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Flowering in a seed orchard of *Pinus sylvestris* L.

Blomningen i en tallfröplantage

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Abstract

Flowering phenology and flowering frequencies were investigated in clones of Swedish and Finnish origin growing in a pine seed orchard at Långtora (lat. 59°43', long. 17°08', alt. 15 m). One purpose was to estimate the gene contribution of individual clones to the progeny.

The frequencies of female and male strobili were estimated in 1973–1975. The onset and duration of both female receptivity and pollen dispersal were recorded. The pollen density in the seed orchard was estimated.

Great clonal variation prevailed in the seed orchard with respect to the frequency of female and male flowering as well as the onset and duration of female receptivity and pollen dispersal.

A good agreement in flowering frequencies and phenological characteristics of the clones between different years was observed. The great variation in onset and duration of receptivity and pollen dispersal from year to year was influenced to a great extent by the prevailing temperature conditions in the spring, different years.

The calculations of the genetic composition of the progeny revealed that the gene contribution of the analysed clones varied considerably. This was mainly due to differences in the frequency of flowering.

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1 Introduction

As pointed out in a previous paper (Eriksson *et al.* 1973) the frequency of flowering and the point of time for flowering of the clones in a seed orchard is of importance for the genetic composition of the seed material harvested in the seed orchard. Since the clones in many seed orchards originate from different regions, the synchronization of flowering may not be complete. The long distance transfers may influence the vegetative growth as well as the amount of flowering. Mostly, a transfer to the south causes an increase in the frequency of flowering but a decrease in vegetative growth (cf. Johnsson *et al.* 1950). The first phenomenon is a consequence of the fact that a tree requires a certain total amount of heat in order to initiate flowering (cf. Sarvas 1970). The second phenomenon is a consequence of a photoperiodic response of the plants. Thus, the critical night length causing the cessation of growth is reached earlier in the season at a southern latitude than at the place of origin. Following long distance transfers from north to south the over-all reduction in vegetative growth may reduce the total amount of flowering in a particular clone, although the flowering per branch may be regarded as prolific.

Such phenomena make it necessary to carry out detailed investigations of the frequency with which different combinations occur in the seed harvested in a seed orchard. Since few marker genes are available, the evaluation has to be carried out on records of the flowering abundance and the point of time of flowering. These data are then combined to obtain the final estimate of the genetic composition of seed in the seed orchard. For all calculations, random mating is assumed to be prevailing. The prerequisites for panmixis to occur were listed by Eriksson *et al.* (1973) and they are presented once more below:

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

In the present investigation clones included in a seed orchard at Långtora approximately 30 km west south-west of Uppsala were studied with respect to

1. the number of female strobili per graft
2. the number of male strobili per graft
3. the point of time for receptivity of the ovules
4. the point of time for pollen dispersal

A preliminary phenological investigation of the flowering was carried out in 1972. This was followed by a more extended examination during the period 1973–1975.

2 Material and methods

A varying number of plus tree clones in a seed orchard at Långtora (lat. 59°43′, long. 17°08′, alt. 15 m) was included in the present investigation, which was carried out during the years 1972–1975. The origin of the clones is indicated in Figure 1. The clone numbers C 5001–C 5010 refer to the clones of Finnish origin. These clones are marked differently in the figures showing the performance of individual clones. The seed orchard was established in 1962–1964. The spacing was 5×5 metres. In 1972 only the phenological aspects of flowering were studied, whereas the frequency of flowering was added to the investigation during 1973–1975. In 1973, 17 clones were examined phenologically. Owing to increased flowering the number of clones could be raised to 20 in 1974 and 1975. It has to be added that the estimation of the frequency of male and female strobili comprised all 36 clones in the seed orchard.

This estimation was carried out in five randomly selected blocks in the seed orchard. The counting of all female and male strobili on a graft turned out to be too laborious. Therefore, the counting was restricted to certain branches on which all strobili were recorded. The numbers thus obtained were multiplied to get an estimate of the total number of strobili per graft.

A great variation of flowering intensity between blocks was noted. This variation was most pronounced in 1973. The intensity of male flowering was in this year nearly 15.4 times higher in the best block than in the poorest one.

