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Alpo Luomajoki

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Differences in the Climatic Adaptation of Silver Birch (*Betula pendula*) and Downy Birch (*B. pubescens*) in Finland Based on Male Flowering Phenology

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Male flowering was studied at the canopy level in 10 silver birch (*Betula pendula* Roth) stands from 8 localities and in 14 downy birch (*B. pubescens* Ehrh.) stands from 10 localities in Finland from 1963 to 1973. Distributions of cumulative pollen catches were compared to the normal Gaussian distribution. The basis for the timing of flowering was the 50 per cent point of the anthesis-fitted normal distribution. To eliminate effects of background pollen, only the central, normally distributed part of the cumulative distribution was used. Development up to the median point of the distribution was measured and tested in calendar days, in degree days (> 5 °C) and in period units. The count of each parameter began on and included March 19.

Male flowering in silver birch occurred from late April to late June depending on latitude, and flowering in downy birch took place from early May to early July. The heat sums needed for male flowering varied in downy birch stands latitudinally but there was practically no latitudinal variation in heat sums needed for silver birch flowering. The amount of male flowering in stands of both birch species were found to have a large annual variation but without any clear periodicity.

The between years pollen catch variation in stands of either birch species did not show any significant latitudinal correlation in contrast to Norway spruce stands. The period unit heat sum gave the most accurate forecast of the timing of flowering for 60 per cent of the silver birch stands and for 78.6 per cent of the for downy birch stands. Calendar days, however, gave the best forecast for silver birch in 25 per cent of the cases, while degree days gave the best forecast for downy birch in 21.4 per cent of the cases. Silver birch seems to have a local inclination for a more fixed flowering date compared to downy birch, which could mean a considerable photoperiodic influence on flowering time of silver birch. Silver birch and downy birch had different geographical correlations.

Frequent hybridization of birch species occurs more often in northern Finland in than in more southern latitudes. The different timing in flowering caused increasing scatter in flowering times in the north, especially in the case of downy birch. The chance of simultaneous flowering of silver birch and downy birch so increased northwards due to a more variable climate and also higher altitudinal variations. Compared with conifers, the reproduction cycles of both birch species were found to be well protected from damage by frost.

Keywords male flowering, timing of flowering, pollen catch, heat sum, photoperiodism, adaptation, ecophysiological differences, seasonality, hybridization, *Betula*.
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Contents

Application and Abbreviation of Terms

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

Annual heat sum – the total degree-day sum of the whole growing season.

Anther residues – shed stamens sampled in funnels at the stand and dried and weighed to quantify male flowering (see Koski and Tallqvist 1978).

Anthesis – the time of dehiscence of pollen and pollen dispersal.

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

Biofix – identical to zero point, or 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 applied, so the d.d.-sum grows daily by $(\bar{t} - 5)$ d.d.

Ecological latitude – means altitude-corrected latitude in which the cooling effect of a higher altitude is simulated by a higher latitude. Also called the ecophysiological latitude (Wiersma 1985).

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 condition seldom persists 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.

LD – abbreviation for long day in photoperiodic studies.

Linsser's law – Linsser (1867) held that the heat sum needed for a given stage of development should, in well-adapted populations, remain the same at any locality when divided 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 (of active period) within one hour at 10 °C is equivalent to 5 period units according to Sarvas (1972). This curvilinear regression has the merit of also considering low temperatures which are effective during e.g. microsporogenesis.

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.

Z – a test function for the significance of correlations.

$$z = \tfrac{1}{2}\ln\left(\frac{1+r}{1-r}\right)$$, in which r is the sample correlation coefficient.

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 (quiescence) as the zero point of the entire annual cycle.

50 pcc – 50 per cent completion. Can also be called median of a distribution.

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 and was the designer of this study. In 1974, following his death the collection of data ceased. This was unfortunate, as the material was already considered to be unique in terms of geographical coverage and duration.

The English text was edited by Dr. Ashley Selby. Professors Erkki Annila, Heikki Hänninen and Veikko Koski as well as two anonymous referees made valuable suggestions concerning the manuscript. I extend my sincere thanks to all mentioned.

1 Introduction

Downy birch (*Betula pubescens* Ehrh.) occurs throughout Finland, although a subspecies (mountain birch (ssp. *czerepanovii* (Orlova) Hämet-Ahti) occurs in the northernmost parts of the country and at high altitudes. Silver birch (*Betula pendula* Roth) does not thrive in the far north, at least not abundantly. While both species belong to the four dominant economically valuable trees in Finland (the other two being Scots pine and Norway spruce), silver birch is not present everywhere as it can not grow on wetlands as can downy birch (Sarvas 1949). (Tree names in this study follow Hämet-Ahti et al. 1992.)

The two superficially similar species have genetical and ecophysiological differences. Silver birch is considered a diploid species (2n = 28) and downy birch tetraploid (2n = 56, Woodworth 1929). Sarvas (1974) found seed dormancy weak in silver birch (cf. Vanhatalo et al.) but well developed in downy birch. On the other hand, Myking and Heide (1995) found no significant difference in the chilling requirement of buds of the two species.

Sarvas (1952) studied both species for the basic differences in male flowering and seed setting. The self-recording pollen samplers used already resembled the improved model used in later studies. One stand of each species was under study for five (downy birch) or six years (silver birch). No heat sum follow-up was then arranged although temperatures during the anthesis itself were monitored.

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

The aim of this study is to analyze whether there are systematic differences in the flowering parameters, their geographical correlations or in adaptation to climate between the two birch species. Are the effects of temperature and the light factor equal for both species, and do they differ from those controlling Norway spruce and Scots pine? Is Linsser´s principle of proportional heat sums (Linsser 1867) valid for birch species? Do the parameters employed (d.d. and p.u. heat sums, flowering day) give consistent results in different years? How can the easier hybridization of the two birch species in Northern Finland be explained? Is there any benefit in using the idealized pollen distribution curve mean as a reference compared to simple observations of the day of maximum pollen release?

To answer these questions, the within-year and the between-year variations in the timing of anthesis involved were measured and tested with the three parameters using two alternative reference points, median of anthesis and peak pollen catch day. The geographical variation of pollen catches was also measured and possible geographical correlations were sought.

2 Material and Methods

2.1 Pollen Recording

This study concentrates on the features of pollen dispersal (anthesis) of male flowering in silver birch and downy birch stands (Table 1, Fig. 1) in Finland from 1963 to 1973. The material was collected at the former Department of Silviculture of the Finnish Forest Research Institute. Similar studies were made in late 1940‘s, early 1950´s (Sarvas 1952) and early 1960‘s, but in 1963 a more reliable model of rotating pollen registering equipment was available.

The material consists of 73 complete annual registrations of antheses (years/stands) from in 10 stands of *Betula pendula* and 103 annual registrations in 14 stands of *B. pubescens*. No single stand was studied in all of the eleven years of the period from 1963 to 1973, but four stands were studied in ten consecutive years (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 practices 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 were 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 where two nearby stands (Rovaniemi XX and XXI) shared one measurement point. The accuracy of the meters was checked two to three times a day.

The pollen catch was counted microscopically from the recording bands and the results were prepared in terms of the 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, as reported by Luomajoki (1993a, 1993b, 1995). 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. Regression lines of best fit within the interval from minus 2 standard deviations to plus 1.6 standard deviations from the mean (from 2.3 to 94.5 per cent) were drawn by SYSTAT/SYGRAPHC C Multivariate General Linear Hypothesis computer program (Wilkinson 1990). The cumulative daily catches, considered as percentages of the total catch, approximately locate (on probability paper) on a single line, thus indicating a nearly normal distribution. However, the early and the late observations usually deviated from normality (truncated normal distribution, see Hald 1952), so that the first percentages were slightly larger than expected while the last ones were smaller than expected (Fig. 3). This problem is largely created by background pollen (pollen contamination) and was controlled by empirically determined limits.

Omitting the tails of the distribution that deviated from normality (under –2.0 and over +1.6 SD) seemed justifiable because a line with a closer fit using central points (percentages) near the mean was achieved, thus alleviating the effects of secondary pollen. The standard deviation was also readable from the inclination of the computed regression line of best fit giving an approximation of the variation within a single anthesis. The mean (the 50 per cent point of the theoretical distribution) itself was unbiased by the dispersion.

The onset and the termination of flowering were judged on the basis of the first and last pollen catches (with no restriction) on the registering band. Minimal pollen catches were not used for timing purposes. Only pollen catch total sums of

Table 1. Stand characteristics and years of study (see also Fig. 1).

Stand	Locality	Latitude	Longitude	Elevation(m)	Age, years in 1970	Years of study	Years of minimal pollen catch	Origin and remarks
Betula pendula								
Bromarv VI	1	60°02'	23°03'	5	40	1967–73		Local.
Hammarland III	2	60°14'	19°44'	20	44	1965–69	1965	Local.
Hartola 571	6	61°45'	25°54'	173	63	1965–69		Local. Clear cut in 1983.
Punkaharju LIV	7	61°49'	29°18'	90	59	1964–73		Local.
Punkaharju LXIII	7	61°48'	29°19'	88	32	1964–72		Curly birch, var. *carelica* (Mercklin) Hämet-Ahti. Origin Aulanko, Finland.
Kerimäki 543	8	61°50'	29°23'	86	66	1965–73		Local. Clear cut in 1978.
Vilppula V	9	62°04'	24°29'	150	38	1965–69		Local.
Rovaniemi XXI	10	66°21'	26°45'	114	113	1964–73	1968, long distance transport in 1966	Local.
Rovaniemi XXVIII	10	66°21'	26°41'	251	44	1967–73		Local.
Kittilä, Sätkenä I	11	67°44'	24°51'	220	95	1964–66,68–69,71	1966	Local.
Betula pubescens								
Tuusula 12	3	60°22'	25°02'	45	52	1964–73		Local. Thinned in 1970.
Heinola 568	4	61°10'	26°04'	82	52	1964–71		Local.
Heinola 569	4	61°11'	26°00'	87	53	1964–71		Local.
Padasjoki VIII	5	61°24'	25°03'	106	42	1965–69		Local.
Punkaharju XIV	7	61°48'	29°20'	85	43	1964–65,67–73		Local.
Punkaharju L	7	61°48'	29°20'	90	70	1963–71		Local.
Punkaharju LX	7	61°48'	29°20'	83	38	1964–73		Local.
Vilppula 153	9	62°03'	24°30'	120	68	1964–69		Local.
Rovaniemi XVII	10	66°21'	26°38'	170	123	1964–65,67–73		Local.
Rovaniemi XX	10	66°21'	26°45'	108	118	1964–65,67–73	1968	Local.
Kittilä, Sätkenä II	11	67°44'	24°50'	205	88	1964–66,68–71	1966,68–69	Local.
Kittilä, Pallas VI	12	68°01'	24°17'	295	Unknown	1965–69	1966	Local. Mountain birch, ssp. *czerepanovii* (Orlova) Hämet-Ahti.
Enontekiö II	13	69°00'	20°53'	510	58	1964–69	1965–66,69	Local. Mountain birch, ssp. *czerepanovii* (Orlova) Hämet-Ahti.
Utsjoki II	14	69°44'	27°03'	224	Unknown	1965–66,68–69	1966,69	Local. Mountain birch, ssp. *czerepanovii* (Orlova) Hämet-Ahti.

