).

Many of the factors involved are evidently naturally correlated with latitude. This is true for the simulated migration distances, the average heat sums at a locality, the age of a stand and the dominant height of a stand (which was not included in the data). Partial correlations, in which the effects of latitude are removed, were therefore helpful. These partial correlations were generally weaker than the original geographical correlations (with the exception of the longitude). Nevertheless, all of the geographical partial correlations relevant to timing were highly significant (Table 3b).

From 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. The trees were in all cases of sufficient age to avoid any youth-bound effects in timing, and the northern stands are generally older still than the southern stands. A warm summer seems to increase

the heat sums needed for flowering in the two following years which should usually indicate later flowering. The partial correlation between the length of anthesis in days and the d.d. sum of the previous year is also significant (Table 3b).

The correlations shown in Tables 3a and 3b were also respectively calculated on a stand basis ( $n = 21$ ), but are not shown as separate tables for the sake of clarity. This extra calculation was strictly a safety 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 ( $n = 153$ ) in the calculations gave very similar correlation coefficients to those in Tables 3a and 3b with respect to significance classes. The only clear exceptions were correlations involving longitude and stand age which were no more significant in material grouped on a stand basis. Nevertheless, the respective partial correlations with longitude (the effects of the latitude removed) were highly significant on a stand basis as were those shown in Table 3b. Two further differences were found. The highly significant partial correlation between the period unit heat sum (at 50 per cent anthesis completion) and the degree-day heat sum of the previous year (Table 3b) dropped to an almost significant level while the non-significant correlation between the days since March 19 to anthesis and the degree-day heat sum of two years ago (Table 3b) turned highly significant in the standwise calculation process.

### 3.4 Differences between years

Table 4a gives a comparison between the years from 1966 to 1969. With yearly material from 18 to 20 stands the statistical significance criteria

Table 4a. Differences between years in correlations of heat sums and durations (1966: n = 18, 1967: n = 20, 1968: n = 20, 1969: n = 19).

	Period March 19th to anthesis 50 % completed											
	In period units			In degree days > 5 °C			In days			1969		
	1966	1967	1968	1966	1967	1968	1966	1967	1968			
Latitude	-0.676 **	-0.625 **	-0.749 ***	-0.653 **	-0.628 **	-0.630 **	-0.346	-0.643 **	+0.867 ***	+0.915 ***	+0.936 ***	+0.963 ***
Ecological latitude	-0.720 ***	-0.665 ***	-0.754 ***	-0.645 **	-0.657 **	-0.654 **	-0.335	-0.629 **	+0.865 ***	+0.903 ***	+0.900 ***	+0.960 ***
Longitude	+0.500 *	+0.463 *	+0.421	+0.437	+0.623 **	+0.504 *	+0.757 ***	+0.533 *	-0.254	-0.208	+0.003	-0.110
Distance from EE	-0.782 ***	-0.739 ***	-0.781 ***	-0.781 ***	-0.870 ***	-0.767 ***	-0.963 ***	-0.830 ***	+0.675 **	+0.724 ***	+0.639 **	+0.542 *
Distance from SE	-0.879 ***	-0.821 ***	-0.936 ***	-0.885 ***	-0.914 ***	-0.845 ***	-0.741 ***	-0.917 ***	+0.960 ***	+0.960 ***	+0.899 ***	+0.921 ***
Degree days of previous year	+0.791 ***	+0.747 ***	+0.859 ***	+0.706 ***	+0.751 ***	+0.729 ***	+0.530 *	+0.692 ***	-0.928 ***	-0.953 ***	-0.917 ***	-0.975 ***
Degree days of 2 years ago	+0.810 ***	+0.734 ***	+0.835 ***	+0.767 ***	+0.783 ***	+0.717 ***	+0.481 *	+0.789 ***	-0.933 ***	-0.951 ***	-0.933 ***	-0.975 ***

\* 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 = 18, 1967: n = 20, 1968: n = 20, 1969: n = 19).

	Period March 19th to anthesis 50 % completed											
	In period units			In degree days > 5 °C			In days			1969		
	1966	1967	1968	1966	1967	1968	1966	1967	1968			
Longitude	+0.809 ***	+0.702 ***	+0.787 ***	+0.663 **	+0.917 ***	+0.759 ***	+0.861 ***	+0.781 ***	-0.750 ***	-0.816 ***	-0.333	-0.754 ***
Distance from EE	-0.808 ***	-0.643 **	-0.847 ***	-0.786 ***	-0.906 ***	-0.685 ***	-0.968 ***	-0.851 ***	+0.838 ***	+0.815 ***	+0.624 **	+0.856 ***
Distance from SE	-0.771 ***	-0.690 ***	-0.863 ***	-0.806 ***	-0.897 ***	-0.765 ***	-0.926 ***	-0.886 ***	+0.870 ***	+0.844 ***	+0.523 *	+0.864 ***
Degree days of previous year	+0.855 ***	+0.846 ***	+0.762 ***	+0.435	+0.855 ***	+0.706 ***	+0.766 ***	+0.404	-0.783 ***	-0.690 ***	-0.180	-0.593 **
Degree days of 2 years ago	+0.849 ***	+0.834 ***	+0.750 ***	+0.633 **	+0.907 ***	+0.680 ***	+0.742 ***	+0.759 ***	-0.751 ***	-0.692 ***	-0.242	-0.701 ***