To get a more equal contribution of all blocks to the total flowering in this seed orchard the following correction was made. The number of strobili for every graft was multiplied by the factor characteristic for the block in question. This factor (f) was derived in the following way:

$$f = \frac{100}{\sqrt{\text{total flowering in the block}}}$$

After this correction the ratio between the best and the poorest block in the example mentioned above became 3.9 instead of 15.4.

The examination of the point of time for receptivity and pollen dispersal was made on 50 strobili of each clone. From each clone 50 male and 50 female strobili were labelled. The labelling of the strobili was attempted in such a way that the strobili selected should be as representative as possible for the growth position of the strobili within the crowns. With a few exceptions, four grafts, one in each of four replications, were included in the investigation. In replications 1 and 3, 13 strobili were labelled while 12 strobili were labelled in replications 2 and 4.

The sparse flowering of some grafts in replication 4 made it necessary to label more than 13 strobili on the grafts in replications 1–3. In all cases 50 strobili were investigated. The assessment of receptivity and pollen shedding was performed in the way described in chapters 4 and 5.

The total amount of pollen within the seed orchard was determined by the aid of a pollen-catching device constructed by Sarvas (1962). This was kindly placed at our disposal by Dr Veikko Koski, The Institute for Forest Research, Helsinki, which is herewith thankfully acknowledged.

The maximum and minimum temperatures were recorded daily during the period of examination. Lack of money made it impossible to record the temperature ahead of this period, which is necessary for a determination of the heat quantity needed for reaching a certain developmental stage. However, a high measure of parallellism between the temperature observations at

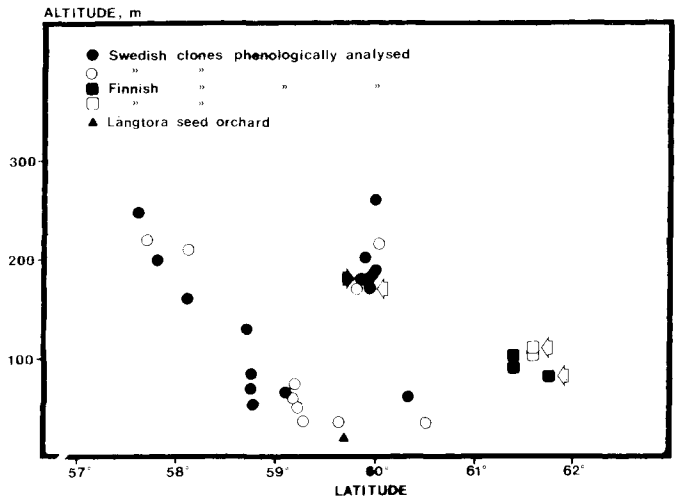


Figure 1. Schematic presentation of the origin of the clones growing in the seed orchard. The arrows mark instances with one clone more of the same origin.
◗ means that this clone was analysed phenologically
◗ means that this clone was not analysed phenologically
One of the Finnish clones was omitted due to its unknown altitude.

Långtora and those at Ultuna (a meteorological station 30 km east north-east of Långtora) was found. The correlation coefficients for the relationship between the maximum and the minimum temperatures at the two localities amounted in 1974 to 0.969*** and 0.909***, respectively.

The temperatures at Långtora were in most cases more extreme in comparison with Ultuna. Because of the good agreement of the temperature measurements from the two localities as well as the greater completeness of the data from Ultuna we preferred to use the latter in our calculations. In Figures 18–21, the daily mean temperature at Ultuna during the period for receptivity and pollen dispersal is demonstrated.

3 The frequency of flowering

As pointed out above, the frequencies of female and male flowering were estimated during the years 1973–1975. The relationship between the flowering of two different years was determined by a correlation analysis. The data from this analysis are compiled in the table below. As can be seen from the high correlation coefficients there is quite a strong relationship, indicating that those clones which flowered abundantly in 1973 did so also in 1974 and 1975. Therefore, in order to illustrate the clonal variation in the frequency of flowering, it may suffice to show the average flowering frequency for the years 1973–1975. This is done in Figures 2–3.