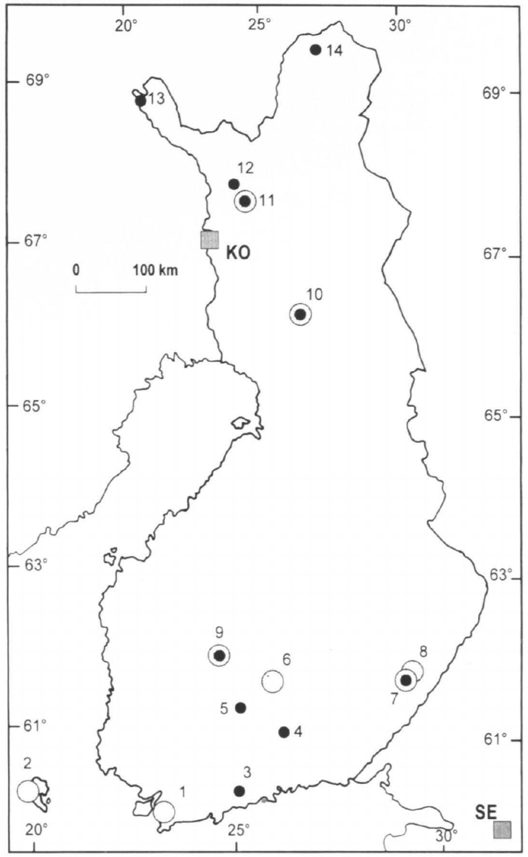

Fig. 1. Localities of stands studied. One to three stands of each species were studied at each locality. The localities were in latitudinal order: 1. Bromarv (annexed in 1977 to Tenhola parish and later to Tammisaari in 1993), 2. Hammarland, 3. Tuusula, 4. Heinola, 5. Padasjoki, 6. Hartola, 7. Punkaharju, 8. Kerimäki, 9. Vilppula, 10. Rovaniemi, 11. and 12. Kittilä 13. Enontekiö and 14. Utsjoki. Localities where *Betula pendula* was studied are marked with a stippled circle (○) and those where *B. pubescens* was studied with a solid dot (●). The KO- and SE-points are references for calculations of hypothetical migration distances.

15 pollen grains/mm² (a purely technical value for the elimination of obvious contamination cases) or larger were used to determine the required point of 50 per cent completion of anthesis. The restriction regarding a minimal pollen catch for anthesis 50 pcc was needed to prevent background pollen from giving spurious timing data. This can, nevertheless, happen if continuous strong southerly winds occur at the time when the more southerly stands flower. One such case of long-distance pollen transport (Hjelmroos 1991, Hjelmroos and Franzen 1994) was detected in this study (stand Rovaniemi XXI of silver birch in 1966). This and two cases of minimal pollen catch for silver birch were excluded from timing studies, as well as ten cases of minimal pollen catch for downy birch.

The results were obtained as flowering days, degree days and period units with corresponding variation coefficients (CV). A comparison of various units on a mere variation coefficient basis is not unproblematic. However, CV-data will also be presented to allow a comparison with previous studies (Luomajoki 1993a, 1993b).

A comparison of all three parameters was also made on the basis of days (Table 2b) to test the real forecast value of each parameter. 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 stand-own 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.

2.2 Temperature Data

Temperatures in Finland varied such that in the southernmost stand of silver birch the average annual heat sum over the thirty year period from 1951 to 1980 was 1350 degree-days (over +5 °C), with a minimum value of 1110 d.d. and a maximum value of 1550 d.d., respectively. At the coldest (second northernmost) downy birch stand the average was 515 d.d., with a minimum value of 250 d.d. and a maximum value of 740 d.d., respectively, as calculated from database of Ojansuu and Henttonen (1983). Annual variations in temperature sums were also greater in the north than in the south (Fig. 2).

Temperature data from thermographs located at tree-top level in the stands with matching pollen recorders were processed to give two kinds of

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 19 to 50 per cent anthesis completion In period units	CV%	In degree days>5°C	CV%	In days	CV%	Period March 19 to peak pollen catch day In days	CV%
Betula pendula													
Bromarv VI	1	April 25–June 5	7(7)	26.0	28.2	2652	6.7	49.3	23.0	58.9	4.3	58.0	6.1
Hammarland III	2	April 26–June 3	4(5)	28.4	23.8	2668	6.9	50.8	12.8	62.0	9.2	62.6	7.5
Hartola 571	6	May 5– June 2	5(5)	18.4	49.2	2695	7.3	56.2	22.0	61.4	2.7	60.6	3.8
Punkaharju LIV	7	May 6–June 1	10(10)	18.0	32.1	2608	5.6	58.1	13.6	60.9	3.5	59.8	5.0
Punkaharju LXIII	7	May 1–May 31	9(9)	17.6	34.8	2577	6.2	54.9	15.7	61.7	3.3	59.9	5.0
Kerimäki 543	8	April 30–June 5	9(9)	19.1	45.3	2623	8.2	58.0	15.3	61.9	1.5	60.1	4.4
Vilppula V	9	May 3–June 1	5(5)	17.2	49.9	2708	4.7	59.0	11.5	59.4	7.2	58.4	8.5
Rovaniemi XXI	10	May 17–June 18	8(10)	15.2	47.9	2820	9.9	60.0	18.4	76.1	5.8	76.4	5.9
Rovaniemi XXVIII	10	May 23–June 18	7(7)	13.0	35.3	2679	5.7	62.6	9.7	77.7	4.8	77.9	4.7
Kittilä, Sätkenä I	11	May 25–June 22	5(6)	12.8	52.5	2551	8.2	57.6	11.3	78.8	7.5	78.2	7.3
Betula pubescens													
Tuusula 12	3	May 5–June 7	10(10)	24.1	26.0	3300	10	73.9	14.9	63.5	5.2	66.8	9.1
Heinola 568	4	May 4–June 8	8(8)	22.9	32.2	3213	7.8	73.3	10.2	64.5	5.0	62.9	8.7
Heinola 569	4	May 5–June 8	8(8)	22.1	35.0	3316	9.1	78.4	13.8	64.9	5.0	64.5	7.6
Padasjoki VIII	5	May 5–June 9	5(5)	20.2	52.7	3379	13	72.0	14.4	67.2	7.1	67.8	8.3
Punkaharju XIV	7	May 11–June 7	9(9)	19.6	21.1	3215	6.5	73.2	8.6	67.4	5.0	66.7	6.1
Punkaharju L	7	May 7–June 9	9(9)	18.8	37.8	3227	7.3	79.6	14.0	66.4	7.6	65.1	9.4
Punkaharju LX	7	May 10–June 9	10(10)	18.9	27.5	3168	7.8	72.4	10.5	67.3	5.8	66.8	6.9
Vilppula 153	9	May 8–June 10	6(6)	21.8	41.9	3466	7.4	77.5	12.8	68.5	6.3	67.5	5.0
Rovaniemi XVII	10	May 23–June 22	9(9)	18.8	21.4	3014	7.8	73.3	20.4	77.7	5.7	77.6	6.2
Rovaniemi XX	10	May 24–June 22	8(9)	19.0	20.9	3069	11	70.5	16.8	77.4	5.9	77.8	6.7
Kittilä, Sätkenä II	11	May 21–June 19	2(5)	14.8	59.6	2742	11.0	69.5	33.6	74.5	4.7	77.2	13.9
Kittilä, Pallas VI	12	May 21–June 26	4(5)	14.6	48.8	3125	7.8	75.5	15.7	88.5	9.1	84.0	16.1
Enontekiö II	13	June 2–July 19	3(6)	11.5	116.0	2833	5.9	57.5	18.5	98.7	5.1	99.0	5.3
Utsjoki II	14	June 11–July 3	2(4)	9.8	116.2	2859	3.3	63.5	5.6	99.0	1.4	98.5	0.7

* Figures in brackets include the years of minimal pollen catch that were not suitable for timing studies.
Duration of anthesis and peak pollen catch day were recorded also for minimal pollen catches.

Table 2b. Comparison of timing parameters on a day basis (stand means). Period March 19 th to 50 per cent anthesis completion. (n = 70 (73) for *B. pendula*, n = 93 (103) for *B. pubescens*)[1]

Stand	Locality	Period units converted to days Predicted days Mean	Mean of annual deviations [2]	CV %	Degree days>5°C converted to days Predicted days Mean	Mean of annual deviations [2]	CV %	Days Observed days Mean	Mean of annual deviations [2]	CV %
Betula pendula										
Bromarv VI	1	58.4	1.51	3.7	59.0	2.86	6.4	58.9	1.92	4.3
Hammarland III	2	61.3	4.13	9.1	62.8	4.25	9.1	62.0	4.00	9.2
Hartola 571	6	60.4	2.32	4.8	61.0	5.20	11.1	61.4	1.28	2.7
Punkaharju LIV	7	61.0	1.20	2.7	63.4	2.40	4.6	60.9	1.34	3.5
Punkaharju LXIII	7	61.4	1.51	3.3	63.0	2.44	5.1	61.7	1.70	3.3
Kerimäki 543	8	61.8	1.23	3.2	63.9	2.35	4.9	61.9	0.59	1.5
Vilppula V	9	60.2	2.96	6.6	64.6	4.48	8.4	59.4	3.28	7.2
Rovaniemi XXI	10	76.6	3.13	5.2	76.8	3.25	5.6	76.1	3.16	5.8
Rovaniemi XXVIII	10	77.9	2.73	4.7	78.4	2.78	4.6	77.7	2.90	4.8
Kittilä, Sätkenä I	11	78.8	3.44	5.2	81.6	3.28	5.8	78.8	4.64	7.5
Mean			2.42			3.33			2.48	
Betula pubescens										
Tuusula 12	3	63.1	1.72	4.3	64.0	2.40	5.1	63.5	2.60	5.2
Heinola 568	4	63.5	2.25	4.5	65.1	3.13	5.9	64.5	2.63	5.0
Heinola 569	4	64.3	1.75	3.4	66.0	3.00	5.9	64.9	2.66	5.0
Padasjoki VIII	5	67.0	1.60	3.7	68.0	2.40	5.5	67.2	3.12	7.1
Punkaharju XIV	7	67.3	1.85	3.8	67.4	3.16	6.3	67.4	2.84	5.0
Punkaharju L	7	66.4	3.19	6.3	67.6	4.15	8.6	66.4	3.83	7.6
Punkaharju LX	7	67.2	2.16	4.3	67.2	3.40	6.6	67.3	3.30	5.8
Vilppula 153	9	68.0	2.33	4.4	69.0	3.67	6.9	68.5	3.00	6.3
Rovaniemi XVII	10	77.7	3.26	5.1	78.4	3.38	5.8	77.7	3.70	5.7
Rovaniemi XX	10	77.6	3.13	4.9	78.0	3.50	5.9	77.4	3.63	5.9
Kittilä, Sätkenä II	11	77.0	1.00	1.8	80.5	4.50	7.9	74.5	2.50	4.7
Kittilä, Pallas VI	12	88.0	4.50	7.0	91.0	2.00	3.2	88.5	5.75	9.1
Enontekiö II	13	98.3	2.44	3.6	98.7	2.44	3.3	98.7	3.56	5.1
Utsjoki II	14	99.0	1.00	1.4	99.5	0.50	0.7	99.0	1.00	1.4
Mean			2.30			2.97			3.15	

[1] Figures in brackets include the years of minimal pollen catch that were not suitable for timing studies. [2] Absolute values

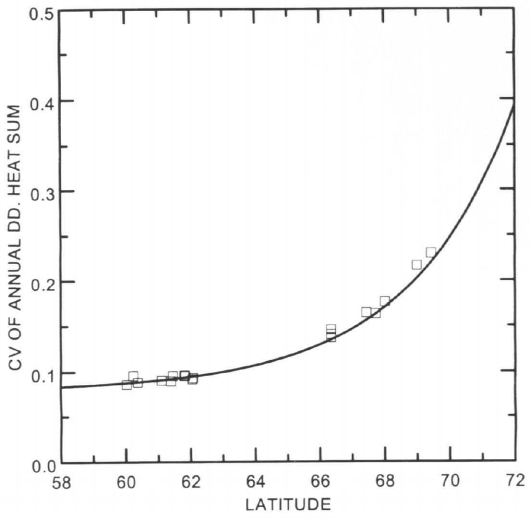

Fig. 2. The coefficient of variation of annual degree-day heat sums for the birch stands studied. On the vertical scale 0.1 is equivalent to 10 per cent. Based on data by Ojansuu and Henttonen (1983). The equation for the curve is $Y = 0.07815 + e^{-12.56349+0.00222\,X2}$.

