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Flowering in a clone trial of *Picea abies* Karst

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Abstract

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The female and male flowering frequency were studied in a clone trial of Picea abies at Röskär nine kilometers north-east of Stockholm. During 1971 the extension in time of pollen shedding and female receptivity was recorded following daily examination of individual strobili.

The data obtained revealed a great variation in female as well as male flowering between the clones. Only a part of this variation could be attributed to differences in height of the clones. Great yearly variations in flowering of individual grafts were noticed.

Based on the flowering frequency as well as the pollen shedding and female receptivity during each day, the expected contribution of the different clones to the offspring was calculated. According to the calculations four of the clones contributed 55 per cent of the genes to the offspring. Many (66) of the 190 theoretically possible combinations among the 20 clones occurred in a lower frequency than 0.1 per cent.

The consequences of the data obtained for the genetic composition of the seed orchard progeny were discussed.

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Introduction

Flowering of the clones growing in a seed orchard are of importance for two different reasons.

1. As a limiting factor with respect to the amount of seed produced in the seed orchard
2. As a determinant of the genetic set-up of the seed material harvested in the seed orchard

The first reason is quite obvious since it determines the profitability of the seed orchard. On the other hand the second one may be less understandable for a layman. Therefore, reason number two will be discussed in more detail below.

At the first glance it might be expected that the gene frequencies of the clones in the seed orchard and the seed produced in the orchard are exactly the same. The prerequisite for the equilibrium situation is "panmixia" or expressed in another way "random mating" (including selfing). This ideal situation can easily be distorted by a lot of different factors. The main prerequisite of panmixia might be broken down to a series of factors:

1. the number of male gametes/clone is the same for all clones
2. the number of female gametes/clone is the same for all clones
3. the fertilization is completely random which means that
   a) time of flowering is completely synchronous
   b) the sperm nuclei of each clone have the same probability of reaching the ovules of each clone
   c) no incompatibility exists
4. no genetic factors cause any differences in embryo viability in any way
5. no fertilization with pollen originating from outside growing trees occurs
6. all clones have the same self-fertility.

Deviations from any of the prerequisites listed above might distort the equilibrium. (The unusual situation that several deviations balance each other may however occur.) Therefore, it is hardly believed that any of the seed orchards established shows exactly the same gene frequency in the parent generation as in the offspring generation.

Slight deviations are probably without practical importance. If the deviations are large the consequences ought to be discussed. The genetical variation may be unacceptably small. Further, the actual genetic value of the seeds may deviate considerably from the mean value of the parents, and this may decrease the value of the progeny testing for a prediction of the genetic value of the clones in a seed orchard. The deviation may be positive as well as negative. It might be judged desirable to take measures to improve a situation caused by deviations from the prerequisites listed above.

The greatest deviation from the equilibrium situation would appear if a self-fertile clone contributes to the majority of the gametes in a seed orchard. This might cause the formation of inbred seeds which in turn might cause a severe inbreeding depression. Thus Eriksson (1972) reported a reduction of the volume production in *Picea abies* by 50 per cent following selfing. It should be pointed out that such an extreme situation will hardly ever appear in any of the clonal seed orchards composed of more than 30 different clones.

To get a firmer base for a further discussion concerning the importance of deviations from the equilibrium situation it was found worthwhile to study the following factors:

A. the number of male and female strobili/graft
B. the point of time for the pollen shedding
C. the point of time for the receptivity of the female strobili.

The study was performed in a clone trial of *Picea abies*, Based on the data from this investigation it will be possible to estimate the gene contribution of the individual clones to the filial generation.

A phenological study of the clones is also of importance for the composition of the second generation seed orchards if they will be built up by clones from the first generation seed orchards.

Johnsson (1965) pointed out that the effective number of clones in a seed orchard was lower than the real one depending on variation in fertility and the moment of the flowering. The pronounced differences concerning male and female flowering also contribute to a reduction of the effective number of clones. The importance of the flowering characteristics have also been discussed by Andersson (1967). Thus, there seems to be a need for a quantitative estimation of the effect on the genetic set-up in the seed orchard progeny caused by the flowering characteristics.

Material and methods

The clone trial used for this investigation was established in 1959 by the Co-ordination Committee for Forest Tree Breeding and Genetics. Four years old grafts belonging to 22 different clones of *Picea abies* were used. The clones growing in this trial constitute selected plus trees from southwestern Sweden (O- and P-counties). The stands in which the selections were performed were in some cases non-indigenous. Thus, ten of the clones are of French origin and four of them are of German origin. The rest of the clones (8) originate from autochtonous stands. The clones are listed in Table 1. The clone trial is located at Grabbtorp, Röskär, nine kilometres north-east of Stockholm.

The clone trial consists of five complete replicates with 22 plots, each plot comprising 5 grafts planted in a line. The plots within the replicates were randomised irrespective of the origin of the clones. Some of the grafts have not survived. Partly they were replaced by grafts of the same age but a few clones are represented with less than 25 grafts. The empty spots have probably not yet any influence on the flowering of neighbouring grafts since the spacing is 3 metres within rows and 4 metres between rows. Around the trial two rows with spruce seedling plants were planted. The total area of the trial is 6600 m^2.

From 1967 and onwards the number of female strobili of each graft has yearly been counted. The number of male strobili has simultaneously been estimated.

In 1967, 1968 and 1969 all male strobili were counted. As the number of strobili increases by the size of the grafts the counting becomes more and more tedious. It is not realistic to count all strobili in a graft with thousands of strobili. Therefore some method of estimation had to be used. In 1970 a counting of all strobili growing on one graft of each clone was performed. The number of strobili in the other grafts were estimated. In 1971 a method of estimation was used. If the number of male strobili exceeded 100 an estimate of the total number of strobili was based on the number of male strobili on some branches. Using this technique it is assumed that the estimate usually falls within 25 per cent of the true

Table 1. Clones included in the clone trial at Röskär

Clone	French (F) German (G) Swedish (S)	Height (cm) mean 67 and 71	Remarks
O 1000	F	155.4	
O 1001	F	209.6	
O 1002	F	130.8	1.2
O 1003	F	251.6	
O 1004	F	214.9	2
O 1005	F	208.8	
O 1006	F	192.6	
O 1007	F	238.6	
O 1008	F	268.3	
O 1009	F	223.5	
O 2000	G	229.5	
O 2001	G	212.3	
O 2002	G	195.9	
O 2003	G	263.2	
O 2006	S	278.6	
O 2008	S	192.6	1
O 2011	S	143.6	
O 2012	S	112.9	
O 2013	S	280.9	
O 2014	S	138.2	
P 2001	S	179.7	
P 2002	S	339.1	

Remark 1. These clones has not been included in the analysis of variance as they are not represented in all blocks (p. 14).
Remark 2. These clones are not included in the imaginary seed orchard (p. 28) as the number of female strobili 1971 was too low to make an estimation of the receptive period.

value. The total relative error of a whole clone ought to be lower, but no reliable estimate of the systematic error can be given.

The study of the point of time for the pollen dispersal and the receptivity of female strobili was done during 1971. As regards the pollen dispersal 50 male strobili from each clone except for the clones O 1002 and O 1004 were labelled. The sparse female flowering was the reason for the exclusion of these clones. Labelling was attempted in such a way that the strobili examined should be as representative as possible for the growth positions of the male strobili within the crown of a particular graft. Mostly the labelling comprised four grafts (12 or 13 strobili on each) from each clone.

When a pollen cloud could be seen following a faint vibration of the part of a twig where the strobilus was growing, it was noted that this particular strobilus dispersed pollen. We are aware that this technique might indicate a pollen dispersal on a day when no spontaneous pollen dispersal took place owing to a too high air humidity (cf. Sarvas 1955). However, this seemed to be the only way to record the pollen shedding of a certain strobilus during a series of days. This technique also constitutes the only way to estimate the total duration of the pollen dispersal of individual strobili. In contrast to automatic recordings of the pollen density in the air our method discriminates between the pollen shedding of different clones. We also believe that our method constitutes a reliable basis for a calculation concerning the relative contribution of the different clones to the pollen cloud. Moreover, the simultaneous use of our technique and an automatic recording of the pollen density would offer an opportunity to estimate the contribution of pollen from outside growing trees to the pollen cloud of a seed orchard.

The labelling of the female strobili was done in almost the same way as for the male strobili. It has to be mentioned that the sparse flowering of some clones necessitated that more than 13 strobili from a certain graft had to be labelled in a few cases. The classification of the strobili with respect to receptivity was done in almost the same way as by Brøndbo (1971). A strobilus was regarded as receptive when a few cone scales were in a perpendicular position to the axis of the strobilus. The appearance of the stages will be presented and discussed below.

The temperature data used for the calculations of the temperature sums were obtained from the meteorological station situated 700 metres to the west of the clone trial.

Flowering frequency

Yearly variations in flowering

An evaluation of whether or not any differences exist between the clones with respect to frequency of female or male strobili per graft may be unreliable if the evaluation is based on data obtained a certain year. This is conditioned by the cyclic rhythm of flowering in *Picea abies* which was first carefully analysed by Tirén (1935). The periodicity of flowering in *Picea abies* has later on been reported on several occasions *e.g.* Sarvas (1968) and Hagner (1965). Such a periodicity is not confined to *Picea abies* but seems to be of general occurrence in many conifers (see *e.g.* Baron 1969, Bramlett 1972, Rehfeldt *et al.* 1971, Schubert and Rietveld 1970). A summary of the data published before 1942 was presented by Baldwin (1942).

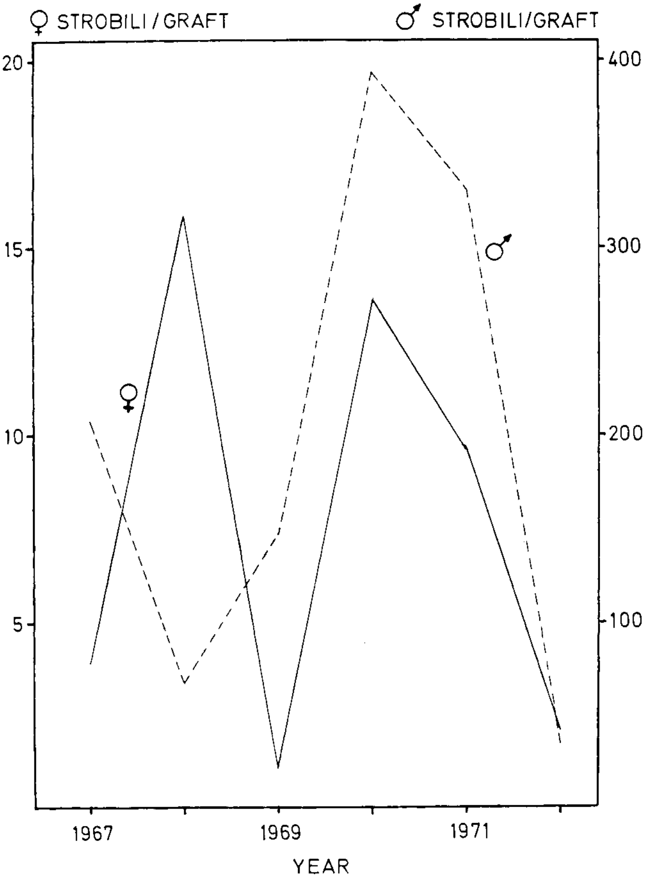

Figure 1. The mean number of female and male strobili per graft of 22 clones of *Picea abies* growing in a clone trial at Röskär (9 km northeast of Stockholm). The grafting was done in 1955.

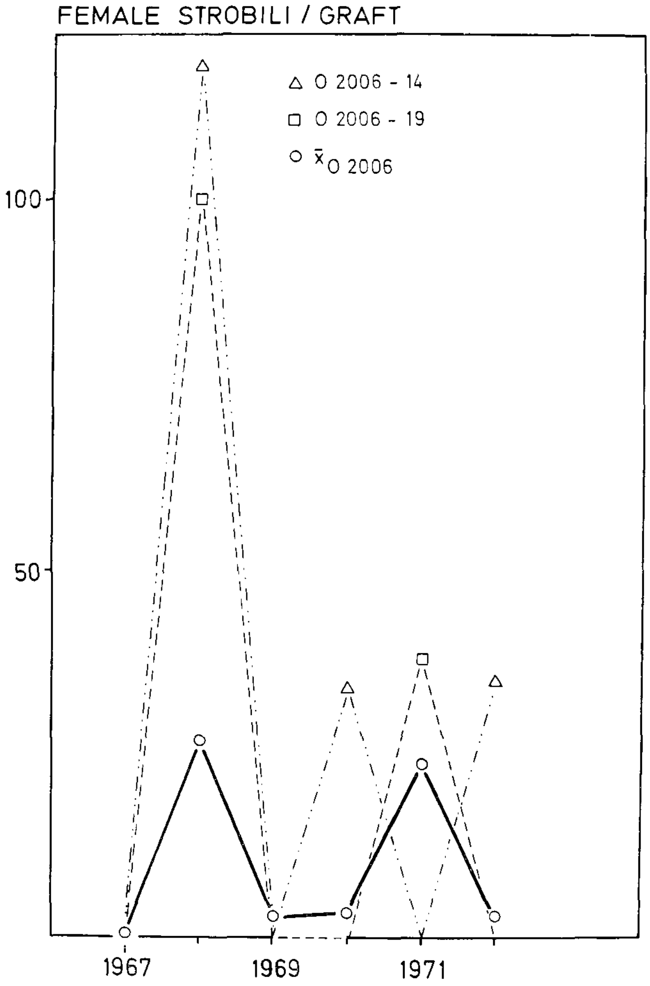

Figure 2. The mean number of female strobili per graft in a clone of Swedish origin. The number of female strobili of two individual grafts is also demonstrated.