are stricter. The significance of correlations in relation to longitude suffered mostly from instability owing to the smaller number of observations, but the situation improved when the effects of latitude were removed in partial correlations (Table 4b). Otherwise, the geographical correlations were quite stable and significant with only a single exception of latitudinal correlation, that of 1968 for degree days (Table 4a). In partial correlations, year 1968 was also inconsistent with respect to durations in days (Table 4b).

There were also systematic differences between the years even though parallel geographical correlations were maintained at all times. A difference can be seen between the years 1967 and 1969 both in terms of p.u. heat sums and days (Figs. 8 and 9). In 1969 the heat sums at 50 per cent completion of anthesis tended to be higher than average and anthesis also occurred later in calendar time. In 1967 the respective values were lower (earlier) than average.

From Tables 3a, 4a it is clear that there were no noteworthy differences between the latitude and the ecological latitude. Altitudinal effects were found not to be prominent in this material, and thus were not studied further.

### 3.5 Adaptation

The heat sums needed for reaching the point 50 per cent completion of anthesis were weighted by the average annual heat sum of a locality and given as a percentage. This method had already been suggested by Reaumur (cit. Sarvas 1972, Robertson 1973) and Linsler (1867) and gives information on the adaptability of species at various localities. This method was only applicable on a degree day basis (data from Finland is shown in Figs. 14 and 15) as the additional materials from localities south of Finland were only measured in this form. With the aid of this additional southern reference material it becomes evident that the adaptation of the Scots pine suffers considerably north of a latitude of about 63° (Fig. 10, cf. also Fig. 16). The value for the Utsjoki stand is shown, but was ignored in curve shaping owing to the high value obtained in the standardized residuals test (Fig. 11).

Variation inherent in each yearly anthesis was also concomitantly found to vary geographically in the heat sums. The yearly variation in addition to the between-the-years variation increased northwards and along the simulated migration routes from southeast to northwest and from east

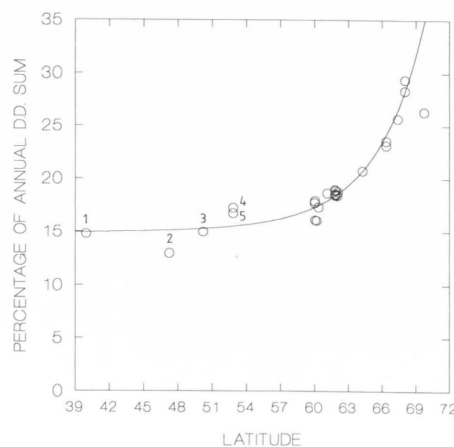


Fig. 10. The proportion of the average annual d.d. heat sum needed for 50 per cent anthesis completion. Years 1951–1980 were used for the average annual d.d. sum. The unnumbered circles are stand averages from Finland. The points south of Finland are 1. Catak, Turkey, years 1971–1973 (Boydak 1975), 2. Kamon, Hungary, years 1981–1984; a collection of Hungarian grafts, not a natural stand (Koski 1987), 3. Bedovice, CSSR, year 1959 (Sarvas 1967 referring to Chalupa 1964), 4. Eberswalde, Germany, year 1968 (author's own unpublished material: anthesis 50 per cent completed at 347 d.d.) and 5. Eberswalde, Germany, years 1933 and 1936 (Sarvas 1967 referring to Scamoni 1955). The value for Utsjoki (at 69°44') was ignored in shaping the curve  $Y = 14.849 + e^{-5.036+0.00165 X^2}$  ( $R^2 = 0.958$ ).

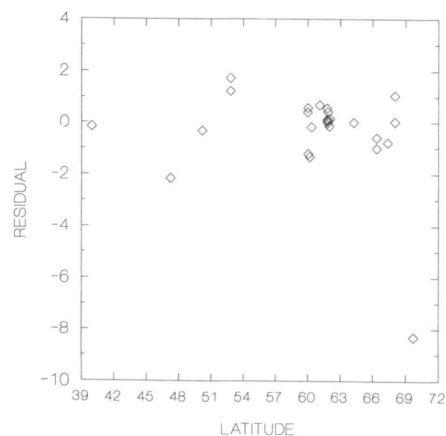


Fig. 11. The standardized residuals test for values in Fig. 10. The value for Utsjoki is certainly an outlier.