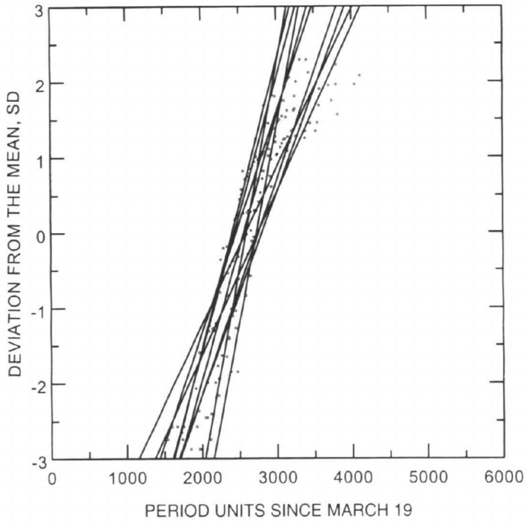

Fig. 4. Cumulative pollen catches of *Betula pendula* stand Punkaharju LIV in 1964–73. Points between –2 to +1.6 standard deviations were used to position the lines. Catches beyond these limits are also shown.

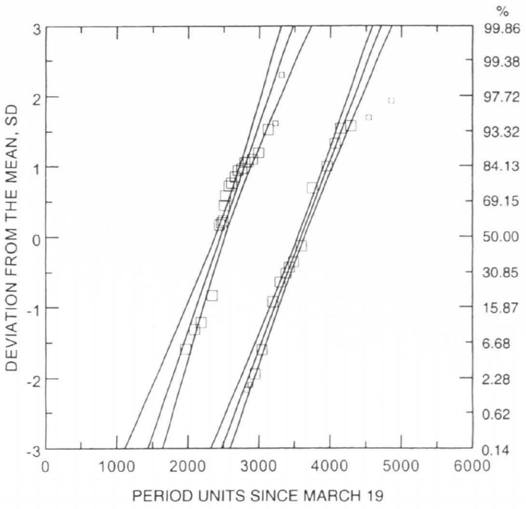

Fig. 3. Cumulative distribution of pollen catches of *Betula pendula* stand Punkaharju LIV (on the left) and *B. pubescens* stand Punkaharju L (right) in 1965. The central larger squares were used to position the regression line while the smaller ones beyond the limits of –2 and +1.6 standard deviations were excluded. The equivalents of steps of the ordinate in SD (left side) are given in per cent on the right side.

temperature sums to be used as phenological parameters. The first was a daily degree-day sum (over +5 °C) and the other a more specific 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 unit a "period unit".

Creating and testing ecophysiological models was begun by finding the mean of each anthesis as a period unit sum. The daily accumulation of p.u. units was computer-tabulated at intervals of two hours during growing season for all the stands and years of study. The relevant degree-day heat sums and dates were also readable from the same computer sheet. Three alternative measures (phenological parameters) of the mean of each anthesis were thereby generated. The parameters are compared in Table 2a and 2b: each coefficient of variation is a measure of the between-years variation. Evidence of long distance pollen transport caused the rejection of one observation cycle from the timing data (Rovaniemi XXI in 1966). The most extreme onset and termination dates of antheses are also presented standwise in Table 2a.

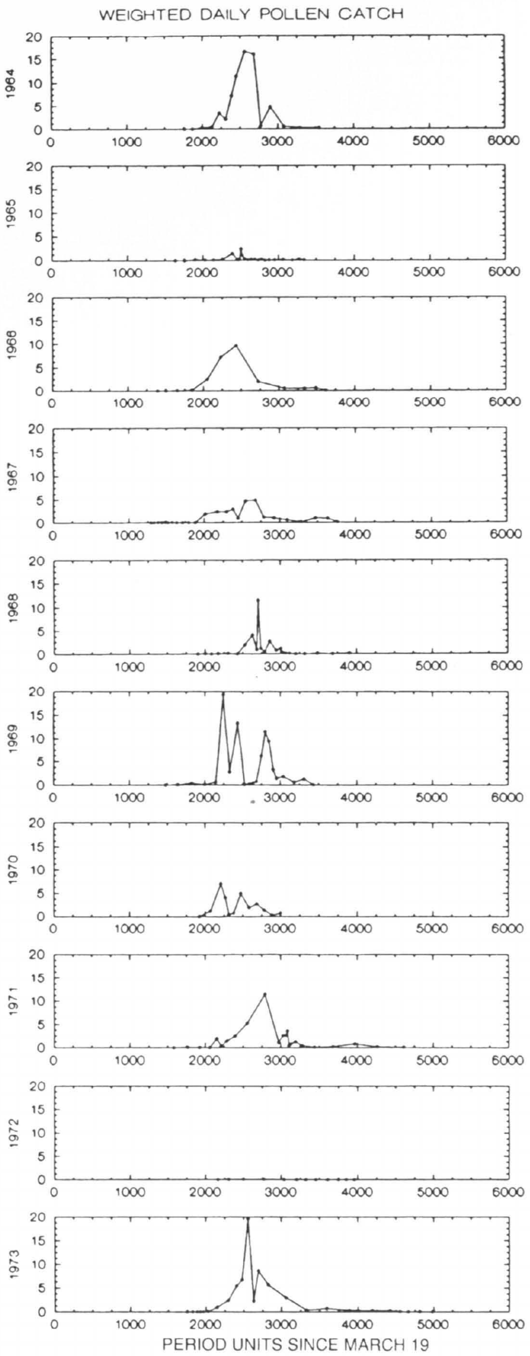

Fig. 5. Pollen catches of the *Betula pendula* stand Punkaharju LIV in 1964–73. The daily catches per mm² were divided by the period unit heat sum of each day (the ordinate). Compare to Fig. 4.

A physiologically meaningful biofix of the 19th of March (see Luomajoki 1995) was chosen for this study. It matches with the first day with 12 hours of sunhours (measured from the upper edge of the sun). This day is close to the astronomical vernal equinox on March 21. Biofix problems are little studied on species levels, but evidence from long observation series supports a fixed biofix rather than one that depends on physiological stage (Häkkinen 1999).

In the present study, earlier starting dates were impossible owing to shortcomings of early temperature data. The data in a few cases had to be supplemented with the temperature recordings taken from near-by stands. With regard to the timing of anthesis, all dates considerably later than March 19th produced 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 in mild winters it reduced the period unit sums in southern Finland in certain years compared to a biofix of e.g. February 1. As a reference point, the date for the median of the theoretical pollen distribution was compared with the peak pollen catch day in terms of variability.

Diagrams showing the progress of anthesis were drawn up from the daily average pollen catches transformed by dividing by each daily period unit temperature sum. Examples of the diagrams are shown in Fig. 5. Compare this form of presentation to Fig. 4 in which the same years of the same site (Punkaharju LIV) are shown on probability paper.

2.3 Other Variables

Latitudes and longitudes were used in calculating correlations to expose the usual geographical trends. Finland is quite flat, with the highest altitudes occurring in the north. To simulate an increase in altitude as equivalent to an increase in latitude (i.e. create the so-called ecological or ecophysiological latitude) would thus just stretch the latitudinal scale in an uncomplicated manner from the south to the north. Considering the stand altitudes made no difference to geographical correlations in previous studies (Luomajoki 1993a, 1993b) so altitudes could be omitted from correlation calculations. The sample stands lie at altitudes from 5 to 510 meters.

Finnish forests are paleobotanically young owing to the relatively recent (ca. 10 000–8000 years B.P.) deglaciation of the country. Birch species invaded Finland first, shortly before Scots pine and long before Norway spruce. Two geographical locations were chosen as reference points for calculating hypothetical migration distances. Kolari (called the KO-point, 67°20'N lat. and 23°47'E long.) was the last glaciated area of Finland (see Kujansuu 1967, Ignatius et al. 1980, Manner and Tervo 1988). The other reference point was located at the 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). With help of these reference points migration effects can be studied from both ends: advancement of populations towards Kolari, the last glaciated area, and from Karelian Isthmus towards later stand localities. For simplicity, seas and other waterways were not considered in this scheme.

Anther residues and seed crop data by Koski and Tallqvist (1978) were used for the calculations presented in Table 4. Many of the factors studied are evidently naturally correlated with latitude and comparing two such correlation coefficients may only show the mutual dependency of the latitude. The connection with latitude is real for the simulated migration distances, the average annual heat sums at any given locality and the age of a stand. Partial correlations, in which the effects of latitude are removed, are therefore necessary when judging the nature of correlations found.

3 Results

3.1 Flowering Characteristics

Both birch species flowered abundantly but irregularly. The variation between years was high and cases of no measurable pollen catch were observed in both species for *Betula pendula* once and for *B. pubescens* on five instances. Years of no flowering occurred in the northernmost stands of both species, more in the case of in downy birch, which extends northwards far more than silver birch, and so is more exposed to the effects of the harsh climate. The range of total (annual) pollen catches in silver birch in the 73 cases recorded was very large, 0.0–9424.5 grains/mm^2 (CV = 1.158, standwise 0.566–1.767). The range in downy birch in the 103 cases was almost equally large, 0.0–9085.9 grains/mm^2 (CV = 1.519, standwise 0.751–1.882).

3.2 Timing of Anthesis

Of the two species, silver birch was the earlier flowerer. Male flowering in silver birch was commenced as early as April 25 in southern Finland and it could extend to as late as June 22 in northern Finland (Table 2a). Male flowering in downy birch began as early as May 4 in southern Finland and it could extend to as late as July 19 in northern Finland (Fig. 6). The relative level of air temperatures during spring and early summer influenced the timing in an individual year. Locally, in the individual stands, the occurrence of anthesis over several years remained rather constant in calendar time, although there is a difference between the two species in this respect.