In a previous report (Eriksson 1972) it was shown that the frequency of female and male flowering varied considerably from year to year in this particular clone trial. The data from the French, German, and Swedish clones were illustrated separately. Except for 1971 the three categories were completely in phase with each other both with respect to female flowering and male flowering. In Figure 1 the average number of female strobili per graft is illustrated independent of their origin. Before a discussion of this diagram is done it should be mentioned that the flowering before 1967 was sparse in all clones.

As seen from Figure 1 the female flowering shows two peaks, one during 1968 and a second during 1970—1971. The extension of the second peak over two years can to its greatest extent be attributed to the profuse flowering of four Swedish clones during 1971: O 2006, O 2013, P 2001, and P 2002. Two of them flowered abundantly during 1970 too.

The best way to detect the yearly variation in flowering is probably to study the number of strobili on individual grafts.

Figure 2 was drawn to exemplify the necessity of studying individual grafts to reveal the yearly fluctuations in flowering.

In this figure the average number of female strobili per graft in clone O 2006 is illustrated for the period 1967—1972. In addition, the number of strobili of two of the 25 grafts belonging to this clone is demonstrated. Both grafts flowered profusely in 1968. After 1969 only one of the grafts, No. 19, is in phase with the general pattern of flowering in this clone. Thus, in 1970 and 1972 No. 14 showed peaks in contrast to No. 19. On an individual tree basis it may be stated that a year of abundant flowering is followed by a poor one. This agrees well with the statements by Tirén (1935). Recently Bastide and Vredenburch (1970) as well as Rehfeldt *et al.* (1971) have used sophisticated statistical calculations to evaluate the influence of different climatic factors on the flowering.

The male flowering which starts earlier than the female flowering in *Picea abies* is not believed to influence the seed set to the same extent as the female flowering. Except for the years 1968 and 1972, sufficient amounts of pollen have probably been produced.

It is interesting to note that the male and female flowering was not in phase with each other during the first three years 1967—1969.

Finally it should be added that the flowering of *Picea abies* during 1972 was extremely poor all over Sweden. It is probable that an interaction between climatic factors and the vegetative status of the trees are responsible for the poor flowering in 1972. As for the clone trial studied an analysis of the influence of external and internal factors on the flowering has to be postponed for another five to ten years.

Flowering and tree height

There are evident differences between the clones concerning the abundance of flowering (cf. Table 2, where the percentage of

Table 2. The percentage of strobili and calculated gametic contributions in the imaginary seed orchard (cf. p. 28)

Clone	Strobili			Gametes transmitted		
	Female[1]	Male[1]	Mean	Female	Male	Mean
	x_1	x_2	x_3	$y_1 = x_1$	y_2	y_3
O 1000	1.80	1.11	1.45	1.80	0.41	1.10
O 1001	1.75	2.22	1.98	1.75	1.29	1.52
O 1003	1.70	1.83	1.76	1.70	1.01	1.36
O 1005	1.79	1.05	1.42	1.79	0.42	1.11
O 1006	5.69	1.36	3.52	5.69	0.78	3.24
O 1007	4.19	12.71	8.45	4.19	6.08	5.13
O 1008	4.27	9.07	6.67	4.27	2.75	3.51
O 1009	0.52	3.70	2.11	0.52	1.58	1.05
O 2000	3.74	0.92	2.33	3.74	0.44	2.09
O 2001	3.06	2.79	2.92	3.06	2.67	2.87
O 2002	6.09	3.43	4.76	6.09	2.55	4.32
O 2003	1.64	2.38	2.01	1.64	5.30	3.47
O 2006	11.30	22.62	16.94	11.30	23.40	17.35
O 2008	4.17	6.76	5.46	4.17	17.95	11.06
O 2011	1.33	1.17	1.25	1.33	5.01	3.17
O 2012	1.59	1.45	1.52	1.59	0.72	1.16
O 2013	18.58	4.17	11.38	18.58	2.52	10.54
O 2014	1.76	1.12	1.44	1.76	1.95	1.85
P 2001	10.33	4.94	7.63	10.33	4.48	7.40
P 2002	14.70	15.20	14.95	14.70	18.69	16.70

[1] Remark. 1 per cent corresponds to 2.09 female flowers/graft resp. 50.2 male flowers/graft.
$r_{x_1 x_2} = 0.54$; $\Sigma x_1 x_2 = 789.233 = 7.89\,\%$ selfing; $r_{x_3 y_3} = 0.931$; $r_{x_2 y_3} = 0.831$

strobili in 20 of the clones is presented). In 1971 the difference in flowering frequency between clones was highly significant (cf. below). In Figures 3—4 the mean number of strobili is plotted against the mean height for each clone (means for 5 years used). Evidently there is a strong relationship between the clone height and the clone flowering. It may be mentioned that Sarvas (1968) found a positive correlation between the amount of pollen and cones produced per m² ground area and the dominant height of a stand. Recently Remröd (1973) reported that the frequency of female flowering in *Picea abies* was dependent on the size of the grafts. Thus, it is justified to ask the question to what degree the differences in flowering within and between the clones can be attributed to the variation in height. Therefore, it would be desirable to adjust the flowering for the height.

Before any further calculations are performed the problem of suitable transformations has to be discussed.

The flowering varies considerably. This complicates the analysis of variance. The variance of the flowering increases with increasing flowering, which means that the basic prerequisite for an analysis of the variance, the constant variance of the experimental error, is not fulfilled. The fact that the flowering is increasing faster than linearly by the height will also complicate the analysis of the relationship between flowering and height. It might be added that the analysis would be improved if the exact relationship between the height and the number of potential positions within the crown for female or male strobili was known. In lack of knowledge of an exact relationship the square root transformation of the number of strobili was chosen as it seems to be biologically probable that the number of strobili increases by the area of "the surface" of the tree, at least concerning trees of some metres in height.

Another alternative may be to make a logarithmic transformation of the height (x) as well as the number of strobili (y) and then find the least square solution within plots for the regression equation

$$\log y = C_1 + C_2 \log x.$$

If $C_2 = 2$ this is similar to the square root transformation used. In the study by Sarvas (1968) referred to above, the following relationships were obtained between the amount of pollen grains (y_1 g/m²) or the number of cones (y_2/m²) produced and the dominant height of a stand (x—x covers the range 20.5—28.0 m)

$$\log y_1 = -2.459 + 1.991 \log x$$
$$\log y_2 = -4.661 + 3.404 \log x$$

With respect to the male flowering Sarvas' data is in excellent agreement with the assumptions of proportionality between the height and the square root of the number of strobili. As regards female flowering the agreement is not as good. However, such a strong dependence on the height as found for female flowering by Sarvas can hardly be valid over all heights.

The effect of using the square root transformation on the clonal mean values may be studied by comparing Figures 5—6 with Figures 3—4. The deviations from the regression line is more independent of height if the transformation is used. The correlation is somewhat, but only slightly improved.

For further calculations an adjustment for each tree was carried out in the way described below.

It is assumed that the flowering of a graft may be expressed by

$$Y_{ij} = \mu + \beta(X_{ij} - \overline{X}) + \alpha_j + \varepsilon_{ij} \qquad (1)$$

Y_{ij} denotes the square root of the number of strobili of the i:th graft within the j:th plot
μ is a mean effect
X_{ij} denotes the height of the i:th graft within the j:th plot
$\overline{X}$ is a "standard height"
β denotes a constant regression coefficient
α_j is a "plot effect of the j:th plot". Thus α_j denotes the joint effect of clone and block
ε_{ij} is a trial error of the i:th graft of the j:th plot. ε_{ij} is expected to be approximately normally distributed with a constant variance independent of the other parameters involved.

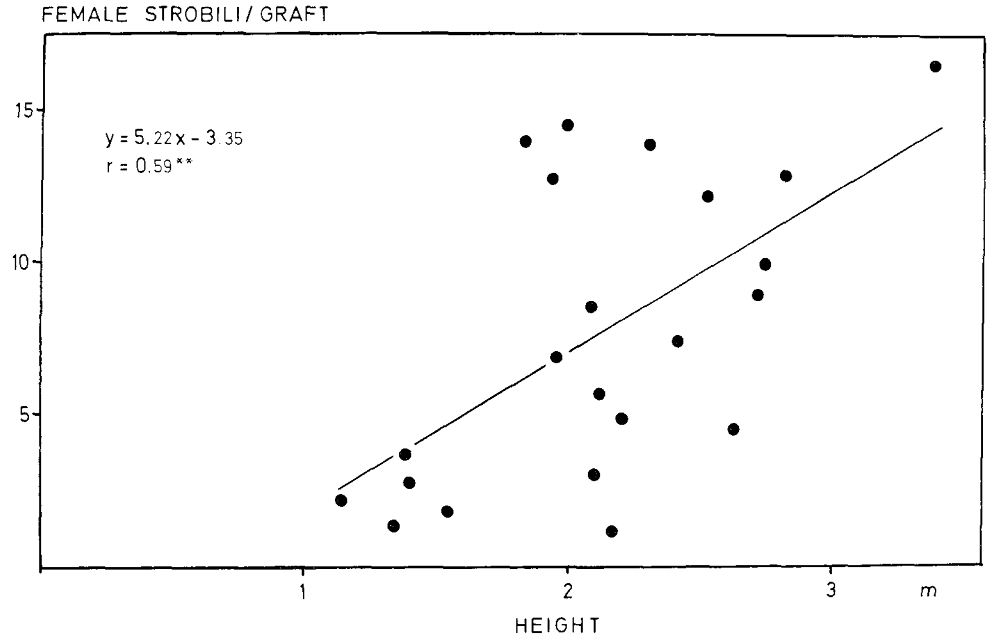

Figure 3. The relationship between the mean female flowering per graft of the *Picea abies* clones growing in a clone trial at Röskär (9 km northeast of Stockholm) during the period 1967—1972 and their mean heights (average heights of the measurements carried out in 1967—1971).

It is assumed that α_j and ε_{ij} are independent of X_{ij}, if the correct value of β is used.

In such a case all dependence on the “concomitant” variable, the height, can be released by studying the variable Z, the number of strobili adjusted for height

$$Z_{ij} = Y_{ij} - \beta(X_{ij} - \bar{X}) = \mu + \alpha_j + \varepsilon_{ij} \qquad (2)$$

instead of Y_{ij}

β can be estimated within each plot, when α_j is a constant

$\hat{\beta} = \frac{\Sigma(X-\bar{X})(Y-\bar{Y})}{\Sigma(X-\bar{X})^2}$, when $\Sigma(X-\bar{X})(Y-\bar{Y})$ and $\Sigma(X-\bar{X})^2$ are calculated within plots. (Thus $\bar{X}$ and $\bar{Y}$ refers to plot means.)

An estimate for the whole material can easily be obtained by summing up the values of $\Sigma(X-\bar{X})(Y-\bar{Y})$ and $\Sigma(X-\bar{X})^2$ for all plots and calculate a pooled estimate of β. After that the adjusted height Z is calculated and an ordinary analysis of variance is performed.

The mean number of female and male strobili was calculated for the years 1967—1971 for each graft (the number of female strobili was actually multiplied by 10 for technical reasons). This complicates the interpretation somewhat. Then the square root was calculated (Y_{ij}). Since the calculation was started with a determination of an arithmetical mean an emphasis is given to years with a profuse flowering. Thus, the clones which contribute much to the flowering a year with a low frequency of flowering and less a year with abundant flowering will get a lower mean value than clones with a reverse performance. For each tree the mean value of the height 1967 and 1971 (X_{ij}) was determined.

Based on the pooled value of the regression of the flowering on the height (cm) the following expressions were obtained:

Female:

$$Z_{ij} = Y_{ij} + 0.020961\,(214.02 - X_{ij}) \qquad (3)$$

Male:

$$Z_{ij} = Y_{ij} + 0.043088\,(214.02 - X_{ij}) \qquad (4)$$

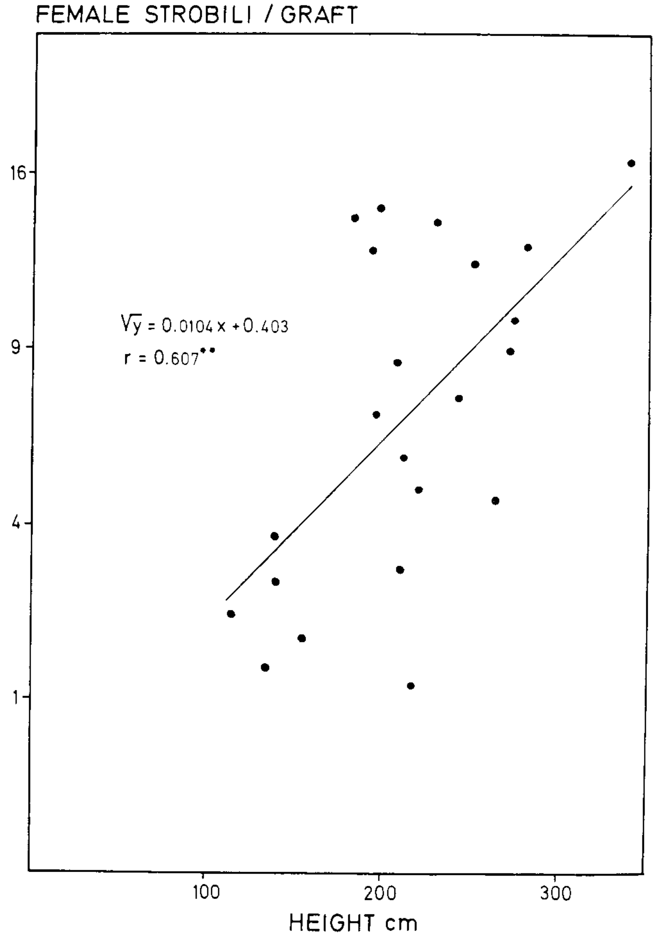

Figure 4. The relationship between the square root of the female flowering per graft of *Picea abies* clones growing in a clone trial at Röskär (9 km northeast of Stockholm) during the period 1967—1972 and their mean heights (average heights of the measurements carried out in 1967—1971).

