Variation in Flowering Abundance and Its Impact on the Genetic Diversity of the Seed Crop in a Norway Spruce Seed Orchard

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The variation in flowering abundance 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). The flowering variation in 1984–1996 was studied at the annual, clonal and graft level. In addition, the genetic diversity of an imaginary seed crop was estimated using a concept of status number.

The between-year variation was large in both female and male flowering. Differences in flowering abundance among the clones were large and statistically significant in all the years studied. The average broad-sense heritability values for female and male flowering were 0.37 and 0.38, respectively, but varied considerably from year to year. The correlations between the flowering abundance of the clones in different years were usually positive and significant. However, the correlations for two pairs of successive good flowering years showed that the same clones usually flowered well in the first year in both pairs of years, and the other clones in the second year. The clonal differences in flowering could not be explained by geographic origin, but were more dependent on the graft size. Our results demonstrate that the variation in the ramet number, flowering abundance and pollen contamination must be included when estimating the genetic diversity of the seed crop in a seed orchard. The relative status number of the seed orchard was 84% of the number of clones when the variation in the ramet number was included. The relative status numbers after adjusting for the variation in female and male flowering were on the average 46 and 55%, respectively, and 59% when adjusting for both genders together. Pollen contamination increased the status number considerably.

Keywords *Picea abies*, clone, ramet, status number, census number
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1 Introduction

The results of forest tree breeding are utilised through artificial regeneration. Most of the seed for artificial regeneration in Finland is nowadays produced in clonal seed orchards consisting of genetically superior trees. Because the number of seed orchards, number of clones per seed orchard and total number of clones are rather limited in Norway spruce (*Picea abies* (L) Karst.) seed orchards (Nikkanen et al. 1999) especially, it is important to pay attention to the genetic diversity of the regeneration material produced in seed orchards.

Variation in flowering affects the genetic diversity of the seed crop. The between-year variation in the abundance of flowering and seed crop of Norway spruce is large (Blomqvist 1876, Heikinheimo 1932, 1948, Tirén 1935, Koski and Tallqvist 1978). The periodicity of abundant flowering is irregular, and the occurrence of good flowering years is the more infrequent, the more northern is the region in question (Koski and Tallqvist 1978). The annual variation in flowering can primarily be explained by climatic factors. High temperatures during the differentiation of flower buds promote abundant flowering (Lindgren et al. 1977, Pukkala 1987). The weather in early and mid-summer is crucial, because the differentiation of flower primordia takes place not later than July. The seed crop of Norway spruce can be predicted rather well on the basis of the June and July temperatures in the two preceding summers (Pukkala 1987).

The variation in flowering abundance is also large between trees within a stand (Sarvas 1968, Koski and Tallqvist 1978), and between clones within a seed orchard (Skrøppa and Tutturen 1985, Ruotsalainen and Nikkanen 1989, Kjær 1996). When Norway spruce is planted in a locality where the summer temperatures are higher than those to which it is genetically adapted, it responds by enhancing female flowering (Skrøppa and Tutturen 1985). In Finland, as well as in the other Nordic countries, Norway spruce and Scots pine (*Pinus sylvestris* (L.)) seed orchards have often been established at sites with a warmer climate than that from which the selected plus trees originate, and where the orchard seed is to be used (Sarvas 1970, Werner 1975, Ilstedt and Eriksson 1982, Skrøppa and Tutturen 1985).

For estimating genetic diversity in natural populations, Wright (1931) introduced the concept of effective population size. Since then, the concept has been developed and applied by many population geneticists and plant breeders, mainly focusing on two alternative aspects; the inbreeding effective population number and the variance effective population number (Crow and Kimura 1970, Crow and Denniston 1988, Muona and Harju 1989, Caballero 1994, Burczyk 1996, Kjær 1996). Because effective population size describes the rate of change in a population, Lindgren et al. (1996, 1997) developed the concept of status number, which is a more functional measure of the state for a non-changing population, like a seed orchard crop. The application of status number for estimating the genetic diversity of seed orchards or seed orchard crops has been discussed by Kjær and Wellendorf (1997, 1998), Lindgren and Mullin (1998), Kang and Lindgren (1998) and Ruotsalainen et al. (2000), and is continued in the present work.

Various aspects of flowering and seed crop have been intensively studied in a Norway spruce seed orchard, Heinämäki, in southern Finland (Ruotsalainen and Nikkanen 1989, Nikkanen 1993, 1995, 2000, Puhakka 1993, Hämäläinen 1994, Pakkanen et al. 2000). This seed orchard was selected for the study in 1983 because it was one of the first Norway spruce seed orchards to start reasonable flowering. It also well represents the specific problems encountered in Finnish Norway spruce seed orchards: clonal-row design, pollen contamination and transfer of clones from north to south. Due to the long time series of flowering this seed orchard offered excellent material for the present study.

The aim of this study was to determine the magnitude and characteristics of flowering variation in a Norway spruce seed orchard, and to try to explain the variation on the basis of clonal and environmental factors. The variation in flowering abundance and pollen contamination was used to estimate their effect on the genetic diversity of the seed crop produced in the seed orchard.

2 Material and Methods

2.1 Basic Information and Management of the Seed Orchard

The variation in flowering abundance was studied in Norway spruce seed orchard no. 170 (Heinämäki) established in 1968 at Korpilahti, southern Finland (62°13'N, 25°24'E). The seed orchard consists of 67 clones originating from latitudes 64°–67° N in northern Finland (Fig. 1). The effective temperature sum (+5 °C threshold) of the seed orchard location was 1100 d.d., and that of the plus tree locations varied from 820 to 1070 d.d. (Nikkanen et al. 1999).

Information about the geographic origin of the clones was obtained from the National Register of forest genetics. The geographic data were used to calculate predicted climatic variables for the original growing sites of the plus trees. This was done by a program (ILMA) that interpolates climatic variables to any location in Finland using the measurements made at weather stations (Ojansuu and Henttonen 1983). The original geographic data and climatic variables derived from it were used to explain the clonal variation in flowering.