The average duration of anthesis in different stands varied between 12.8 and 28.4 days (CV = 0.443) in silver birch and between 9.8 days and 24.1 days (CV = 0.410) in downy birch (Table 2a,

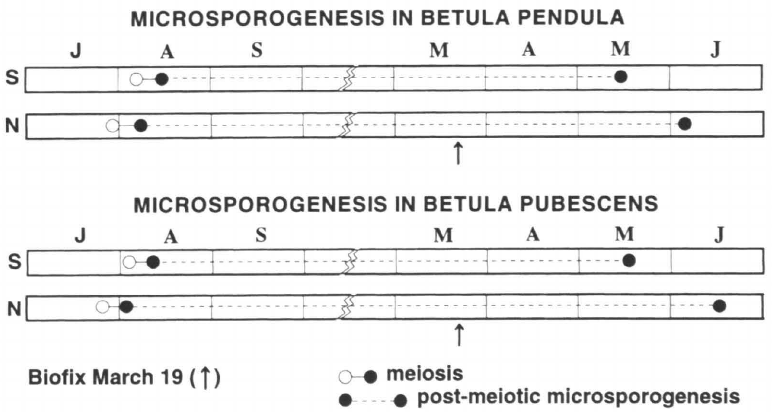

Fig. 6. A diagrammatic presentation (July to June of the second year) of the timing of microsporogenesis in silver and downy birch in southern (60°N lat., marked **S**) and northern (68°N lat., marked **N**) Finland. Open points ( ) mark the estimated time when pollen mother cells were in leptotene, solid points (●) next to it mark the tetrad stage 50 ppc (Luomajoki 1986) and the solid points to the right mark anthesis 50 ppc (from this study).

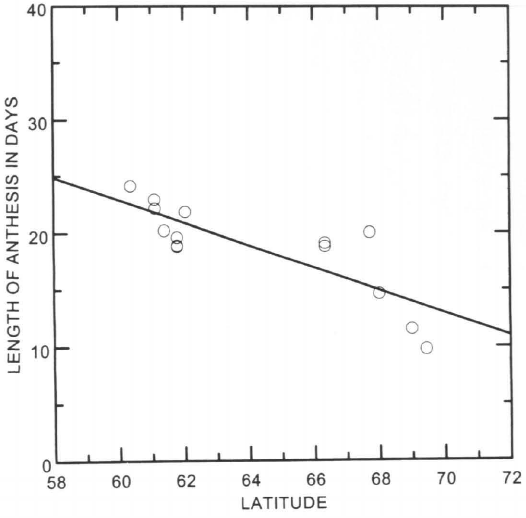

Fig. 7. The average length of anthesis in days in *Betula pubescens* stands. The regression line is: Y = 82.499 – 0.994 X. Significance of the slope: $P < 0.000$.

Fig. 7). This was assessed from the recorded pollen catches, so these duration figures are somewhat susceptible to effects of secondary pollen. Moderate coefficients of variation between years in each stand were found for silver birch: 23.8 to 52.5 per cent. Considerably higher cofficients were measured for downy birch: 20.9 to 116.2 per cent (Table 2a).

3.2.1 Simple Heat Sum Basis

The performance of the three parameters was evaluated in two ways: using coefficients of variation of the stand data straight, and subsequently on a day basis, when the annual deviations in heat sums had been converted to days using expected and observed heat sums. In the basic, unconverted data, the period from March 19th to median of anthesis in silver birch varied from 2551 to 2820 period units in stand means (Table 2a, Fig. 8). The respective coefficients of variation ranged from 4.7 to 9.9 per cent. D.d. heat sums varied during the same period from 49.3 to 62.6 degree days (Fig. 9). The respective coefficients of variation were from 9.7 to 23.0 per cent. In calendar time, the period under study ranged from 58.0 to 78.2 days (Fig. 10), with the coefficient of variation ranging from 4.4 to 8.5 per cent. In this basic data (Table 2a), calendar days were the least variable measure of timing in eight of the ten stands. Period units varied least in two stands, whilst degree days were always more variable than the two other parameters.

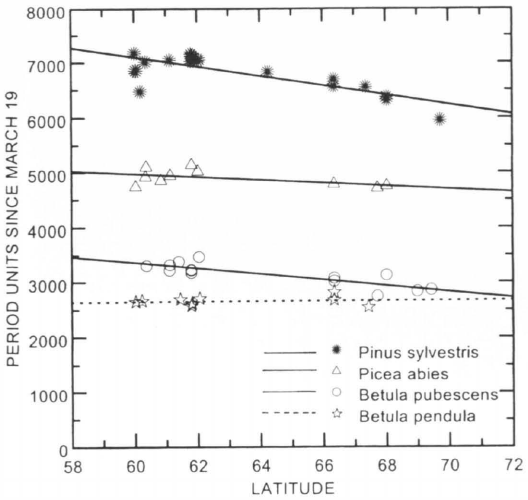

Fig. 8. The required period unit sum for the median of anthesis with reference to latitude of the stand. The regression lines are: Y = 2451.5 + 3.284 X (R^2 = 0.0) for *B. pendula* (2 outliers) and Y = 6571.8 – 53.522 X (R^2 = 0.704) for *B. pubescens*. The slope is highly significant ($P < 0.000$) for *B. pubescens*, not significant for *B. pendula*. This figure was completed with two regressions derived from earlier material (Luomajoki 1933a, 1993b). Upmost: *Pinus sylvestris* (Y = 12263.8 – 86.135 X, R^2 = 0.619), and below it *Picea abies* (Y = 6625.6 – 27.600 X, R^2 = 0.243). The slope is highly significant ($P < 0.000$) for *Pinus*, not significant for *Picea*.

In both birch species, the occurrences of maximum pollen release were also observed. A pairwise comparison with anthesis 50 pcc day and maximum pollen release as reference points showed that peak pollen catch for silver birch occurred in average 0.67 days earlier than anthesis 50 pcc. The peak pollen catch day was a more variable reference point than the median of anthesis in seven of the ten stands. The average difference between peak pollen catch day and median of anthesis does not tell all, however. Owing to large variations individual deviations between the two parameters could be as large as seven days.

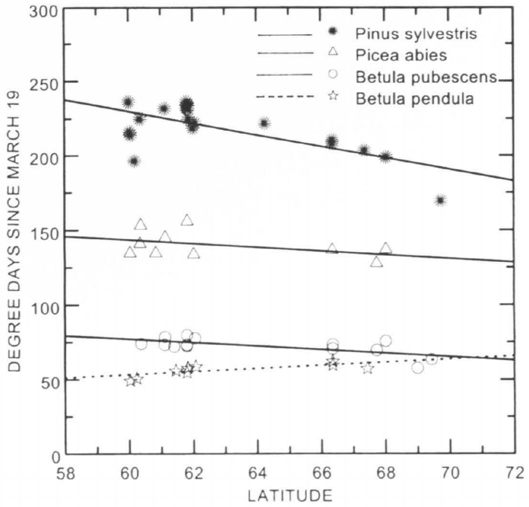

Fig. 9. The required degree-day sum for median of anthesis with reference to the latitude of stand. The regression lines are: Y = –10.713 + 1.070 X (R^2 = 0.449) for *Betula pendula* and Y = 146.464 – 1.158X (R^2 = 0.419) for *B. pubescens* (1 outlier). Significance of the slopes: *B. pendula* (P = 0.020), *B. pubescens* (P = 0.007). This figure was completed with two regressions derived from earlier material (Luomajoki 1933a, 1993b). Upmost: *Pinus sylvestris* (Y = 464.8 – 3.919 X, R^2 = 0.488), and below it *Picea abies* (Y = 219.5 – 1.264 X, R^2 = 0.109). The slope is highly significant ($P < 0.000$) for *Pinus*, not significant for *Picea*.

Downy birch required higher heat sums to flower. In the basic data, the period March 19 to the median of anthesis varied from 2742 to 3466 period units in stand means (Table 2a, Fig. 8). Respective coefficients of variation ranged from 3.3 to 12.6 per cent. Degree days for the same period varied from 57.5 to 79.6 (Fig. 9), and the respective coefficients of variation ranged from 5.6 to 33.6 per cent. In calendar time, the period under study varied from 63.5 to 99.0 days (Fig. 10) with coefficients of variation from 1.4 to 9.1 per cent. In this basic data (Table 2a) calendar days were the least variable measure also for downy birch. This was true in twelve of the fourteen stands. Period units varied least in two stands. As in the case of silver birch, degree days always varied the most.

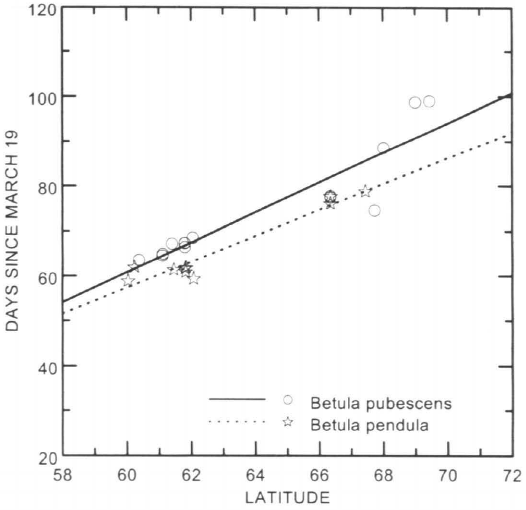

Fig. 10. The durations from March 19 in days needed for anthesis 50 pcc with reference to latitude of locality. The regression lines are: Y = 116.219 + 2.893 X (R^2 = 0.921) for *Betula pendula* (2 outliers) and Y = 139.235 + 3.334 X (R^2 = 0.835) for *B. pubescens* (1 outlier). The slopes of the regressions are both highly significant ($P < 0.000$).

A pairwise comparison reveals that peak pollen catches occurred in downy birch on average 0.15 days earlier than the median of anthesis. The maximum pollen release day was a more variable reference point than the median of anthesis in twelve stands, and so it was the better reference point only twice, judged by coefficients of variation of days elapsed since biofix (Table 2a). While the average deviation from median was very slight, solitary differences of up to 13 days were observed.

3.2.2 Heat Sums Converted to a Day Basis

The annual deviations in days (derived from expected and observed heat sums) proved smaller that the heat sum CV basis might lead to expect. The results of the comparison of parameters are shown in Table 2b. For silver birch, on a day basis, period units were the least variable measure of timing in five of the ten 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 parameter in two stands and, as noted above, being equal in accuracy with period units in one stand. Degree days, on the other hand, suffered in the comparison, producing the least variation only in one stand and being equal to period units in another (Table 2b).

For downy birch, of a comparison of parameters on a day basis produced radically different results from the simple heat sum CV basis. Period units performed best in as many as eleven of the fourteen stands, while degree days were the most accurate in the remaining three stands. The performance of calendar days was inferior to heat sums (Table 2b).

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 median of anthesis fell close to the stand mean. In most years, this coincidence occurred only in single stands. However, in 1964 this phenomenon occurred in as many as five downy birch stands, and in 1971 in four stands of the same species. On the other hand, the maximum distribution of values for silver birch was recorded in 1968 (stand Vilppula V) when the range between forecasts was as large as 14 days. In 1964 (stand Kittilä, Sätkenä II) a range of 13 days was observed for downy birch.

The mean deviations (absolute values) in days between the expected and the observed days are also given in Table 2b. These mean deviations do not correlate fully with the day parameters' coefficients of variation (long used as the customary measure) of the same table. The reason for this is that the coefficient of variation involves squared annual deviations, while the mean of annual deviations involves only simple (unsquared) values. Nevertheless, in the present material using the mean of annual deviations, rather than the coefficient of variation, would make no difference to the order of the performance of the parameters in either species.