Clonal and interblock variations in flowering

For further analysis of variance the following model was assumed:

$$Z_{kl} = \mu + c_k + b_l + \varepsilon_{kl} \qquad (5)$$

where

Z_{kl} = plot mean of the flowering (square root of number of strobili of the k:th clone in the l:th block at a standard graft height of 214 cm. From a mathematical point of view equations (3) and (4) are valid even if Z_{ij}, Y_{ij} and X_{ij} are replaced by the plot means, which simplifies the calculation work.

μ = a mean effect

c_k = the additional effect of the k:th clone

b_l = the additional effect of the l:th block (thus α_j of equation (1) and (2) has been divided into a block and a clone effect)

ε_{lk} = "experimental error" (Not identical to the "experimental error" of equations (1) and (2). This "experimental error" includes variation between plot means and interactions between blocks and clones.)

Instead of using missing value techniques, the analysis was restricted to 20 clones which were represented in all plots.

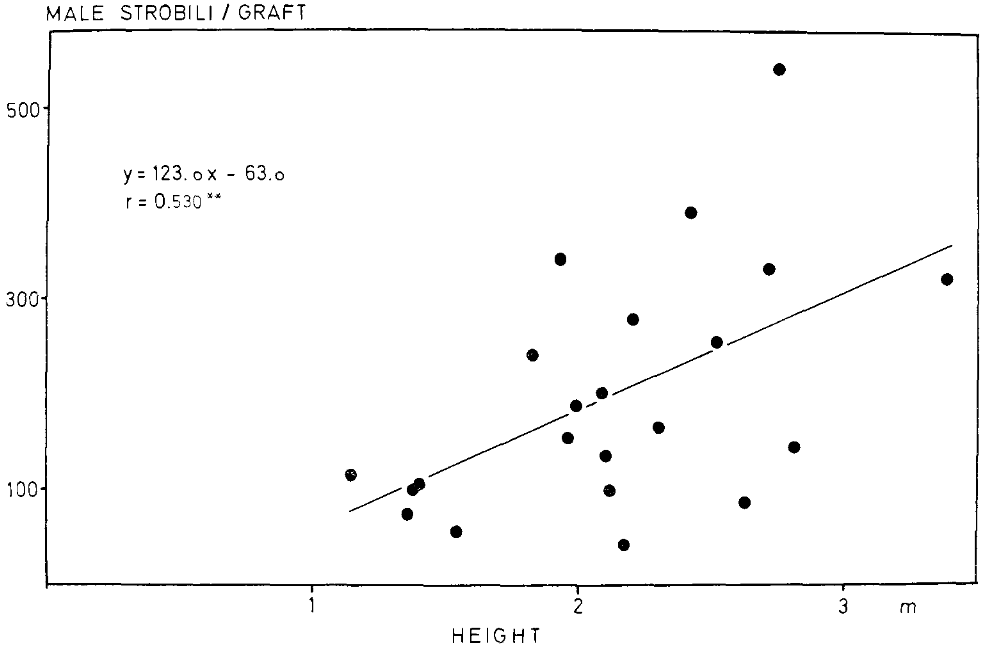

Figure 5. The relationship between the mean male flowering per graft of *Picea abies* clones growing in a clone trial at Röskär (9 km northeast of Stockholm) during the period 1967—1972 and their mean heights (average heights of the measurements carried out in 1967—1971).

Analysis of variance, female strobili

Source	Square sum	Degrees of freedom	Mean square	Estimate of
Between blocks	27.180	4	6.795	$\sigma^2 + 20\sigma_b^2$
Between clones	648.053	19	34.108	$\sigma^2 + 5\sigma_c^2$
Residual	335.712	76	4.417	σ^2
Total	1010.945	99		

F between blocks = 1.538 (not significant)
F between clones = 7.722 ($p < 0.001$)

	%	
$\sigma_b^2 = 0.189$	1.1	$\sigma_b = 0.345$
$\sigma_c^2 = 5.9382$	56.7	$\sigma_c = 2.437$
$\sigma^2 = 4.417$	42.2	$\sigma = 2.102$

H^2 = repeatability of plot mean = 0.567

Analysis of variance, male strobili

Source	Square sum	Degrees of freedom	Mean square	Estimate of
Between blocks	25.20	4	6.300	$\sigma^2 + 20\sigma_b^2$
Between clones	1423.19	19	74.905	$\sigma^2 + 5\sigma_c^2$
Residual	507.44	76	6.677	σ^2
Total	1955.83	99		

F between clones = 11.21 ($p < 0.001$)

	%	
$\sigma_b^2 =$ 0 (negative)	0.0	$\sigma_b = 0$
$\sigma_c^2 = 13.645$	67.1	$\sigma_c = 3.694$
$\sigma^2 = 6.677$	32.9	$\sigma = 2.584$

H^2 = repeatability of plot mean = 0.671

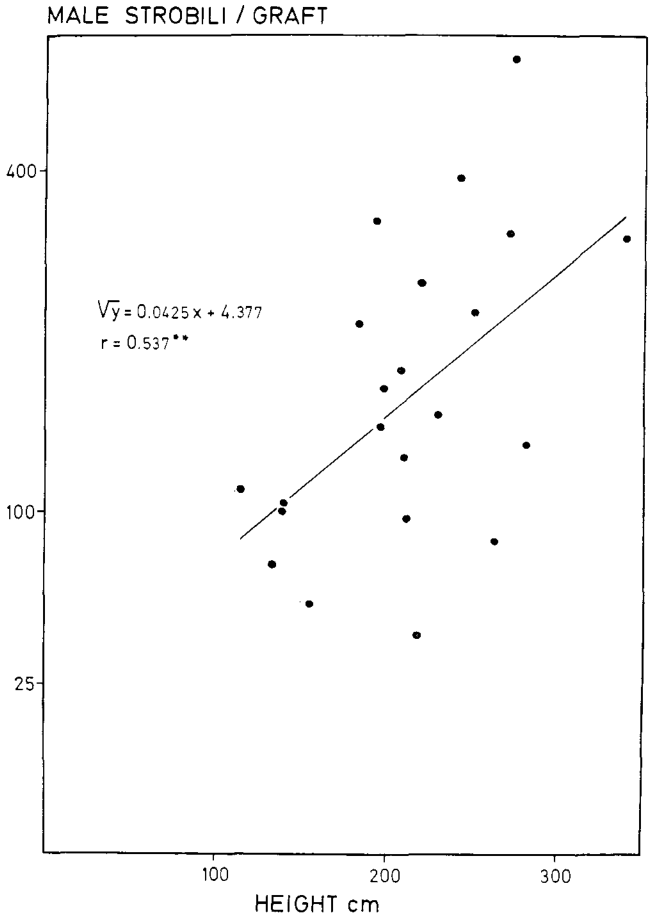

Figure 6. The relationship between the square root of the male flowering per graft of *Picea abies* clones growing in a clone trial at Röskär (9 km northeast of Stockholm) during the period 1967—1972 and their mean heights (average heights of the measurements carried out in 1967—1971).

In an analysis of variance of the untransformed data of flowering of 1971 only and not adjusted for height the following variance components and significancies were obtained:

	Female %	Male %
σ_b^2	3.8	16.4
σ_c^2	62.9	41.6
σ^2	33.3	42.0

Significance	Female	Male
Between blocks	$0.01 < p < 0.05$	$0.001 > p$
Between clones	$0.001 > p$	$0.001 > p$
H^2	0.629	0.416

Block differences. No block differences were obtained by height adjusted flowering data accumulated for several years. The block differences obtained 1971 might thus be due to differences in height between blocks or interaction between blocks and year. A more detailed study of the differences between years is planned to take place, when more data have been accumulated. The possibility of an influence of the block height will be discussed.

Following exclusions of all data which did not fit into an ortogonal design "balanced mean values" were calculated (Table 3).

The figures for flowering are derived from data of five years flowering. They constitute the root of the mean of the squares of individual grafts. The heights (cm) are the means of the two years 1967 and 1971. The figures are not exactly comparable with those presented in the previous analysis of variance as data has been excluded to get balance. The difference in height between blocks was found to be significant ($p < 0.001$). The figures for male flowering seem to be closely correlated with the block height. For the figures for female flowering no correlation is indicated. Thus height differences between the blocks may cause differences in male flowering between blocks.

Clone differences. As is quite evident from the analysis of variance presented above there are strongly significant differences between clones both with regard to female and male flowering compared at a standard height. The "mean" number of strobili per year and graft is presented in Figures 7—8. "Mean" number means the square of the square root plot means at a standard height of 214 cm. The "means" are thus not simple arithmetic ones (the arithmetic means will generally be a little higher). For ranking purposes the presented means are slightly superior as they are less dependent on the occurrence of individual grafts with an abundant flowering.

Table 3. Balanced mean values of female and male flowering and heights.

	Female strobili	Male strobili	Height cm
Block 1	8.24	15.98	261.8
2	8.85	12.98	193.5
3	8.59	13.96	222.2
4	8.21	13.56	203.7
5	8.91	14.40	249.4

The correlations between height-adjusted number of strobili (Figures 7—8) and height (Table 1) were calculated:

r female strobili – height = 0.28
r male strobili – height = 0.044

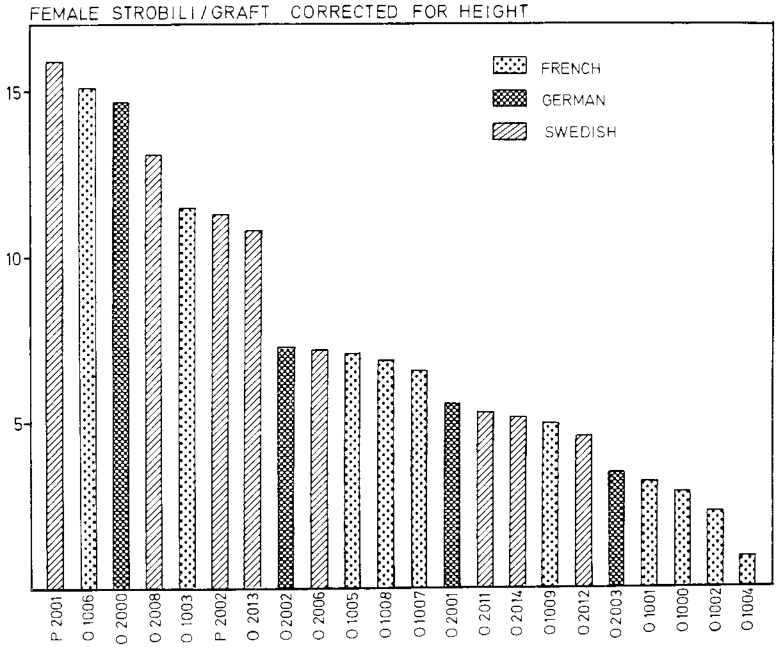

Figure 7. The number of female strobili per graft of 22 clones of *Picea abies* growing in a clone trial at Röskär (9 km northeast of Stockholm). The numbers are adjusted to a standard height of 214 cm (cf. the text).

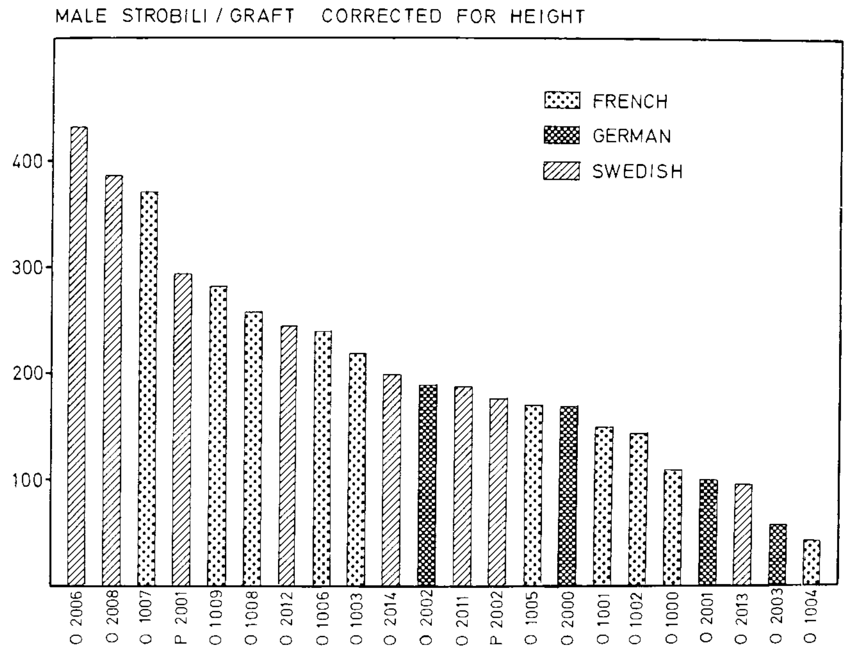

Figure 8. The number of male strobili per graft of 22 clones of *Picea abies* growing in a clone trial at Röskär (9 km northeast of Stockholm). The numbers are adjusted to a standard height of 214 cm (cf. the text).

(The calculations are meaningful as the adjustment of height was done based on the within plot variance.)

Neither of the correlations is significant. However, there is a slight indication that the most fast growing trees also have more female strobili at an equal height. It may be regarded as promising that the height growth does not even reduce the flowering capacity when the clones were compared after the adjustments of the flowering to a standard height. Since there was a direct and strong relationship between tree growth and non-adjusted flowering it means that the favour of a good growth for an increase of the flowering will be still more accentuated.

The relation between fast growth and number of female strobili found is in agreement with the reports of Sarvas (1968) and Remröd (1973). In this connection it might be mentioned that Johnsson (1973) found a positive correlation between breeding value for height and seed production in a progeny test of Scots pine clones from a seed orchard.