The seed orchard is 13.2 ha in area, and is partly located on abandoned agricultural land (6.0 ha) and partly on forest land (7.2 ha) on a hill (160–190 m asl) sloping gently to the south and steeply to the east and west (Fig. 2). The grafts were planted in the orchard using a clonal-row design with ramets of each clone in two or more rows distributed in different parts of the orchard. The spacing of the grafts was 3.5 × 6.5 m, the ramets of the same clone being located 6.5 metres from each other. In 1987 one half of the orchard was thinned systematically by removing every third graft, and in 1994 the other half of the orchard in the same way (Fig. 2). The average number of ramets per clone was 56 before the first thinning, 47 after it, and 39 after the second thinning. In the early part of the study period the seed orchard was surrounded by old Norway spruce forest which was cut down in winter 1994.

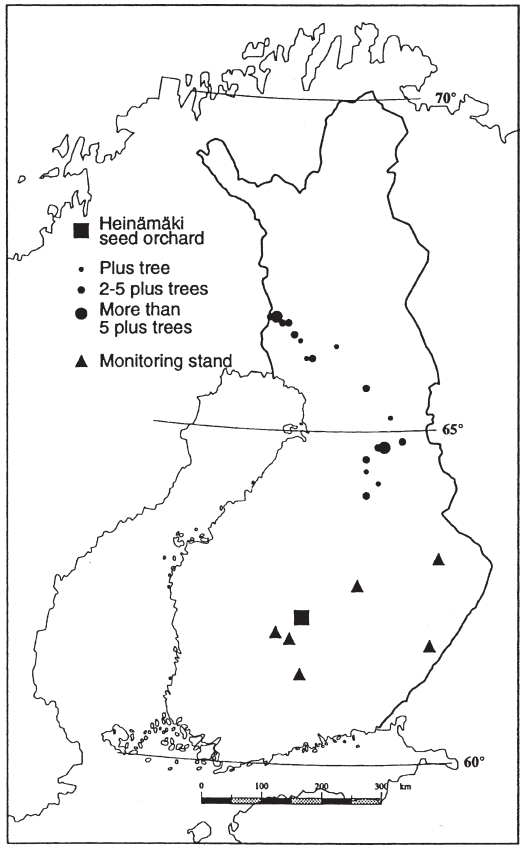

Fig. 1. Location of the Heinämäki seed orchard and the origin of its clones, and the monitoring stands for flowering abundance.

2.2 Soil and Weather Data of the Seed Orchard

The nutrient concentrations and pH of the seed orchard soil were determined in 1993 (Hämäläinen 1994). In order to estimate the variation in the nutrient status, the seed orchard was divided into 20 plots and soil samples were taken down to a depth of 5–15 cm at 20 points on each plot. The samples were bulked to give one composite sample per plot. Plant-available phosphorus, potassium, calcium and magnesium were determined by extraction with 1N ammonium acetate (pH 4.65), and pH on a soil sample/water suspension. The results were used as independent

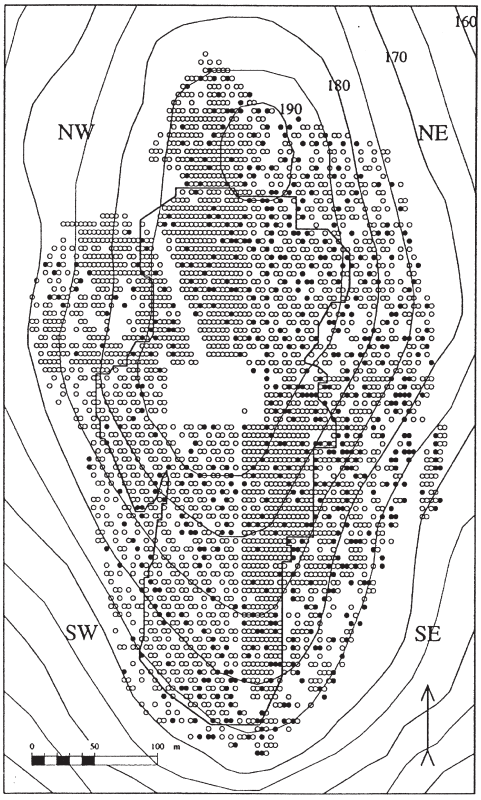

Fig. 2. The Heinämäki seed orchard in 1993. The orchard is situated on a hill and divided into four sections (NW, NE, SW and SE). Two of the sections (NE and SW) were thinned systematically in 1987, and the rest of the orchard in 1994. The border line between the abandoned agricultural (in the middle) and forest land, and the altitude contours are marked on the map. The sample grafts observed after 1988 are also marked.

Table 1. The concentrations of plant available phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) and pH (soil/water) in the soil of the Heinämäki seed orchard in 1993.

Nutrient	Agricultural land		Forest land		Total	
	x̄	CV %	x̄	CV %	x̄	CV %
P mg/l	1.9	49.1	1.7	50.1	1.8	50.2
K mg/l	64.0	19.4	60.3	26.7	62.3	23.1
Ca mg/l	680.9	23.4	360.3	42.4	527.6	42.4
Mg mg/l	34.6	27.4	34.4	50.6	34.5	40.1
pH	5.8	2.8	5.4	1.9	5.6	4.3

Table 2. The annual effective temperature sums and mean temperatures of the study period recorded at the Jyväskylä Weather Station of the Finnish Meteorological Institute.

