Reproductive Phenology in a Norway Spruce Seed Orchard

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Reproductive phenology was studied in a Norway spruce seed orchard, located in southern Finland (62°13'N, 25°24'E), consisting of 67 clones from northern Finland (64°–67°N). Timing of flowering was determined on the basis of data recorded by a pollen catch meter during 1984–1995, and visual observations made on grafts in 1989, 1992, 1993 and 1995. The genetic and environmental factors affecting female and male phenology, and reproductive synchronisation were studied.

The between-year variation in the timing of flowering was more than three weeks. However, when it was defined on the basis of the effective temperature sum, the variation was smaller. No phenological reproductive isolation was found between the seed orchard and surrounding natural forests. The duration of the receptive period of the seed orchard varied from 5 to 8 days, and anthesis determined on the basis of airborne pollen from 5 to 10 days. The receptive period started about one day earlier than anthesis, except in one abnormally warm flowering period when female and male flowering started simultaneously. In general, the flowering periods of the different clones overlapped. The clonal differences in the phenology of receptivity were in most cases statistically significant, but in pollen shedding they were not. The broad-sense heritability estimates were higher for female than for male phenology. Environmental factors, conversely, had a stronger effect on male phenology. A wide graft spacing and a graft position that favoured solar radiation on the lower parts of the crown promoted early pollen shedding and, subsequently, better reproductive synchronisation between female and male flowering.

Keywords *Picea abies*, flowering, receptive period, pollination, reproductive synchronisation
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1 Introduction

Reproductive synchronisation, together with a balanced production of female and male strobili, random mating, minimal selfing and isolation from non-orchard pollen sources, are the basic biological assumptions when determining the genetic efficiency of wind pollinated seed orchards (Blush et al. 1993). However, many of these requirements are difficult to fulfil. In order to determine the degree of flowering synchrony of seed orchard clones, the reproductive phenology of a seed orchard has to be characterised. Data on the timing and duration of female receptivity and pollen release are needed for this purpose. Several different techniques have been developed for collecting and presenting data on reproductive phenology, the method applied depending on the species, conditions and accuracy requirements (Jonsson et al. 1976, Wheeler 1983, El-Kassaby et al. 1984, Griffin 1984, Erickson and Adams 1989, El-Kassaby and Reynolds 1990). In addition to knowing the variation in flowering phenology in the seed orchard, it is also important to be aware of the timing of pollen shedding outside the seed orchard compared to pollen shedding and female receptivity inside the orchard.

Numerous studies have shown that non-synchronous flowering is a serious problem in seed orchards of many coniferous species in the temperate region: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (El-Kassaby et al. 1984, 1988, El-Kassaby and Askew 1991), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (El-Kassaby and Reynolds 1990), radiata pine (*Pinus radiata* D. Don) (Griffin 1984), loblolly pine (*Pinus taeda* L.) (Askew 1988, Askew and Blush 1990), and black pine (*Pinus nigra* Arnold) (Matziris 1994). In a colder climate, more simultaneous flowering has been reported in seed orchards of Scots pine (*Pinus sylvestris* L.) (Jonsson et al. 1976, Pulkkinen 1994, Burczyk and Chalupka 1997) and black spruce (*Picea mariana* (Mill) B.S.P.) (O'Reilly et al. 1982), but no information is available about Norway spruce (*Picea abies* (L.) Karst.) seed orchards. The only studies on the reproductive phenology of Norway spruce are the work carried out on flowering and the seed crop in natural stands by Sarvas (1968), the flowering study in a four-year-old clone trial by Eriksson et al. (1973), and the study on the climatic adaptation of Norway spruce in Finland by Luomajoki (1993).

The seed orchards in Finland have been established using clones originating from geographically and climatically limited areas (Sarvas 1970, Koski 1980, Nikkanen et al. 1999). This was done in order to ensure the adaptability of the seed orchard material to its utilisation area, which has usually been planned to be the same as that of the clone origins. Simultaneous flowering of the seed orchard was also aimed at by limiting the clone origin. Another measure directed at the phenology of the seed orchards was to locate the seed orchards of northern origin (like the studied one) in the southern parts of the country. In addition to enhanced flowering and better seed ripening, this was done in order to achieve phenological isolation between the seed orchard clones and surrounding forests (Sarvas 1970). The hypothesis was that the temperature sum required for the onset of flowering would be smaller in trees adapted to northern conditions than in those adapted to more southern conditions (Sarvas 1962, 1968, 1970). No phenological isolation has been found in Scots pine (Pakkanen and Pulkkinen 1991, Pulkkinen 1994), and no results from this or from any other measures directed at reproductive phenology in seed orchards have been reported for Norway spruce.

The aim of this study was to determine the phenological variation in female and male flowering in a Norway spruce seed orchard, and to describe the timing of the shedding of pollen. An additional aim was to determine the extent to which genetic and environmental factors affect flowering phenology, and to discuss the possible consequences of variation in reproductive phenology for the seed crop produced in the seed orchard.