As seen from Figure 7 there was a tendency in the Swedish clones to produce more female strobili than the French ones. The German clones are intermediary. As regards male flowering the Swedish clones seem to be somewhat more outstanding than was the case for the female flowering (Figure 8).

A great variation in female flowering between different clones of *Picea abies* growing in a clone archive in Grimstad (S-county), in western Sweden was reported by Nilsson and Wiman (1967). They studied the flowering at the age of 9, 11 and 22 years. Only at the age of 22 years did a considerable flowering occur, which means that the information with respect to flowering is limited to just one year. Therefore, knowing the great yearly fluctuations in flowering, it is hard to draw any definite conclusions with respect to clonal variation in female flowering from the data presented

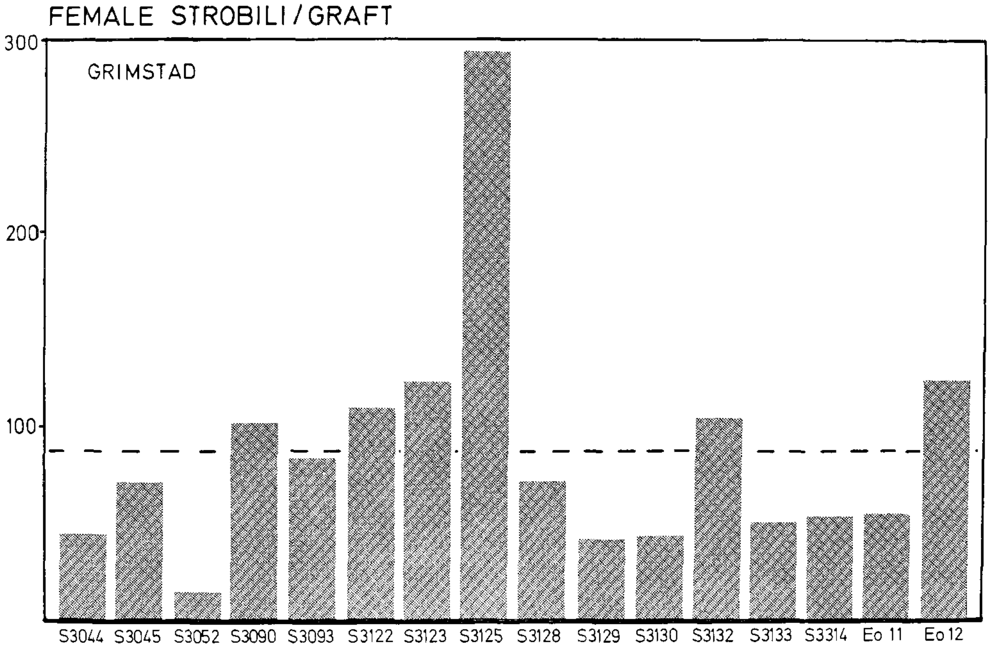

Figure 9. The mean number of female strobili per graft of some *Picea abies* clones growing at Grimstad. The means refer to observations made 22, 24 and 25 years after grafting. Original data emanate from Ljunger (presented as a table in Andersson *et al.* 1972).

by Nilsson and Wiman. However, the female flowerings have been recorded in this clone archive two more years, 1969 and 1970 (Andersson *et al.* 1972, the original data were offered to these authors from Ljunger, who will give a detailed presentation of those data later on). Based on the data presented by Andersson *et al.* (1972) we have calculated the average number of female strobili per graft for the three years 1967, 1969 and 1970. These years were rich in female flowering which means that the number of strobili per graft will show up much higher than if the average flowering had been based on data from a continuous series of years. As seen from Figure 9 the average female flowering of these 14 clones varied considerably.

Similar observations of differences in the flowering of Norway spruce clones growing in a clone archive in Southern Sweden have been observed by Kiellander (personal communications).

In this context it may be worth mentioning that striking differences in flowering frequency between trees in a stand of *Picea abies* have been reported by Eliason and Carlson (1968). The flowering of the Norway spruce trees studied in their investigation was recorded 12—18 years after the planting of the stand.

A clonal difference with regard to flowering is not confined to *Picea abies* among the conifers. Thus, Johnsson (1961) showed a significant difference in seed production of individual clones of *Pinus silvestris.* Similar differences have *e.g.* been reported for *Pinus rigida* (Barnes and Bengtson 1968), *Pinus taeda* (Bergman 1968), *Pinus monticola* (Bingham and Rehfeldt 1970), *Pinus echinata* (Bramlett 1972), and *Pseudotsuga menziesii* (Orr-Ewing 1969).

Pollen dispersal

In 1971 the pollen dissemination started on May 14 and lasted to the very end of May. The duration of the pollen dispersal from individual strobili will be discussed below.

We have preferred to illustrate the time of the pollen dispersal by selecting two clones, *viz* the earliest starting one and the latest starting one (cf. Figure 10). The average of all clones is also demonstrated in Figure 10. The curves of the two clones resemble each other, the only important dissimilarity being the dislocation in time between the two curves.

The plotting of the percentages against the time is of some value for the artificial pollinations in the seed orchards. However, the temperature conditions which have proven to be responsible for the onset of anthesis (Sarvas 1970 b) are not stable but vary from year to year. Therefore, to obtain information less dependent on the temperature conditions in a particular year it is better to relate the pollen dispersal to a temperature sum of the type $\Sigma(t_m - 5)$, in which t_m = the daily mean temperature of the days with a temperature exceeding +5°C. A critical temperature of +5°C has been shown to be a figure which well describes some biological processes (Sarvas 1967 b). However, in our material the development proceeded even on days with a temperature below +5°C. As an example of this it might be mentioned that the temperature sum remains constant from May 22 to May 25 if

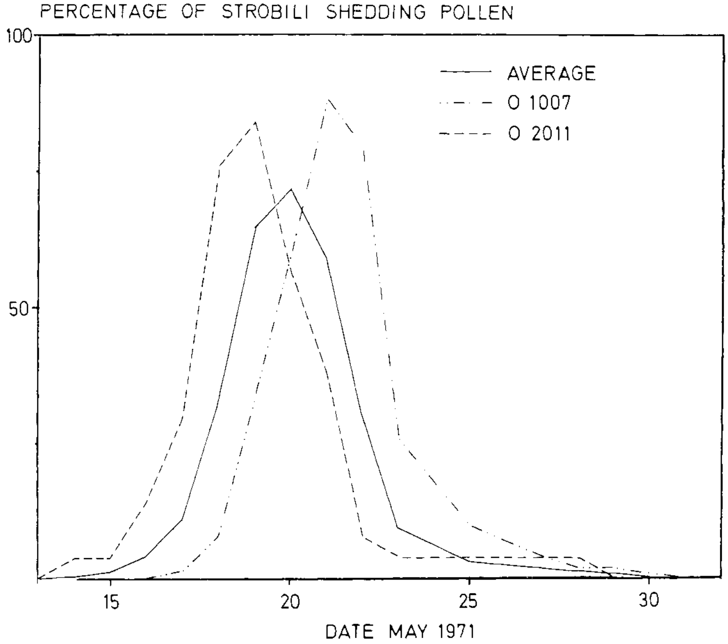

Figure 10. The average percentage of strobili shedding pollen from 22 clones of *Picea abies* on different occasions during May 1971. The percentage of strobili shedding pollen in the earliest clone O 2011 and the latest clone O 1007 is also demonstrated.

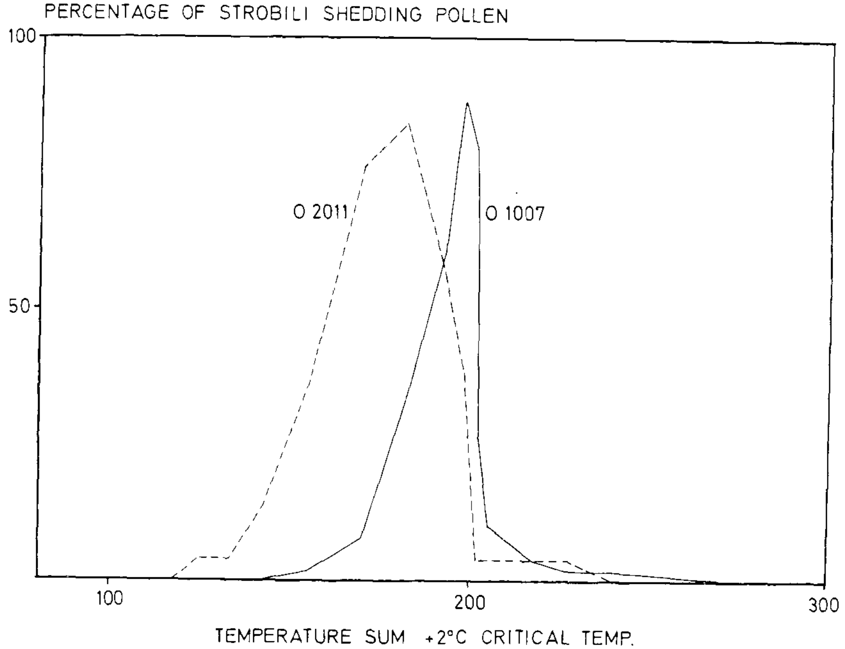

Figure 11. The relationship between the number of strobili shedding pollen in the clones O 2011 and O 1007 and the temperature sum $\Sigma(t_m - 2)$.

+5°C is selected as the critical temperature. In clone O 1007 the percentage of strobili shedding pollen decreased from 78 to 10 during those days which suggests that +5°C is not the best choice of critical temperature. In this context it has to be recalled that our observations were made on the same strobili during a series of days. Therefore statistical fluctuations owing to the examination of different strobili are excluded.

Since the lowest temperature during the pollen dispersal amounted to +2.9°C we will use +2°C as a critical temperature. This will be done without stating that +2°C is the best choice of critical temperature from a biological point. An estimation of the critical temperature must be based upon analyses during more than one year.

In Figure 11 the pollen dispersal of the clones O 1007 and O 2011 is plotted against the temperature sum: $\Sigma(t_m - 2)$. In this case the pattern of the two clones differs considerably. The occurrence of any inherent differences of the clones has to be evaluated after examination during different years.

The average duration of the pollen dispersal of individual strobili of the 22 clones varied between 2.2 and 4.1 days. This difference may partly be attributed to the fact that the strobili of the late clones dispersed pollen when the temperature was lower than when the early clones shed their pollen.

Since the clone trial consists of clones originating from three different geographic areas it is of interest to investigate whether any differences between the three types of clone occur. The temperature sum (+2°C as critical temperature) for onset of pollen dispersal in 50 per cent of the strobili was determined for each clone. To obtain a measure of the duration of the pollen dispersal the curves showing the percental pollen shedding was used. In this case the difference between the ascending and descending parts was read at the 50 per cent level in the curves. As seen from Figure 12 the sequence of the onset of pollen dispersal was: Swedish—German—French. Based on an analysis of variance it could

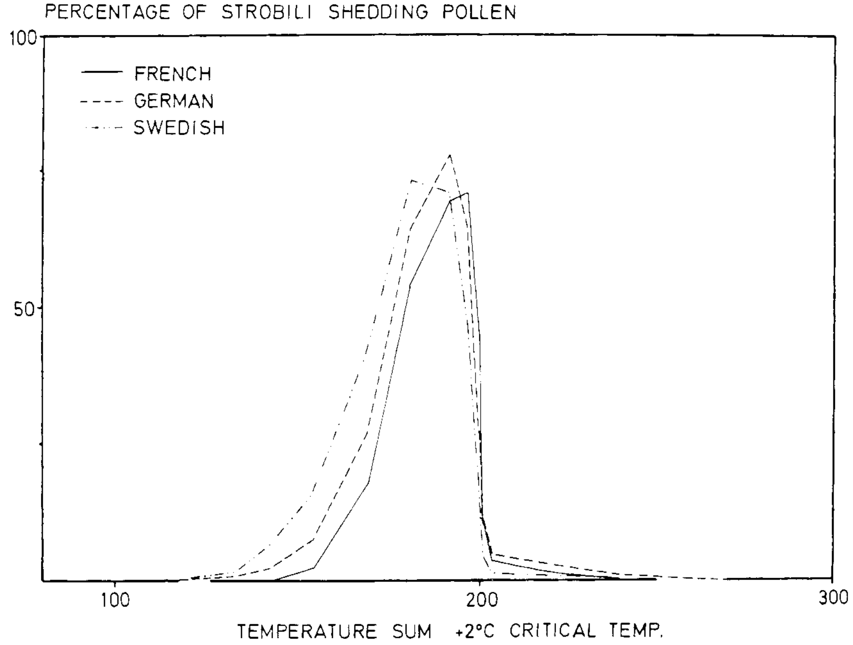

Figure 12. The average percentage of strobili shedding pollen in the clones of French, German and Swedish origin.

be disclosed that the difference was significant at the one per cent level. With respect to the duration of the pollen dispersal there was a significant difference at the five per cent level.

According to Sarvas (1967 b) the populations are adapted to the climatic conditions prevailing on their growth localities in the way that *e.g.* anthesis occurs when 17 per cent of the yearly temperature sum—$\Sigma(t_m - 5)$—is reached. In agreement with this it was expected that the anthesis would start earlier in the Swedish clones than in the French and German clones which was also the case in our investigation.

The development of the female strobilus

In Brøndbo's paper (1971) the appearance of six different phases during the development of the strobilus was demonstrated. Since we have a few more stages to consider we have found it worthwhile to present a complete set-up of photographs to facilitate further discussion.

In Figure 13 a bud is seen which is completely protected by bud scales. The appearance of the strobilus in Figure 14 is of frequent occurrence. Although the apex of the strobilus is covered with bud scales, receptive ovules may occur in the central part of the strobilus. In Figure 15 a strobilus is seen in which most of the ovules are receptive. A bending down of the ovuliferous scales had taken place in the strobili of Figures 16 and 17. In these cases only a few scales close to the apex of the strobilus are placed at a right angle to the axis of the strobilus. The strobilus in Figure 18 shows a bending down of all the scales, which is a clear indication that receptive ovules are no longer present. After some time the scales start to bend upwards (Figure 19) and finally a completely closed cone has been formed (Figure 20).