Year	Temperature sum (> +5 °C)	Mean temperature				
		Annual	May	June	July	August
	d.d.	°C				
1982	999	2.9	8.1	10.0	16.5	14.2
1983	1220	3.4	10.6	13.4	16.6	13.5
1984	1211	3.6	12.3	12.8	15.0	13.2
1985	1141	0.8	7.7	13.3	15.3	14.8
1986	1154	2.5	10.2	16.4	16.3	12.1
1987	892	0.6	7.0	12.7	14.2	10.5
1988	1331	3.0	9.5	15.8	19.2	13.2
1989	1254	4.7	9.9	15.6	15.8	13.4
1990	1059	3.9	8.4	13.1	14.7	14.2
1991	1086	3.7	6.0	12.5	16.5	15.0
1992	1176	3.6	10.4	15.2	13.3	12.7
1993	994	2.9	11.6	10.6	15.1	12.5
1994	1143	2.8	6.6	12.5	18.2	14.1
1995	1263	3.7	8.2	16.5	14.7	14.2
1996	1070	2.6	7.7	13.0	13.8	16.1
Average in 1982–96	1133	3.0	9.0	13.6	15.7	13.6
Average in 1961–90	1129	2.6	8.7	14.1	15.7	13.6

variables to describe the differences in flowering abundance or graft size. The results of the soil analyses grouped into agricultural and forest land are shown in Table 1.

The weather data for the study period were obtained from the Jyväskylä weather station of the Finnish Meteorological Institute, located 25 km north-east from the seed orchard. The weather data consisted of annual, monthly and daily mean temperatures (including effective temperature sum, d.d.) from 1982 to 1996. The annual mean temperatures and temperature sums, and some important monthly mean temperatures are shown in Table 2.

2.3 Measuring Flowering Abundance and Size of the Grafts

Both female and male flowering were studied. The number of flowers was recorded every year during 1984–1996, the observations being made during flowering in May and June. The number of male flowers on sample branches was counted and used to evaluate the total number of male flowers on a graft. In 1984 when the study was started, 10 sample grafts per clone were selected systematically to cover representatively the whole seed orchard. After the first thinning in 1987 the number of sample grafts was 5, but in 1988 it was returned to 10 using systematic selection. No changes in the number of sample grafts were subsequently made. However, the second thinning in 1994 and natural mortality decreased the number of sample grafts to a minimum of 4 and average of 7 in 1996. The total number of grafts on which flowering abundance was measured varied from 650 to 478.

The height and diameter of the sample grafts were measured in all years except 1994. The width of the crown was measured in 1993. The average height of the grafts in 1984 when the flowering study started was 4.9 m, the clonal means varying from 3.0 to 7.2 m. Twelve growing periods later in 1996 the average height was 10.4 m, varying from 6.5 to 13.4 m. Thus the average annual height growth of the grafts during the study period was 42 cm. The size of the graft was used as one of the independent variables to describe flowering abundance.

The flowering abundance in natural stands, used as comparisons when the annual variation in flowering was studied, was obtained from 6 monitoring stands in different parts of southern and central Finland (Fig. 1) (Hokkanen, unpublished data).

2.4 Data Analysis

The annual variation in female flowering was explained using the model for predicting a seed crop developed by Pukkala (1987). The formula predicting the seed crop (*SI*) in southern Finland (Pukkala 1987, p. 138; corrected for a printing error) is

$$SI = 175.35 + 0.05144\left(\frac{K_1 + H_1}{2}\right)^2 - 5.9860\left(\frac{K_2 + 2H_2}{3}\right) \quad (1)$$

where K_1 and K_2 are the mean temperatures of June one and two years before flowering, respectively, and H_1 and H_2 are the respective mean temperatures of July.

The variables measured on the grafts in the seed orchard were used in the statistical analyses as such, as well as after some transformations. In order to describe the changes in flowering between successive years new variables were created by subtracting the number of flowers in one year from that in the following year.

Because the number of flowers had a skewed and non-normal distribution, a non-parametric Kruskall-Wallis test was used to test the statistical differences between the clones. For the same reason the Spearman rank correlation procedure was used to calculate the strength of the linear association between different variables. Stepwise regression analysis was used to obtain models that best explained the variation in flowering. The variance components for estimating heritability values were obtained by analysis of variance. All these analyses were performed by SPSS® Base 8.0 statistical software (SPSS Inc. 1998).

Broad-sense heritabilities (h_B^2) (= clonal repeatability) were determined on a single-graft basis for each study year separately using formula (2) (Sokal and Rohlf 1995). The procedure is similar to that described in Matziris (1993). Standard errors for the estimates were determined using the approximate formula given by Becker (1984).

$$h_B^2 = \frac{s_c^2}{s_c^2 + s_e^2} \quad (2)$$

where s_c^2 is the variance component for clonal differences, and s_e^2 is the environmental variance.

Genetic diversity of the seed orchard and the seed crops was described using the status number (N_S), which is derived from group coancestry (Θ) (Lindgren et al. 1996, 1997, Lindgren and

Mullin 1998). The status number for the seed orchard crop was calculated according to Lindgren and Mullin (1998) using formula (3), which assumes that the seed orchard clones are not related to each other and have no inbreeding.

$$N_S = \frac{1}{\sum_{i=1}^{n} p_i^2} \quad (3)$$

where p_i can be any clonal proportion measured in the seed orchard (female or male flowering, graft proportion).

When the effect of pollen contamination was considered, the status number was calculated according to Lindgren and Mullin (1998), and Ruotsalainen et al. (2000)

$$N_S = \frac{1}{\sum_{i=1}^{n} \left(f_i + (1-2M)m_i \right)^2} \quad (4)$$

where f_i is the proportion of clone i of the female flowers and m_i is the corresponding value for male flowering. Both f_i and m_i sum up to 0.5. M is the proportion of migrating genes in the seed crop. Here also the clones were assumed to have no relatedness and no inbreeding. A further assumption was that the contaminating pollen is not related to itself or to the seed orchard clones.