2 Material and Methods

2.1 The Seed Orchard

The variation in flowering phenology was studied in Norway spruce seed orchard no. 170, Heinämäki, established in 1968 at Korpilahti,

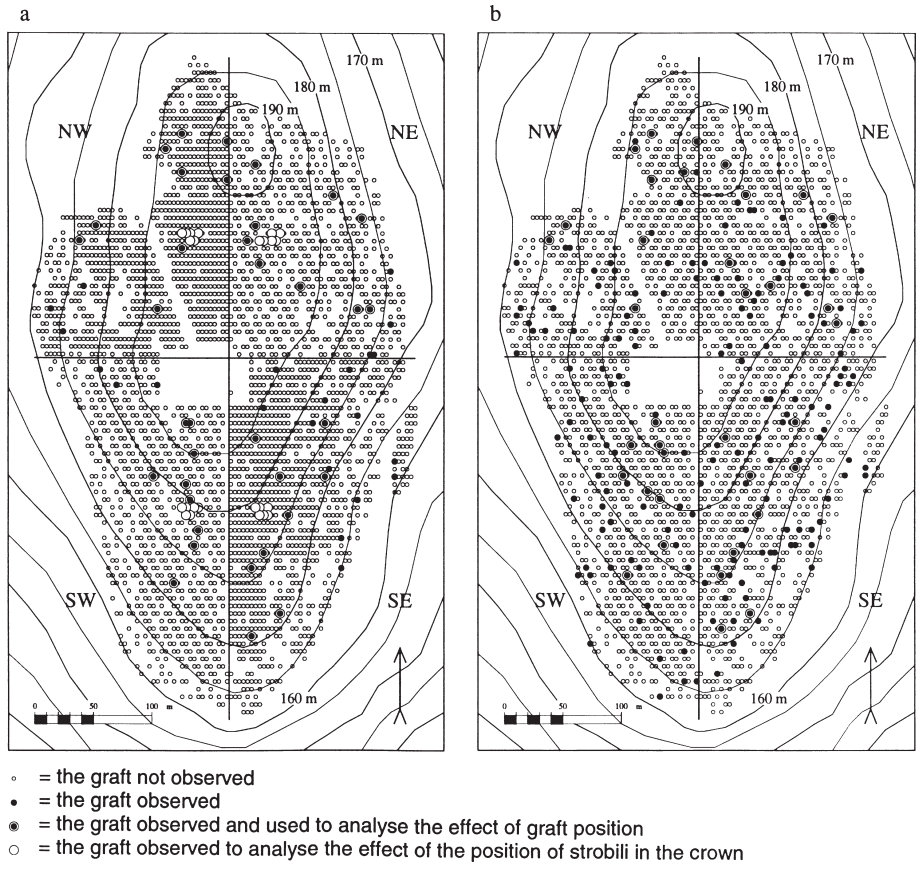

Fig. 1. The Heinämäki seed orchard before (a) and after (b) thinning in 1994. Grafts on which the phenological stage of the female and male flowers were observed are marked.

southern Finland (62°13'N, 25°24'E). The seed orchard consists of 67 clones originating from latitudes 64°–67°N in northern Finland (for more detailed information see Nikkanen and Ruotsalainen 2000).

The seed orchard is 13.2 ha in area, and is located on a hill (160–190 m asl) sloping gently to the south and steeply to the east and west (Fig. 1). The grafts were planted in the orchard using a clonal-row design with ramets of each clone in two or more rows. The spacing of the grafts was 3.5×6.5 m, the ramets of the same clone being located 6.5 m from each other. In 1987 half of the orchard was thinned systematically by removing every third graft, and in 1994 the other half of the orchard thinned in the same way. The different sections of the seed orchard before the thinning in 1994 were: north-western unthinned section (NW), north-eastern thinned section (NE), south-eastern unthinned section (SE), and south-western thinned section (SW) (Fig. 1).

The position of the grafts were determined in 1993 by means of a tachymeter (Nikon A20) and a field computer (Geonic 1000). The equipment was used to create a three-dimensional coordinate system covering the studied area (Lähde et. al. 1992).

The spacing of the grafts was calculated by counting the number of grafts within a radius of 12.62 m (i.e. 500 m^2) around each graft. In addition, a slope index for the position of each graft was calculated for a circle of the same size. The slope index was calculated from the direction and gradient of the slope using formula (1).

$$I = 1 + \frac{\alpha - 5}{15} \times \frac{s - 90}{90} \quad (1)$$

where α is the slope angle (if $\alpha < 5°$ then $\alpha = 5°$ and if $\alpha > 20°$ then $\alpha = 20°$), s is the slope direction (deviation from north, degrees). The slope index has values ranging from 0 (north with 20°) to 2 (south with 20°). The spacing and the slope index were used as environmental factors to explain the differences in flowering phenology.

The measurements and results concerning the abundance of flowering and the growth characteristics of the grafts, e.g. height, diameter, and crown width, are given in Nikkanen and Ruotsalainen (2000).