In some of the clones investigated the stages shown in Figures 17 and 18 do not occur. Instead a direct development from the appearances in Figures 16 and 17 to the appearance in Figure 19 occurs. This complicates the comparison of the duration of the receptive period in different clones.

In this context it should be mentioned that Brøndbo (1971) showed that strobili of the appearance shown in Figure 16 gave a few or no filled seeds following pollination at that stage. Sarvas (1968) pointed out that there exists at the apex and the base of the strobilus a "number of cone scales, on which organically deficient ovules are developed". Based on these observations we have preferred to consider the strobili shown in Figures 14—15 as receptive. This still constitutes an oversimplification since only a part of the ovules in all the strobili of the type shown in Figure 14 are receptive. However, a daily examination of the individual ovuliferous scales of 1000 strobili can impossibly be carried out.

To get a quantitative measure regarding a possible difference between the clones with respect to the onset of the receptivity the temperature sum $\Sigma(t_m - 2)$ needed to reach 50 per cent receptive strobili was determined for each clone in the diagrams. The duration of the receptivity was also read in those diagrams. In this case the difference between the ascending and descending parts of a curve at the 50 per cent level was used as the parameter investigated.

The data obtained are presented in Figure 21. Analogous to the situation in the male strobili the onset of the receptivity took place in the following sequence: Swedish—German—French. However, an analysis of variance revealed that there was no significant difference between the French, German and Swedish clones with respect to the onset of the receptivity. On the other hand there was a highly significant ($p < 0.001$) difference between the categories with respect to the duration of the receptive period. This difference can to a great extent be attributed to the difference in pattern of development between the German clones on the one hand and the French and Swedish clones on the other hand. In the German clones the stages illustrated in Figures 16—18 were in many cases absent. We believe that the receptivity does not persist all the time the strobili of the German clones remain in the developmental stages shown in Figure 15. This means that the receptivity is probably exaggerated in the clones

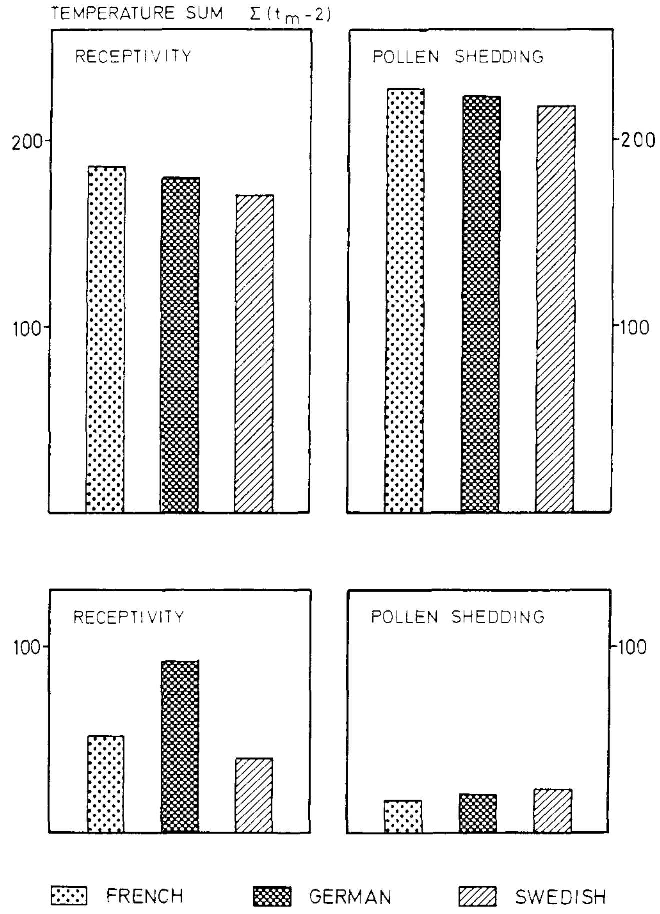

Figure 21. Above the temperature sums—$\Sigma(t_m - 2)$—required for reaching 50 percental receptivity and pollen shedding in the French, German, and Swedish clones of *Picea abies* are illustrated. Below the temperature sums required for the duration of the receptivity and pollen shedding of the French, German and Swedish clones of *Picea abies* are demonstrated. Further explanations are given in the text.

showing this pattern of development. Therefore, an exterior examination of the strobili is not in all cases sufficiently decisive for a judgement whether or not a strobilus is receptive.

In Figures 22—23 the receptivity of two extreme clones is demonstrated. The Swedish clone P 2001 showed all the stages illustrated in Figures 13—19 whereas 90 per cent of the strobili in the German clone O 2000 passed directly from the stage shown in Figure 14 to the one shown in Figure 19. The pollen dispersal, which is also illustrated in Figures 22—23 occurred during the period of receptivity in the German clone (Figure 23) whereas the peak in pollen dispersal occurred during the very end of the receptive period in clone P 2001. In this context it might be added that Wright (1953) reported that the receptivity of a female flower of Norway spruce lasted for one week. Wright made his observations in Pennsylvania, USA.

It is worth mentioning that the receptivity of the Swedish clone O 2008 started extraordinarily early. As a consequence of this, only a few strobili were still receptive at the onset of the pollen dispersal. Thus, when the average pollen shedding of all clones exceeded ten per cent of the male strobili for

Figures 13—16. Various stages during the development of the female strobilus of *Picea abies*. Photo: Kjell Lännerholm.

Figures 17—20. Various stages during the development of the female strobilus of *Picea abies*. Photo: Kjell Lännerholm.

Figure 24. Frost-damaged strobili showing different stages of wilting. Photo: Kjell Lännerholm.

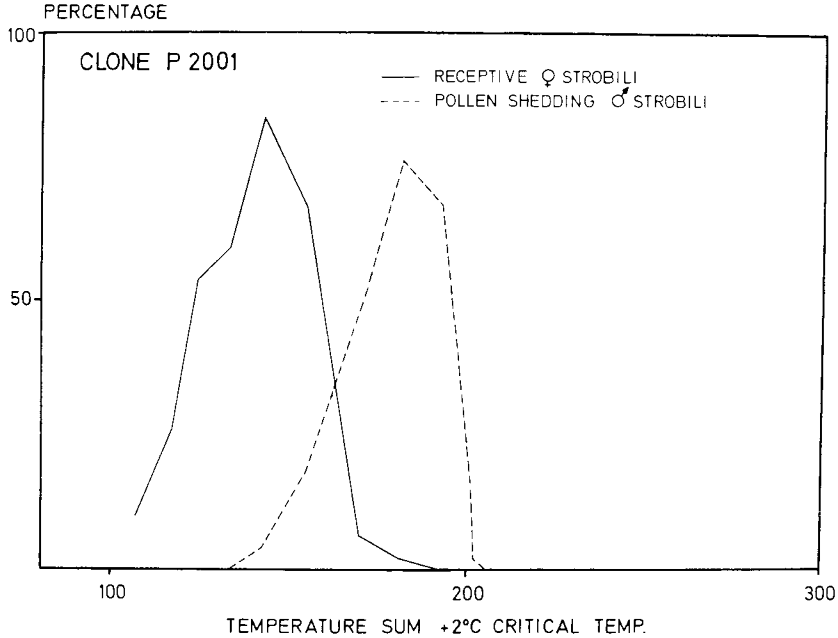

Figure 22. The percentage of receptive strobili and the percentage of strobili shedding pollen in clone P 2001 (Swedish origin) plotted against the temperature sum $\Sigma(t_m - 2)$.

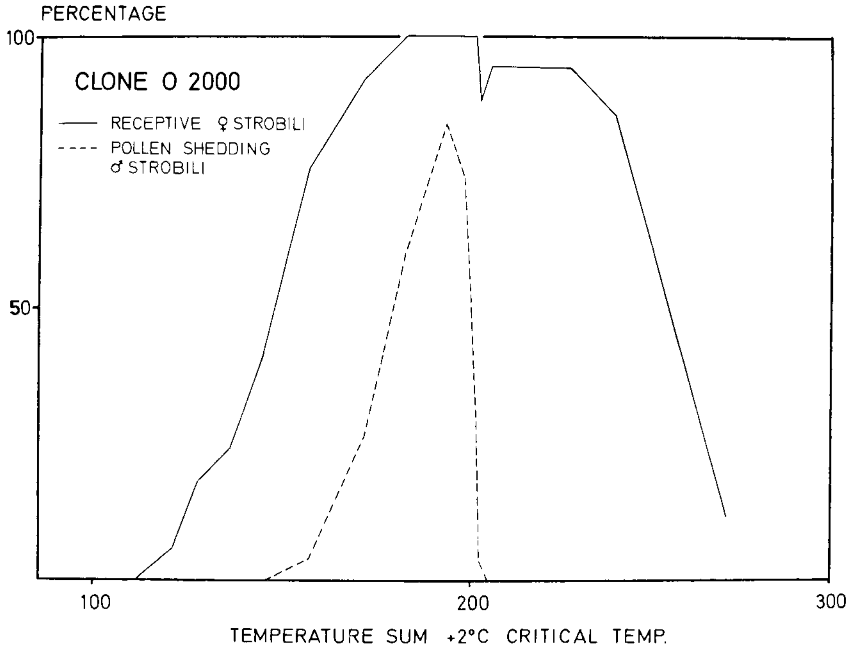

Figure 23. The percentage of receptive strobili and the percentage of strobili shedding pollen in clone O 2000 (German origin) plotted against the temperature sum $\Sigma(t_m - 2)$.

the first time, the receptivity of clone O 2008 had dropped to four per cent. In spite of its abundant female flowering this clone cannot contribute much to the progeny via its female germ line since this is more or less out of phase with the pollen dispersal of the other clones. This is not fully reflected by the later presented methods used for calculating the values of Table 7. On the other hand clone O 2008 dominated the pollen cloud during the first days. As a consequence of this clone O 2008 as father contributes heavily to the genetic set-up of the progeny.

Finally, it should be mentioned that 35 per cent of the labelled strobili were irreversibly frostdamaged during the night of the 23rd—24th May when the temperature dropped to −3°C at the meteorological station. This observation suggests that the female strobili are very sensitive to exposure to frosts (even slight ones) during this phase of the development. Some frostdamaged female strobili are illustrated in Figure 24.

Comparison of the female and the male development

This comparison will be done with the starting point in Figure 21. It is seen from this figure that the onset of the receptivity in the female strobili took place at a lower temperature sum than the pollen dispersal. This finding was independent of the origin of the clones. With the exception of the four German clones the receptivity passed its maximum at a lower temperature sum than the peak of the pollen dispersal (cf. Figure 21). This confirms earlier statements (cf. Sarvas 1968) that *Picea abies* is characterized by protogyny.

The mean difference between the onset of female flowering and the onset of male flowering (measured as the difference between the temperature sum $\Sigma(t_m - 2)$ at 50 per cent pollen shedding and 50 per cent receptive strobili) is 44.9 (it means *e.g.* 5 days with a mean temperature of 11°C). The standard deviation for individual clones amounted to 16.1 (or 1.8 days at 11°C).

The protogyny is one way of avoiding self pollinations. Since this seems to be a common phenomenon in *Picea abies* it might be assumed that this is the case for the German clones too. This is another indication that the duration of the receptivity of the German clones is exaggerated.

Even if the duration of the receptivity of the strobili in some cases is exaggerated our data have disclosed that the time for pollen dispersal is shorter than that for the period of female receptivity. This agrees with observations for *Pinus silvestris* (Sarvas 1967 a), and *Larix decidua* (Barner and Christiansen 1960).

Genetic set-up of the progeny

Calculations

The calculations below refer to an imaginary seed orchard comprising 20 clones. Each clone is represented by exactly the same number of grafts. The clones O 1002 and O 1004 were excluded since no reliable estimates of the receptive period could be obtained owing to a too limited female flowering in these clones. The removal of these clones may have some influence concerning the interference between the results obtained in the imaginary seed orchard and a real seed orchard. Further, it should be added that a provenance seed orchard with such a combination of French, German, and Swedish clones has not been established in Sweden.

Several assumptions had to be made in order to be able to calculate the genetic set-up of the progeny of the imaginary seed orchard. Since the main emphasis was paid on the flowering frequency and the time of flowering, the prerequisites 3 b—c, 4, 5 and 6 (cf. page 5) were assumed to be fulfilled. Further prerequisites will be discussed below. Evidently the calculations presented are based on many somewhat uncertain assumptions. Therefore, the calculations ought not to be regarded as an exact description of the genetic set-up of the seed produced in the imaginary seed orchard but rather as an approach to an understanding of the importance of the deviations from the situation of random mating.

The composition of the pollen cloud

The following prerequisites must be fulfilled to be able to carry out the calculation:

1. The estimate of the number of male strobili is correct from a statistical point of view.
2. The amount of pollen contributing to the pollen cloud is the same (irrespective of the clone) for all strobili shedding pollen simultaneously.
3. All pollen grains have the same viability and life time in the cloud irrespective of its origin.

For each clone the number of male strobili per graft is known. These numbers are transferred to a percentage of strobili of the total number of strobili formed in the clone trial (Table 2). If the percentage for a certain clone is multiplied by the percentage of strobili shedding pollen grains on a certain day (Table 4) a relative measure of the contribution of that clone on this particular day is obtained. This relative measure was divided by the total relative measures of all clones for that day and after that multiplied by 100 in order to transfer the figures into percentages. In Table 5 the percental composition of the pollen cloud for each day is demonstrated.

The occurrence of different combinations

Besides the three prerequisites for the calculation of the pollen cloud composition, the following ones must be fulfilled to be able to calculate the genetic set-up of the seeds produced in the hypothetical seed orchard:

1. The amount of pollen grains available is not a limiting factor after May 14.
2. The clones are 100 per cent self-fertile. (The effect of this assumption is discussed later.)
3. The number of fertilizations each day is proportional to the number of receptive female flowers within each clone.

