ADAPTATION OF MICROSPOROGENESIS OF EXOTIC CONIFERS IN FINLAND

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ABSTRACT

The phenology of microsporogenesis was studied in 15 exotic conifers in Finland. Eleven native broadleaf and 4 native coniferous species were used as comparison species. Meiotic disorders were studied in 7 exotics and 7 native species. The timing of anthesis was measured using both degree days (>5° C) and period heat sum units. Period units were clearly a better measure of the timing of anthesis in early spring, when degree day accumulation was minimal, although later in the season, degree days could also be used. No regular failure of male meiosis was found in the native species studied. Among the exotics, failure of male meiosis was frequent in *Larix gmelinii* (Rupr.) Rup. and also occurred in some years in *Larix sibirica* Ledeb. Of the 15 species studied, *Abies sibirica* Ledeb., *Larix sibirica* Ledeb., *Picea mariana* (Mill.) B. S. P., *Pinus cembra* L. and *Pinus peuce* Griseb. were the best adapted to the Finnish climate in terms of health and offspring production.

Key words: adaptation, microsporogenesis, exotic conifers

INTRODUCTION

About 60 exotic conifers grow in Finland in addition to numerous species that have been introduced but which have failed completely. The adaptation of species varies considerably, but only about 20 species can be regarded as "hardy" (LÄHDE *et al.* 1984). Not all of these hardy species produce offspring in Finland; LÄHDE *et al.* (1984) found 13 species capable of at least "fair regeneration". These exotic conifers enrich Finnish silvicultural diversity considerably, since only four native species grow in Finland and of these only two species are economically significant.

Fifteen exotic conifers were studied in terms of timing of anthesis, and of these, 7 species were also studied for occurrence of meiotic disorders at male meiosis. The stands studied were limited to 3 locations in southern Finland. At these locations (Figure 1), Finnish native species were also studied for a comparison. Eleven broadleaf and four coniferous native species were studied for timing of anthesis and, of these, four broadleaf and three coniferous species for occurrence of meiotic disorders.

The aims of this study were to compare the phenology of male meiosis between species, to observe possible failures of microsporgenesis that affect regeneration, and to more precisely define the frost sensitivity and crossability of both the exotic and native species reported in records made in the arboreta. These findings were compared with published silvicultural observations on the regeneration of these species.

MATERIALS AND METHODS

Ten to 30 male buds were excised daily either from each tree or from a population of 10 trees, 1–6 times a day, depending on air temperatures (LUOMAJOKI 1977, 1984, 1995). Each sample was handled separately. The buds were bisected longitudinally (one half being discarded), and each half bud was put in fresh fixative containing 9/11 (v/v) glacial acetic acid/absolute ethanol. A pooled squashed sample from 10–30 fixed bud halves was subsequently prepared in acetic (or formic) orcein on 4–6 slides. From 400–600 pollen mother cells from each pooled squashed sample were inspected under the microscope. The samples were checked for meiotic disorders.

Mature, thinned stands several hectares in area were classified as normal stands for pollination (SARVAS 1962). Antheses were measured in each stand at tree-top height with 1–3 self-recording pollen samplers (model SARVAS–VILSKA 1963, see SARVAS 1968). The mean of daily pollen catches was used when more than one sampler was used. A Fuess (Berlin Steglitz) thermograph was also placed at tree-top height in each stand.

The pollen catch was counted from the recording bands with the aid of a microscope. The results were presented in terms of daily catches of the recorders, catch averages, cumulative sums and cumulative percentages of the pollen catch (SARVAS 1972). The cumulative percentages were plotted with the Systat/Sygraph computer program (WILKINSON 1990) in which