It should be noted in reading Table 2b that only the observed day column (on the right) gives the original day data based on observations: stand means of annual deviations varied from 0.59 to 4.64 days for silver birch and from 1.00 to 5.75 days for downy birch. As simple, unsquared figures the deviations have a real, concrete meaning: namely, the mean difference of the expected and the observed dates in days. The two scales converted from period units and degree days (the two columns furthest left) are hypothetical and only show where the observed heat sums fell on a day scale compared to the expected heat sums, and the consequent deviations.

3.3 Timing-related Geographical Correlations

3.3.1 Correlations

Correlations can be dealt either with on a yearly, individual anthesis basis or on a stand basis. As far as timing of flowering is concerned, the yearly basis is appropriate, because the greatest source of variation are differences between years. Air temperatures are important, not productivity-related site factors. On the other hand, both levels were studied in correlations with total pollen catch.

Period units for silver birch at the median of anthesis did not correlate significantly with any of the independent variables (latitude, longitude, the SE-point or the KO-point) nor with the age of stand nor degree days of either previous year or 2 years earlier. On the contrary, period unit sums at the median of anthesis for downy birch correlated highly significantly with all of the mentioned factors with the only exceptions of age (significant) and longitude (not significant) as seen in Table 3a.

Degree days did not produce significant correlations with either species. Interestingly, the correlation coefficients of the two species differed often also by sign, and in the case of correlation with latitude, both coefficients were almost significant ($P < 0.05$) and had opposite signs (Table 3a).

The correlations with the median of anthesis in days reached highly significant levels with every variable for downy birch, but for silver birch, longitude failed to produce a significant coefficient. Again, the remaining variables produced highly significant correlation coefficients also for silver birch (Table 3a). A summary of the latitudinal correlations in four tree species is presented in Table 7.

The length of anthesis (i.e. the pollen season) in period units was significantly correlated with latitude and degree days of two years earlier for downy birch but no significant correlation coefficients for silver birch were obtained. On the other hand, latitude, distance to the KO-point, degree days of previous year, as well as those of 2 years earlier, each correlated with the length of anthesis in days of silver birch at a highly significant level. On the contrary, none of the variables correlated significantly with length of anthesis in days of downy birch (Table 3a). In many respects, the two species thus showed opposite trends in timing-related correlations. In neither species, did the age of stand correlate significantly with either measure of the length of anthesis.

Table 3a. Correlations of heat sums and durations involved in anthesis. Upper figures are for *Betula pendula* ($n_1 = 69$) and lower figures for *Betula pubescens* ($n_2 = 93$).

	Period from March 19 th 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	0.116	0.293*	0.899***	–0.178	–0.395***
	–0.432***	–0.231*	0.861***	0.322**	0.254*
Longitude	–0.102	0.201	–0.051	–0.280*	–0.310*
	0.030	0.149	–0.369***	0.012	–0.174
Distance from SE-point	0.159	0.103	0.789***	0.068	–0.111
	–0.380***	–0.243*	0.845***	–0.178	–0.067
Distance to KO-point	–0.133	–0.289*	–0.897***	0.176	0.390***
	0.391***	0.171	–0.748***	0.155	0.162
Degree days of previous year	–0.079	–0.221	–0.855***	0.289*	0.425***
	0.433***	0.255*	–0.815***	0.263*	0.163
Degree days of 2 years earlier	–0.033	–0.203	–0.777***	0.127	0.420***
	0.531***	0.261*	–0.703***	0.295**	0.248*
Age of stand ($n_2 = 88$)	0.209	0.194	0.577***	0.020	–0.157
	–0.300**	–0.043	0.711***	0.030	–0.108

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

Table 3 b. Partial correlations of heat sums and durations involved in anthesis: effects of latitude removed. Upper figures are for *Betula pendula* ($n_1 = 69$) and lower figures for *Betula pubescens* ($n_2 = 93$).

	Period from March 19 th 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	–0.112	0.186	–0.278*	–0.271*	–0.305*
	–0.125	0.082	–0.198	–0.064	–0.236*
Distance from SE-point	0.110	–0.206	0.335**	0.332**	0.336**
	0.109	–0.078	0.168	0.121	0.247*
Distance to KO-point	–0.198	0.035	–0.044	–0.017	–0.043
	–0.081	–0.176	0.514***	–0.214*	0.065
Degree days of previous year	0.038	0.058	–0.392**	0.266*	0.185
	0.113	0.110	–0.175	0.140	0.066
Degree days of 2 years earlier	0.136	0.108	0.010	–0.056	0.170
	0.360***	0.126	0.301**	0.214*	0.259*
Age of stand ($n_2 = 88$)	0.178	0.007	–0.006	0.179	0.139
	0.043	0.094	–0.070	0.314**	0.170

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

3.3.2 Partial Correlations

With respect to distances from the KO- and SE-points, partial correlations with period units were not significant, nor with degree days at anthesis 50 pcc (Table 3b). Significant partial correlation coefficients of the day parameter were divided so that correlations with distance from SE and with degree days of the previous year were significant for silver birch, while correlations with distance to Kolari and with degree days of 2 years earlier were significant for downy birch (Table 3b). These inequalities could be taken for differences between the two species in their ancient migration history and, respectively, for different reaction patterns in timing during consecutive years. 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 but, surprisingly, the length of anthesis in period units had a significant partial correlation with the age of stand in downy birch (a random correlation?). Both measures of length of anthesis (p.u., days) were correlated with distance from the SE-point for silver birch.

3.4 Differences Between Years

The efficiency and stability of the three parameters could be demonstrated by comparing just two years, 1968 and 1969, with each parameter. These years were taken because the material from these two years is standwise complete (critical with silver birch) which also provides the best statistical reliability. Period units for downy birch (the two upper lines) behaved uniformly indicating good match between the two years (Fig. 11). This was expected owing to a highly significant correlation coefficient between period units and the latitude (Table 3a). There is little conformity between 1968 and 1969 in period units for silver birch (Fig. 11) the regressions being divergent. Better uniformity could not be expected owing to a low, non-significant latitudinal correlation coefficient (Table 3a).

Degree days fared much worse. There is large discrepancy between the two years in both species (Fig. 12). The correlation coefficients between d.d. –sums and latitude were not significant in either species, albeit almost significant at $P < 0.05$, and they also had opposite signs. Considering days since March 19, the regressions are very uniform, the two lower regression lines pertaining to silver birch (Fig. 13) indicating earlier flowering. All of the regression lines lie almost parallel. This agrees well with the large, highly significant latitudinal correlation coefficients (Table 3a).

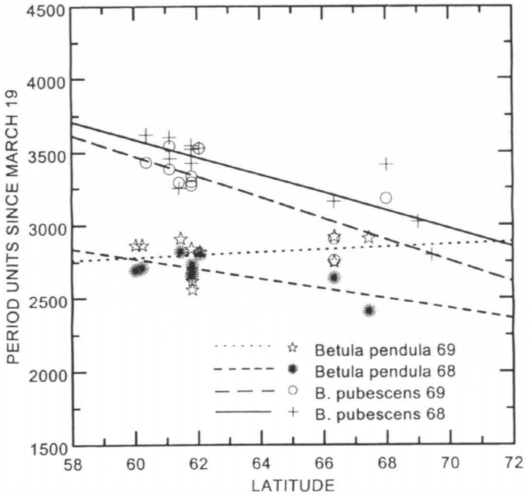

Fig. 11. Fair consistency achieved in the performance of the period unit parameter (since March 19) versus the latitude in comparison of the years 1968 and 1969 at each stand.

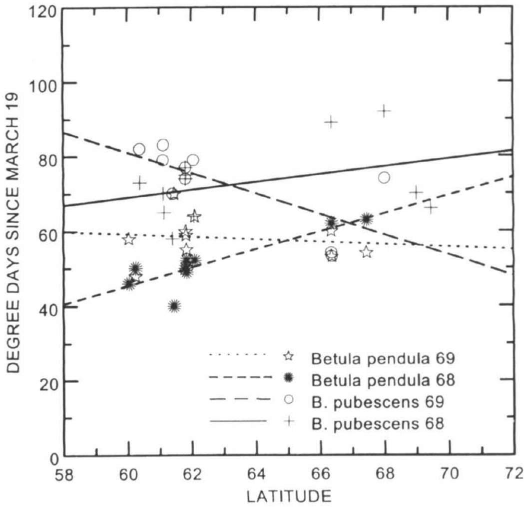

Fig. 12. Poor consistency of the degree-day (since March 19) parameter versus the latitude in 1968 and 1969 at the stands studied.

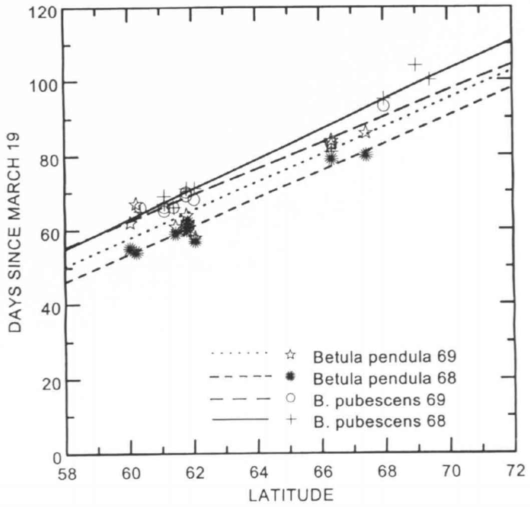

Fig. 13. Excellent consistency of the days (since March 19) parameter versus the latitude in 1968 and 1969 at each stand. In 1968 the separation of flowering dates of the two species was far larger than in 1969 (cf. Table 6).

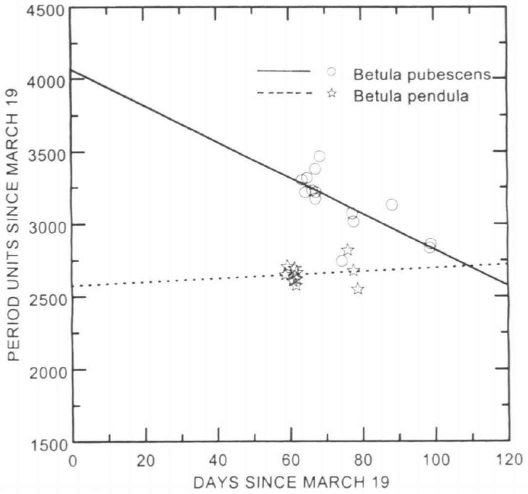

Fig. 14. *Betula pendula* and *B. pubescens* stands in a dual-parameter co-ordinate system. Silver birch varies only in with respect to days. Downy birch varies with respect to days and period unit sums. The slope of the regression is significant for *B. pubescens*, not significant for *B. pendula*.

It is not meaningful to compare the significance of the slopes of these regressions owing to relatively small yearly materials. A comparison of the three parameters can be made on a more general basis from the whole material (see Figs. 8 to 10 and the respective legends). Any two of the parameters can also be tested in a common co-ordinate system. Combining period units as the ordinate with observed days as abscissa explicitly shows the ecophysiological difference in the timing of flowering of the two species (Fig. 14). Generally speaking, silver birch only varies with respect of days. Downy birch varies with respect to both period unit heat sums and calendar days.