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

	Variation within each yearly antheses in period units (n = 153)		Variation of period unit sums between years at each stand (n = 20)	
	Correlation	Partial correlation with effects of latitude removed	Correlation	Partial correlation with effects of latitude removed
Latitude	+0.200 *	-	+0.0571 **	-
Ecological latitude	+0.193 *	-0.040	+0.515 *	-0.410
Longitude	-0.186 *	-0.188 *	+0.006	-0.083
Distance from EE	+0.296 ***	+0.232 **	0.470 *	+0.275
Distance from SE	+0.296 ***	+0.250 **	+0.558 *	+0.162

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

Table 6. Correlations with total pollen catch (n = 156; for seeds/m<sup>2</sup>, n = 143).

	Correlations	Partial correlations with effects of latitude removed
Latitude	-0.486 ***	-
Ecological latitude	-0.468 ***	+0.025
Longitude	+0.031 ***	+0.372 ***
Distance from EE	-0.500 ***	-0.335 ***
Distance from SE	-0.584 ***	-0.373 ***
Age of stand	-0.234 **	+0.034
Length of anthesis in days	+0.160 *	+0.139
Degree days of previous year	+0.649 ***	+0.547 ***
Degree days of 2 years ago	+0.356 ***	-0.187*
Anther residues	+0.618 ***	+0.512 ***
Seeds/m <sup>2</sup>	+0.490 ***	+0.384 ***

to west (Table 5). The correlation between yearly variation and latitude in terms of period units was almost significant while the correlations regarding distances from EE-point and SE-point were highly significant. The latter two remained so even when the effects of latitude were removed (Table 5).

The between-the-years variation in flowering time in terms of period unit heat sums also increased significantly ( $r = 0.571^{**}$ ) in a northerly direction. The variation along the two hypothetical migration routes increased at an almost significant level (Table 5).

### 3.6 Pollen catch

The total pollen catches measured were relative, rather than quantitative values due to the natural

effects of wind and rain. However, the catches were correlated to anther residues assessed in the same stands (n = 148; figures from Koski and Tallqvist 1978) at a highly significant level  $r = 0.618^{***}$  (Table 6). The effect of the amount of pollen catch on seed production (n = 143) was also highly significant ( $r = 0.490^{***}$ ). In addition, both correlations remained significant when the effects of latitude were removed.

Likewise, the yearly d.d. temperature sums in the preceding year were correlated at a highly significant level with the pollen catch (Table 6). The relevant partial correlation, free from latitudinal effects, was also highly significant ( $r = 0.547^{***}$ ). The yearly temperature sums measured two years earlier had less effect on pollen catches with a negative partial correlation value ( $r = -0.187^*$ ). The stand ages were only significant with latitude which was due to northern

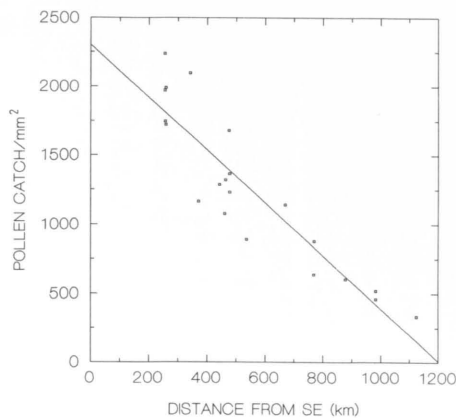


Fig. 12. The dependence of size of pollen catch on distance to SE-point. The values used are stand averages. The regression line shown is  $Y = 10092.2 - 139.8 X$  ( $R^2 = 0.578$ ).

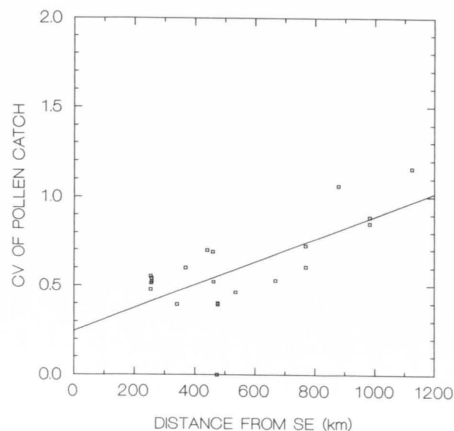


Fig. 13. The dependence of coefficient of variation of pollen catch in stand averages on distance from SE-point. The regression line is  $Y = 0.24792 + 0.00064X$  ( $R^2 = 0.487$ ).

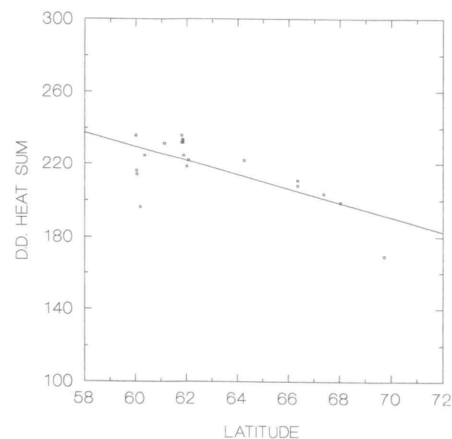


Fig. 14. The required degree-day heat sums as stand averages for reaching the 50 per cent anthesis completion. Used together with average annual heat sums (Fig. 15) to calculate Linsser's quotient. The regression line is  $Y = 464.93 - 3.9197 X$  ( $R^2 = 0.513$ ).