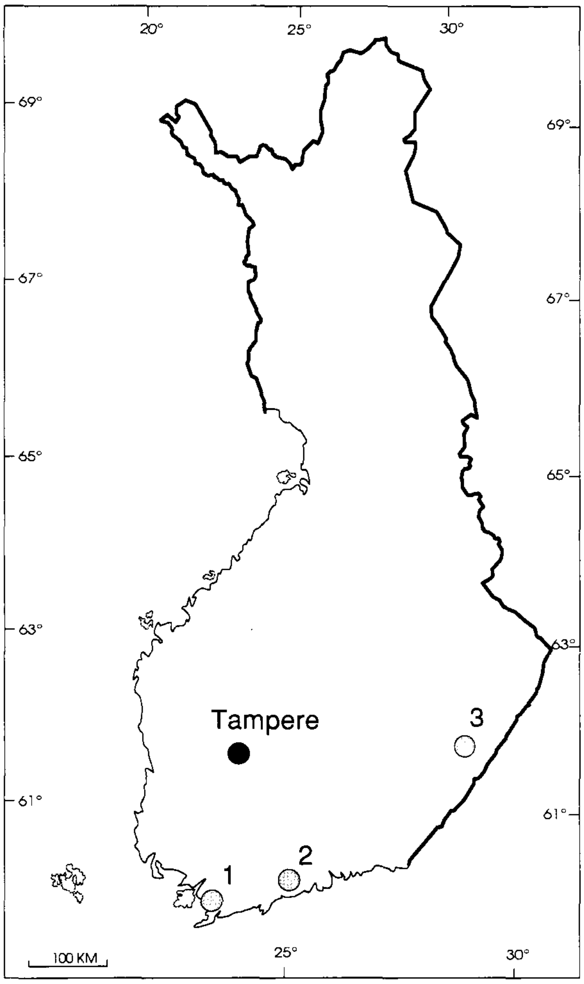

Figure 1 Location of stands studied: **1**. Bromarv, **2**. Tuusula, **3**. Punkaharju. For reference, Tampere, the IUFRO XX World Congress site, is also shown.

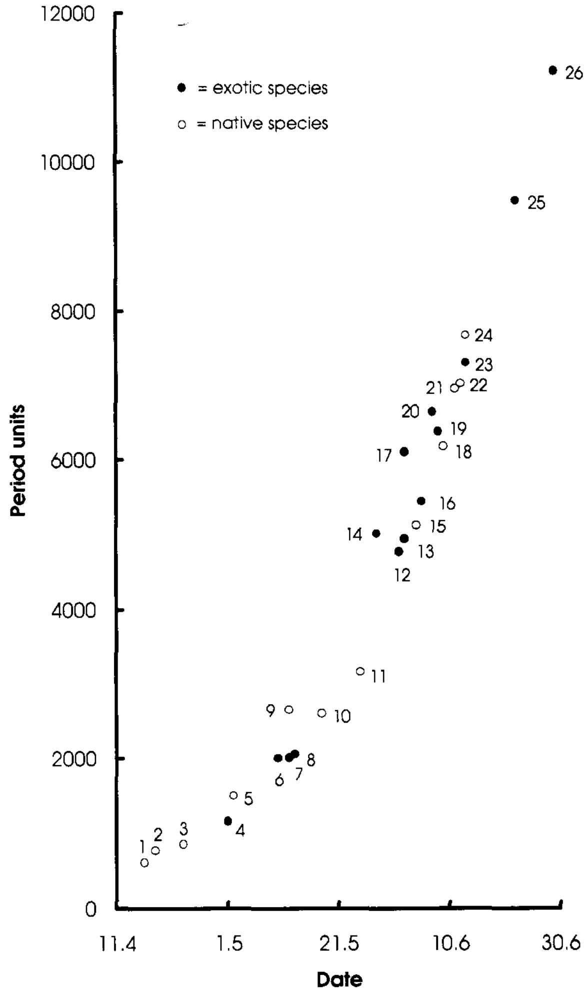

Figure 2 Period unit heat sum average and corresponding average date at 50% completion of anthesis for the stands of each species shown: 1 – *Alnus incana* (∘), 2 – *Corylus* (∘), 3 – *A. glutinosa* (∘), 4 – *Thuja* (•), 5 – *Populus* (∘), 6 – *Larix gmelini* (•), 7 – *L. sibirica* (•), 8 – *L. decidua* (•), 9 – *Taxus* (∘), 10 – *Betula pendula* (∘), 11 – *B. pubescens* (∘), 12 – *Abies balsamea* (•), 13 – *A. veitchii* (•), 14 – *Picea glauca* (•), 15 – *P. abies* (∘), 16 – *A. sibirica* (•), 17 – *P. omorika* (•), 18 – *Quercus* (∘), 19 – *P. mariana* (•), 20 – *Pinus banksiana* (•), 21 – *Juniperus* (∘), 22 – *P. sylvestris* (∘), 23 – *P. contorta* (•), 24 – *P. mugo* (∘), 25 – *P. cembra* (•), 26 – *P. peuce* (•)

the ordinate scale was a Gauss integral with a linear abscissa scale. The abscissa showed the cumulative temperature sum at the end of each day (corresponding to the measurement of the cumulative pollen catch). Because of the effects of secondary pollen on anthesis data (LUOMAJOKI 1993), exclusion of points outside the central zone from –2 to +1.2 was necessary to position the regression line. The point of 50 per cent completion of each stage was used as a criterion for attaining a given stage. The 50 per cent point is unbiased by standard deviation. Only timing, not the viability of pollen, was studied. One series of observations of anthesis in Norway spruce was rejected because of a minimal pollen catch (Bromarv I in 1968) to avoid bias by secondary pollen from neighbouring stands.