Correlation between flowering in different years	r
♀ 1973–1974	0.878***
♀ 1973–1975	0.705***
♀ 1974–1975	0.866***
♂ 1973–1974	0.847***
♂ 1973–1975	0.827***
♂ 1974–1975	0.908***

According to the ranking of the clones, the summed percentages within each quarter of the clones are illustrated.

From Figure 2, showing the frequency of female strobili, in 1973–1975 it may be seen

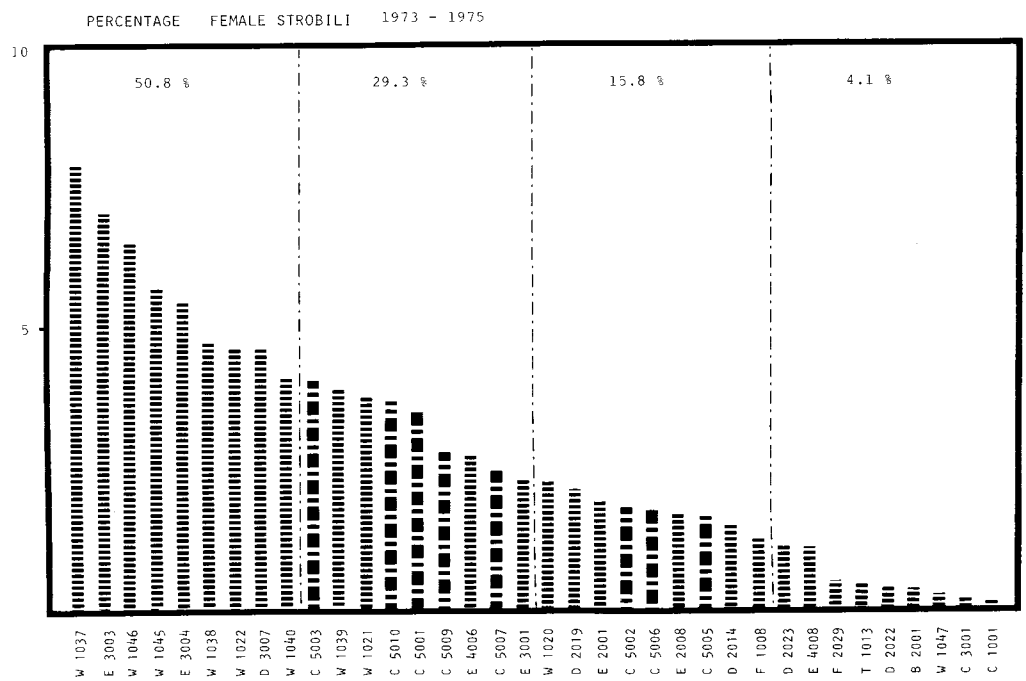


Figure 2. The mean percentage of the female strobili during the years 1973–1975 of all 36 clones growing in the seed orchard.