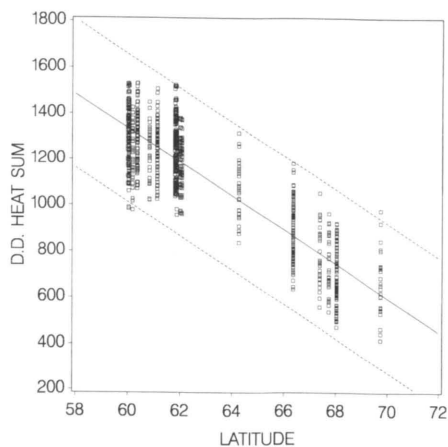


Fig. 15. Annual heat sums in 1951-1980 at research stand localities. A simulation program by Ojansuu and Henttonen (1983) based on temperatures measured at 80 (in 1951) to 157 (in 1979) stations was used. The regression line is  $Y = 5764.5 - 73.8 X$ , with confidence limits at 99 per cent level.

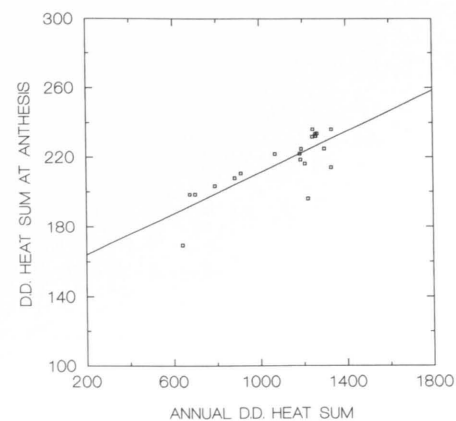


Fig. 16. Stand averages of required d.d. heat sums for 50 per cent anthesis completion with reference to local annual d.d. heat sums. The regression line is  $Y = 152.03 + 0.05916 X$  ( $R^2 = 0.642$ ). Compare to Fig. 10 where the dimension of latitude is added.

stands being older than southern stands. When the effects of latitude were removed, the partial correlation approached zero (Table 6).

All the pollen catch-related geographical correlations including both latitudes, the longitude and migration distances were highly significant. When the effects of latitude were removed the remaining correlations were also highly significant. This means that pollen catches diminish in a northward and westward direction (Table 6).

## 4 Discussion

### 4.1 Sampling

The method used for pollen sampling was influenced by the effects of rain, atmospheric humidity and windless periods (see Käpylä 1984). Therefore the study of dehiscence of pollen sacks and the flight of pollen by the recording apparatus used for timing purposes was not methodologically as accurate as the microscopical inspection earlier phases of microsporogenesis (Luomajoki 1984, 1986a, 1986b).

Sarvas (1972) found that delays to anthesis caused by atmospheric factors were somewhat

self-corrective in that the progress of anthesis was increased after withdrawal of the disturbance, e.g., the rain. The result of such external factors is a pollen distribution curve that is not so near the hypothetical normality. Pollen diagrams nearer the proportions of a Gaussian normal curve can be obtained if daily pollen catches are weighted by dividing them with the daily p.u. heat sums (see Fig. 4) as shown by Sarvas (1972). Removal of the effect of natural variability in heat accumulation renders a cleaner picture of the physiological trend.

The atmospheric factors mentioned seemed to

Table 7. Variation between years in pollen catches ( $n = 20$ ).

	Correlations	Partial correlations with effects of latitude removed
Latitude	+0.846 ***	-
Ecological latitude	+0.821 ***	-0.203
Longitude	-0.012	-0.227
Distance from EE	+0.565 **	+0.346
Distance from SE	+0.796 ***	+0.253

Pollen catch as related to distance from SE is shown in Fig. 12.

Along with a diminishing of pollen catches the variability of the pollen catches increased. Variation coefficients for between-the-years pollen catch differences at each stand increased latitudinally northwards and along the two simulated migration routes (Fig. 13). In relation to latitude was calculated a correlation of  $r = 0.846^{***}$  (Table 7), and to distance from SE-point a correlation of  $r = 0.796^{***}$ . Along the suggested migration route from EE-point the variability of pollen catches increased less conspicuously at  $r = 0.565^{**}$ .

Stand XXII at Kerimäki differed from the other stands (including stands XX and XXXIII at Kerimäki) in that it had on one occasion received urea fertilization (Table 1). However, no clear fertilization effects on flowering could be observed; the three stands at Kerimäki remained almost identical in flowering behaviour.

have a greater effect on the time to peak pollen catch than the time to mean pollen distribution. The self-corrective effects discussed by Sarvas (1972) can alleviate the problems of mean disturbance, but maximal pollen emission requires dry and windy weather. Accordingly, the theoretical distribution mean was the better reference point.

No calculations involving the median, i.e. the point when accumulation of pollen actually reaches the 50 per cent level, were shown in this paper. But it should be mentioned that use of the median also leads to larger variation. The median and also the peak pollen catch (included) are daily values while the 50 per cent point of the normal distribution can be read with a higher accuracy. So it pays to first fit the nearest normal distribution and then take the 50 per cent point.