The weather data for the study period were obtained from the Jyväskylä weather station (located 25 km north-east from the seed orchard) of the Finnish Meteorological Institute, where the temperature conditions were very close to those in the seed orchard. The weather data consisted of daily mean temperatures (including effective temperature sum, d.d., > +5°C) from 1984 to 1995, as well as cloudiness and precipitation during the flowering period.

2.2 Observations of Flowering Phenology

The timing and amount of airborne pollen were studied by means of a recording pollen catch meter (Sarvas 1962). The pollen catch was measured in the seed orchard from 1984 to 1995, and on a hill, where the environmental conditions were similar to those in the orchard, located about 1 km to the south-east from it from 1987 to 1995. The results obtained with the pollen catch meter provide information about the actual timing of flowering, the mean flowering day being the day when 50% of the total pollen catch was recorded. The duration of anthesis was defined by excluding pollen catches beyond the limits of –2 and +1.2 standard deviations, i.e. including in primary anthesis the period from 2.3 to 88.5% of the total pollen catch of the season (Luomajoki 1993). This was done in order to eliminate secondary pollen.

The phenological stage of the female and male flowers was observed on seed orchard grafts in 1989, 1992, 1993 and 1995. In 1989 the observations were made on 7 randomly chosen clones, in 1992 and 1993 on 21 randomly chosen clones with sufficient flowering abundancy, and in 1995 on 65 out of the 67 seed orchard clones. The observations on the phenological stage of the flowers were made on 3 grafts per clone. The sample grafts were the same in 1992 and 1993, and also in 1995 except for the few cases where they had been removed in thinning, had died or were not flowering. In those cases they were replaced with the nearest grafts of the same clone. This experimental design made it possible to study the effect of graft position in the seed orchard together with clonal variation. The effect of graft position was further studied by analysing randomly chosen grafts from four different sections of the seed orchard (Fig. 1), nine grafts per section in 1992, 1993 and 1995. In 1992 the effect of the position of strobili in the crown (height above ground level and exposure of the branch) was also studied on 24 separate sample grafts from 18 different clones (Fig. 1).

When studying the clonal and environmental variation in flowering phenology, the stage of development of the female strobili was determined by observing the top of the graft with binoculars, and the stage of the male strobili by observing pollen shedding from the sample branch on the southern side of the graft at a height of two to three meters. Phenological observations were made daily, or every second day depending on the weather and the stage of phenology. During warm, dry weather the observations were made every day whenever possible, and during cold, wet weather every second day. The observation round was planned to take no longer than two or three hours in order to ensure that the phenological stage would not have changed during the round. In 1995 when all the clones were included in the study, the observation round was divided into three separate rounds, each including one ramet per clone. The effect of the position of the strobili was investigated on 10 branches per graft by observing one branch at differing crown exposures in every flowering whorl.

The phenological stages of the female strobili were classified as follows: (0) strobili not yet receptive, i.e. completely protected by bud scales,

(1) strobili partly receptive, i.e. partly covered with bud scales and partly open, (2) strobili fully receptive, i.e. cone scales at a right angle and most of the ovules receptive, (3) strobili started to close, i.e. cone scales had started to bend upwards, and (4) strobili closed, i.e. all the cone scales bent. The stages for male strobili were: (0) pollen not yet shed, (1) small amount of pollen ready to be shed, (2) considerable amount of pollen being shed, and (3) almost all pollen shed.

2.3 Data Analysis

In 1992 when the effect of flower position in the crown was investigated, the phenological stages were used in the calculations as such, while in all the other cases the dates when a certain phenological stage had been reached were used in the calculations. The dates of stage 2 in both female and male phenology represented the timing of female receptivity and of pollen shedding. When observations were not made every day, the date of the phenological stage was interpolated.

When the dates of the phenological stages were used in the analysis, a non-parametric Kruskall-Wallis test was used to determine the statistical differences between the clones, and the Spearman rank correlation procedure to calculate the strength of the linear association between different variables. Because the used day scale was so coarse that the observations fell in only a few classes, a non-parametric test and rank correlation procedures were used. When the phenological stages were used instead, the normal score transformation was performed before the analysis of variance and the Tukey post-hoc test using the GLM General Factorial procedure. All the analyses were performed by SPSS® Base 8.0 statistical software (SPSS Inc. 1998).

Broad-sense heritabilities (h_B^2) (= clonal repeatability) were estimated on the basis of a single graft using the formula of Sokal and Rohlf (1995, p. 214) as described in Nikkanen and Ruotsalainen (2000).

3 Results

3.1 Variation in the Timing of Flowering

The between-year variation in the timing of pollen shedding was large (Fig. 2). When the years with poor anthesis were excluded and seven years (1985, 1986, 1987, 1989, 1992, 1993 and 1995) out of the twelve were examined, the mean flowering date varied from May 15 to June 6, the average being May 28. The effective temperature sum of these dates varied from 122 d.d. to 159 d.d., the average being 141 d.d. (Table 1). The timing of anthesis measured outside the seed orchard did not differ from that in the orchard. The duration of primary anthesis varied from 5

Table 1. Duration of primary anthesis, the weather conditions and the effective temperature sums during primary anthesis in the Heinämäki seed orchard in different years.