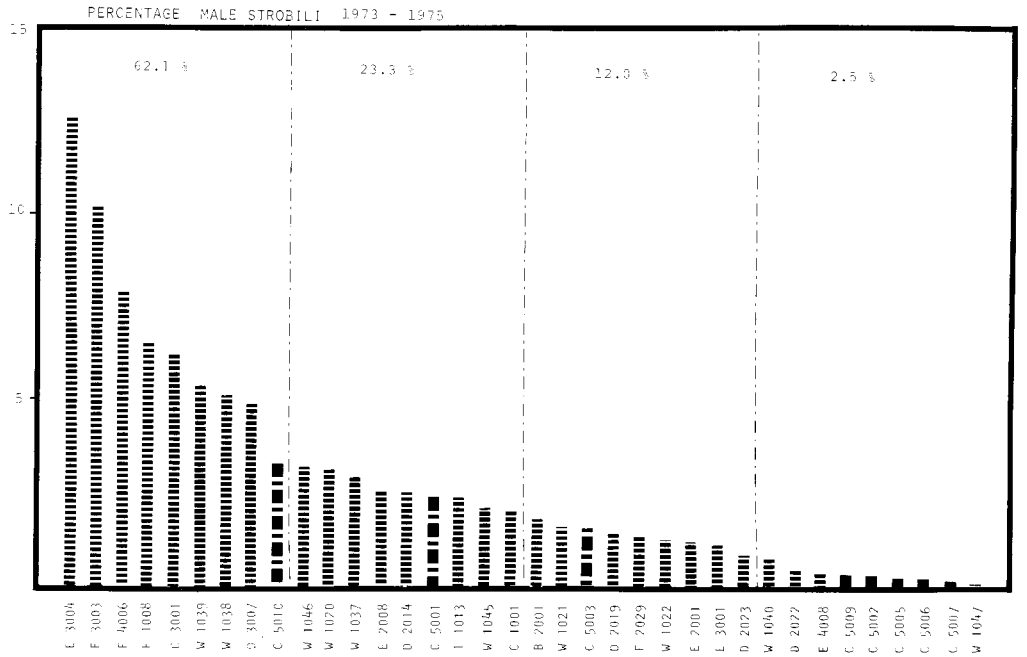


Figure 3. The mean percentage of the male strobili during the years 1973–1975 of all 36 clones included in the seed orchard.

that the nine most abundantly flowering clones reached the 50 per cent level, whereas the corresponding figure for the nine poorest clones did not amount to more than four per cent.

The clones of Finnish origin are mostly small compared to the rest of the clones. In spite of this no Finnish clone belonged to the poorest quarter when considering the female flowering. It is not probable that these clones will compete vegetatively with the other clones. Therefore one cannot anticipate a leading position of any one of them in the future. In this context it is worth mentioning that Karrfalt *et al.* (1975) reported a variation in flowering between Scots pine provenances which they attributed to differences in size.

The abundant flowering of clone W 1037 is due to the fact that mostly 3–5 female strobili were present at the same shoot apex.

As regards the male flowering the difference between the poorest and the most abundantly flowering clones is still more pronounced than for the female flowering (Figure 3). This may be due to the fact that in Scots pine male flowering starts at an older

Table 1. The loss of female strobili during receptivity and during the development of the conelets.

Year	Percentage decrease in number of female strobili during		Total reduction
	Receptivity	The development of the conelets	
1972	4.0	—	—
1973	7.88	15.89	22.53
1974	10.21	25.60	33.20
1975	61.79	—	—

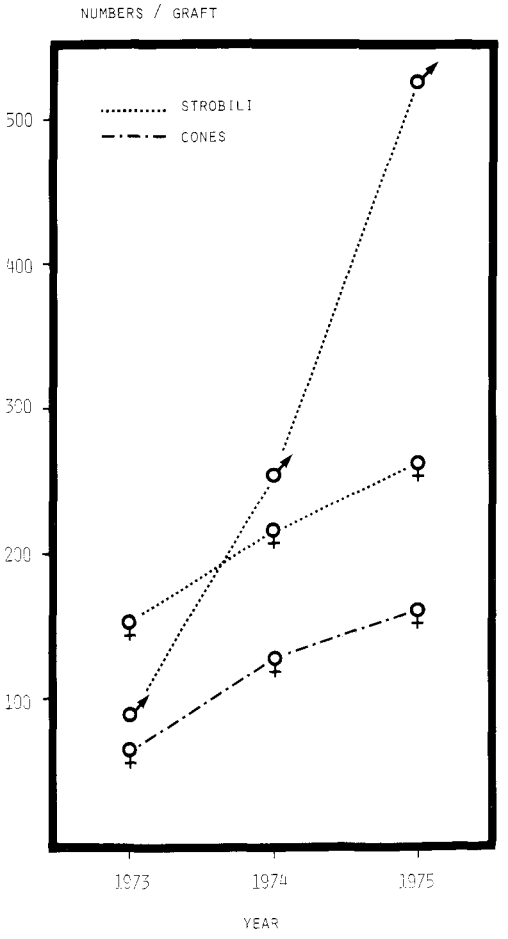


Figure 4. The estimated number of female and male strobili per graft as well as the number of one-year old cones during the period 1973–1975.

age than female flowering. As may be seen from Figure 3 the eight Finnish clones were ranked with the poorest male flowering clones.

The clone C 3001 was characterized as an abundant male flowering clone whereas the frequency of female flowering was very low. In spite of that, a weak correlation between female and male flowering of all clones, including C 3001, ($r=0.414^{*}$) was obtained. Omitting C 3001, the r-value increased somewhat, $r=0.479^{**}$.