The status number for combined proportion of female and male flowering ($c_i = f_i + m_i$) was also weighted with the graft proportions (g_i). The weighted proportions were calculated using formula (5)

$$p_i = \frac{g_i c_i}{\sum g_i c_i} \quad (5)$$

The status numbers were estimated for the seed orchard and the seed crops adjusting for several sources of variation. The first factor to be considered was the variation in ramet number. In this adjustment the clonal ramet contributions (p_i) were inserted in formula (3), it being assumed that there are no clonal differences in flowering abundance. The next step was to assume an equal number of ramets per clone, and to study the effect of variation in flowering abundance on status number. This was done separately for female and male flowering, and also for the combined flower contribution. When the variation in female or male flowering was studied separately, it was assumed that the contribution of the other sex was the same as that of the studied one. The study was brought closer to the real situation when both the variation in ramet numbers and flowering abundance were combined using formulae (5) and (3). Finally the status numbers for the seed crop were estimated by considering the variation in ramet numbers and flowering abundance, and assuming different levels of pollen contamination (formula 4). The rationale in this kind of stepwise approach is that it shows the possibilities of utilising different levels of information about the genetic contribution of the clones in estimating the genetic diversity of the seed crop.

3 Results

3.1 Annual Variation in Flowering

The year-to-year variation in flowering was large in both female and male flowering (Table 3). During the 13-year study period there were six years (1987, 1989, 1992, 1993, 1995 and 1996) when flowering was fairly abundant, five years (1984, 1985, 1986, 1990 and 1991) when it was poor, and two years (1988 and 1994) when there was no flowering in the orchard.

Flowering was the most abundant in 1996, when the average number of female flowers per graft was 87 and male flowers 17 300. The maximum number of female flowers per single graft was 680 and of male flowers 100 000. However, the percentages of flowering grafts were greater in 1989 and 1993 than in 1996 (Table 3).

The model predicting the annual seed crop (formula 1) on the basis of the temperature data of two previous summers gave a rather good fit ($r = 0.71$, $p = 0.007$) when the formula for southern Finland was used (Fig. 3). The formula for northern Finland (Pukkala 1987) gave a poorer prediction ($r = 0.41$, $p = 0.163$).

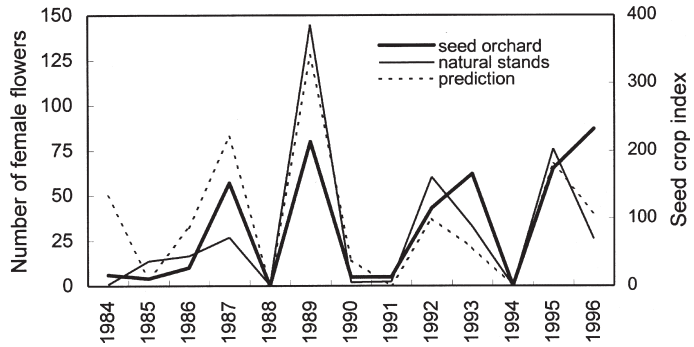

Fig. 3. Annual variation in the number of female flowers in the Heinämäki seed orchard and in 6 natural stands in southern and central Finland, and the predicted seed crop using Pukkala's (1987) model.

Table 3. The percentages of flowering grafts, clonal mean, minimum and maximum values for the number of flowers, and the broad-sense heritability values for the number of flowers in the Heinämäki seed orchard in different years.

Year	Percentage of flowering grafts		Number of female flowers / graft			Number of male flowers / graft			Broad sense heritability	
	Female	Male	Mean	Min	Max	Mean	Min	Max	Female	Male
1984	36	59	6	0	33	310	0	1770	0.19	0.30
1985	31	48	4	0	39	530	0	6390	0.44	0.41
1986	44	88	10	0	127	1080	0	4950	0.37	0.33
1987	77	91	57	0	196	1700	10	7300	0.42	0.49
1988	0	0	0	0	1	90	0	980		
1989	96	99	80	0	454	4900	73	16950	0.27	0.35
1990	54	91	5	0	18	550	4	2010	0.17	0.46
1991	31	66	5	0	20	620	0	2570	0.36	0.39
1992	90	83	43	0	278	2190	0	6880	0.39	0.39
1993	95	99	62	0	202	2080	184	5230	0.42	0.40
1994	0	0	0	0	0	0	0	1		
1995	82	83	65	0	396	12500	0	47200	0.46	0.40
1996	79	98	87	0	496	17300	1207	65000	0.63	0.30
Average	55	70	33			3373			0.37	0.38
sd	33	33	32			5158			0.12	0.06

3.2 Clonal Differences in Flowering Abundance

Differences in flowering abundance among the clones were large (Table 3) and statistically significant ($p \leq 0.000$) in all the years studied. The proportion of clones that did not flower at all was largest when flowering was poor. In the years of abundant flowering all the clones in the seed orchard flowered. For female flowering such years were 1989, 1992, 1993 and 1996, and for male flowering 1987, 1989, 1990, 1993 and 1996. Broad-sense heritability estimates for flowering abundance varied considerably from year to year (Table 3). The average heritability estimates for female and male flowering were slightly higher

Table 4. The Spearman rank correlation coefficients of the clones (significance in parentheses) between female and male flowering in different years (diagonal), and between years in female (above diagonal) and male flowering (below diagonal) in the Heinämäki seed orchard.

Year		1987	1989	1992	1993	1995	1996
		Female					
1987		0.58 (0.000)	0.49 (0.000)	0.48 (0.000)	0.55 (0.000)	0.32 (0.009)	0.44 (0.000)
1989		0.72 (0.00)	0.39 (0.001)	0.74 (0.000)	0.51 (0.000)	0.38 (0.002)	0.39 (0.001)
1992	Male	0.70 (0.000)	0.85 (0.000)	0.56 (0.000)	0.30 (0.013)	0.64 (0.000)	0.23 (0.068)
1993		0.52 (0.000)	0.65 (0.000)	0.55 (0.000)	0.17 (0.182)	–0.01 (0.962)	0.73 (0.000)
1995		0.60 (0.000)	0.79 (0.000)	0.84 (0.000)	0.56 (0.000)	0.56 (0.000)	–0.17 (0.161)
1996		0.18 (0.148)	0.27 (0.030)	0.21 (0.092)	0.47 (0.000)	0.08 (0.530)	0.38 (0.001)

Table 5. The Spearman rank correlation coefficients (significance in parentheses) between female and male flowering, and origin (latitude) of the clones and size (height, breast height diameter and crown volume) of the grafts in the Heinämäki seed orchard.