Two types of heat sum were used, the conventional degree day heat sum (>5 °C) and the curvilinear period unit system of SARVAS (1972). The latter system was actually used for timing of anthesis and daily degree day values were taken only as a popular reference. The names of the species studied are according to HÄMET-AHTI *et al.* (1992).

RESULTS

The species are arranged in Table 2 in phenological order at 50 per cent completion of anthesis (see also Figures 2 and 3). The stands of each species are listed from south to north. The three parameters (period units, degree days >5 °C and calendar days, all three dating

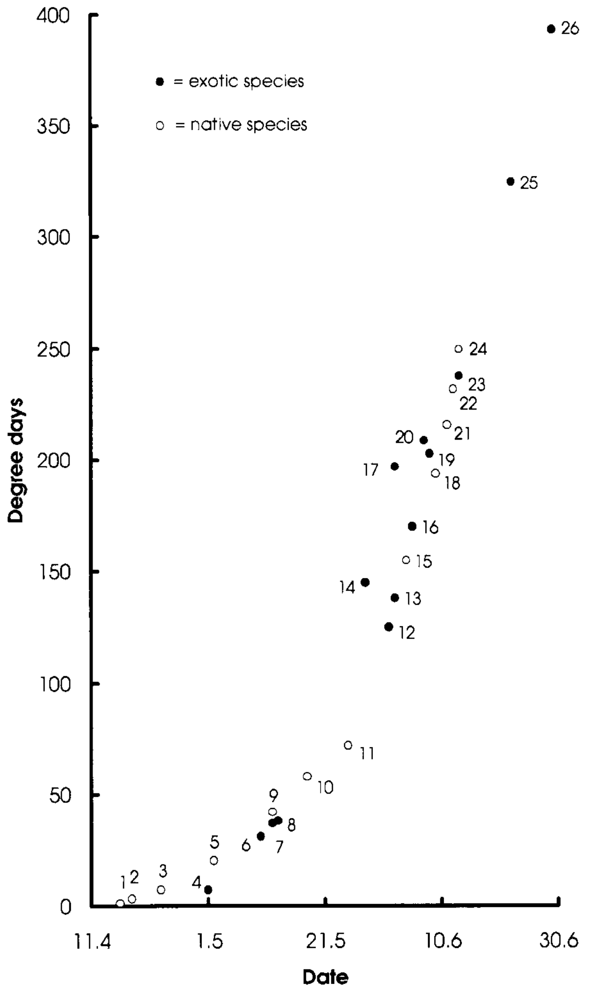

Figure 3 Degree day heat sum average and corresponding average date at 50% completion of anthesis for the stands of each species shown (Tree species as in Figure 2)

from March 19) did not always agree precisely in terms of phenological order. Degree days varied more than period units and very low figures were actually involved for the earliest flowers. Later in the season the usefulness of degree days improved.

Simultaneous flowering of related species can lead to crosses between species. Flowering of *Larix* and *Abies* species did overlap within these genera, making conditions favorable for crossing where the stands of different species were close to each other. Crosses within the genus *Larix* and the genus *Abies* were actually common. Although there were hybrid seedlings within the stands, it was not possible to explain definitively why *Larix gmelinii* (stand 267) produced seeds at Punkaharju in years 1970 and 1971 (KOSKI & TALLQVIST 1978) when male meiosis of this continental species failed owing to premature onset of meiosis in November – December of the previous year. Stands of both *Larix decidua* and *L. sibirica* are nearby.