#### 4.2 Statistical distribution

The distributions found in biological developmental processes can show deviation from statistical normality when temporal distributions are limited in that very early and very late occurrences of a stage vs. the mean are impossible. Mathematically this means that the tails of the Gaussian normal curve are cut shorter and the first and last observations of a stage occur at a lower frequency than that expected with normal probability (see also Törnevik 1982).

The measured distributions of pollen were found to deviate from normality by overfrequency at the beginning of pollen season and by considerable underfrequency towards the end of the pollen season. In expecting this basic biological trend to show underfrequency at both ends of the distribution, the overfrequency found at the beginning of the pollen season must be regarded as being more pronounced than expected and the underfrequency at the end less severe than judged by the theoretical normal curve alone.

The reason for the distortions of the ends of the pollen distribution is due to secondary pollen. This concept includes both long-distance dispersal of pollen and re-floated pollen (Krzywinski 1977, Hänninen 1984). Dimensions of long-range dispersal of pollen were reported by Koski (1970). As a result of prevailing south-western winds such long-distance dispersal usually brings relatively small amounts of pollen that are detected on the recording band before the anthesis has actually begun in the stand under study. This background pollen also adds to the initial low

catches of the anthesis. After the peak of anthesis there is a large amount of local stand produced pollen that flies and circulates before falling to the ground. Re-floated pollen can contribute to the disformation of the distribution towards the end of the anthesis. However, Sarvas (1972) pointed out that a portion of the released pollen remains in pollen sacs or emerges after a delay thus affecting release rate and the pollen catches recorded.

#### 4.3 Pollen catch

The total pollen catch figures cannot be used for highly accurate pollen production calculations as the method was designed for timing studies. The equivalence between pollen catches and pollen crop measured by anther residues was nevertheless quite good. However, the correlation coefficient was not nearly as high as that reported by Sarvas (1962), who used on that occasion globe samplers (picture in Sarvas 1962 p. 44) to estimate the amount of pollen. Totally different method of sampling explains some of the difference between the two estimates.

The distortions of the distribution caused by rain and windless weather that hamper recording also affect pollination. This similarity explains the relatively high correlation between seed crop and pollen catches.

Flowering capacity and, consequently, the pollen crop are dependent on the dominant height of trees (Sarvas 1962, Koski & Tallqvist 1978). This partly explains the diminishing pollen catches from south to north in addition to the temperature factor. The fairly high partial correlation found between pollen catches and the temperatures of the previous summer is no surprise as the generative buds develop during the summer prior to anthesis. However, the correlation of pollen catches with temperatures measured two years earlier was low and the partial correlation where the effects of latitude were removed was a negative one ( $r = -0.187^*$ ). This situation could be explained by the fact that consecutive years with abundant flowering are rather infrequent (Koski & Tallqvist 1978). The seed crop of Scots pine also correlates negatively to summer temperatures measured two years earlier (Pukkala 1987).

#### 4.4 Timing parameters

Beyond the main aim of this study, the flowering

phenology of Scots pine, the value of the three phenological parameters adopted was assessed. The first, days in calendar time, was on average a surprisingly good alternative. The traditional degree-day system, however, was a far inferior explanatory parameter in this material. On the basis of a limited data set, Sarvas (1967) believed that degree days were a better measure than days. The third alternative, the relatively unknown period unit heat sum system was found to narrowly be the best of all. As heat sum system it provides better prediction of anthesis in a single year, let alone an exceptional year, than calendar time. Period units were only slightly superior to days in describing the average occurrence of anthesis at each stand. However, if a single figure was needed to describe the occurrence of anthesis without reference to latitudinal effects, period units would be the best choice followed by degree days. The steep slope in the regression between days and latitude renders days the worst single-figure estimator of the three.

The better predictions in days in western and southern areas of Finland, and in period units in the eastern and northern continental areas may have a climatic background. A similar division of areas was shown by Laaksonen (1976b) in his climatological study of temperatures in Finland in October and January. The October temperatures are interesting because they supposedly greatly contribute to the chilling needed by trees for dormancy and to the synchronization of the whole annual cycle (Sarvas 1974). However, the basis for the division of the areas studied by Laaksonen (1976b) are complex and technical. Accordingly, no single factor can be found that explains the geographically different performance of days or period units.

#### 4.5 Geographical trends

Parallel changes with increasing phenological variation towards north can be found in heterozygosity clines. Hiltunen et al. (1975) and Tigerstedt et al. (1979) found a cline in the recessive low 3-carene allele. Frequencies of the recessive allele increased northwards (or towards lower annual d.d. sums). High variation in timing of microsporogenesis was found by Rozhdstven-skii (1981) in northern Siberia and by Luomajoki (1984) in northern Finland, which corresponds to the anthesis results presented here.