Year	Latitude ×		Height ×		Diameter ×		Crown volume ×	
	Female flowering	Male flowering	Female flowering	Male flowering	Female flowering	Male flowering	Female flowering	Male flowering
1987	0.21 (0.097)	–0.11 (0.361)	0.37 (0.002)	0.57 (0.000)	0.33 (0.007)	0.60 (0.000)	0.36 (0.003)	0.46 (0.000)
1989	0.07 (0.577)	–0.26 (0.037)	0.59 (0.000)	0.50 (0.000)	0.60 (0.000)	0.55 (0.000)	0.64 (0.000)	0.49 (0.000)
1992	–0.13 (0.308)	–0.21 (0.095)	0.55 (0.000)	0.56 (0.000)	0.50 (0.000)	0.63 (0.000)	0.54 (0.000)	0.56 (0.000)
1993	0.12 (0.358)	–0.28 (0.022)	0.19 (0.130)	0.42 (0.001)	0.16 (0.197)	0.47 (0.000)	0.34 (0.006)	0.27 (0.026)
1995	–0.16 (0.199)	–0.33 (0.006)	0.38 (0.002)	0.48 (0.000)	0.39 (0.001)	0.51 (0.000)	0.32 (0.009)	0.42 (0.000)
1996	0.17 (0.176)	–0.07 (0.598)	0.001 (0.994)	0.17 (0.180)	–0.09 (0.478)	0.33 (0.006)	0.10 (0.422)	0.19 (0.124)

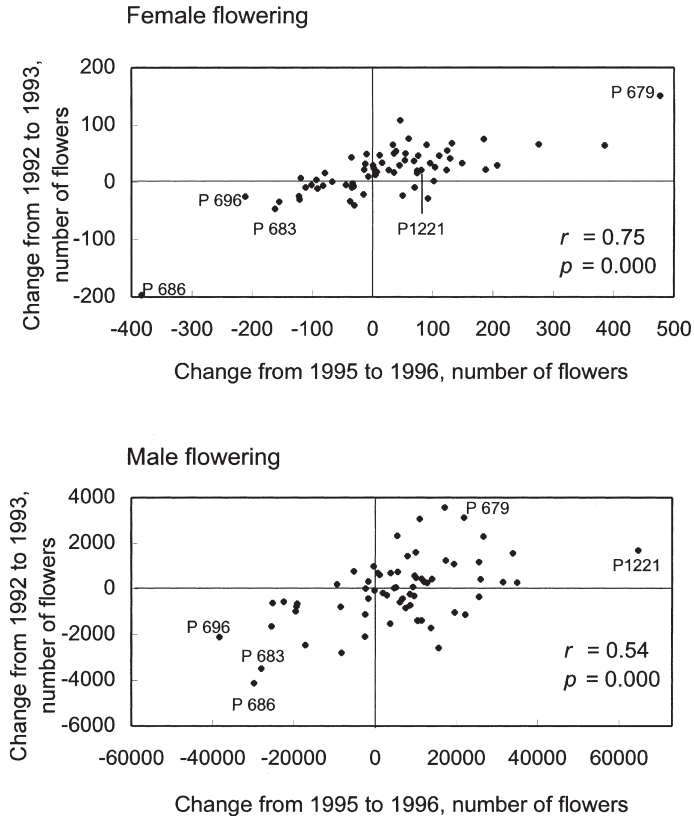

Fig. 4. Stability in the change of flowering abundance between two different pairs of years in the Heinämäki seed orchard. Some extreme clones are labelled.

than those for the height (0.30) and diameter (0.32) of the grafts.

Only the six fairly good flowering years (1987, 1989, 1992, 1993, 1995 and 1996) were included in a more detailed examination of clonal differences. The correlation coefficients between female and male flowering of the same years were always positive and statistically significant, with the exception of 1993 (Table 4). Also the correlation coefficients from year to year were usually positive and significant, and in general slightly higher in male than in female flowering (Table 4). However, in some cases the correlations between years were complex. In female flowering the correlation coefficients of successive years (1992 and 1993; 1995 and 1996) were rather low, 0.30 and –0.17, respectively, and in the latter case negative and not significant. On the other hand, when the first years of these two pairs of years (1992 and 1995), and correspondingly the second years (1993 and 1996) were compared, the correlation coefficients were significant and high, 0.64 and 0.73, respectively. The changes in flowering abundance between two successive good flowering years showed a persistent pattern for the two pairs of years (Fig. 4).

When the clonal differences in flowering were studied on the basis of geographic origin using correlation analysis, no correlation was found between female flowering and latitude, while there was a significant negative correlation between male flowering and latitude in 1989, 1993 and 1995 (Table 5). Male flowering decreased with increasing latitude of origin. The correlation coefficients between the average height of the grafts and flowering were significant in the studied years, except for 1993 and 1996 in female flowering, and for 1996 in male flowering. The

correlation coefficients between flowering and the other variables describing the graft size (diameter at breast height and crown volume) were very similar to those with height (Table 5). Clones with larger grafts had more abundant flowering.