Year	Duration of anthesis days	Number of rainy days	Number of sunny hours [1]	Mean [2] temperature °C	Timing of anthesis Start	Median d.d.	End
1985	8	3	7.7	8.3	100	124	130
1986	7	6	5.3	9.6	130	159	162
1987	8	6	3.5	12.5	89	134	149
1989	10	3	12.1	12.0	79	122	148
1992	6	0	14.3	17.0	101	148	173
1993	6	2	9.4	13.8	108	143	163
1995	5	1	13.2	20.1	93	152	169
Average	7	3	9.4	13.3	100	141	156

[1] per day
[2] during the anthesis

to 10 days, the average being 7 days.

During the seven years examined, there were large differences in the onset of spring and in the weather during flowering (Table 1, Fig. 2).

Both female and male phenology was observed visually on the seed orchard grafts in 1989, 1992, 1993 and 1995. The time difference in the start of the receptive period of the female flowers between the earliest and the latest graft varied from 2 (1995) to 4 (1993) days, and in the start of pollen shedding from 3 (1995) to 6 (1993) days. The average duration of the receptive period of the grafts was 4.0, 3.7, 4.0 and 2.6 days in 1989, 1992, 1993 and 1995, respectively. The receptive period of the whole seed orchard varied from 5 (1995) to 8 (1993) days. On the average, the receptive period of an individual graft started from 4 (1989) to 0 (1995) days earlier than pollen shedding on the same graft.

3.2 Clonal Differences in Flowering Phenology

The phenological observations made in 1992, 1993 and 1995 were used in the statistical analyses. The clonal differences in the start and duration of the receptive period were statistically significant ($p < 0.05$) in all cases, apart from the start of receptivity in 1992 (Table 2). The average broad-sense heritabilities for the start and duration of the receptive period were 0.28 and 0.36, respectively, and for the start of pollen shedding 0.17 (Table 2).

The Spearman rank correlation coefficients of the clones between the years in the start and the duration of the receptive period were positive and in most cases statistically significant. The correlation coefficients between the start and duration of the receptive period were always negative, and in 1992 and 1995 statistically significant (Table 3a), i.e. the early clones had a longer receptive period than the late ones. The ranking of the clones between the years in the start of pollen shedding was statistically significant in all cases (Table 3b). The ranking of the clones between female and male phenology was statistically significant only in 1992 (Table 3c).

The differences between the clones in the start of the receptive period were 1, 3 and 1 day and in

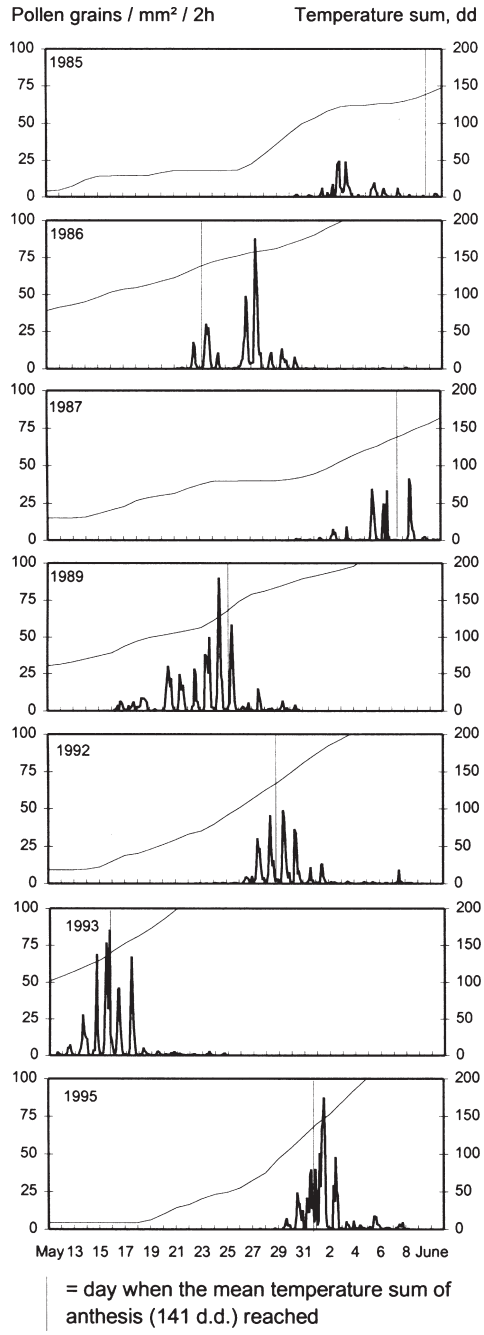

Fig. 2. The number of pollen grains captured in the Heinämäki seed orchard during flowering seasons of moderate or abundant anthesis, and accumulation of the effective temperature sum (> 5°C) based on temperature measured at Jyväskylä Weather Station.