The data from 1972–1975 indicate that a decrease in the number of female strobili originally found, occurred both during receptivity and during the development of the conelets. The results are compiled in Table 1. The percentages of female strobili lost during receptivity were extremely high in 1975. This was probably a consequence of the protracted development caused by unfavourable weather conditions. Losses occurring during the development of the conelets were measured as the difference between the number of one-year old cones and the number of female strobili at the end of the receptivity (approximately at the stage shown in Figures 11–12) in the preceding year (Figure 4, Table 1). From column 4 in Table 1 it may be seen that the total reduction is considerable.

4 The development of the female strobilus

As far as we know, no complete sequence of photos showing the different phases of development of the female strobilus of Scots pine has been published. Therefore, we found it worthwhile to present a complete series of photos illustrating these stages. This will also facilitate the understanding of how the calculations of the gene transfer to the next generation were carried out.

In Figure 5 a bud is seen which is completely protected by bud scales. At the next stage, shown in Figure 6, the apex of the strobilus is no longer covered by bud scales. The ovules are probably not receptive at this stage. However, pollen grains may get inside the bud scales and if they survive they might be able to take part in a fertilization. Therefore, such buds should not be included in controlled matings. In Figures 7–8 (▲) the strobilus has grown considerably and receptive ovules are certainly present in the upper part of the strobilus. These two stages during the strobilus development were designated by a triangle during the phenological examination. In Figure 9 (●) a strobilus is shown in which most of the ovules are receptive. Such a strobilus got the circle as its symbol during the phenological examination. If no pollen dispersal had taken place previously and abundant pollen is prevailing, a maximum amount of pollen could be expected to reach the pollen chambers at this stage.

The next photo, Figure 10 (/), shows a strobilus in which the ovuliferous scales have increased in thickness to such an extent that the pollen grains can no longer reach the pollen chamber. Thus, the receptivity is passed. The last two photos, Figures 11–12, show the process of bending down of the entire strobilus.

In Figures 13–16 the pattern of development for receptivity in the earliest and the latest clone each year is demonstrated. "Early" and "late" refer to the dates for reaching 25 per cent receptivity. Also the average receptivity of all clones studied in a particular year is illustrated. Thus, these figures give information on the pattern of development for receptivity.

The clonal variation is best seen in Figure 17 in which the duration of receptivity from the stage shown in Figure 7 to the stage shown in Figure 10 is demonstrated for all clones. In this context it should be added that the recording of the development in 1972 was made in a slightly different way. Therefore, only data from 1973–1975 are illustrated in Figure 17. The clones were arranged according to the date for onset of the receptivity in 1975.

The clonal variation as regards the reaching and duration of certain stages was analysed numerically, as presented below. For each graft the average date at which the stages shown in Figures 7, 9 and 10 respectively, were reached, was calculated. Furthermore, the duration of different phases of development was calculated by subtracting the figures obtained for the stages shown in Figure 7 and 9 from the figure for the stage shown in Figure 10. A two-way analysis of variance was carried out for the onset of the three different stages as well as for the duration of the two phases.

The variance ratios are listed in Table 2. As can be seen from this table the clonal differences were found to be great for all characteristics studied and for all years.

Furthermore, Figures 13–17 reveal that the onset of receptivity varies considerably from year to year. Thus, 1973 is characterized by a late and comparatively fast development in contrast to 1975 with an early onset and a protracted receptivity.