The northernmost stand studied at Utsjoki showed considerable exaggeration of the expect-

ed trends. However, an unknown source of error or a genetical difference compared with the rest of stands can not be excluded, and the limited data of sufficient pollen catch from four years (out of six measurements) warrants no conclusions.

The geographical correlations and partial correlations involving both latitudes and both simulated migration distances were very stable in this material irrespective of the statistical methods used. However, different grouping of the material affected correlation coefficients involving the longitude, the age of the stand and the effects of the d.d. sum of the two previous years (cf. Chapters 3.3 and 3.4) and uncovered some instability in these correlation coefficients.

Difference between the south and north can naturally be explained in terms of adaptation. The between-the-years variation in heat sums at anthesis and in pollen catches together with the variation within yearly antheses (in terms of period units) was more pronounced in the roughly southeast to northwest direction (i.e. the distance from SE-point) than in purely a latitudinal direction. That the duration of anthesis in days was not geographically correlated is a consequence of three counteracting factors. The pollen crop is smaller in the north which tends to shorten the anthesis, whilst the lower temperatures and the higher within-anthesis variation in the north tend to protract the anthesis. These effects tend to nullify each other.

The reason for deviation of geographical trends from south to north might be found in Finnish glaciation history. The timetable of the reinvasion of the Scots pine into Finland is roughly known, e.g., from palynological studies (see Alho 1990). The more or less arbitrarily chosen points (EE and SE) served only to reveal trends, not to explore the true reinvasion routes that can not be assessed with the material studied.

Geographical patterns and clines that deviate from a southerly to northerly direction have been used to suggest reinvasion routes of trees in North America on base of distribution of oleoresin composition in *Picea glauca* (Moench) Voss (Wilkinson et al. 1971) and on basis of distributional characteristics of isozyme polymorphism in *Larix laricina* (Du Roi) Koch (Cheliak et al. 1988).

#### 4.6 Adaptation

The adaptation of Scots pine was appraised using proportions of degree-day heat sums. Ac-

ording to Linsser (1867) the heat sum needed for a given stage should, in well-adapted populations, remain proportionally the same at any locality when weighted by the average annual heat sum. This principle also largely holds for the flowering of Scots pine. Sarvas (1967, 1970a) found that limits of adaptability of the flowering cycle are reached in Finland. Sarvas (1970b: Fig. 7) was, however, inclined to believe that quite an abrupt cessation of adaptation occurred in a region he called the marginal zone.

Adaptability in Linsser's sense could be tested more rigorously in this study. The d.d. heat sums needed for attaining 50 per cent completion of anthesis (Fig. 14) as well as the local annual heat sums (Fig. 15) continued to decrease right up to the timberline. There is thus also quite good adaptive parallelism with clinal characteristics of vegetative growth (Hagner 1970a, 1970b, Mikola 1982). Linsser's quotient, however, could not hold the usual 14 to 17 percent range (typical of flowering of Scots pine in large areas of Europe, see Koski 1991) in central or northern Finland. That anomaly can be taken as an indication that the limits of the adaptive capacity had been reached. There is no sharp boundary, instead, the failure of complete adaptation leads in a progressively higher Linsser's quotient.

On basis of flowering phenology it is fair to suggest that north of a latitude of 63° the limits adaptability are already achieved. This latitude is roughly equivalent to an average annual heat sum of 1000 to 1050 degree days. This is also near the level at which Scots pine reaches an anatomically estimated seed maturation level of about 98 per cent (Sarvas 1970b) in an average year. Considering that it is impossible for all seeds to germinate for genetical reasons this is the equivalent to full adaptation. Sarvas (1970b) called the area south of this limit the optimum zone of Scots pine. In areas north of the 63° N.lat. limit full maturation is only reached in years with above-average temperature. At the timberline full or almost full maturation of Scots pine seeds seldom occurs, perhaps but once in a century (Renvall 1912, Siren 1961, Henttonen et al. 1986). However, the frequency of good seed years can be higher if several warm years follow in succession each other as happened in the 1920's and 1930's (Hustich 1948).

It has been suggested that insufficient time has elapsed for full adaptation of tree species in Finland during and after their reinvasion following the last glaciation event. It is more likely that our trees have not had time enough to adapt after a

warm period of about 5000 to 7000 years ago during the Holocene. At that time the Scots pine timberline was considerably further north and at a higher altitude (Eronen 1979, Alho 1990).

Today the offspring of local stands survive best at about one hundred kilometres south of their origin (Remröd 1976, Mononen 1987, Koski 1989). How much gene flow (Koski 1970, Chung 1981) contributes to this situation is not known. The once pineless areas tend to be repopulated during warm periods as seen in the 20's and 30's (Hustich 1958).

It has been proposed that our conifer forests are in danger owing to a global warming of the climate (Hänninen 1990, 1991). This warming is expected as a consequence of increased atmospheric concentration of the so called greenhouse gases, e.g. carbon dioxide. The present environmental basis has been forgotten, however. There is of course no guarantee that the vegetative growth and the generative development in Scots pine are perfectly in line in terms of adaptation. But in the light of the adaptation of the generative cycle about a half of Finnish Scots pine forests are at present not fully adapted to our cold climate. Therefore a moderate warming (up to roughly three degrees Celsius in annual average temperature) would be quite beneficial rather than damaging for our Scots pine forests. This amount of warming would be on a par with temperatures of 5000–7000 years ago.