3.5 Adaptation

The heat sums needed for reaching the median of anthesis were divided by the average annual heat sum of a locality and given as a percentage. The method had already been suggested by Reaumur (cit. Sarvas 1972, Robertson 1973) and Linsser (1867) and gives information on the adaptability of species to various localities. This method was only applicable on a degree day basis (Figs. 9 and 16) owing to the need for measured annual heat sums for each locality.

Downy birch adapted only moderately in terms of degree-day sums needed for the median of anthesis ($P = 0.012$, Fig. 15). In silver birch there was no such adaptation, the trend being the opposite but without being significant ($P = 0.123$, Fig. 15). This finding is new for the species studied so far: silver birch does not adapt at all latitudinally in terms of temperature sums needed for flowering (see also Fig. 9). The curves in Fig. 16 were mostly shaped by the change of the local annual heat sums and not by the change in the heat sums needed for reaching the median of anthesis.

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 at a highly significant level with anther residues assessed in the same years in the same stands (figures from Koski and Tallqvist 1978) in both birch species (Table 4). For silver birch ($n = 72$) the correlation coefficient was

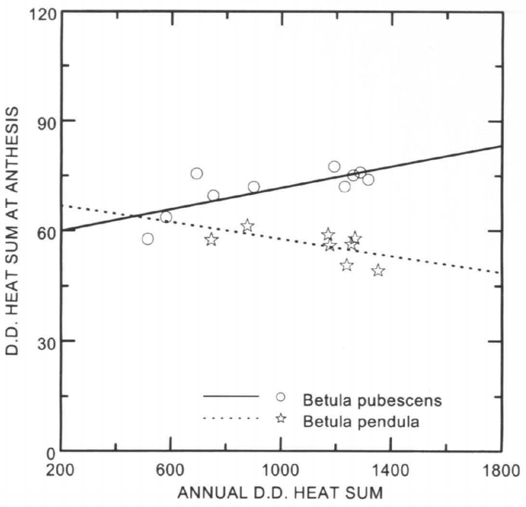

Fig. 15. The relation of the degree-days needed for anthesis 50 pcc to the average annual d.d. sum of the locality. The regression lines are: $Y = 69.028 - 0.011\ X$ ($R^2 = 0.241$) for *Betula pendula* ($P = 0.123$) and $Y = 56.906 + 0.015\ X$ ($R^2 = 0.514$) for *B. pubescens* ($P = 0.012$); 2 outliers.

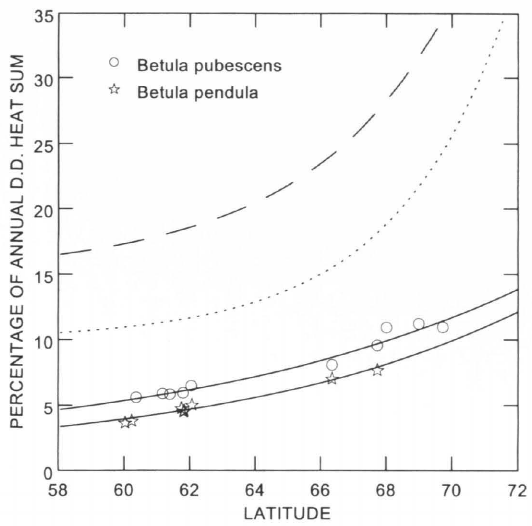

Fig. 16. The proportion of the average local annual d.d. sum needed for the median of anthesis. The trend visible is mostly due to latitudinal change in annual d.d. sums of the locality. The curve equations are: $Y = e^{-0.482439+0.000601\ X2}$ ($R^2 = 0.978$) for *Betula pendula* and $Y = e^{-1.185184\ +\ 0.000709\ X2}$ ($R^2 = 0.963$) for *B. pubescens*. Corresponding curves were earlier published of *Pinus sylvestris* and *Picea abies* over a wider latitude range (Luomajoki 1993a, 1993b). Parts of those curves were added to this figure (*Pinus* = long dashes, *Picea* = short dashes).

r = 0.779*** and for downy birch (n = 103) it was r = 0.692. The effect of the amount of pollen catch on seed production also was highly significant for both species. Again, silver birch reached the higher coefficient (r = 0.807***) compared with downy birch (r = 0.608***). Both correlations remained highly significant for both species when the effects of latitude were removed.

In both species, pollen catches were correlated with the annual d.d. temperature sums of the preceding year at a highly significant level (Table 4). The relevant partial correlations, free from latitudinal effects, were both highly significant. The temperatures measured two years earlier had no positive effect on pollen catches for silver birch. However, for downy birch a highly significant partial correlation was found. The age of the stand had little influence except for downy birch (r = –0.338***). When the effects of latitude were removed, the correlation approached zero in both species (Table 4).

Latitudinally, a highly significant negative correlation coefficient (r = –0.390***) was found for downy birch. For silver birch, on the other hand, the pollen catch correlated with longitude (r = 0.381***), the corresponding partial correlation also being significant (r = 0.402**). Interestingly, the correlations along the hypothetical migration route (distance from SE-point) for both species were highly significant. Considering this from the reverse viewpoint, the correlation with distance to Kolari (the KO-point or last glaciated area) was highly significant only for downy birch (r = 0.380***). No periodicity was found in the annual pollen catches of either species. Nevertheless, pollen catches of both species correlated (also partial correlations) with degree days of the previous year.

With respect to stand averages, the corresponding correlations (Table 4) of pollen catch with anther residues (Fig. 18) and seed crop (Fig. 19) were highly significant for silver birch and significant for downy birch. On the other hand, degree days of the previous year were significant only for downy birch. Likewise, the temperatures of two years earlier correlated at a significant level for downy birch. The geographical correlations for pollen catch stand averages (the regression on latitude shown in Fig. 17) were similar to those based on yearly values at a lower significance level. The longitudinal correlation for silver birch was not significant at the stand level (Table 4).

Variation coefficients reflecting pollen catch differences between years were found to vary little geographically (Table 5).

Table 4. Correlations with total pollen catch. Upper figures are for *Betula pendula* ($n_1 = 72$, 10 stands) and lower figures for *B. pubescens* ($n_2 = 103$, 14 stands). For partial correlations. $n_1 = 62$ and $n_2 = 93$ throughout.

	Yearly observations		Stands	
	Correlations	Partial correlations with effects of latitude removed	Correlations	Partial correlations with effects of latitude removed
Latitude	–0.258* –0.390***	– –	–0.404 –0.707**	– –
Longitude	0.381*** 0.194	0.402** 0.054	0.632 0.377	0.771* 0.170
Distance from SE–point	–0453*** –0.388***	–0.389** –0.062	–0.771** –0.709**	–0.740* –0.169
Distance to KO-point	0.276* 0.380***	0.206 0.005	0.429 0.689**	0.285 0.065
Length of antesis in days	0.026 0.039	–0.093 –0.167	0.018 0.638*	–0.560 0.099
Degree days of previous year	0.448*** 0.509***	0.480*** 0.459***	0.539 0.722**	0.656 0.314
Degree days of 2 years earlier	0.131 0.212*	–0.203 –0.406***	0.518 0.706**	0.601 0.095
Age of stand ($n_2 = 93$)	–0.143 –0.338***	0.043 –0.083	–0.196 –0.615*	0.123 –0.140
Anther residues. g/m² ($n_1 = 63$, $n_2 = 93$)	0.779*** 0.692***	0.747*** 0.643***	0.888*** 0.652**	0.876** 0.326
Seeds/m2 ($n_1 = 63$, $n_2 = 93$)	0.807*** 0.608***	0.781*** 0.546***	0.901*** 0.683**	0.870** 0.410

3.7 Occurrence of Simultaneous Flowering in *Betula pendula* and *B. pubescens*

Silver birch has to be considered the earlier flowerer of the two species, as reported in Chapter 3.2 (see Figs. 10 and 13). However, simultaneous flowering in the two species occurred in some years and both species locally shared the same anthesis 50 pcc day. Partial overlapping of flowering time was common. The inclination to simultaneous flowering had a latitudinal correlation, as can be seen in Table 6. Although the average separation in days of the flowering times of the two species does diminish in the north, it is not directly apparent from Fig. 10 and there is difference between years (Fig. 13). A separation of seven days between adjacent stands at median of anthesis was observed in 1968 at Kittilä.

In downy birch, the scatter in days increases northwards (see Fig. 10) and cases of nearly simultaneous flowering were far more common at Rovaniemi (66°21') than in the south of Finland. Cases of a perfect matching of flowering times occurred only at Rovaniemi. On the other hand, silver birch is relatively rare and the present material is limited, in northernmost Finland (e.g. at Kittilä), and so there was little chance of observing simultaneous flowering there.

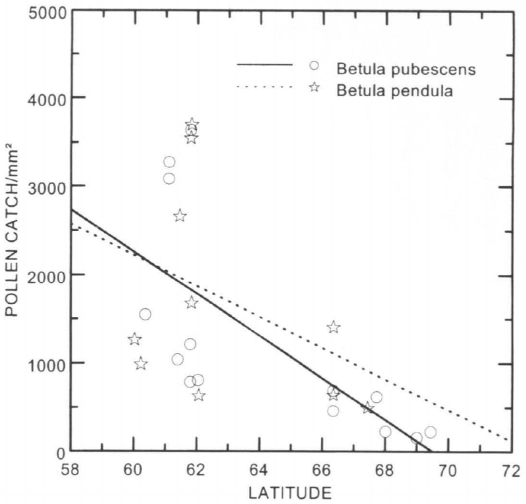

Fig. 17. Pollen catch per mm^2 of the two species with reference to latitude in the stands studied (n = 10 for *Betula pendula*, n = 14 for *B. pubescens*). The regression lines are: Y = 12800.1 – 176.318 X ($R^2 = 0.055$) for *B. pendula* and Y = 16519.1 – 237.690 X ($R^2 = 0.418$) for *B. pubescens*; 1 outlier.

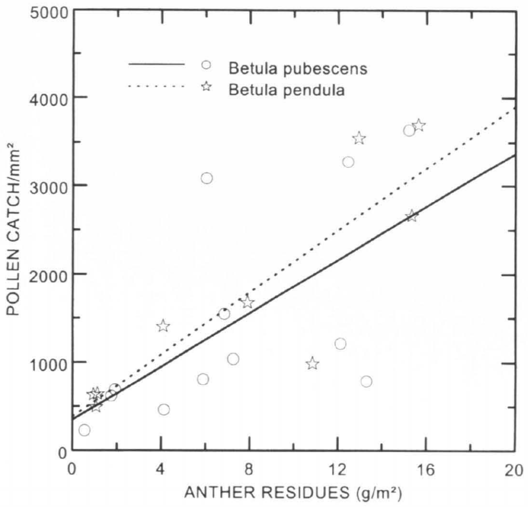

Fig. 18. Pollen catch per mm^2 with reference to anther residues (g/m^2) in birch stands of the two species. The regression lines are: Y = 381.7 + 176.518 X ($R^2 = 0.719$) for *Betula pendula*; (1 outlier), and Y = 344.3 + 151.356 X ($R^2 = 0.332$) for *B. pubescens*.