Comparisons of the exotic species with the native species showed that there were no regular failures of male meiosis in the native species. However, the continental *Larix* species often suffered such failures. In addition to *Larix gmelinii, L. sibirica* had suffered in some years from insufficient adaptability to the Finnish climate. Of the fifteen species studied (Table 2) five (*Abies sibirica*, *Larix sibirica*, *Picea mariana*, *Pinus cembra* and *P. peuce*) were found most adapted in terms of health and offspring production. The seed germination percentage is given in general terms for some species in Table 2. Offspring production is listed according to LÄHDE *et al.* 1984 with one exception, *Pinus cembra*, for which new knowledge was available. Remarks in Table 2 indicate problems at meiosis and seed germination. Frost sensitivity notes and observations of fungal attacks are listed in Table 1.

DISCUSSION

The progress of anthesis is strongly temperature-dependent. The period unit heat sums given in Table 2 are better suited to a comparison between species than to one between dates. Anthesis progresses more slowly in early spring than during the warmer summer period. Cold spells also prolong anthesis. However, the size of the pollen crop also influences the duration of the pollen season; a large crop has a longer period of pollen shedding and a small crop has a shorter period. Large crops and close proximity of flowering periods between closely related species usually increase the possibility of species crossing.

Larix hybrids were reported by LÄHDE *et al.* 1984, NAPOLA 1993, NIKKANEN 1993 and RUOTSALAINEN 1993. The very productive and intentionally-produced hybrid *Larix decidua* × *L. sibirica* (LÄHDE *et al.* 1984) occurs within the stands studied. *Abies* hybrids are known to occur at localities where *Abies* species are grown together or in adjacent stands. They have been found, for example, at Solböle, Bromarv and at Mustila, Elimäki. Mustila is a private arboretum located between the Tuusula and Punkaharju experimental areas.

Although many hybrid combinations within genera *Abies* and *Larix* may occur, only a few possibilities for interspecific crossing exist within the exotic genera studied. The cross between *Picea omorika* and *P. mariana* is possible (MIKKOLA 1970), but it was not observed in the experimental areas. The cross between *Pinus banksiana* and *P. contorta* is also known to exist (RUSSELL & HONKALA 1990).

Native species of a region usually do not cross, and no interspecific crossing is possible between these four native coniferous species studied. Among the broadleaf

Table 1 Stand characteristics and years of study

Species	Stand	Latitude	Longitude	Elevation	Age, years in 1970	Years of study	Origin and remarks
Abies balsamea (L.) Miller	Tuusula 275	60°20'	24°59'	45	44	1965–69	Canada, New Brunswick. Some windthrow in 1981,1989. Damage by various fungi.
Abies sibirica Ledeb.	Bromarv 244 Punkaharju 45	60°02' 61°48'	23°03' 29°19'	13 102	41 79	1965–69 1964–74	Russia, Valamo island. Origin unknown. Windthrow in 1985. Largely clear cut in 1993.
Abies veitchii Lindley	Bromarv 218	60°03'	23°03'	24	42	1964–65, 67–69	Japan, Hokkaido.
Alnus glutinosa (L.) Gaertner	Tuusula 3	60°22'	25°02'	50	100	1964–67	Local. Selective thinning in 1980.
Alnus incana (L.) Moench	Tuusula XLI Punkaharju LXII	60°20' 61°48'	24°58' 29°19'	50 81	34 44	1963–69 1967–74	Local. Light thinning in 1967. Local
Betula pendula Roth	Bromarv VI Punkaharju LIV Punkaharju LXIII	60°02' 61°49' 61°48'	23°03' 29°18' 29°19'	5 90 88	40 59 32	1967–73 1964–73 1964–72	Local Local Curly birch, var. ***carelica*** (Mercklin) Hämet–Ahti. Origin Aulanko, Finland.
Betula pubescens Ehrh.	Tuusula 12 Punkaharju XIV Punkaharju L Punkaharju LX	60°22' 61°48' 61°48' 61°48'	25°02' 29°20' 29°20' 29°20'	45 85 90 83	52 43 70 38	1964–73 1964–65, 67–73 1963–71 1964–73	Local. Thinned in 1970. Local Local Local
Corylus avellana L.	Bromarv V Punkaharju I	60°02' 61°48'	23°02' 29°19'	7 87	Variable Unknown	1965, 67–69, 73 1973–74	Local Origin Finland, Bromarv, Framnäs.
Juniperus communis L.	Punkaharju D 38	61°48'	29°19'	91	44	1973–74	Origin Finland, Leppäkoski. The stand died naturally in 1980–84.
Larix decidua Miller	Punkaharju 80	61°49'	29°19'	93	94	1963, 67–68, 70–74	Origin unknown.
Larix gmelinii (Rupr.) Rupr.	Punkaharju 267	61°49'	29°20'	81	42	1973	Origin Russia, Sakhalin. Thinned in 1952 and 1957.
Larix sibirica Ledeb.	Punkaharju, Montell Punkaharju 49	61°48' 61°49'	29°19' 29°19'	105 106	97 79	1968–73 1963, 67–74	Origin unknown (Russia). Treetop metering. Origin unknown (Russia).
Picea abies (L.) Karsten	Bromarv I Tuusula XXX Tuusula XXXIV Punkaharju LII	60°02' 60°21' 60°22' 61°49'	23°05' 25°02' 24°59' 29°20'	27 53 50 92	126 91 67 96	1963–74 1964–67, 69–73 1967–73 1964–74	Local. Clear cut in 1976. Local Local. 400 kg urea/ha given in winter 1967–68. Origin Finland, Lammi. Clear cut in 1975–76.