Table 4. The daily percentage of male strobili shedding pollen in the clone trial of *Picea abies* at Röskär

Clone	Date May 1971														
	14	15	16	17	18	19	20	21	22	23	25	27	28	29	31
O 1000					12	54	86	80	54	8					
O 1001				2	42	86	88	70	18	6	4				
O 1002			4	12	40	62	72	70	52	12	12	6	6	2	
O 1003				4	34	64	74	70	46	12	2	2			
O 1004	4	8	16	30	44	62	80	62	14						
O 1005				2	14	46	60	70	38	8	2	2	2		
O 1006			2	6	22	54	64	60	30	12	4	4	2		
O 1007				2	8	34	60	88	78	26	10	4	2	2	
O 1008					4	50	62	62	46	12	2	2			
O 1009				2.0	8.2	44.9	59.2	67.3	51.0	14.3	4.1	2.0	2.0	2.0	2.0
O 2000				4	26	60	84	74	32	4					
O 2001		2	4	10	24	60	76	42	4						
O 2002					12	52	70	88	70	42	20	14	10	4	
O 2003	2	2	6	16	46	84	82	54	8	2					
O 2006			8	16	38	78	76	48	24	10	2	2	2		
O 2008	2	4	8	18	54	84	70	34	6	2					
O 2011	4	4	14	36	76	84	56	38	8	4	4	4	4		
O 2012				6	30	82	72	32	8						
O 2013				8	22	52	76	80	52	22	6	4	2		
O 2014		2.0	14.3	30.6	51.0	65.3	65.3	36.7	8.2						
P 2001			4	18	48	76	68	40	16	2					
P 2002		2	8	12	42	80	68	24	4						

Table 5. The daily composition of the pollen cloud in the clone trial of *Picea abies* at Röskär (per cent)

Clone	Date May 1971														
	14	15	16	17	18	19	20	21	22	23	25	27	28	29	31
O 1000					0.44	0.91	1.4	1.6	1.9	0.83					
O 1001				0.45	3.1	2.9	2.8	2.9	1.3	1.3	2.7				
O 1003				0.73	2.1	1.8	1.9	2.4	2.7	2.1	1.1	1.8			
O 1005				0.21	0.49	0.73	0.90	1.4	1.3	0.79	0.65	1.0	1.6		
O 1006			0.61	0.82	0.99	1.1	1.2	1.5	1.3	1.5	1.7	2.7	2.0		
O 1007				2.5	3.5	6.6	10.9	20.6	31.7	31.2	39.2	25.1	19.5	54.5	
O 1008					1.2	6.9	8.1	10.4	13.3	10.3	5.6	9.0			
O 1009				0.74	1.0	2.5	3.1	4.6	6.0	5.0	4.7	3.7	5.7	16.0	100
O 2000				0.36	0.80	0.84	1.1	1.3	0.94	0.34					
O 2001		7.5	2.6	2.8	2.2	2.5	3.0	2.2	0.36						
O 2002					1.4	2.7	3.4	5.6	7.7	13.6	21.2	23.8	26.4	29.5	
O 2003	20.8	6.4	3.3	3.8	3.6	3.0	2.8	2.4	0.61	0.45					
O 2006			41.4	36.2	28.6	26.8	24.7	20.0	17.3	21.3	13.9	22.3	34.7		
O 2008	58.9	36.2	12.4	12.2	12.1	8.6	6.8	4.2	1.3	1.3					
O 2011	20.2	6.2	3.8	4.2	3.0	1.5	0.94	0.82	0.30	0.44	1.4	2.3	3.6		
O 2012				0.87	1.4	1.8	1.5	0.85	0.37						
O 2013				3.3	3.0	3.3	4.5	6.2	6.9	8.6	7.7	8.2	6.4		
O 2014		3.0	3.7	3.4	1.9	1.1	1.0	0.76	0.30						
P 2001			4.5	8.9	7.9	5.7	4.8	3.6	2.5	0.93					
P 2002		40.7	27.8	18.3	21.2	18.5	14.8	6.7	1.9						

Table 6. Percentage of receptive female strobili of the clones of *Picea abies* growing at Röskär on different occasions during May 1971

Clone	Date May 1971																	
	11	12	13	14	15	16	17	18	19	20	21	22	23	25	27	28	29	31
O 1000		28	78	84	92	100	100	80	69.4	16.7	4.2							
O 1001			11.6	14.0	18.6	44.2	69.8	69.8	60.5	30.8	17.9	17.9	17.9	18.2	18.2	18.2	18.2	3.0
O 1003		2.1	10.4	12.5	14.6	41.7	81.3	95.8	95.7	52.3	2.3							
O 1005				4	8	40	70	88	92	50	4							
O 1006		4	8	12	12	46	78	100	100	100	66	6						
O 1007		4	28	38	44	66	80	100	100	98	66	10	2					
O 1008			4	4	8	36	56	96	100	36.7	8.3	2.1	2.1					
O 1009			10	40	60	70	100	100	90	60	10	10						
O 2000			6	18	24	42	76	92	100	100	100	100	87.8	94.3	94.3	94.3	85.7	11.8
O 2001		16.3	32.7	49.0	63.3	85.7	97.9	100	100	97.7	77.3	29.5	13.6	4.5	5.0	5.0		
O 2002		44	64	68	80	92	96	100	100	81.3	8.3	2.1						
O 2003					2.0	30.6	67.3	100	100	100	91.8	91.8	91.5	97.4	97.4	97.4	86.5	2.8
O 2006		24	66	64	68	38	12	2										
O 2008	62	88	94	24	24.5	10.2	4.1											
O 2011				7.9	13.2	65.8	89.5	97.4	94.6	21.6								
O 2012		16	42	54	60	86	92	30	20	4								
O 2013			6.1	10.2	18.4	47.9	78.7	89.4	80.4	43.5	22.2	6.7	4.4	3.8	3.8	3.8		
O 2014		18	38	54	64	77.6	87.5	20.8	16.7									
P 2001		10	26	54	60	83.7	67.3	6.1	2.0									
P 2002				10	18	48	75.5	98.0	95.9	61.2	32.7	26.5	22.4	22.2	22.7	18.2	15.9	

Table 7. Percental contribution of each possible crossing combination to the offspring of an imaginary seed orchard

♂ ♀	O 1000	O 1001	O 1003	O 1005	O 1006	O 1007	O 1008	O 1009	O 2000	O 2001
O 1000	.004	.018	.014	.004	.011	.041	.025	.013	.006	.032
O 1001	.008	.026	.021	.010	.017	.207	.065	.060	.008	.035
O 1003	.009	.032	.022	.026	.015	.077	.051	.024	.011	.044
O 1005	.010	.036	.025	.009	.017	.086	.059	.027	.012	.047
O 1006	.043	.120	.091	.036	.057	.422	.262	.114	.043	.148
O 1007	.028	.075	.059	.023	.038	.281	.168	.075	.028	.113
O 1008	.025	.090	.064	.022	.041	.226	.154	.068	.029	.111
O 1009	.002	.007	.006	.002	.004	.023	.014	.007	.003	.015
O 2000	.023	.056	.052	.029	.049	.764	.210	.202	.018	.049
O 2001	.020	.052	.040	.017	.028	.237	.126	.058	.018	.080
O 2002	.026	.085	.061	.022	.044	.231	.152	.073	.029	.177
O 2003	.011	.026	.025	.012	.022	.355	.095	.081	.008	.020
O 2006	.001	.007	.008	.002	.021	.023	.001	.007	.003	.396
O 2008	.000	.001	.002	.000	.006	.007	.000	.002	.001	.142
O 2011	.005	.023	.016	.005	.012	.048	.032	.016	.007	.036
O 2012	.002	.009	.008	.002	.009	.024	.010	.007	.004	.049
O 2013	.100	.334	.260	.097	.178	1.189	.650	.316	.113	.483
O 2014	.001	.009	.008	.002	.009	.021	.008	.007	.003	.056
P 2001	.002	.021	.025	.007	.043	.076	.008	.023	.011	.330
P 2002	.088	.265	.206	.091	.162	1.737	.663	.398	.085	.309
Σ	.408	1.292	1.013	.418	.783	6.075	2.753	1.578	.440	2.672

4. The number of seeds obtained per strobilus is the same in all clones.

During the first (May 14—16) or last (May 25—31) days the total amount of pollen was comparatively low. It is probable that some receptive ovules remained unfertilized because of insufficient amounts of pollen. Therefore, the contribution of pollen from the early flowering clones will probably be somewhat exaggerated.

The occurrence of different combinations among the 20 clones may be estimated by the available information of the daily composition of the pollen cloud, (Table 4) the percentage of female strobili per graft (Table 2) and the percentage of receptive female strobili per graft for each day and clone (Table 6).

To get relative contributions, the percentage of receptive female strobili (the estimate covering the stages demonstrated in figures 14—15 cf. above) was multiplied by the percental contribution of pollen from each male clone. Such a multiplication was carried out for all days during the period of receptivity. Those relative numbers were added up over all the days for each combination of the clones. Within a female clone those sums are proportional to the contribution of each male clone as a father to the offspring of the particular female clone. By division of the total sum of all fathers of that female clone the proportions of each father were calculated. By multiplying those proportions by the number of female strobili per graft for each "female" clone new relative numbers are obtained. Finally, those numbers are expressed in per cent of the grand total. In that way the percentage of each possible crossing combination has been obtained (Table 7).

To clarify the calculations an example with actual figures will be given. At May 12, 28 per cent of the female strobili in clone O 1000 are receptive (Table 6), but no fertilizations can take place until May 14, as no pollen is available before this date.

O 2002	O 2003	O 2006	O 2008	O 2011	O 2012	O 2013	O 2014	P 2002	P 2001	Σ
.013	.121	.414	.416	.115	.012	.031	.041	.083	.387	1.801
.107	.056	.445	.184	.054	.014	.063	.028	.081	.259	1.748
.024	.068	.482	.218	.056	.019	.048	.034	.105	.334	1.699
.029	.065	.531	.207	.052	.022	.052	.036	.115	.356	1.793
.125	.205	1.556	.627	.154	.063	.194	.103	.331	.997	5.691
.084	.189	1.051	.603	.155	.041	.126	.075	.218	.762	4.192
.077	.149	1.238	.487	.119	.051	.128	.085	.269	.837	4.270
.007	.024	.131	.087	.023	.005	.013	.011	.027	.105	0.516
.420	.075	.821	.225	.079	.022	.184	.033	.112	.322	3.745
.080	.135	.750	.445	.117	.027	.098	.055	.144	.538	3.065
.073	.341	1.461	1.151	.304	.052	.134	.128	.298	1.242	6.084
.198	.025	.374	.072	.028	.010	.086	.013	.049	.132	1.642
.002	1.198	1.266	4.228	1.176	.008	.028	.237	.181	2.509	11.302
.000	.459	.371	1.609	.542	.002	.009	.079	.054	.880	4.166
.016	.051	.403	.170	.045	.015	.035	.030	.085	.278	1.328
.005	.107	.386	.373	.105	.008	.022	.041	.073	.349	1.593
.446	.687	5.199	2.247	.594	.186	.576	.371	1.077	3.472	18.575
.004	.123	.409	.435	.123	.007	.023	.046	.076	.391	1.761
.005	.785	2.312	2.767	.785	.027	.093	.279	.392	2.333	10.324
.839	.442	3.798	1.398	.383	.131	.574	.221	.707	2.208	14.705
2.554	5.305	23.398	17.949	5.009	.722	2.517	1.946	4.477	18.691	100.000

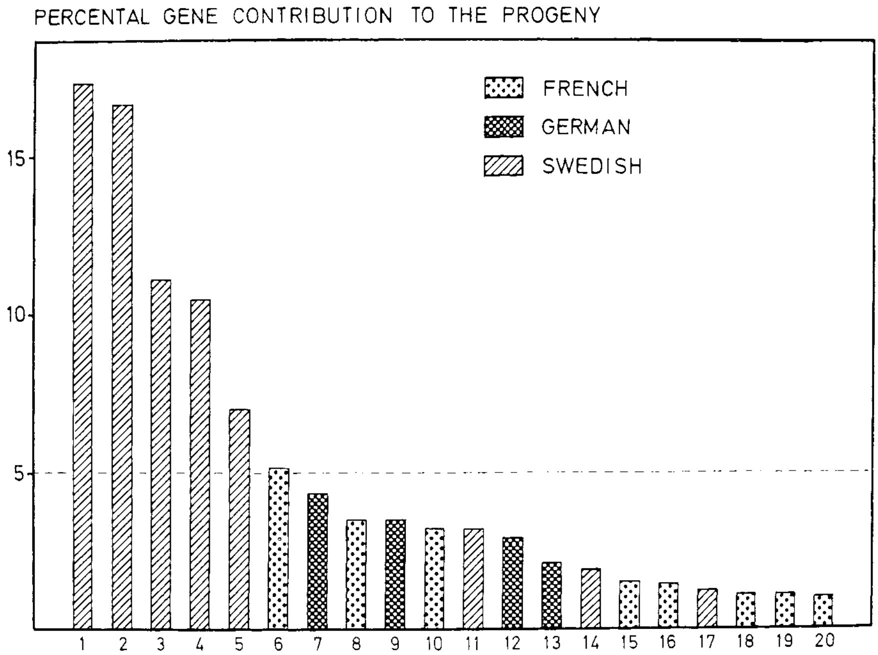

Figure 25. The percental gene contribution to the progeny of individual clones based on the frequencies of male and female strobili as well as the time of flowering. The dashed line illustrates the anticipated percentage if all prerequisites for random mating were fulfilled.