Table 2. The significance of clonal differences in the Kruskall-Wallis test, and the broad-sense heritability for the start of receptivity and pollen shedding and for the duration of receptivity in the Heinämäki seed orchard.

Year	Significance of clonal differences			Broad sense heritability		
	♀ Start	♀ Duration	♂ Start	♀ Start	♀ Duration	♂ Start
1992 [1]	0.090	0.014	0.062	0.22	0.42	0.21
1993 [1]	0.019	0.022	0.109	0.41	0.41	0.24
1995 [2]	0.030	0.010	0.332	0.21	0.26	0.05

[1] data from 21 clones
[2] data from 58 (♀) and 60 (♂) clones

Table 3. The Spearman rank correlation coefficients of 21 clones (significance in parentheses) between years a) in the start and duration of the receptive period, b) in the start of pollen shedding, and within different years c) in the start of the receptive period and pollen shedding in the Heinämäki seed orchard.

a

Female	Start 1992	Start 1993	Start 1995	Duration 1992	Duration 1993
Start, 1993	0.58 (0.006)				
Start, 1995	0.44 (0.050)	0.35 (0.130)			
Duration, 1992	–0.53 (0.014)	–0.26 (0.254)	–0.24 (0.300)		
Duration, 1993	–0.31 (0.173)	–0.32 (0.155)	–0.05 (0.829)	0.66 (0.001)	
Duration, 1995	–0.36 (0.121)	–0.22 (0.354)	–0.66 (0.002)	0.71 (0.000)	0.54 (0.014)

b

Male	Start 1992	Start 1993
Start, 1993	0.45 (0.040)	
Start, 1995	0.49 (0.028)	0.45 (0.046)

c

	Start 1992	Start 1993	Start 1995
Female × male	0.53 (0.013)	0.26 (0.254)	0.38 (0.101)

Table 4. The average phenological stages of female and male strobili in different crown exposures and heights in 1992, and significance for differences in ANOVA after normal score transformation. The average phenological stages marked with different letters differ significantly from each other, $p < 0.05$ in the Tukey post-hoc test.

Exposure and height in the crown				Gender and date of observations	
				♀ May 26 or 27	♂ May 28
				Phenological stage of flowers	
W + E	N	> 4 m		a 1.33	a 1.71
	S			a 1.59	a 1.80
				a 1.17 + 1.40 a	a 1.79 + 1.77 a
p for differences between exposures				0.840 [1]	0.900 [2]
W + E	N	≤ 4 m			a 1.30
	S				b 1.66
					a, b 1.50 + 1.86 b
p for differences between exposures					0.010 [3]

[1] data from 51 observations
[2] data from 136 observations
[3] data from 90 observations

the start of pollen shedding 3, 5 and 2 days in 1992, 1993 and 1995, respectively. The average duration of the receptive period of the clones was 4.2 (varying from 3 to 5), 5.0 (3–7) and 3.2 (2–5) days in 1992, 1993 and 1995, respectively.

No correlation was found between female or male phenology and the geographic origin of the clones. Neither was there any correlation between the phenology and the number of flowers, except in 1995 when the receptive period started the earlier ($r = –0.30$, $p = 0.022$) the more abundant was the flowering. When the average size of the grafts and the phenology was examined, statistically significant correlation was found between the crown volume and the start of receptivity in 1995 ($r = 0.40$, $p = 0.002$), and the start of pollen shedding in 1995 ($r = 0.30$, $p = 0.021$) and in 1993 ($r = 0.52$, $p = 0.016$), i.e. flowering started later in the clones with a large crown.

3.3 Environmental Effects on Flowering Phenology

In 1992 the receptive period in the whole graft usually started within one day, but there were 1 to 3 days differences in the start of pollen shedding. In the strobili situated in the upper part of the crown (> 4 m) pollen started to shed earlier than in the lower part. In the lower part the exposure in the crown also affected pollen shedding (Table 4).

The differences in flowering phenology between the randomly chosen grafts growing in different sections of the seed orchard (see Fig. 1) were more significant in male than in female phenology (Table 5). In the northern sections of the orchard pollen shedding took place later than in the southern sections.

Environmental factors had a stronger effect on male than on female phenology also when the larger data set for 1995 was examined. The slope index (the direction and gradient of the slope)

Table 5. The average number of days, counting from May 1, when the receptive period and pollen shedding started in four different sections (9 grafts / section) of the Heinämäki seed orchard, and the statistical significance of the differences in the Kruskall-Wallis test.

Section of the seed orchard	Start of receptive period Year			Start of pollen shedding Year		
	1992	1993	1995	1992	1993	1995
NW Thinned in 1994	26.0	13.1	31.1	28.0	16.0	31.7
NE Thinned in 1987	26.0	13.7	31.2	27.8	15.1	31.8
SE Thinned in 1994	25.7	12.4	30.9	26.8	13.9	31.1
SW Thinned in 1987	25.8	13.2	31.0	26.8	14.0	31.1
p for differences between sections	0.264	0.081	0.476	0.001	0.021	0.003

Table 6. The Spearman rank correlation coefficients of the grafts (significance in parentheses) between the start of receptivity and pollen shedding, and some environmental factors.