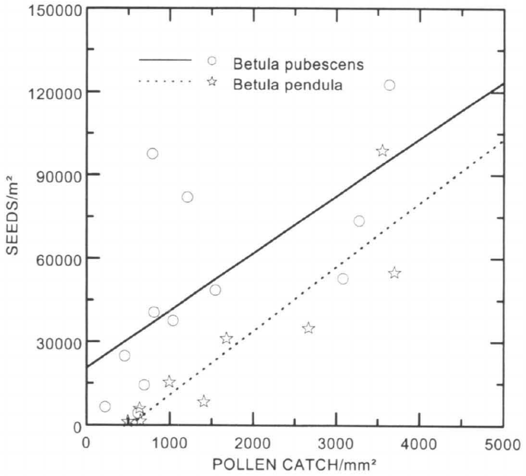

Fig. 19. Production of seeds/m^2 with reference to pollen catch in the birch stands studied. The regression lines are: Y = –12145.1 + 22.989 X ($R^2 = 0.780$) for *Betula pendula* and 20590.9 + 20.600 X ($R^2 = 0.377$) for *B. pubescens*. There is an outlier in both regressions.

Table 5. Correlations of the between-years variation in pollen catches in the stands studied. Upper figures are for *Betula pendula* ($n_1 = 10$) and lower figures for *B. pubescens* ($n_2 = 14$). For partial correlations, $n_2 = 12$.

	Correlations	Partial correlations with effects of latitude removed
Latitude	–0.016 0.208	– –
Longitude	–0.163 –0.364	–0.163 –0.372
Distance from SE-point	0.105 0.267	0.173 0.353
Distance to KO-point	0.034 –0.240	0.209 0.139
Age of stand ($n_2 = 12$)	0.048 –0.047	0.079 –0.576*

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

Table 6. Simultaneous flowering in *Betula pendula* and *B. pubescens*.

Locality (latitude)	Number of stands	Common flowering years (no.)	Instances of same flowering day (anthesis 50 pcc)	Difference of one day at anthesis 50 pcc
Punkaharju (61°48')	5	7	–	–
	4	2	–	1966(2x), 72
	3	1	–	
Vilppula (62°03')	2	5	–	–
Rovaniemi (66°21')	4	7	1967(2x), 69(2x), 70 71(2x), 72(2x), 73(4x)	1967, 69, 70(2x), 71(2x)
	3	2	–	1964(2x), 65
Kittilä (Sätkenä) (67°44')	2	4	–	1964, 69

4 Discussion

4.1 Sampling

The two birch species studied here join Scots pine and Norway spruce that were studied earlier (Luomajoki 1993a, 1993b) using the same methods, and can thus be compared. The biofix adopted, March 19, is the same even if the photoperiodic needs of the trees are not necessarily the same. The choice, made on grounds of a 12 hour day length, conforms well with the date of March 21, as calculated by mathematical optimization by Häkkinen et al. (1998).

Two main differences can be found between the flowering of birch species and the flowering of Scots pine. Deviations from normality (found by the probability paper method applied to each species) were larger for Scots pine than for birches. Overfrequency in the beginning of the pollen season and the considerable underfrequency towards the end of the pollen season found in Scots pine (Luomajoki 1993a) were less problematic with birch species. There was practically no overfrequency at the beginning of birch anthesis and the manifestation of underfrequency at the end of anthesis was far less conspicuous for birches (cf. Sarvas 1952). This meant that a larger part of the anthesis could be used to position the line of best fit on the probability paper. A range from –2.0 to +1.6 standard deviations could be used compared to a more limited range of –2.0 to +1.2 standard deviations for Scots pine and Norway spruce.

On the other hand, the two birch species flower in close succession in calendar time; an average deviation of six days was found at Punkaharju between the two silver birch stands and the three downy birch stands. This is in accordance with Sarvas´ (1952) notes from the Helsinki region. In some years at some localities, the difference can be smaller. The pollen grains of the two birch species are quite similar and their only difference is a practically statistical difference in size (see Mäkelä 1996). This means that in adjacent sample stands pollen clouds of each species´ pollen can disturb measurements in both stands, i.e. towards the end of the pollen season of silver birch and in the beginning of the pollen season of downy birch. This did not considerably affect timing of anthesis 50 pcc owing to the empirically sought limits adopted (–2.0 to +1.6 SD). It did disturb accurate measurement of the duration of anthesis, however.

In his early study, Sarvas (1952) had not yet employed either temperature sums nor probability paper. His results concerning "strongly concentrated pollination over a few initial days" in birches are in a conflict with the present results. Sarvas may have observed the pollination event during abnormally warm or windy weather.

4.2 Flowering Characteristics

Both birch species were earlier flowerers than Norway spruce. Flowering of birches resembles that of Norway spruce in terms of variability between years. However, the maximum pollen crop levels were much higher in birch species, being numerically over five times that of Norway spruce (Luomajoki 1993b). A clear difference was also found in the latitudinal factor: the variation coefficient of pollen catches does not grow latitudinally in birches (Table 5) as it grew in Scots pine and Norway spruce (Luomajoki 1993a, 1993b). Considerable amounts of pollen and small pollen size make long-distance pollen transport in birch possible and probable (e.g. Koski 1970, Tyldesley 1973, Hjelmroos 1991, Hjelmroos and Franzén 1994). Variability of pollen crops in birches between years may not have similar biological causes as in the flowering of Norway spruce. Insects harm the male catkins of birch (Juutinen 1974) but this does not have the same grave consequences for birch reproduction than, e.g., seed-damaging insects have on Norway spruce reproduction (Annila 1981, Fenner 1991). Moreover, birch seeds are shed quickly and therefore do not remain for too long on the trees as potential food for foraging insects or birds.

4.3 Timing Parameters

Overlapping pollen seasons mostly hampered the estimation of the end of anthesis in silver birch and, respectively, the beginning of flowering in downy birch. This in turn impeded the measurement of the duration anthesis in both species. However, the results showing slightly shorter durations for downy birch than for silver birch were actually quite logical owing to the higher temperatures (and the faster development) during the later flowering time of downy birch.

As previously experienced, the peak pollen catch day was a poorer reference point than anthesis 50 pcc. This was the case for both birch species and it was also so for Scots pine and Norway spruce studied previously (Luomajoki 1993a, 1993b). However, the use of maximum pollen release (Di-Giovanni et al. 1996) is straightforward compared with the present method and also saves the researcher from background pollen worries.

In the basic data, the period unit, was the least variable parameter for both species. Likewise, observed days scored as the second best choice and degree days was the poorest in both cases. On a converted calendar day basis (Table 2b), the annual deviations between the expected and the measured heat sums proved moderately small. For silver birch, the converted calendar day basis also resulted in the period unit becoming the best parameter, followed by days actually observed. Degree days scored only a marginal success when judged on a converted calendar day basis (Table 2b). For downy birch, on a converted calendar day basis, the period unit was the superior parameter, degree days also performed well, but observed days failed totally.

The use of the basic heat sum data can be defended for its simplicity or from interest in the heat sums themselves. On the other hand, the 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. Critical comparison of the parameters thus requires the conversion of heat sums to a day basis. For silver birch, period units was the best parameter in 50 per cent of the stands (i.e. splitting each tie case and giving 5 per cent units to each rival). Calendar days would score 25 per cent this way, leaving 15 percent for degree days. For downy birch, on the other hand, period units dominated with a 78.6 per cent score while degree days obtained the remaining 21.4 per cent. Observed days did not score.

Of the three parameters, none was really bad for either species. This result was probably due to contribution of both temperature and photoperiod in the control of birch flowering. Different accuracy of the models tells to which extent a factor is likely to be contributing in either species. This approach supports the conclusion that flowering in downy birch is very much temperature-dependent. The mean of deviations of converted period units for downy birch was the smallest in the study (2.30 days). On the other hand, anthesis in downy birch can not be forecasted in days with equal accuracy. Silver birch follows the calendar time considerably more closely. However, the mean of deviations of converted period units is the smallest of the three parameters for silver birch (2.42 days) followed closely by observed days (mean 2.48 days; Table 2b). This kind of balance could mean a partly photoperiod-induced control of flowering in silver birch.

Andersen (1991) also suggested that forecasts of the *Betula* pollen season required a photoperiodic parameter (without specifying species). Downy birch adapts latitudinally both in terms of period unit sums and degree day sums. Heat sums did not reflect adaptatation in the case of silver birch at all (see Figs. 8, 9 and 14). This suggests the importance of temperatures for flowering in the case of downy birch but less so for the flowering of silver birch. Such latitudinal independence from adaptation to temperatures has not been recorded earlier.

In certain years, notably in 1964 (except for northernmost Finland), and in 1971, all parameters tended to give the same forecast for most downy birch stands. Also in Norway spruce in 1971 all parameters agreed well (Luomajoki

Table 7. Latitudinal correlations with flowering (anthesis 50 pcc) parameters in four species.

Species	Source	n	Parameter (counted since March 19) Period unit sum	Degree-day sum	Flowering day
Betula pendula		70	0.116	0.293*	0.899***
Picea abies	Luomajoki 1993b	70	–0.245*	–0.172	0.900***
B. pubescens		93	–0.432***	–0.231*	0.861***
Pinus sylvestris	Luomajoki 1993a	153	–0.584***	–0.491***	0.807***

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

1993b). Large forecast ranges for birches extending to two weeks were found in some years (e.g. in 1968) when the accumulation of degree days halted due to persistent low temperatures. Apart from the synchrony of parameters, 1963 was an early year for flowering of the downy birch as it was for flowering of Scots pine (Luomajoki 1993a).

4.4 Geographical Trends

Silver birch lacks noteworthy latitudinal heat sum correlations even though the correlation between the latitude and degree days was almost significant ($P < 0.05$). Curiously, that correlation was positive, which means a really "avant-garde" behaviour. In all other species studied so far, heat sum latitudinal correlations have been negative (Table 7). As downy birch had an almost significant negative correlation between the latitude and degree days, the difference between the correlations in the two species in terms of z (Sokal and Rohlf 1995) can be considered highly significant. The correlation between latitude and period units for downy birch was negative and highly significant. Latitudinal heat sum correlations for downy birch numerically fall between Norway spruce and Scots pine, which is the most explicitly latitudinally adapted of the species so far studied (Table 7). In terms of calendar days, the latitudinal variation was high in both birch species, as well as in the two conifers studied earlier (Table 7). This correlation was highest for the two species (*Betula pendula* and *Picea abies*) which are also likely to be affected by photoperiodic control of flowering in addition to the control by temperatures.

Partial geographical correlations (Table 3b), with latitude removed, gave a more reliable picture of the geographical relationships than the straight correlations that were constantly high owing to effects of latitude and parallel factors. Silver birch correlated significantly with distance from the SE-point, while downy birch correlated highly significantly to distance to the KO-point, the last glaciated area in Finland. Other geographical partial correlations were not significant. This also agrees with the current migration theories: downy birch followed the retreating glacier into northern Finland as a pioneer tree species and silver birch probably followed later from southeast, together with Scots pine (Alho 1990, Luomajoki 1993a). According to refugium theories (cf. Seppä 1996 for *Pinus*) the Finnish downy birch populations could also stem from several sources, the southern and one or more northern refugia. This also justifies the reverse angle used here in testing migration routes: correlation with distance to the KO-point rather than with distance from some source. Generally speaking, the preservation of such old traits in populations is doubtful. However, there are no pressures of selection in birches that are likely to change old patterns (see Chapter 4.6). Assumptions based on migration history (see also Luomajoki 1993a, 1993b for Scots pine and Norway spruce) can be applied inductively as long as no new knowledge provides a better explanation for the different correlations observed for the individual species.