3.3 Factors Affecting Flowering Abundance

The average number of female flowers per graft was 40% higher on the agricultural land than on the forest land, and the average number of male flowers 8% higher. For female flowering the difference was statistically significant ($p \leq 0.05$) in 1987, 1989, 1992 and 1993 (when six years of abundant flowering were analysed), but for male flowering only in 1996. The average height of the grafts in 1995 was 10.7 m (±0.11) on the agricultural land and 9.5 m (±0.13) on the forest land. The correlation between the height and flowering of the grafts was statistically significant ($p \leq 0.005$) for both female and male flowering in every year, the average Spearman rank correlation coefficient of six years for female flowering being 0.36 and for male flowering 0.44.

Differences in flowering abundance between the clones were investigated using stepwise regression analysis. The variables analysed were geographical latitude (lat) and longitude (lon) of the plus tree, average height (h), breast height diameter (dbh), crown width (wid) and crown volume (vol) of the grafts of each clone. The results for both female and male flowering in six separate years are shown in Table 6. The regression model for female flowering in 1992 included three statistically significant independent variables (dbh, in addition to vol and wid, $R^2 = 0.61$), while in the other cases there were two or less (Table 6). In general, female flowering was best

Table 6. Statistically significant regression equations with one and two independent variables for female and male flowering at the clonal level in the Heinämäki seed orchard.

Year	Intercept	First term			Second term			
		Variable	Coefficient	p	Variable	Coefficient	p	R^2
Female								
1987	–44.13	wid	2.67	0.001				0.15
1989	–4.04	vol	2.27	0.000				0.51
1989	175.13	vol	5.00	0.000	wid	–7.32	0.007	0.56
1992	–4.54	vol	1.31	0.000				0.51
1992	118.68	vol	3.19	0.000	wid	–5.04	0.001	0.59
1993	No significant regression							
1995	4.74	vol	1.65	0.000				0.23
1995	201.76	vol	4.65	0.001	wid	–8.05	0.029	0.29
1996	No significant regression							
Male								
1987	–1230	dbh	258.4	0.000				0.32
1989	–5255	dbh	707.6	0.000				0.31
1992	–3819	dbh	346.0	0.000				0.40
1992	–2520	dbh	213.6	0.011	vol	27.4	0.042	0.44
1993	–1150	dbh	172.6	0.000				0.21
1993	–784	dbh	294.4	0.000	wid	–69.0	0.013	0.29
1995	–36000	h	483.6	0.000				0.26
1995	–43652	h	372.0	0.001	lon	39.6	0.028	0.31
1996	–10287	dbh	1347.3	0.001				0.15
1996	–22790	dbh	2406.9	0.000	vol	–263.8	0.015	0.23

Note: wid = crown width, vol = crown volume, dbh = breast height diameter, h = graft height, lon = longitude of the clone origin

explained by crown volume, and male flowering by breast height diameter. The geographical origin of the clone was included in the model only in the case of male flowering in 1995.

3.4 Genetic Diversity in Seed Orchard Crops

The status number of the seed orchard was 56 when the variation in the number of ramets per clone was considered. This was equivalent to 84% of the number of clones (census number) in the orchard. The variation in female flowering had a considerable influence on the status number of the seed crop when the ramet number was assumed to be the same for all the clones, and male flowering was assumed to follow female flowering. The average status number after adjusting the variation in female flowering was 31 (46% of the census number), the variation between different years ranging from 12 to 48 (Table 7). The status number after adjusting for the variation in male flowering in the same way

Table 7. Estimated absolute (N_s) and relative (N_r) status numbers of the seed crop of the Heinämäki seed orchard after adjusting for different variation sources in the genetic contribution of the clones and for pollen contamination.

Year	Equal ramet number			Weighted with ramet number				
	Flowering of			Flowering of both genders				
	female	male	both genders	Percentage of pollen contamination				
				0	25	50	75	100
Absolute status number, N_s								
1984	22	28	31	32	40	50	61	75
1985	14	16	24	19	25	33	43	52
1986	12	33	23	17	21	25	31	37
1987	37	42	44	36	47	61	83	116
1989	41	43	48	37	48	63	87	121
1990	37	40	46	37	48	64	87	121
1991	24	31	37	31	39	49	62	76
1992	39	41	44	33	42	56	78	113
1993	48	49	55	42	55	75	105	153
1995	32	33	38	29	39	51	70	98
1996	31	44	44	36	44	56	73	95
Average	31	36	39	32	41	53	71	96
sd	11	9	9	7	10	14	21	34
Relative status number, N_r (%)								
1984	33	43	46	49	61	75	93	113
1985	21	24	36	29	38	51	65	79
1986	18	50	35	26	32	38	46	56
1987	56	63	64	55	70	92	125	176
1989	62	65	72	56	73	96	131	183
1990	56	60	70	56	73	97	132	183
1991	37	48	56	47	59	75	94	115
1992	59	62	66	50	64	85	118	171
1993	73	74	83	64	84	113	159	232
1995	49	50	57	44	58	77	106	148
1996	47	67	66	55	67	85	110	144
Average	46	55	59	48	62	81	107	145

as for female flowering was 36 (55%), ranging from 16 to 49. It was always higher than the status number adjusted for female flowering. When female and male flowering were considered together, the average status number was 39 (59%). When the status number of the seed crop was adjusted for all these three sources of variation, i.e. ramet number, female flowering and male flowering, it decreased to 32 (48%) on the average (Table 7).

The estimated effect of pollen contamination on the status number of the seed crop was large (Table 7). Even moderate pollen contamination (25%) increased the average status number from 32 to 41. The status number increased with increasing pollen contamination. With total background pollination it was 96, which is 45% higher than the census number of the seed orchard (Table 7).

The status number for the seed crop adjusted for variation in female flowering increased with increasing number of female flowers ($r = 0.65$, $p = 0.032$). For male flowering the corresponding dependence was weaker ($r = 0.29$, $p = 0.394$).