Table 1 (continued)

Species	Stand	Latitude	Longitude	Elevation	Age, years in 1970	Years of study	Origin and remarks
Picea glauca (Moench) Voss	Punkaharju 221	61°48'	29°20'	87	42	1973	Origin Canada, Alberta, Olds. Insect and storm damage. Thinned in 1950, 1952, 1958 and in 1963. Sanitary cutting in 1995.
Picea mariana (Miller) Britton, Sterns & Poggenb.	Punkaharju 217	61°48'	29°20'	87	42	1969, 72–73	Origin Canada, New Brunswick. Sanitary thinning in 1994.
Picea omorika (Pančić) Purkyně	Punkaharju 358	61°48'	29°20'	83	38	1973	Origin unknown (Serbia). Thinned in 1969.
Pinus banksiana Lamb.	Bromarv 106	60°02'	23°03'	35	43	1973	Origin Canada, Saskatchewan, Prince Albert. Thinned in 1950. Snow damage in 1952-53.
	Bromarv 139	60°02'	23°03'	42	42	1973	As above, but thinned also in 1970.
Pinus cembra L.	Punkaharju 100	61°48'	29°20'	88	46	1963–74	Origin unknown.
	Punkaharju 248	61°48'	29°20'	83	43	1964, 67–71	Unknown. 400 kg urea/ha given in 1967-68
Pinus contorta Douglas ex Loudon var. *latifolia*	Punkaharju 99	61°48'	29°20'	89	45	1965–71 , 73	Canada, British Columbia, Long Lake
Pinus mugo Turra	Punkaharju 235	61°48'	29°19'	101	41	1973–74	Origin Switzerland, Engadin. Thinned in 1952 and 1959.
Pinus peuce Griseb.	Bromarv 40	60°02'	23°03'	40	46	1965–73	Origin Bulgaria, Rila Mts.
	Bromarv, Bergö	60°02'	23°01'	5	Unknown	1967, 70–73	Single tree, origin unknown.
	Tuusula 111	60°22'	24°59'	53	46	1965–69	Bulgaria, Rila Mts. Clear cut in 1991.
	Punkaharju 278	61°48'	29°20'	79	39	1968–71	Bulgaria, Pirin Mts.
	Punkaharju 306	61°48'	29°19'	88	40	1964–74	Bulgaria, Pirin Mts. 400 kg urea/ha given in 1967–68.
Pinus sylvestris L.	Bromarv 559	60°00'	23°05'	32	110	1964	Local
	Bromarv II	60°02'	23°03'	41	84	1964–69	Local
	Bromarv III	60°03'	23°03'	35	63	1965–73	Local
	Tuusula XXXII	60°21'	25°01'	70	144	1964–69	Local
	Punkaharju I	61°48'	29°19'	91	147	1963–74	Local
	Punkaharju XLV	61°48'	29°19'	106	119	1964–74	Local
Populus tremula L.	Tuusula XXXIII	60°21'	25°01'	70	144	1964–66, 68–69	Local
	Punkaharju, Likolahti	61°48'	29°19'	80	ca.40	1974	Local
Quercus robur L.	Punkaharju 90	61°48'	29°19'	96	45	1963–74	Origin Finland, Bromarv, Framnäs. Frost damage in 1986–87.
Taxus baccata L.	Bromarv 310	60°03'	23°03'	9	39	1965–68	Origin Finland, Åland, Jungfruskär. Bad frost damage in 1984–85.
Thuja occidentalis L.	Punkaharju D 19	61°48'	29°19'	97	45	1966–69, 71–74	Origin Canada, Ontario.