Phenology in 1995	Altitude of grafts	Spacing of grafts	Slope index	Spacing / slope index
Start of [1] receptivity	0.25 (0.001)	0.20 (0.012)	–0.07 (0.363)	0.20 (0.010)
Start of [2] pollen shedding	0.40 (0.000)	0.26 (0.001)	–0.22 (0.004)	0.28 (0.000)

[1] data from 162 grafts
[2] data from 171 grafts

correlated significantly with the start of pollen shedding, but not with the start of female receptivity (Table 6). Pollen shedding started the earlier, the more southerly directed and the steeper was the slope, and the later the more northerly directed and the steeper it was. The spacing of the grafts correlated with both female and male phenology such that flowering started earlier when the spacing was wide. The correlations were stronger when the spacing was weighted by the slope index. In addition, the position of the graft was significantly correlated with both female and male phenology, i.e. the higher the position the later flowering.

3.4 Reproductive Synchronisation

Pollen shedding on the first grafts in the seed orchard usually started at about the same time as female receptivity. On the average, however, the female flowers developed earlier than the male flowers, because the proportion of receptive grafts or clones increased at a faster rate than the proportion of grafts or clones shedding pollen, except in 1995 (Fig. 3). All the clones in the seed orchard were simultaneously receptive on at least one day. On this day (May 26 in 1992, May 14 in 1993 and May 31 in 1995) 62, 81 and 88% of the clones, respectively, had started to shed pollen. The proportion of pollen captured by the pollen catch meter on that day was 3, 12 and 20%, and up to that day 4, 26 and 33% of the total pollen catch, respectively. In 1992 all the 21 clones were able to participate in the pollination of all the clones, but in 1993 four out of the 21 clones (P391, P1208, P1217 and P2306) had passed receptivity before the last three clones (P391, P496 and P2578) had started to shed pollen. In 1995 all 60 clones producing male strobili were able to pollinate all 58 clones bearing female strobili.

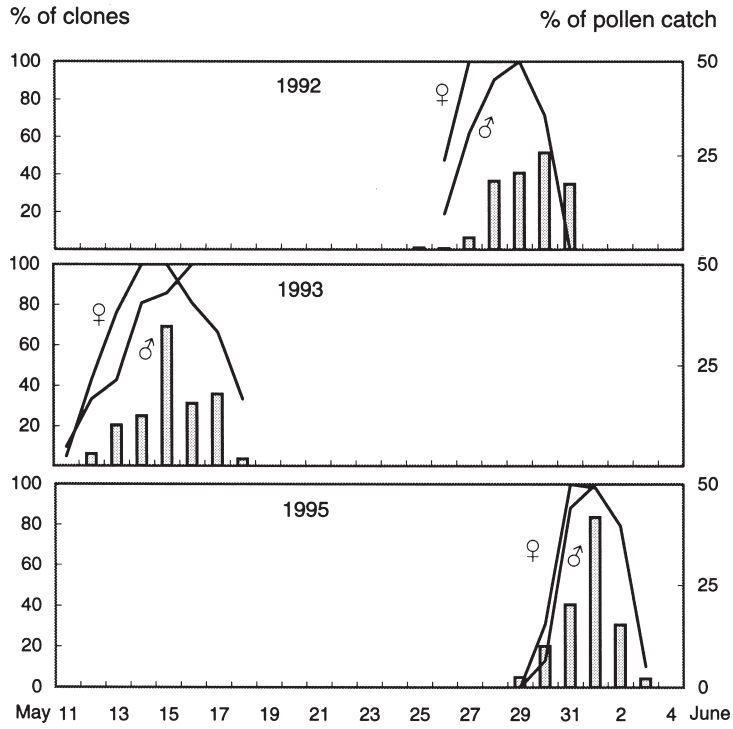

Fig. 3. The development of female receptivity and pollen shedding at the clonal level, and the proportions of pollen catches (bars) by pollen catch meter in 1992, 1993 and 1995.

4 Discussion

In southern Finland, Norway spruce flowers in the latter half of May or in the beginning of June. The midpoint date of anthesis, which represents the average date of flowering, varied in this study from May 15 to June 6, the average date being May 28 (Fig. 2). The average temperature sum that had accumulated by these days was 141 d.d.(Table 1), which was the same temperature sum as Sarvas (1968) obtained for a natural stand in southern Finland in two different years, and close to the figure (134 d.d.) Luomajoki (1993) obtained for a natural stand located near the seed orchard. The range of 37 d.d. between the lowest and highest temperature sum values for the midpoint dates of anthesis corresponds to 6–7 days calculated using the average daily temperatures during the flowering period. This is much smaller than the difference of 23 days observed in this study. The result that the temperature sum explained the timing of flowering better than the date is in accordance with the findings and conclusions of Sarvas (1968, 1972) and Koski (1991), but contrary to that of Luomajoki (1993).