4 Discussion

In Norway spruce the between-year variation in flowering abundance and cone crop is large (Blomqvist 1876, Heikinheimo 1932, 1948, Tirén 1935, Koski and Tallqvist 1978). Many attempts have been made to explain this variation (e.g. Lindgren et al. 1977, Pukkala 1987). In our study the variation in female flowering could be explained reasonably well using Pukkala's (1987) model for predicting the seed crop index for southern Finland on the basis of the temperature data of the two previous summers. The greatest incompatibility between the prediction and the number of flowers in the seed orchard was observed in the two cases where there was good flowering in two successive years (Fig. 3). The model predicted a decreasing seed crop index for the latter years, but in these cases the flowering in the seed orchard actually increased. In the natural stands the abundance of flowering better followed the predicted value. The reason for the different behaviour of the seed orchard grafts was either their northern origin or the special conditions prevailing in the seed orchard.

The large, statistically significant variation between the clones in flowering abundance (Table 3) is in accordance with earlier results from Norway spruce in both natural stands and seed orchards (Sarvas 1968, Eriksson et al. 1973, Koski and Tallqvist 1978, Skrøppa and Tutturen 1985, Kjær 1996), as well as with other conifer species (Varnell et al. 1967, Jonsson et al. 1976, Bhumibhamon 1978, Koski and Tallqvist 1978, Schoen et al. 1986, Matziris 1993).

The broad-sense heritability estimates (Table 3) for female flowering were about the same or lower than those reported for the cone crop of other conifers (Varnell et al. 1967, Matziris 1993, Savolainen et al. 1993). Unfortunately, results for male flowering are scarce. The only comparable result concerns the heritability of pollen production in Scots pine (Savolainen et al. 1993), which was about the same as that for male flowering in our study. It is noteworthy that in our study with Norway spruce, as well as in the study of Savolainen et al. (1993) with Scots pine, the flowering characteristics had higher broad-sense heritabilities than height growth. The considerable amount of genetic variation in flowering characteristics is in contrast with the hypothesis of low variation in fitness-related characteristics (Falconer and Mackay 1996). This is not, however, the first time that this has been observed. Large genetic variation has been reported in other studies on flowering (see references above), as well as in other fitness-related characters (Harju et al. 1996). This apparent contradiction is discussed in other studies (Harju et al. 1996, Kjær 1996, Ruotsalainen 1998).

The broad-sense heritability estimates obtained in this study can be considered to be overestimates, because the seed orchard was not established using a random design. In the clonal-row design used here the ramets of a single clone were usually growing in two to four rows in different parts of the seed orchard. The effect of non-random distribution of the ramets on the heritability was examined by re-analysing the data after removing 12 clones with the most concentrated distribution. In most cases this data screening had no marked effect on the heritability estimates, but in the years with the highest

heritabilities the estimates decreased somewhat in both female and male flowering. Therefore the broad-sense heritability estimates can be regarded as rather reliable.

The finding that the correlation in female flowering between two successive good flowering years was poor (Table 4) is in accordance with the results for Norway spruce (Kjær 1996), white spruce (*Picea glauca* (Moench) Voss) (Schoen et al. 1986) and black pine (*Pinus nigra* Arnold) (Matziris 1993). In male flowering the changes in flowering abundance between successive years were not as great as those in female flowering, as also shown by Kjær (1996). The correlations for two pairs of successive good flowering years showed that there exist genotypes that have a different response to climatic factors: some clones flowered well in the first year, and other clones in second year. This tendency was especially clear in female flowering.

Our result that the same clones tend to have a large number of both female and male flowers (Table 4) is in accordance with earlier results for Norway spruce (Skrøppa and Tutturen 1985, Kjær 1996, Kjær and Wellendorf 1997), black spruce (*Picea mariana* (Mill) B.S.P.) (O'Reilly et al. 1982, Caron and Powell 1989) and white spruce (Schoen et al. 1986). Kang and Lindgren (1998) did not find any statistically significant correlation between female and male flowering in three pine species (*Pinus densiflora* Sieb. & Zucc., *P. thunbergii* Parl. and *P. koraiensis* Sieb. & Zucc.), but Nikkanen and Velling (1987) reported low positive correlation between female and male flowering in Scots pine. It should be kept in mind, however, that our results, as well as most of the other results cited above (with the exception of Kjær 1996), are based on phenotypic or clonal (genotype) means. In Scots pine the phenotypic and environmental correlations between female and male flowering are usually positive, but genetic correlation negative (Savolainen et al. 1993). However, the correlation between genotypic means gives a rather good approximation of the real genetic correlations if the genotypes are represented by a sufficient number of randomised ramets. Kjær (1996) also obtained from moderate to high genetic correlations between female and male flowering in a Norway spruce seed orchard. Thus there seem to be some differences in the mode of sexual allocation between spruces and pines, spruces having a more equal contribution to female and male flowering. One explanation for the differing correlations between female and male flowering could be that the correlation tends to be positive at a young age, but turns more negative with increasing sexual maturity (Savolainen et al. 1993). However, in our material there were no signs that the clones were specialising into different sexes with increasing age.

The differing land-use history of the central and outer parts of the seed orchard (agricultural vs. forest land) was reflected in many of the characteristics measured on the grafts. The grafts growing in the more fertile soil on the agricultural land (Table 1) were taller. The flowering abundance correlated in most cases with the size of the graft, and therefore the flowering abundance was affected by both environmental and clonal factors. The clonal variation in flowering was usually explained better by size characteristics of the grafts other than height; female flowering by crown volume and male flowering by breast height diameter (Table 5). The result that tall grafts with a wide crown had more flowers than small ones has also been obtained for grafts in a Scots pine clone bank (Nikkanen and Velling 1987).

Differences in the origin of the clones did not explain the variation in flowering (Table 5). This was contrary to expectations (Eriksson et al. 1973, Skrøppa and Tutturen 1985). In our study the origin of the clones may not have covered a sufficiently large area to show any clear differences in response to climatic adaptation. In the above studies the material covered large areas, consisting of provenances from Central Europe to Scandinavia.