When there are differences in the point of

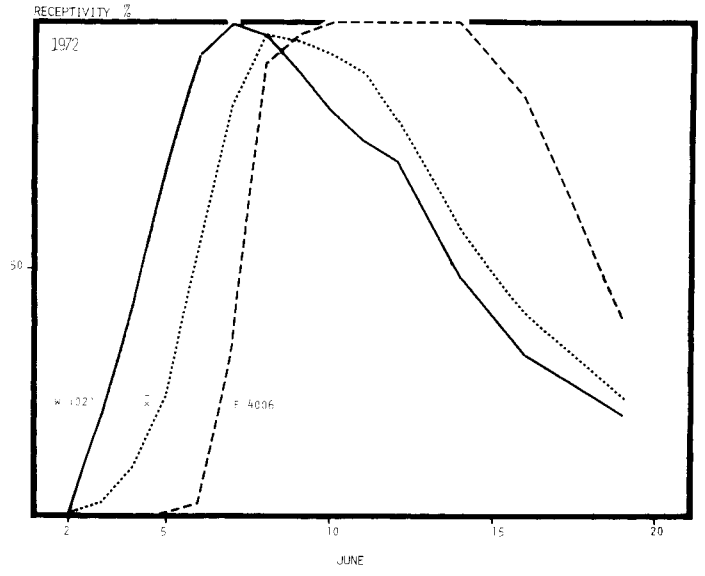


Figure 13. The percentage of strobili containing receptive ovules in June 1972 for the earliest and latest clone, as well as the mean values for all clones.

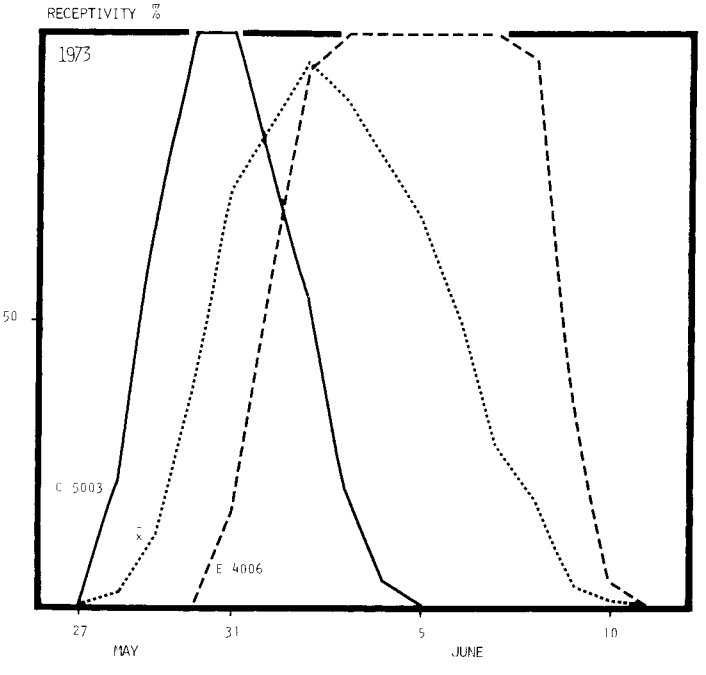


Figure 14. The percentage of strobili containing receptive ovules in May and June 1973 for the earliest and latest clone as well as the mean values for all clones.