On May 14, 84 per cent of the strobili are receptive. Furthermore, it is assumed that O 2003 will give a contribution of 20.8 per cent (Table 5) of the fertilizations that day which means a contribution of $0.84 \times 0.208 = 0.175$ to the cross O 1000×O 2003 on May 14. The next day the same cross will give a contribution of 0.92×0.064 and so on. The total contribution of O 1000×O 2003 (cf. Table 5 and 6) $= 0.84 \times 0.208 + 0.92 \times 0.064 + \ldots = 0.360$. The total sum of all contributions for O 1000 as a mother equals 5.389. This relative number corresponds according to Table 2 to 1.80 per cent of the contribution of the female side. Thus the overall contribution of O 1000×O 2003 can be calculated as $\frac{0.360 \times 1.80}{5.389} = 0.121$ per cent.

This figure is transferred to Table 7. In such a way the contribution of each of the 400 possible combinations has been estimated (Table 7).

It ought to be mentioned that observations from two days, May 24 and May 30, are lacking. Those days were not included in the calculations. Owing to the cold and damp weather those days, it was assumed that no significant numbers of fertilizations took place (cf. Sarvas 1955).

The transmission of genes to the offspring from different clones

By adding the rows or the columns of Table 7 the percental contribution of the different clones as fathers or mothers is obtained. The mean value constitutes the genetic share of each clone in the filial generation. In Figure 25 the clones are arranged according to the sequence in which they contribute genes to the progeny. If all the prerequisites listed in the Introduction are fulfilled, all clones would contribute five per cent to the offspring. Figure 25 reveals that only five clones considerably passed the five per cent level. These five clones were all of Swedish origin. Two of them (O 2006 and P 2002) contributed heavily. In this connection it is worth mentioning that three other Swedish

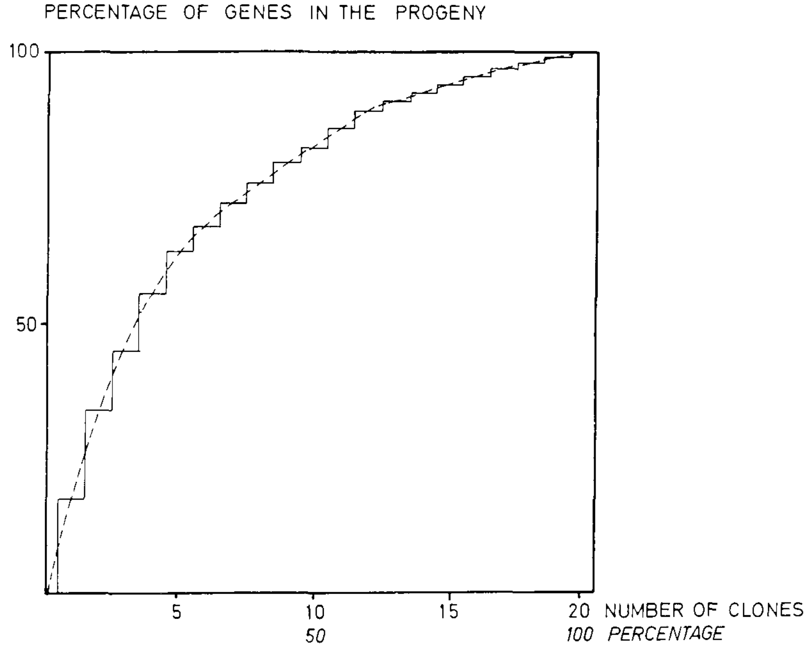

Figure 26. The cumulative percentages of the gene contribution to the progeny of individual clones of *Picea abies*, which are arranged according to their contribution.

clones were poor contributors. None of the French or German clones contributed heavily.

The relation between the poorest (clone O 1009 of French origin) and largest contributor (O 2006) amounted to approximately 1 : 17. It is quite evident that the main bulk of the genes originates from a few clones. To demonstrate this, Figure 26 was drawn. In this diagram the cumulative sum of the clonal contribution is illustrated, the data of the clones were added up in the sequence shown in Figure 25. From Figure 26 it may *e.g.* be seen that four of the clones are responsible for 55 per cent of the genes in the progeny whereas the added percentages of nine other clones did not reach 15 per cent. Thus, there is a considerable lack of balance between the genetic set-up of the parental and filial generations.

The question may be raised whether or not it is worth-while to follow the pollen shedding and the receptivity of the strobili in detail to obtain information about the transmission of genes from different clones. Evidently, there are considerable differences between the number of male strobili and the contribution as a father to the following generation (Table 2) but if the mean contribution on the male and female side (Table 2) is calculated the differences decrease. The mean contributions of the clones calculated with or without knowledge of the moment of pollen shedding and receptivity are strongly correlated ($r = 0.93$). Considering all other uncertain factors it might be stated that it is generally enough to count the number of strobili to obtain information about the genetic set-up of the seed material.

The occurrence of selfing

From Table 7 the number of selfing may be calculated by adding the number on the diagonal from the upper left corner to the lower right corner. The obtained value is 6.905 per cent. If random mating is assumed five per cent would have been expected. With the assumptions given, two factors may cause deviations:

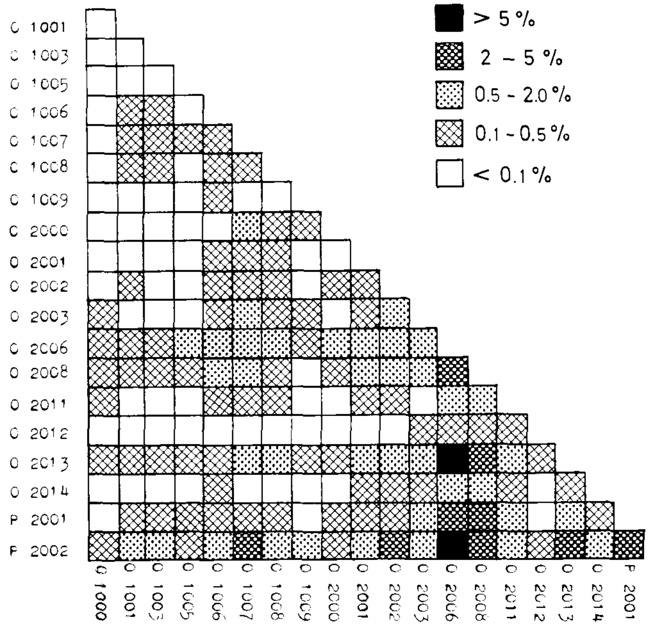

Figure 27. The percentage of the different combinations in the imaginary seed orchard of *Picea abies.*

1. The time difference between male and female flowering is expected to decrease the frequency of self-fertilization.
2. The positive correlation between the amount of male and female flowering (r = 0.54 calculated on the values presented in Table 2) increases the frequency of self-fertilization.

The anticipated amount of selfing if the number of strobili exactly reflected the percentage of gametes transmitted by each clone would be 7.9 per cent (cf. Table 2) which might be compared with 5.0 per cent which would be anticipated without any correlation of the number of male and female strobili (and limited variations between clones). Thus, factor 1 is decreasing the amount of selfing only to a limited extent, and might not be the barrier against selfing which is often assumed, at least not on the clonal level. In addition to the clonal covariation between male and female flowering there is also a covariation on the individual level within clones. The correlation coefficient calculated on transformed values (cf. pp. 17—18) of the number of male and female strobili was 0.52 on the graft level, within the five tree row plots. Probably both factors mentioned, covariation of male and female flowering and differences in the time of flowering will act more strongly on the individual level than on the clonal one.

In practice the occurrence of recessive lethal genes probably decreases the amount of viable inbred seeds considerably (cf. Sarvas 1962, Andersson 1965, Koski 1971). If the reduction of the viable seed yield is the same for all clones this does not affect the relative contribution to the offspring of the different clones. Probably there are, however, large variations in the number of lethal genes in different clones (cf. Franklin 1972), but if the yield of inbreeding generally is low the percental contribution of the genes will not be affected to any considerable extent.

The realization of the theoretically possible combinations

The pairwise mating of 20 clones in all possible directions causes the formation of 190 different combinations. If all crosses have

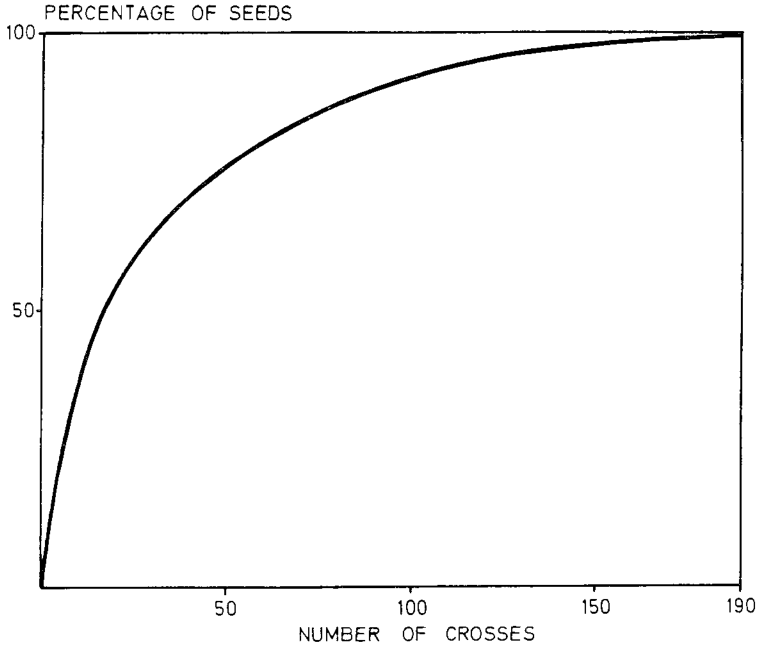

Figure 28. The cumulative percentage of different crossing combinations arranged according to their contribution (selfing being excluded).

the same probability of occurring, 0.5 per cent of the offspring from the seed orchard would originate from each possible combination. In the imaginary seed orchard studied, the percentage of different combinations may be obtained by adding the reciprocal combinations in Table 7. To obtain a visual impression of the importance of different crossing combinations Figure 27 was constructed. Selfing is not excluded. If it were excluded, the borders between the classes would be 5.37, 2.148, 0.537 and 0.104, instead of the percentages given. The data obtained indicate that a few combinations dominate the offspring from the imaginary provenance crossing seed orchard.

To obtain a more quantitative impression Figure 28 was constructed in a way similar to Figure 26. In the figure it is assumed that selfing does not give any seeds.

Significance for predicting the genetic quality of seeds from a seed orchard

To obtain information about the quality of the seed from a genetic point of view the combining abilities of the clones has to be considered.

It is assumed that the general combining ability of the 20 clones was determined without experimental error. As an estimate of the genetic quality of the seeds obtained from the provenance crossing orchard the genetic mean value of the clones is given. Besides other sources of uncertainty, there occur deviations from the predicted value as the clones do not contribute equal parts to the offspring. Furthermore, the presence of specific combination effects causes deviations.

The contribution to the next generation by the i:th clone is designed P_i. P_i values are presented in Figure 25. The mean value of the breeding values of the 20 clones ($=\bar{y}$) will have a variance caused by the deviation of contributions from five per cent.

$$V_{\bar{y}} = \sum_{i=1}^{20}(P_i - 0.05)^2 V_{GCA} = 0.0483 V_{GCA};$$

$$\sqrt{0.0483} = 0.220$$

(V_{GCA} = variance between clones concerning general combining ability).

Thus, the estimate of the genetic quality of the seeds as the mean of the breeding value of the clones will have a variance of 4.8 per cent of the variance between the clones because of the unequal contribution of gametes. If there is a positive correlation between breeding value and flowering as indicated by Johnsson (1973) the deviation may be in a positive direction.

Another reason for possible uncertainty in the genetic quality predicted by the mean of the breeding values is the presence of specific combining effects. An assumption must be made concerning the method of estimating the breeding value and the most simple assumption is that only one parent originates from the imaginary seed orchard in the progeny testing crosses.

The mean value of the specific combining effects is denoted $\bar{z}$. The variance of $\bar{z}$ is $V_{\bar{z}}$.

$$V_{\bar{z}} = \sum_{i=1}^{190} C_i^2 \cdot V_{SCA}$$

V_{SCA} = variance between crosses concerning specific combining ability. C_i = the contribution of each of the 190 crosses possible (calculated by aid of Table 7). Selfing is assumed not to occur, which means that the occurrence of the different combinations has to be divided by $(1.00 - 0.06906)$ as the amount of selfing is 6.906 per cent according to Table 7.

$\sum C_i^2 = 0.02174$

If all combinations occurred with the same frequency a value of $\sum C_i^2 = 190 \cdot \left(\frac{1}{190}\right)^2 =$ 0.00526 would be expected, thus the uneven distribution of combinations means a four-fold increase in the variance of the genetic quality of the seed produced in the imaginary seed orchard, compared to the situation if random mating was prevailing.

A simple example will be given to clarify the magnitude of the error of a prediction:

In a progeny test of the 20 clones of the imaginary seed orchard, all clones were crossed with a large number of common testers originating from the same population as the clones. It is further assumed that the standard deviation of the breeding values was found to be 10 units and $\sqrt{V_{SCA}}$ was also 10 units. The genetic quality of the seed orchard will in such a case be the mean value of the breeding value of the 20 clones which amounts to 100 units. The standard error of this estimation will be

$$\sqrt{0.0483 \cdot 10^2 + 0.0217 \cdot 10^2} = 2.65 \text{ units.}$$

Significance for two clone orchards

There are three factors which must be considered in the choice of clones for a two clone orchard (cf. Andersson 1966).

1. The common offspring of the parents must be of high genetic quality
2. The clones should be good seed producers
3. The amount of self pollinations must be kept down unless the clones are self-sterile.