Table 2 Species in phenological order. Reproduction and vitality

Species	Stand	Status	Years	Anthesis 50 per cent completion (stand average)			Seed producion /m² (2)	Germination percentage (3)	Offspring production (4)	Remarks
				In period units	In degree days >5 °C	Date				
Alnus incana	Tuusula XLI	L	7	765	4	April 20	988			
	Punkharju LXII	L	8	615	1	April 16	4099			
Corylus avellana	Bromarv V	L	5	772	3	April 18	24			
	Punkharju I	M	2	989	4	April 26	NM			
Alnus glutinosa	Tuusula 3	L	4	853	7	April 23	2235			
Thuja occidentalis	Punkharju D 19	E	8	1158	7	May 1	888	High	Poor	
Populus tremula	Tuusula XXXIII	L	5	1496	20	May 2	NM			
	Punkharju, Likolahti	L	1	1556	8	May 14	NM			
Larix gmelinii	Punkharju 267	E	1	2007	31	May 10	26		Poor to fair	Destruction of PMC common owing to premature onset of meiosis. Hybrid offspring.
Larix sibirica	Punkharju, Montell	E	6	2083	40	May 12	NM		Fair	Premature meiosis occurs sometimes.
	Punkharju 49	E	9	2014	37	May 12	465			
Larix decidua	Punkharju 80	E	8	2062	38	May 13	547		Fair	
Taxus baccata	Bromarv 310	M	4	2659	42	May 12	NM			No pollen-years common
Betula pendula	Bromarv VI	L	7	2652	49	May 16	NM			
	Punkharju LIV	L	10	2608	58	May 18	45409			
	Punkharju LXIII	L	9	2577	54	May 19	88071			
Betula pubescens	Tuusula 12	L	10	3300	73	May 21	38252			
	Punkharju XIV	L	9	3214	73	May 25	103821			
	Punkharju L	L	9	3227	79	May 24	84148			
	Punkharju LX	L	10	3167	72	May 25	65887			
Abies balsamea	Tuusula 275	E	5	4776	125	June 1	229	Low	Fair	
Abies veitchii	Bromarv 218	E	5	4951	138	June 2	472	Low	Abundant	
Picea glauca	Punkharju 221	E	1	5021	145	May 28	2541	High	Poor	

Table 2 (continued)

Species	Stand	Status	Years	Anthesis 50 per cent completion (stand average)			Seed production /m² (2)	Germination percentage (3)	Offspring production (4)	Remarks
				In period units	In degree days >5 °C	Date				
Picea abies	Bromarv I	L	12	4735	134	June 3	346			
	Tuusula XXX	L	9	4913	141	June 1	534			
	Tuusula XXXIV	L	7	5095	153	June 1	627			
	Punkharju LII	M	11	5133	155	June 4	665			
Abies sibirica	Bromarv 244	E	5	4706	124	June 3	2153	Moderate		
	Punkaharju 45	E	11	5455	170	June 5	1581	Moderate		
Picea omorika	Punkharju 358	E	1	6113	197	June 2	290	High		
Quercus robur	Punkharju 90	M	12	6186	194	June 9	177			
Picea mariana	Punkharju 217	E	3	6383	203	June 8	1345	High		
Pinus banksiana	Bromarv 106	E	1	6469	198	June 6	NM		None	
	Bromarv 139	E	1	6642	209	June 7	NM		None	
Juniperus communis	Punkharju D38	M	2	6957	216	June 11	NM			
Pinus sylvestris	Bromarv 559	L	1	7167	236	June 14	133			
	Bromarv II	L	6	6854	216	June 13	76			
	Bromarv III	L	9	6848	214	June 11	120			
	Tuusula XXXII	L	6	7012	224	June 12	118			
	Punkharju I	L	12	7027	232	June 12	96			
	Punkharju XLV	L	11	7154	236	June 13	127			
Pinus contorta	Punkharju 99	E	8	7307	238	June 13	17		Poor	Serotinous cones.
Pinus mugo	Punkharju 235	E	2	7677	250	June 13	266		Poor	
Pinus cembra	Punkharju 100	E	12	9491	325	June 22	122	Low to moderate	None under the stand	Slow germination under several years. Dispersal by birds (5).
	Punkharju 248	E	5	9269	315	June 22	NM			
Pinus peuce	Bromarv 40	E	9	10728	367	June 26	297		Abundant	
	Bromarv, Bergö (1)	E	5	10483	360	June 26	NM			
	Tuusula 111	E	5	11553	389	June 28	36	Moderate	Abundant	
	Punkharju 278	E	4	11591	409	June 30	NM	Low		
	Punkharju 306	E	11	11231	394	June 29	241	Low	Abundant	