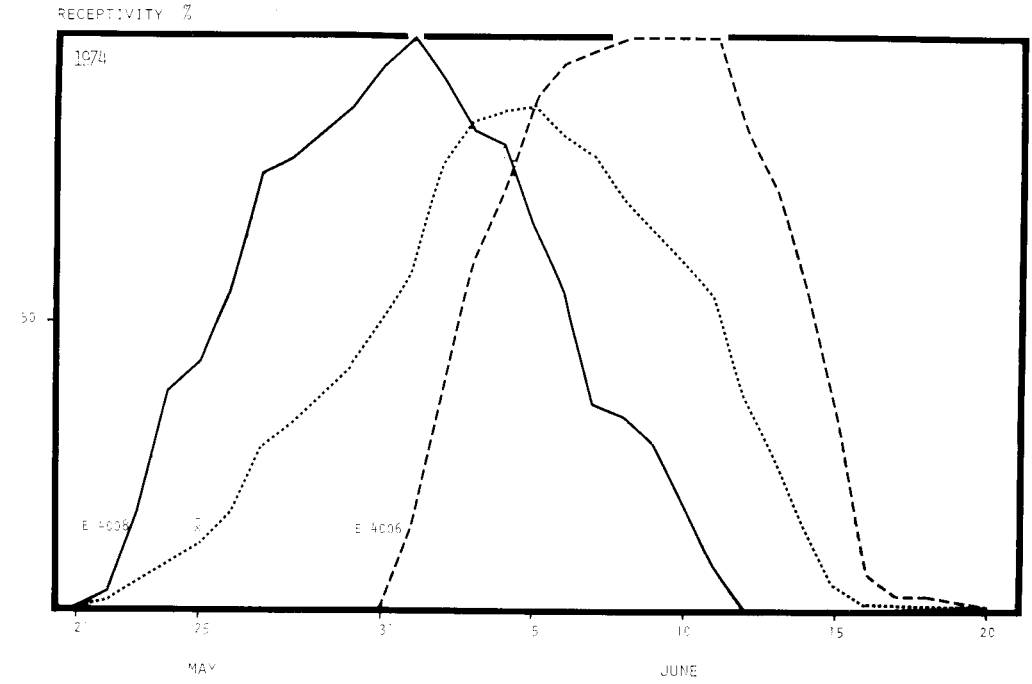


Figure 15. The percentage of strobili containing receptive ovules in May and June 1974 for the earliest and latest clone as well as the mean values for all clones.

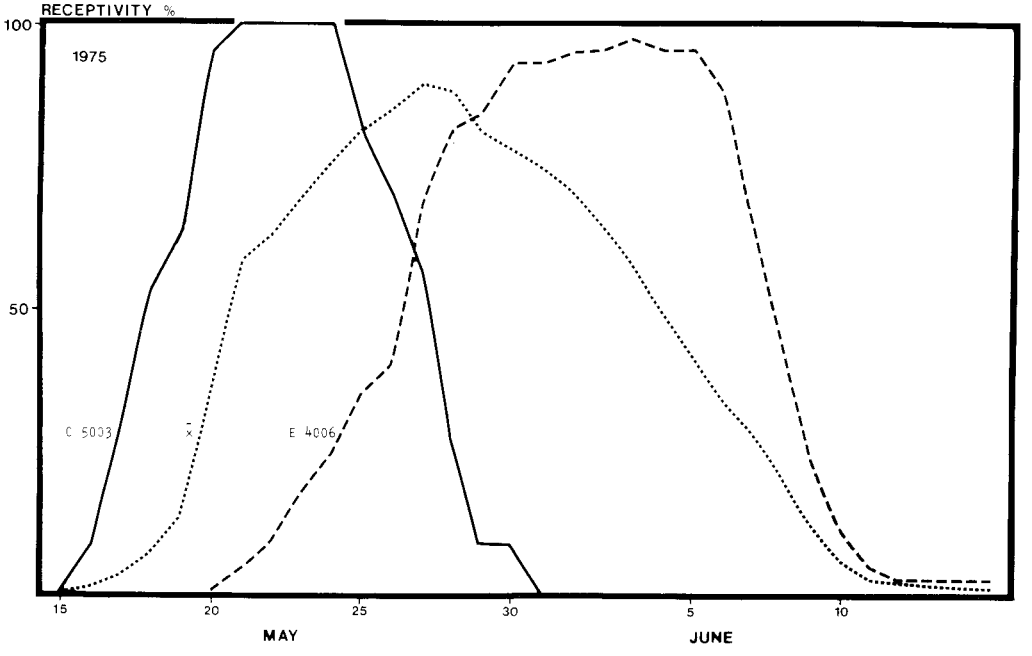


Figure 16. The percentage of strobili containing receptive ovules in May and June 1975 for the earliest and latest clone as well as the mean values for all clones.