The large variance of the contribution of different parent pairs demonstrated in Figures 27 and 28 stresses the need to consider factor 2. However, it is hardly probable that the amount of pollen available is a limiting factor for the seed yield. Therefore, the capacity of the intermediary pollen producers may be underestimated. On the other hand a good pollen production is also requested to decrease the importance of pollen from outside sources. In this context it is worth mentioning that Hadders (1973) treated questions which relate the amount of pollen production within the seed orchard and the contamination of pollen from outside sources.

It seems recommendable to try to find one parent characterized by early and good male flowering and the other parent characterized by late or intermediary and abundant female flowering.

The flowering behaviour of clones designated to be components of two clone seed orchards ought to be studied before a progeny test is carried out. This is due to the poor willingness to flower in some of the clones, which means that only some clones combined in pairs will produce seeds in suf-

Table 8. Percentages of different provenance combinations in the imaginary orchard

	Mating pattern		
♀ ♂	I	II	III
F×F	16	7.17	3.72
F×G	8	2.07	2.03
F×S	16	12.47	15.96
G×F	8	4.80	3.28
G×G	4	1.38	1.74
G×S	8	8.34	9.51
S×F	16	21.07	7.32
S×G	8	6.07	7.20
S×S	16	36.62	49.24
Hybrid seeds	64	54.83	45.30

	Pattern I (percentage of clones)		Pattern II (percentage of strobili)		Pattern III (percentage of contribution)	
	♀	♂	♀	♂	♀	♂
French, F	40	40	21.71	33.05	21.71	14.32
German, G	20	20	14.53	9.52	14.53	10.96
Swedish, S	40	40	63.76	57.43	63.76	74.72

ficient amounts to justify the investments involved in the establishment of a seed orchard. Moreover, a progeny test is more expensive than a study of flowering behaviour. Therefore, we recommend that the progeny test is confined to those combinations which seem promising from a flowering point of view.

The efficiency of the provenance crossing design

Norway spruce seed orchards are in Sweden often designed to give seeds which are partly of a provenance hybrid origin (cf. Andersson and Andersson 1962 and Andersson 1967). Therefore, it was considered to be of interest to study how the imaginary seed orchard functioned as a provenance hybrid seed orchard. As mentioned earlier this hypothetical provenance crossing orchard is composed of 20 clones, eight of French origin (F), four of German (G) and eight of Swedish (S). Nine different types of crossing combination may be obtained according to Table 8. The proportion of provenance hybrid seed is dependent on the mating pattern (cf. below). Different assumptions concerning the mating pattern will be made for demonstration. Selfing is always included in "within provenance", therefore the amount of provenance hybrid seeds obtained may be somewhat underestimated. The consequences of the different assumptions concerning the mating pattern are demonstrated in Table 8.

Without any prior knowledge concerning flowering characteristics it seems logical to assume that random mating is prevailing. This means that the provenances contribute proportionally to the number of clones (cf. Andersson 1967). This assumption is called mating pattern I.

The second approach (II) means that each provenance contributes to each crossing combination proportional to its share of the strobili (cf. Table 2). Thus it is assumed that the flowering in the clones are synchronous. In this case a considerable difference is observed in the distribution of crossing combinations compared with mating pattern I. Crosses within the Swedish provenance dominate especially. However, the number of hybrid seeds decreases slightly. In spite of the differences in the flowering frequency the chances of producing hybrid seeds do not seem to be seriously decreased.

In approach III the situation is studied under the conditions for the imaginary seed orchard and the values of gametes transmitted of each clone (cf. Table 2) are added for each of the nine provenance combinations. A further drop in the number of hybrid seeds produced is obtained. This is mainly due to the predominance of crosses between clones of Swedish origin. This in turn can to a great extent be attributed to the early onset of male flowering in the Swedish clones which means that they act effectively as fathers to the other Swedish clones. In contrast to this much of the pollen originating from French clones is shed after the passing of the receptive period of the female strobili. It might have been expected that the differences in the time of flowering would increase the amount of hybrid seeds, but this mechanism is evidently weak.

To conclude, the number of provenance hybrid seeds will be realized to 75 per cent of the amount expected from the number of participating clones, but the decrease of hybrid seeds compared to expectation might not be serious. From a practical point of view the drop in provenance hybrid seed produced between assumptions II and III is of more interest. This drop was found to approximate 15 per cent.

Concluding remarks

The present investigation has disclosed that the flowering in *Picea abies* shows great yearly fluctuations. This is in good agreement with earlier observations on flowering in this species (Tirén 1935, Hagner 1965). One reason for the fluctuation in female flowering is probably the localization of the female strobili to the apices of the branches. This prevents a good vegetative growth during a year with a profuse female flowering. As a consequence of this there are few positions left in the crown for formation of the generative organs. Therefore, it lasts one or more years before another abundant flowering can take place again. The direct or indirect influence of weather factors like temperature and rainfall on the formation of generative organs in the Norway spruce is certainly of great importance (cf. Tirén 1935, Brøndbo 1971, Remröd 1973). Weather conditions and vegetative conditions must simultaneously be favourable in order to obtain an induction of abundant flowering. At the future localization of the Norway spruce seed orchards the climatic influence on flowering should be considered. It has to be added that the yearly fluctuations in flowering are best studied by examining individual grafts during a series of years.

Conspicuous differences in flowering capacity were noticed between individual grafts. Part of the difference could be attributed to variation in mean height of the clones (Figures 3—6). In spite of the relatively strong correlations between flowering and height a great clonal variability with respect to female as well as male flowering adjusted for height was proven. In Figures 7—8 the flowering at a standard height of 214 cm is demonstrated. From these figures it may be seen that the Swedish clones on an average show a more abundant flowering than the clones of German or French origin at an equal height. It might be added that there was no negative correlation between clone height and the flowering at a standard height. This indicates that a good growth is in no way contradictory to a good flowering. Probably the southern clones require a higher temperature sum (acting direct or indirect) than the domestic clones for development of the same number of strobili. This requirement certainly varies from clone to clone. It seems promising for future establishment of central European clones in Swedish seed orchards that some of the French and German clones ranked as highly as is illustrated in Figures 7—8.

A study of the synchronization of the flowering is of considerable importance for the genetic set-up of the seed produced in a seed orchard. Therefore, the pollen shedding of individual male strobili and the receptivity of individual female strobili were investigated in 20 of the clones growing in the clone trial at Grabbtorp, Röskär (9 km northeast of Stockholm). The temperature requirements for onset of the receptivity and the pollen shedding are shown in Figure 21. As seen from this diagram, the sequence of these events was found to be: Swedish—German—French, both with regard to receptivity and pollen shedding. The German clones were seemingly characterized by an extremely long duration of the receptivity. The real receptivity is probably considerably shorter than could be revealed by the method of examination used.

The twenty clones examined with respect to pollen shedding and receptivity were regarded as components of an imaginary seed orchard. Based upon the receptivity and pollen shedding of the individual clones during different days as well as the frequencies of female and male strobili, the percental gene contribution to the offspring of the various clones was calculated. The results obtained are demonstrated in Figure 25. As may be seen from this figure there is a conspicuous difference between the clones. Assuming random mating and absence of complicating factors every clone would contribute five per cent to the offspring. Only five clones passed the five per cent level considerably, all of them were of Swedish origin. Based upon Figure 26 it can be disclosed that four of the Swedish clones contributed more than 55 per cent to the offspring.

Theoretically 190 different combinations could be realized in the imaginary seed orchard. The estimated percental contribution of the different combinations is illustrated in Figure 27. This figure reveals that many combinations will have an extremely limited influence upon the progeny whereas the combinations O 2006 × O 2013 and O 2006 × P 2002 exert a heavy influence on the progeny.

Some clone pairs have certainly better prerequisites than others to produce a good seed yield. This ought to be considered at an early stage in a program directed to the foundation of two clone orchards.

Since so called provenance crossing seed orchards of the Norway spruce have been established to a great extent in Sweden it is of great interest to estimate the occurrence of provenance hybrid offspring. In the imaginary seed orchard composed of eight French, four German and eight Swedish clones the frequency of provenance hybrids would amount to 64 per cent of the progeny, assuming random mating and equal contribution of all clones. If the frequencies of male and female strobili were considered the amount of provenance hybrids decreased to 55 per cent. If the point of time for pollen-shedding and receptivity were also considered the percentage of provenance hybrids was approximated to be 45 per cent.

Finally it will be stated that a considerable female flowering was noted at the age of 12 years for some of the clones in this clone trial.

Acknowledgements

The present investigation was supported by grants from the Swedish Council for Forestry and Agriculture Research. We are greatly indebted to the head of our department, Professor Enar Andersson, who placed some of the data collected during the sixties at our disposal, as well as for his support and advice during the course of this investigation. We are very grateful to Mr Kjell Lännerholm for drawing the diagrams. Mr Lännerholm is also responsible for the pictures shown in Figures 13—20, and 24.

Sammanfattning

Den föreliggande undersökningen har visat att blomningen hos *Picea abies* uppvisar stora årliga variationer. Detta överensstämmer väl med tidigare iakttagelser av Tirén (1935) och Hagner (1965). Lokaliseringen av honstrobili till skottspetsarna är troligen en av anledningarna till den starkt fluktuerande honblomningen hos gran. Detta förhållande förhindrar en god vegetativ tillväxt under ett år med riklig honblomning. Som en följd av detta finns det få positioner över för bildning av generativa organ. Detta innebär att riklig blomning uppträder högst vartannat år. Det direkta eller indirekta inflytandet av sådana väderfaktorer som temperatur och nederbörd på anläggningen av generativa organ hos gran är säkerligen betydelsefullt (jfr Tirén 1935, Brøndbo 1971, Remröd 1973). Väderförhållanden och vegetativ status måste samtidigt vara tillfredsställande för att en omfattande initiering av generativa organ skall erhållas. Klimatinflytandet på blomningen bör beaktas vid den framtida lokaliseringen av granfröplantager. Det bör observeras att den årliga variationen i blomning bäst kan studeras genom att registrera blomningen hos enskilda ympar under en följd av år.

Påfallande skillnader i blomningskapacitet observerades hos ymparna. Skillnaderna kan delvis tillskrivas variationer i höjd hos dem (jfr figurerna 3—6). Även om man beaktar den stora klonala skillnaden i höjdtillväxt var variationen i blomning mellan olika kloner starkt signifikant. I figurerna 7—8 visas blomningen vid en standardhöjd av 214 cm. Av dessa figurer torde framgå att de svenska klonerna genomsnittligt visar en rikligare blomning än de franska och tyska klonerna vid en standardhöjd. Detta visar att en god tillväxt i detta fall inte varit till nackdel för en riklig blomning. De franska och tyska klonerna kräver troligtvis en högre temperatursumma än de inhemska klonerna för utbildning av samma antal strobili. Detta krav varierar säkert från klon till klon. Det verkar lovande för framtida anläggning av svenska fröplantager med utländska grankloner att några franska och tyska kloner intog en så framskjutande ställning i blomningshänseende som utvisas av figurerna 7—8.

En undersökning av synkroniseringen av blomningen är av stor betydelse för att kunna uppskatta den genetiska sammansättningen hos frömaterialet. Därför studerades pollenspridningen från enskilda hanstrobili och receptiviteten (=froämnenas mottaglighet för pollen) hos enskilda honstrobili från 20 kloner i ett klonförsök vid skogshögskolans försökspark Röskär (9 km nordost om Stockholm). Temperaturkravet för starten av receptiviteten har åskådliggjorts i figur 21. Som framgår av detta diagram ägde starten av dessa skeenden rum i följande ordning: svensk—tysk—fransk. De tyska klonerna karaktäriserades till synes av en extremt lång receptivitet. Den verkliga receptiviteten varade troligen avsevärt mycket kortare tid än vad som kunde avslöjas med den undersökningsmetod som användes.

De tjugo undersökta klonerna betraktades som komponenter i en fröplantage. Baserat på frekvens av hon- och hanblomning samt tidpunkten för receptivitet och pollenspridning hos de enskilda klonerna olika dagar beräknades det procentuella genbidraget till avkomman från de olika klonerna. De erhållna resultaten finns återgivna i figur 25, vilken visar att det är påfallande skillnader mellan klonerna. Under förutsättning att slumpmässig pollinering råder samt att inga komplicerande faktorer stör bilden skulle varje klon bidra med fem procent till avkomman. En nämnvärd passering av femprocentsnivån uppvisades enbart av fem kloner. Alla dessa var svenska. Baserat på figur 26 kan det fastslås att fyra av de svenska klonerna tillsammans bidrog med mer än 55 % av generna till avkomman.

Teoretiskt kan 190 olika kombinationer realiseras i den tänkta fröplantagen. De teoretiskt framräknade bidragen från de olika kombinationerna har illustrerats i figur 27. Denna figur visar att många kombinationer har ett utomordentligt begränsat inflytande på avkomman medan kombinationerna O 2006 × O 2013 samt O 2006 × P 2002 inverkar mycket tungt på avkomman.

Vissa par av kloner har säkerligen bättre förutsättningar än andra att producera en tillfredsställande frökvantitet. Detta förhållande bör beaktas på ett tidigt stadium i ett program som syftar till anläggning av tvåklonsplantager.

Eftersom provenienskorsningsplantager av gran har etablerats i så stor utsträckning i Sverige är det av vitalt intresse att uppskatta frekvensen av provenienshybrider i avkomman. I den tänkta plantagen som hade följande klonsammansättning — 8 franska — 4 tyska — 8 svenska kloner — förväntas frekvensen av provenienshybrider att uppgå till 64 % under förutsättning av slumpmässig pollinering och lika antal gameter hos alla kloner samt att inga komplicerande faktorer stör skeendet. Om man tar hänsyn till att han- och honblomningen varierade hos klonerna sjönk andelen provenienshybrider till 55 %. Om man även tar hänsyn till tidpunkten för pollenspridning och receptivitet uppgår andelen av provenienshybrider till 45 %.

Slutligen skall påpekas att en betydelsefull blomning observerades för första gången vid 12 års ålder hos vissa av de undersökta klonerna.

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