When the factors affecting the clonal variation in flowering were examined by regression analysis, the overall result was that there was great year-to-year variation in the coefficient of determination (Table 6). When two pairs of successive good flowering years were studied, the coefficients of determination were smaller in the latter years. However, the heritability estimates for both female and male flowering were, on the average, slightly larger in the latter years of these pairs of years (Table 3). This could be due to

clonal variation unrelated to the size of the ramets or the origin of the clone. This, again, indicates differing genetic responses to factors regulating flower induction.

Our results demonstrate that the genetic diversity of the seed crop cannot be estimated only on the basis of the census number of the seed orchard, but that variation in the ramet number and flowering abundance as well as pollen contamination must also be considered (Table 7). When the variation in the number of ramets per clone was included, the status number of the seed orchard decreased to 84% of the census number. This decrease in the genetic diversity of a seed orchard is mainly caused by technical difficulties caused by lack of material, mortality etc., which prevent equal numbers of ramets being obtained for each clone. The decrease in status number caused by the variation in ramet number was smaller than that in Norway spruce seed orchards in Finland on the average (Kang et al. 2000), and within the range of variation observed in seed orchards of several other species (Kjær et al. 1995, Kang et al. 2000).

The variation in the abundance of female flowering decreased the status number more than the variation in male flowering (Table 7). The variation among years was also greater after adjusting female flowering than after adjusting male flowering. In Norway spruce, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and noble fir (*Abies procera* Rehder) the relative status number of seed orchard crops after adjusting for the variation in female flowering varies considerably, but has usually been below 50% (Kjær et al. 1995, Kjær and Wellendorf 1998) which is in accordance with our results. In pines the relative status number has usually been higher than that for Norway spruce in our study (Kang and Lindgren 1998, Kjær and Barner 1998). The only available results concerning the effect of male flowering on genetic diversity indicated a lower decrease in status number in mature seed orchards of two pine species (*Pinus densiflora* and *P. thunbergii*) than in our study (Kang and Lindgren 1998). Our observation of the greater influence of variation in female than in male flowering was not unambiguously supported by the results for these pine seed orchards. Whether these results indicate systematic differences between pines and spruces is too early to say.

When both female and male contributions were adjusted together, the relative status number was slightly larger than that obtained after adjusting only for female or for male flowering (Table 7). In Norway spruce seed orchards in Denmark, the relative status numbers after adjusting for fertility variation in both genders was about the same as in our study (Kjær and Wellendorf 1998). According to Kjær et al. (1995), the effective clone numbers (equal to status number) of the seed crops of seed orchards of Norway spruce and noble fir always increase when both male and female flowering are adjusted. An increase in the status number of the seed crop after adjusting for both genders instead of only one, can be expected if there is sexual asymmetry between clones (Savolainen et al. 1993).

The status numbers, obtained after adjusting the fertility variation and weighted with the variation in the ramet number, were about half of the census number, with large annual variation. When pollen contamination was also taken into account, the status numbers clearly increased. The estimated level of pollen contamination in the studied seed orchard in three different years (1989, 1992 and 1993) is about 70% (Pakkanen et al. 2000). With this contamination level the status number of the seed crop after adjusting for all the existing variation would be the same as the census number of the orchard, and double the status number without pollen contamination. These results cannot be compared with those obtained in other studies because, as far as we know, the effect of pollen contamination on the genetic diversity of the seed orchard crop has not earlier been considered quantitatively. The results show that the level of pollen contamination has a great effect on the genetic diversity of the seed orchard crop. In our calculations pollen contamination was assumed to be derived from an infinite population of unrelated trees. If the fertilising pollen grains are related to each other or to the seed orchard clones, then the effect of pollen contamination will be smaller although still considerable (Lindgren and Mullin 1998).

In our study the differences between years with minimum and maximum status number were twofold when pollen contamination was not adjusted (Table 7). The genetic diversity of the

seed crop was the higher, the more abundant was the flowering. A similar result has been reported in other studies using either status number (Kjær and Wellendorf 1998) or other measures of genetic diversity (Ruotsalainen and Nikkanen 1989, Matziris 1993, Kjær 1996). In Scots pine the status number of the seed crop increases along with the seed crop with increasing age (Kjær and Wellendorf 1998), but in Norway spruce the development seems to be more erratic. According to our results, at an older age even a rather low flowering abundancy gives a more balanced seed crop than at a younger age (cf. years 1990–91 with 1984–86).

The results presented here do not concern the real seed crops, but have been predicted on the basis of flowering. However, there are several stages from flowering to seed crop that can affect the clonal contribution and thus the diversity of the seed crop (Sarvas 1968, Sweet 1975, Schoen et al. 1986, Schoen and Cheliak 1987). In a Norway spruce seed orchard the actual seed crop gave almost the same status number as the prediction based on the variation in flowering (Kjær and Wellendorf 1997). In a Sitka spruce seed orchard the relative effective clone numbers based on the number of cones and seeds differed considerably (Kjær et al. 1995). However, as also suggested by Kjær and Wellendorf (1998), monitoring the flowering abundance is a feasible means of obtaining a picture of the genetic diversity of seed crop. Differences between species can influence the feasibility of the method, and more comprehensive studies should be carried out on Norway spruce. Especially, the effect of male flowering and pollen contamination on genetic diversity should be clarified.

This study has demonstrated the large annual and clonal variation in female and male flowering in a Norway spruce seed orchard. On the basis of the differences in flowering abundance, the genetic diversity and the genetic composition of the seed crop varied from year to year. The estimate for the status number after adjusting for the variation in both female and male flowering was on the average 59%, and after adjusting for the variation in ramet number and estimated pollen contamination the same as the census number. The status number proved to be a feasible measure for describing the genetic diversity of the seed orchard crop. However, in order to be able to relate the level of genetic diversity of a seed orchard crop to the situation after natural regeneration, similar studies should also be conducted in natural stands.

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