(1) A single tree on Bergö island; (2) According to KOSKI & TALLQVIST (1978); (3) General lines according to KONTINEN (1994), (low <10, moderate 10–50%, high > 50%); (4) According to LÄHDE *et al.* (1984); (5) See LANNER & NIKKANEN (1990); Status: E – exotic, L – local species, M – moved Finnish origin; NM – not measured; PMC – pollen mother cell

species, the hybrids *Alnus incana* × *A. glutinosa, Betula pendula* × *B. pubescens, B. pendula* × *B. nana* and *B. pubescens* × *B. nana* are sometimes found, although there are known interspecific incompatibility barriers in *Betula* (HAGMAN 1971). In general, overlapping flowering periods of sympatric species of the same genus do not seem to be the rule. Such coincident periods are more common when species have been juxtaposed by moving one or both from the natural range.

Pinus cembra was reported by LÄHDE *et al.* (1984) not to produce seedlings within stands of the species. Although this appears to be the case in the strict sense, LANNER & NIKKANEN (1990) found *P. cembra* seedlings growing outside the stands themselves. The reported explanation was the activity of the bird species *Nucifraga caryocatactes* L., which stores Swiss stone pine seeds in the litter.

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ERRATA

In the paper of **Luomajoki, A.: Adaptation of microsporogenesis of exotic conifers in Finland** ***Forest Genetics*** **3(3):153–160, 1997**, the following errors appeared:

In tables 2 a 3 instead of "Punkharju" there should be "Punkaharju". This error appeared 27 times in both tables.

Since *Pinus mugo* is an exotic tree species in Finland there should be in the caption of Figure 2 full dot instead of empty one.

Thus the correct Figure caption should be:

Figure 2 Period unit heat sum average and corresponding average date at 50% completion of anthesis for the stands of each species shown: 1 – *Alnus incana* (○), 2 – *Corylus* (○), 3 – *A. glutinosa* (○), 4 – *Thuja* (•), 5 – *Populus* (○), 6 – *Larix gmelini* (•), 7 – *L. sibirica* (•), 8 – *L. decidua* (•), 9 – *Taxus* (○), 10 – *Betula pendula* (○), 11 – *B. pubescens* (○), 12 – *Abies balsamea* (•), 13 – *A. veitchii* (•), 14 – *Picea glauca* (•), 15 – *P. abies* (○), 16 – *A. sibirica* (•), 17 – *P. omorika* (•), 18 – *Quercus* (○), 19 – *P. mariana* (•), 20 – *Pinus banksiana* (•), 21 – *Juniperus* (○), 22 – *P. sylvestris* (○), 23 – *P. contorta* (•), 24 – *P. mugo* (•), 25 – *P. cembra* (•), 26 – *P. peuce* (•)

In the paper of **Toda, Y.: Karyomorphological studies of the** ***Taxodiacae. Forest Genetics*** **3(3):141–147, 1996**, the pages in the header should be corrected as follows:

FOREST GENETICS 3(3):141–146, 1996.

In the paper of **Vornam B.: DNA amplification from single pollen grains of beech (*Fagus sylvatica* L.).** ***Forest Genetics*** **3(4):213–216 , 1996** the following errors appeared:

p. 213, left column, line 7 from bottom	instead of "(STARKE & (MÜLLER-STARCK)" should be "MÜLLER-(STARCK)"
p. 214, left column, line 14 from top	instead of "3 5l" should be "3 µl"
p. 214, left column, line 13 from bottom	instead of "to" should be "two"
p. 214, left column, line 7 from bottom	instead of "50 ml" should be "50 µl"
p. 214, left column, line 4 from bottom	instead of "dNTP4s"should be "dNTP's
p. 214, right column, line 15 from top	instead of "10 5l" should be "10 µl"
p. 215, left column, line 3 from top	instead of "rom" should be "from"

We apologize for this inconvenience to the authors of the above mentioned papers and readers of Forest Genetics.