4.5 Differences between Years

Just two single years 1968 and 1969 were compared. This comparison provided information of the usefulness of the parameters, not only of the particular years. Both years included long cool periods in the spring that decreased the usability of degree days. D.d. sums do not grow at all under +5 °C, which might be the reason that led to divergent regressions for both species (Fig. 12). Observed days, instead, gave explicit regressions (Fig. 13), which especially for silver birch were also stable.

4.6 Adaptation

The two birch species are known to prefer different soils, and silver birch, at least, avoids marshy soils. Nevertheless, this does not prevent a comparison of the adaptability of the species to climate. Unfortunately, the comparison was possible only on a degree day, not period unit basis. The latitudinal correlation for degree days was too weak in downy birch to reveal any difference with silver birch in terms of Linsser's quotient (Fig. 16). Silver birch did not adapt at all in terms of the heat sums needed for the flowering. In this respect, birches differ from the conifers studied (Luomajoki 1993a, 1993b). Good adaptation at lower latitudes and, insufficient adaptation at higher latitudes was conspicuous for conifers. No difference between the two birch species is discernible in Fig. 16.

No flowering plant is free from dependency on temperatures. Another aspect is whether temperatures alone determine when stages will be reached within a season. The most striking differences between silver birch and downy birch are visible in latitudinal regressions. The timing of microsporogenesis of both species in the preceding year was influenced by the photoperiod to the degree that the conventional latitudinal sequence of the development stages was reversed (Luomajoki 1986). The tetrad stage of microsporogenesis was reached earlier in the north than in the south of Finland. Subsequently, following winter dormancy, the contribution of the photoperiodic timing seems to weaken in downy birch but to persist in silver birch. The latitudinal regression for median of the anthesis day was very consistent for silver birch, while there was considerably more dispersion in the regression for downy birch (Fig. 10).

In beech (*Fagus sylvatica* L.) budburst is under photoperiodic control (Wareing 1953, Heide 1993a), in addition to obvious chilling needs. Long days also promote budburst in both birch species studied (Heide 1993b) even though the LD requirement was not equally rigorous as it was for beech. Kramer (1994), however, obtained the best predictions for budburst in beech with models incorporating only temperature data.

An important adaptational point is that every phase of the reproduction cycles of birches are well protected from damage by frost. The most delicate phases of microsporogenesis in birch species occur during warm months, July to August (Luomajoki 1986). Anthesis and seed maturation also occur away from unfavourable seasons. So there are no genetic pressures of selection that would cause detectable changes in flowering. On the contrary, microsporogeneses of many conifers (e.g. of *Larix*) suffer from frost damage owing to the totally different seasonality and their insufficient adaptation to the climate of Finland (Eriksson 1968, Luomajoki 1977, 1982).

4.7 Pollen Catch

Geographical correlations with pollen catch were different in the two species: the latitude and the distance to the KO-point gave the highest correlation coefficients for downy birch while the longitude and the distance from the SE-point gave the higher coefficients for silver birch. This is considered as the same pattern of behaviour in downy birch as seen in the timing-related geographic correlations (Table 3a). The variability of pollen catches did not increase in birch species latitudinally as it did in Scots pine and Norway spruce (Luomajoki 1993a, 1993b). However, the level of variability was already high in the south of Finland. This variability can be seen as another characteristic of the two birch species that does not have a latitudinal dimension.

The close relationship between pollen catch and seed set was reported by Sarvas 1962, 1968, Luomajoki 1993a, 1993b, and Sorensen and Webber 1997. The same conclusion has been reached by various methods, irrespective of whether the pollen catch system was active (e.g. Burkard volumetric spore trap, ref. Hjelmroos 1991) or passive.

Nilsson and Persson (1981) found periodicity in *Betula* catches from the Stockholm region. With a little imagination, such periodicity could be also seen in the present material on two instances. Two such cases from a total of 24(10 + 14 stands) seem to be quite incidental, however. Climatic fluctuations can, nevertheless, generate periodicity in biological production in timberline conditions if climatic fluctuation (Pohtila 1993) also is periodic.

4.8 Simultaneous Flowering

The Finnish birch species, the two studied here and *Betula nana* L., seldom cross in southern Finland but they do cross in northern Finland despite some compatibility (see Hagman 1971) problems. These problems are, however, less in the north owing to temperature-dependency of the incompatibility factors (Stern 1963). Kallio et al.(1983) thought that matching flowering times in northern Finland were mainly due to the shortening of the growing season and the reduction of the necessary thermal sums which consequently led to more synchronous flowering and hybridization.

As reported in this study, there was no congruent pattern of reducted heat sums in these two differently behaving species, not at least in terms of degree day heat sums. Heat sums at the median of anthesis for silver birch and downy birch converge in the north (Figs. 8 and 9). The scatter in days for downy birch also grows northwards (Fig. 10). As a result, the occurrence of simultaneous flowering in the two species was really far more common in northern Finland than in the south of the country.

This situation can best be explained by the considerable ecophysiological differences between silver birch and downy birch. The regressions between the latitude and degree days needed for flowering of the two species, are divergent (Fig. 9). Downy birch is more heat sum controlled than silver birch that likely implies photoperiodic control. This causes an increased scatter of the timing of anthesis in the north for downy birch. Climatic variation and altitudinal variation in the north of Finland are also far larger.

There is no detailed knowledge about the ecophysiology and timing of flowering of *Betula nana*. However, it temporally flowers sufficiently close to *B. pendula* and *B. pubescens* to enable hybridization (Kallio et al. 1983). Participation of *B. nana* to hybrids between birch species can perhaps best be explained by altitudinal factors. Considerable differences in timing could only be levelled by the parents of such a hybrid being from different altitudes.

4.9 Final Remarks

The most surprising outcome of this study was to realize how different the two species under study ecophysiologically were in spite of many similarities: e.g. the overall appearance and vast pollen and seed crops. Different responses to the temperature factor and to photoperiodism (e.g. Håbjørg 1978) probably lie at the back of the dissimilarities found.

In the present study only one glaciation, the last one of the quaternarian glaciations, was considered. Several glaciations have contributed to the evolution of many species, however. As many as 21 glaciations (Lowe and Walker 1984) with the respective interglaciations (Zagwijn 1989) have successively occurred in Northern Europe. This has put enormous stress on species (Critchfield 1984), and actually many tree species vanished altogether in Europe. The conditions in Europe and North America differed, however (Davis 1983). The stress of migrations (Zagwijn 1992) on the present species has contributed to their capacity to survive and many different survival strategies were certainly evolved. Successive changes in areal and elevational distribution of species have been reported by several authors (e.g. Hustich 1958, 1983, Sirén 1961, 1993a, 1993b, Hyvärinen 1978, 1987, Eronen 1979, 1981, Eronen and Hyvärinen 1981, Webb III 1981, Davis 1983, Karlén 1983, Lamb 1985, Kullman 1995, 1998, Lescop-Sinclair and Payette 1995, and Szeicz and Macdonald 1995). These changes are the direct outcome of the natural continuous changes of climate (Dzerdzeevskii and Sergin 1972, Harrington 1987) that has never been as static as many people seem to think.

5 Conclusions

1. Both birch species studied flowered abundantly but irregularly with no clear periodicity.
2. The accumulation pattern of pollen catches in both species resembled the cumulative normal distribution more closely than those of Scots pine and Norway spruce studied earlier. The difference was most clearly visible at cumulative percentages above 88 per cent.
3. The flowering periods of silver birch and downy birch overlap to some extent. When inspecting pollen catches, it was not always easy to separate the end of flowering period of silver birch from the beginning of flowering period of downy birch.
4. The choice of a fixed biofix of March 19 for counting parameters was fully justified.
5. The reference point used for timing, the median of anthesis, brought less variation compared to the day of highest pollen catch which preceded the median of anthesis by 0.67 day for silver birch and by 0.15 day for downy birch.
6. All parameters employed (period units, degree days, calendar days) performed at least moderately with both species. So it is probable that photoperiod and temperatures both have an influence on the timing of anthesis of both species.
7. The practicality of the three parameters employed for timing could most accurately be compared when converted on a day basis. Period units were the most accurate for silver birch in 60 per cent of the cases and for downy birch in 78.6 per cent of the cases. The number of days from March 19 was the least variable parameter for silver birch in 25 per cent of the cases. For downy birch, heat sums always served better than the days parameter.
8. Differences between years were manifested in the different usability of methods in successive years. Results from period units and the days parameter were consistent. The degree days method was vulnerable to long cool periods under +5°C which caused variable performance in different years.
9. Period units were found to be the most generally accurate timing parameter. Period units correlated in downy birch highly significantly with latitude, with distances from the SE- and to KO-points, as well as with annual heat sums of the previous year and those of two years earlier. Period units did not correlate with any of these variables mentioned for silver birch.
   The length of anthesis in days in silver birch correlated highly significantly with latitude, the distance to the KO-point and with annual heat sums of the previous year and those of two years earlier, variables for which the respective correlations for downy birch were not significant.
10. Too many factors contribute to latitudinal correlations. So partial correlations with the effects of the latitude removed were employed. Observed days to anthesis 50 pcc had a significant partial correlation in silver birch with the distance from the SE-point while a highly significant partial correlation was found with the distance to the KO-point for downy birch. These correlations might be attributed to the fact that downy birch followed the retreating glacier to Kolari as a pioneer tree species and that silver birch invaded Finland later from southeast.
11. Silver birch has not adapted at all latitudinally in terms of heat sums, while the adaptation of downy birch was highly significant in period units but not in degree days, which nevertheless correlated at an almost significant ($P < 0.05$) level. This indicates that the latitudinal change in d.d. heat sums measured did not considerably affect Linsser's (1867) quotients nor the curves derived from them (Fig. 16). The latitudinal variation of annual heat sums of the localities in question were considered to have shaped the curves.
12. The measured pollen catches correlated with anther residues and seed crop at a highly significant level. Pollen catches of downy birch had a significant latitudinal correlation while silver birch had a significant longitudinal correlation. Silver birch also had a significant partial correlation with longitude and with the distance from the SE-point.

Pollen catches of both species had highly significant correlations and partial correlations with annual heat sums of the previous year.

13. The variability of pollen catches did not have any significant correlations with latitude or longitude in either species. In this behaviour in birches differs from the conifers studied.
14. The preconditions for the generation of hybrids between birch species in northern Finland were favoured by frequent simultaneous flowering. Simultaneous flowering in the north was due to different timing systems related to the ecophysiological differences between the species. A more variable climate and the higher altitudinal variations also have contributed to hybrid generation.
15. Comparison between birches and the two conifers shows that flowering in Scots pine had the strongest latitudinal timing correlations with heat sums, followed by downy birch and then Norway spruce. The timing of flowering in silver birch did not correlate with heat sums. The tendency towards a fixed flowering day locally indicated that photoperiodic regulation was strongest in silver birch.
16. The reproduction cycles of both birch species are relatively well protected from damage by frost. It is difficult to see any selection pressures to change this pattern. Nor are birch seeds likely to be consumed by insects owing to rapid disruption of the female catkins.

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