Hänninen (1991) was concerned with the likelihood of increased frost damage as a result of climatic warming. However, there seems to be certain vaguely known factors that hold back development of Scots pine until March (H. Häggman 1987, J. Häggman 1991). Consequently, the danger of budburst in mid-winter is less likely than that judged only on the existing annual cycle models.

#### 4.7 Generative cycle

Cold and occasionally severe winters necessitate a period of dormancy. A comprehensive review of the concepts and terminology of dormancy is available from Fuchigami et al. (1982) and Hänninen (1986, 1990). For the generative cycle the suggested chilling need (under the so called autumn dormancy, see Sarvas 1974, Hänninen et al. 1985) required for synchronization of the annual cycle seems valuable. A corollary of this theory is that spring development can be affected by the temperatures in the previous late autumn

period. A warm autumn could shift the chilling period to a later date. That could eventually mean a later dormancy break in the spring.

This kind of causality seemed to also apply in this study. Previous year temperature affected the heat sums required for anthesis in the following year (even when latitudinal effects were removed). The point is not, however, that heat sum requirements were different in successive years although temperature sums and dates vary between years (see Figs. 8 and 9). The problem concentrates largely around the mobility of the zero point (biofix) of the heat sum and calendar day scales. There are differences between years regarding the vernal biofix, but there is no good basis for routinely placing the biofix in a physiologically meaningful way. Methodologically, the greatest difficulty arises from the need for a separate biofix in the spring for heat sum calculation while the zero point of the whole annual cycle is more probably in the autumn (Sarvas 1974). The existence of such a point is still uncertain as it is doubtful that any tree species would rely on synchronization by a single factor only once in a year.

The temperature thresholds suggested are sometimes too high (5 °C to 10 °C) for our climate and do not work well. Nevertheless, any heat sum system is likely to introduce a kind of (asymptotic) threshold. On the other hand, using critical daylengths longer than 12 hours for determining the biofix just increased variation in timing. Widely different arbitrary critical daylengths were needed to construct a usable latitudinal bias to allow the development start earlier in the south than in the north.

There is rather good agreement that daylength is neither a significant synchronizing factor at the beginning of the active period (term by Sarvas 1972), nor a little later at the onset of the growing season (Mirov 1956, Roche 1970, Sarvas 1972, Fuchigami et al. 1982, Lumme 1982). It is somewhat of a paradox that in Scots pine the flowering times, on average, showed a rather good correlation with calendar time when the latitudinally bound light factor could not as yet be considered significant as releasing impulse. 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 about direct daylength-induced synchronization.

Further, northern Scots pine grafts transferred to southern Finland flower earlier than southern

grafts (Chung 1981). They should flower later than southern grafts if a variable critical daylength was the impulse needed and if we ignore the possible effects of the grafting stock. Their effects on the timing of flowering are especially not well understood (cf. Schmidting 1991).

#### 4.8 Limiting factors

The predictive value of a curvilinear heat sum system, (e.g. the period unit heat sum in this case), is already now quite good particularly in single years and is, on average, marginally better than calendar time.

Nevertheless, the p.u. system is not sufficiently developed as the regression apparently needs adjustment, especially at the upper region of the curve where a drop in the curve corresponding to retarded development at high temperatures would be more valid.

How well the homogeneity condition (J. Sarvas 1977) of development is fulfilled during the post-meiotic microsporogenesis is not known. The regression by Sarvas (1972) was largely developed from observations of meiosis, an earlier phase of the microsporogenesis.

It is not exactly clear, how much of the variation in period unit sums was due to error in the biofix, to the less than perfect homogeneity of development, the effects of direct radiation (Sarvas 1972, Luomajoki 1977, Pukacki 1980) or, e.g., the effects of sharp fluctuation of temperatures (Ryan 1941, Chung 1981). Being an hourly system, the p.u. system accepts changes in temperature quite well, but very sharp changes are known to interfere with the development rate.

#### 4.9 Final notes

It is natural that timing differences observed at an earlier phase are retained in later phases. The differences seen by Luomajoki (1984) at the tetrad phase of microsporogenesis between the years 1967 and 1969 appeared quite similar in this anthesis material (Figs. 8 and 9). The true range of variation in timing of the anthesis was not revealed by a 12 year study. While this study covered the years from 1963 to 1974, by 1975 far earlier male flowering in Scots pine had occurred (Koski 1991) than was observed in this study.

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## Seloste

### Männyn sopeutuminen Suomen ilmastoon hedekukkimisaikojen valossa

Männyn hedekukinnan ajoittumista eli anteesia ja siitepölymääriä sekä niiden maantieteellisiä korrelaatioita tutkittiin 21 metsikössä 14 koelallalla. Tutkittuja anteeseja oli yhteensä 156. Siitepölymääriä mitattiin Sarvas-Vilksa siitepölymittarilla puiden latvustasolta. Lämpötila kussakin tutkimusmetsikössä mitattiin niinkään puiden latvustasolta.