Anthesis lasted from 5 to 10 days, which is several days less than Luomajoki (1993) obtained for natural stands. The difference is probably due to the more strict delimitation of primary anthesis in this study (2.3–88.5% of the total pollen catch). After the primary period a small amount of pollen, probably partly derived from the surface of the branches and the ground, was caught during a period of 5 to 7 days.

The duration of the receptive period in the seed orchard varied from 5 to 8 days in different years (Fig. 3). The duration of receptivity in the different clones varied from 2 to 7 days depending on the clone and the year. There are no data available from Norway spruce seed orchards

which could be compared with these results. Other results about the receptivity of Norway spruce are also scarce. On the basis of unpublished data collected by the late Professor Risto Sarvas, the receptive period of a stand of 30 trees at Punkaharju lasted for 16, 9 and 10 days in 1966, 1967 and 1968, respectively. In Sweden, Eriksson et al. (1973) found that the receptivity of Norway spruce clones in a young clone trial varied from 7 to 12 days (the whole period lasted 13 days) in 1971 during rather cold weather. Eriksson et al. (1973) discussed how to define receptivity with several examples and figures, and concluded that each model is still an oversimplification since often only a part of the ovules in a strobilus are receptive at one time.

The short and rather simultaneous flowering period observed in this Norway spruce seed orchard is different from that reported for many other conifer species. In Douglas fir seed orchards the duration of flowering period varies from 3 to 4 weeks (El-Kassaby et al. 1984, El-Kassaby and Askew 1991), and the duration of receptivity among families between 5 and 12 days (El-Kassaby and Askew 1991). Sitka spruce functions in the same way, i.e. the duration of the receptive period of the whole seed orchard is about 30 days (El-Kassaby and Reynolds 1990), while in individual clones it is much shorter and in individual strobili it lasts from 6 to 8 days (Owens and Blake 1984). Black spruce and white spruce are more similar to Norway spruce. In a black spruce seed orchard the receptive period of 12 clones lasted 16 days, the average length of the individual clone being 12 days including also partial receptivity (O'Reilly et al. 1982). In white spruce (*Picea glauca* (Moench) Voss) the receptive period for a single strobili is 10 days (Ho 1984). The reproductive phenology of Scots pine, the other common north European conifer, is somewhat different from that of Norway spruce. According to Chung (1981), the receptive period of a female strobilus is about one week (from 3 to 10 days), but the differences between clones are, in many cases, more than one week in a clone bank in southern Finland. In Sweden, Jonsson et al. (1976) found clonal differences to be considerable in a Scots pine seed orchard where the flowering period lasted from 2 to 3 weeks in four different years. Pulkkinen (1994) reported clearly shorter periods for two seasons in a Scots pine seed orchard of northern Finnish origin located in southern Finland. In other pine species the flowering periods are often longer than in Scots pine or in Norway spruce (Nilsson 1981, Griffin 1984, Askew and Blush 1990, Matziris 1994).

In this study female phenology was genetically more strongly determined than male phenology (Table 2). The clonal differences at the start of receptivity were, in most cases, statistically significant but not in pollen shedding, and the broad-sense heritability estimates were higher for female than for male phenology. This can also be looked in the opposite way: the environmental factors had a stronger effect on male than on female phenology. In studies on reproductive phenology, very little attention has been paid to environmental factors. The reason for this has been the relatively small variation between ramets compared to that between clones in many species and seed orchards (Jonsson et al. 1976, Wheeler 1983, Griffin 1984, El-Kassaby et al. 1984, Matziris 1994). For Douglas fir, Erickson and Adams (1989) estimated from Wheeler's (1983) data that the repeatability among ramets within clones for the timing of receptivity was extremely high (0.94). In radiata pine the clonal repeatability for the onset of receptivity was 0.42 and for the start of pollen shedding 0.33 over three years (Griffin 1984), and in black pine the corresponding repeatabilities were 0.69 and 0.23, respectively over two years (Matziris 1994). In the present study the average repeatabilities, i.e. broad-sense heritabilities, over three years were 0.28 and 0.17 for receptivity and pollen shedding, respectively.

Although the clonal differences in flowering phenology in the present study were rather small and affected by environmental factors especially in the case of male flowering, in most cases the ranking of the clones was similar from year to year (Table 3). The correlation coefficients between female and male phenology were positive, but statistically significant only in one year. No results from Norway spruce trees or clones showing the correlation of flowering phenology between years or between female and male phenology within the same year have earlier been presented, but the phenomenon is well known in other coniferous species. In Scots pine the corre-

lation in flowering phenology between clones from year to year is positive and significant (Jonsson et al. 1976, Chung 1981, Pulkkinen 1994, Burczyk and Chalupka 1997). It has also been shown for Douglas fir (El-Kassaby et al. 1984), radiata pine (Griffin 1984), loblolly pine (Askew 1988), and black pine (Matziris 1994), that the order of the onset of receptivity and pollen shedding among clones remains unchanged.