Tutkimuksessa määritettiin tietokonetekniikkaa hyväksikäyttäen siitepölyjakauman kuvaajan muoto kunakin vuonna kussakin metsikössä, laskettiin normaalijakauman mukainen tasoitussuora frekvenssipaperilla, keskihajonta ja 50 prosentin kohta jakautumasta. Viimeksi mainittua 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) kolme mittayksikköä käyttäen: päivinä, tehoisina lämpösummina (d.d. > +5 °C) ja kurvilinearisina ns. period unit -lämpösummina, jotka lasketaan tunneittain mitatuista lämpötiloista. Tutkitut metsiköt kukkivat niin säännöllisesti, että vain yhtenä vuotena yksi metsikkö (Utsjoki v. 1966) ei tuottanut lainkaan siitepölyä. Anteesin 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 soveltaminen tehtiin ATK-ohjelmalla siitepölykertymän 2,3–88,5 % alueella. Prosenttiluvut vastaavat keskiarvoon nähden aluetta  $-2/+1,2$  keskihajonnan yksikköä, mikä on se alue, jolla siitepölyjakauma noudattaa normaalijakaumaa.

Parhaaksi ajoittumisen kuvaajaksi osoittautui period unit -summa, vaikka päiväluku oli keskimäärin melkein yhtä hyvä. Alueellisesti period unit oli parempi Keski-

Itä- ja Pohjois-Suomessa, päiväluku taas Etelä- ja Länsi-Suomessa ja Utsjoella. Tehoisa lämpösumma oli keskimäärin selvästi huonoin mittari. Tämä on vastoin aikaisempia käsityksiä (vertaa Sarvas 1967). Yksittäisenä vuonna period unit -summa on epäilemättä kukkimisajan paras osoittaja, ja poikkeuksellisenä vuonna d.d.-summakin voi olla päivälukua parempi.

Maantieteellisissä korrelaatioissa mänty kukki pohjoisessa odotetusti myöhemmin, ajoittumisen hajonta oli suurempi, siitepölymäärät olivat pienempiä ja siitepölymäärien hajonta suurempi. Yllättävämpää oli, että pääasiallinen vaihtelusuunta näissä korrelaatioissa ei ollut etelästä pohjoiseen vaan suurinpiirtein kaakosta luoteeseen. Tähän tulokseen tultiin laskemalla korrelaatioita Karjalan kannaksen etelälaidalla sijaitsevasta vertailupisteestä (SE-piste) lähtien. Tämä poikkeama totutusta etelä-pohjoisen-suunnasta johtunee siitä, että mänty levisi maahamme kaakosta jääkauden jälkeen (Alho 1990).

Hedekukkimisen vaatima lämpösumma vaihteli myös vuosittain siten, että v. 1969 tarvittiin keskimääräistä korkeampi lämpösumma ja v. 1967 tavallista pienempi lämpösumma. Tämä johtuu kiinteistä nollapisteeistä ajoittumisen määrittämisessä. Lämpösummien laskeminen pitäisikin aloittaa männyn 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 vuosirytmien täsmäys tapahtunee vuosittain syksyisin eikä keväisin.

Hedekukkimiseen tarvittava suhteellinen lämpösumma (kukkimisen lämpösumma jaettuna keskimääräisellä vuotuisella lämpösummalla) pysyy Linsserin lain mukaisesti vakiona Etelä-Euroopasta (ja Aasiasta) Etelä-Suomeen asti. 63. leveysasteen pohjoispuolella tarvittava suhteellinen lämpösumma nousee jyrkästi. Tämä merkitsee, ettei männyn lisääntymissykli enää täysin pysty sopeutu-

maan ilmastoon 63. leveysasteen (vastaa noin 1000–1050 d.d.) pohjoispuolella.

Maassamme on viime aikoina keskuskeltu paljon siitä, että puiden vuosirytmä saattaisi häiriintyä ilmaston lämmetessä. Kukkimisaikojen valossa pohjoinen puolisko Suomen mäntymetsistä on kuitenkin tällä hetkellä vaillinaisesti sopeutunut kylmään ilmastoon, joten ilmaston

lämpeneminen parantaisi männyn elinmahdollisuuksia ainakin Pohjois-Suomessa. Nykyisessä ilmastossa männyn siementaimet menestyvätkin parhaiten noin 100 km etelään päin siirrettynä (Koski 1989). Vielä 5000 vuotta sitten maassamme oli paljon lämpimämpää, ja männyn levinneisyys oli laajempi sekä pohjoiseen päin että korkeussuunnassa (Eronen 1979, Alho 1990).

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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.

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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.

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

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### Käsikirjoitusten ulkoasu

Käsikirjoituksen asun tulee noudattaa sarjan kirjoitusohjeita, joita saa toimituksesta.





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