Differences in the origin of the clones did not explain the clonal differences in flowering phenology, as was also the case in flowering abundance (Nikkanen and Ruotsalainen 2000). In this study the origin of the clones may not have covered a sufficiently large area to show any clear differences in response to climatic adaptation. On the other hand, Eriksson et al. (1973) did not find any significant differences in the onset of the receptivity between origins even though their material covered large areas, i.e. clones ranging from Central Europe to Scandinavia.

In Norway spruce the female flowers are mainly situated at the top of the tree, but the male flowers also in the lower parts. There are obvious differences between the upper and lower part of the graft as regards solar radiation, air flow and humidity. At the top of the grafts the environmental conditions are about the same irrespective of the exposure of the crown and the section of the orchard, but in the lower parts the conditions differ. The findings concerning the differences in the onset of pollen shedding (Table 4) were in accordance with earlier results for Scots pine, i.e. earlier pollen shedding on the southern than on the northern side of the crown (Jonsson et al. 1976), and in the upper and middle parts exposed to the sun than in the lower parts of the crown (Chung 1978). The other finding that pollen shedding started earlier on the eastern than on the western side of the crown was probably due to the warming and drying effect of sunshine on the eastern side before the observations were made in the morning.

Variation between the different parts of the seed orchard was also found in the start of pollen shedding, but not in the start of the receptive period. On the average, pollen shedding started about 1 day earlier on the southern slope than in the northern parts of the orchard (Table 5). When the environmental factors were investigated in more detail in 1995, it was found that both the spacing of the grafts and the slope index (direction and gradient of a slope) affected male phenology especially (Table 6). These results indicate that the wider the grafts are located, the earlier will pollen shedding start, and also that the more southerly directed and steeper the slope is, the denser will it have to be to have the same environmental effect on the start of pollen shedding.

The result that flowering, especially pollen shedding, started later in the clones with a wide crown could be another expression of the need for solar radiation or high temperature. Because the clonal differences in the crown size are large (Nikkanen and Ruotsalainen 2000) and the ramets of the same clone were planted side by side in a north-south direction, the grafts of the wide-crown clones were often overshadowed by the grafts of the same clone, and the flowers on the shaded side of the graft by the graft itself. In addition to the genotype, crown size was also affected by the environment.

The synchronisation of female and male flowering varied from year to year (Fig. 3). In 1995, as a result of the very warm weather, the duration of flowering was short, and the time difference between the clones was small. In this year female and male flowering took place completely simultaneously, and the amount of pollen in the air was also high right from the very beginning of the receptive period. In other years flowering lasted longer, the clonal differences in the timing of flowering being larger and female receptivity developing earlier than pollen shedding. In 1993 some of the 21 clones had passed their receptivity before some of the clones had started to shed pollen. This means that, at least in some years, some of the clones do not participate in the pollination of all the clones in the seed orchard.

It was not possible, on the basis of the results from the pollen catch meters inside and outside the seed orchard, and on the visual observations made on flowering phenology in the seed orchard, to distinguish any time difference between the airborne pollen of non-orchard origin and that released from the seed orchard grafts. The results of the isozyme analysis of the seed from the same seed orchard, which showed that the pollen contamination rate was about 70% in 1989,

1992 and 1993 (Pakkanen et al. 2000), also indicate that there is no phenological isolation between the seed orchard and the surrounding natural forests, as had been assumed by Sarvas (1970). Neither has any isolation been achieved in the case of Scots pine. In the seed orchards of northern Finnish origin the rates of pollen contamination have been 33% (Harju and Muona 1989) and from 45 to 76% (Pakkanen and Pulkkinen 1991) in different orchards and in different years. In addition to a lack of phenological isolation, Pulkkinen (1994) has proposed that one of the reasons for the high pollen contamination would be metandry, i.e. the phenomenon in which the female flowers are receptive before the male flowers on the same trees shed pollen, which is characteristic for both pine and spruce (Sarvas 1968). According to Pulkkinen (1994), this is even overemphasised in Scots pine seed orchards of northern origin established to the south. Harju and Nikkanen (1996) have shown that, when pollination in Scots pine seed orchard is restricted to the pollination peak, pollen contamination is lower than during the period of less abundant pollen release at the beginning of female receptivity. This also indicates that delayed pollen shedding of the seed orchard grafts could be one reason for the high pollen contamination.

This study has demonstrated that wide spacing of grafts promotes early pollen shedding. The position of the grafts on the southern slope also has a similar effect and shortens the time difference between female receptivity and pollen shedding. Pakkanen et al. (2000) found that pollen contamination in the thinned parts of the seed orchard is in some cases lower than that in the unthinned parts. All this suggests that it is essential in Norway spruce seed orchards to keep the orchard open enough to ensure more solar radiation and better ventilation for the lower parts of the crown. Adequate thinning can be used to promote early pollen shedding and decrease pollen contamination through better reproductive synchronisation and, subsequently increase the genetic efficiency of the seed orchard.

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