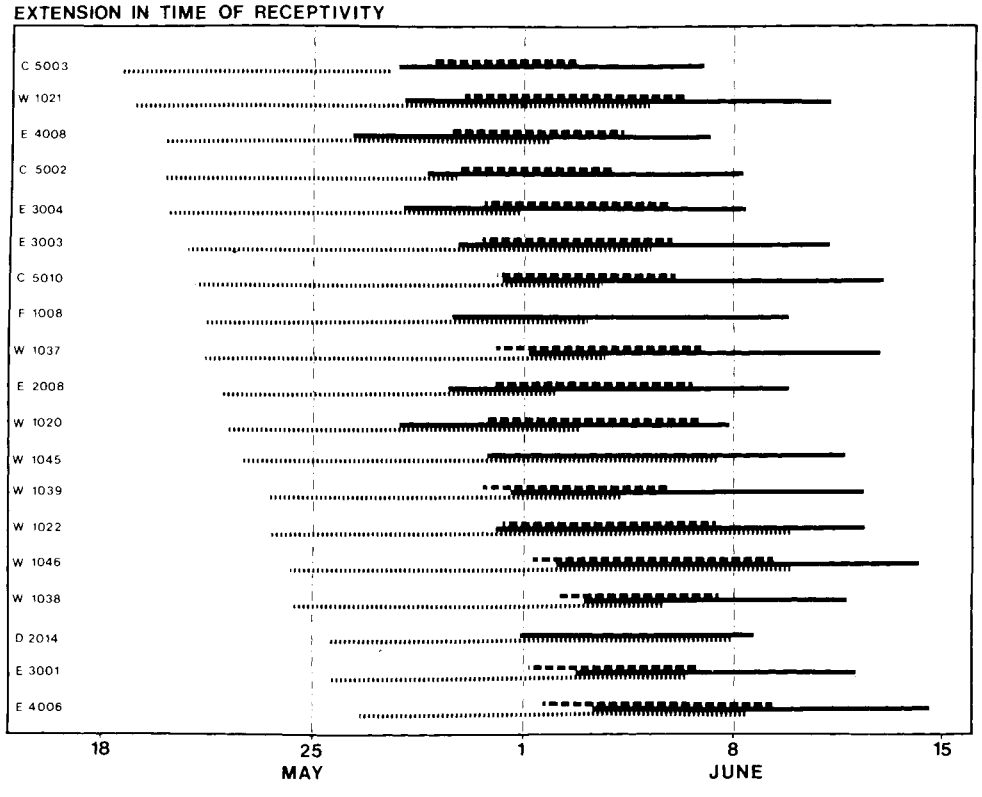


Figure 17. The extension in time of the receptive period measured as the difference between the stages shown in Figures 10 and 7 for each clone and each year ▬ ▬ ▬ 1973 ▬▬ 1974 ▮▮▮▮▮ 1975.

time for the appearance of a certain stage of development it is mostly expected that the temperature is responsible for the observed differences. To illustrate the influence of the temperature conditions on the onset and duration of receptivity, the differences at the 20 per cent level between the ascending and descending parts of the curves referring to the mean values in Figures 14–16 are indicated in Figures 19–21.

To get some quantitative estimation of this influence, the temperature sums based on the daily mean temperatures – $\Sigma(t_i - 5)$ – needed to reach 50 per cent receptivity were

Table 2. Analysis of variance with respect to phenology of the female flowering.

Year	Source of variation	DF	Point of time for onset of the stage shown in			Joint duration of the stages shown in Fig. 7 and 9	Duration of the stage shown in Fig. 9
			Fig. 7 (▲)	Fig. 9 (●)	Fig. 10 (/)		
1972	Clone	14	18.12***	31.77***			
	Replication	3	7.05***	6.10**			
1973	Clone	15	27.29***	20.89***	33.00***	10.88***	16.16***
	Replication	3	1.10	3.15*	1.96	0.82	1.17
1974	Clone	18	40.89***	23.20***	31.92***	31.70***	35.14***
	Replication	3	1.60	0.65	0.73	3.26*	0.66
1975	Clone	18	29.66***	27.51***	30.33***	25.34***	25.01***
	Replication	3	1.81	1.54	0.46	1.42	1.56

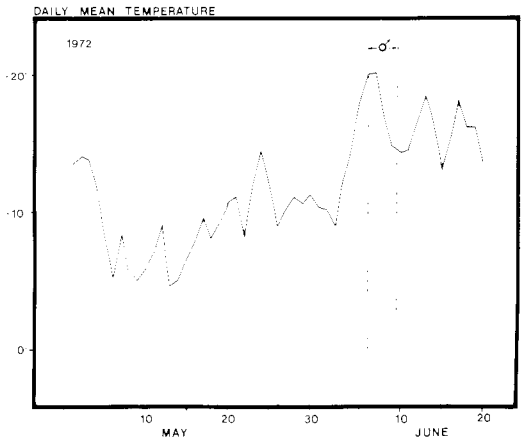


Figure 18. The daily mean temperature from May 1 to June 20, 1972 at Ultuna approximately 30 kilometres east north-east of Långtora. The arrow indicates the duration of the pollen dispersal measured as the difference between the ascending and descending part at the 20 per cent level of the curve showing the mean value for all clones in Figure 25.

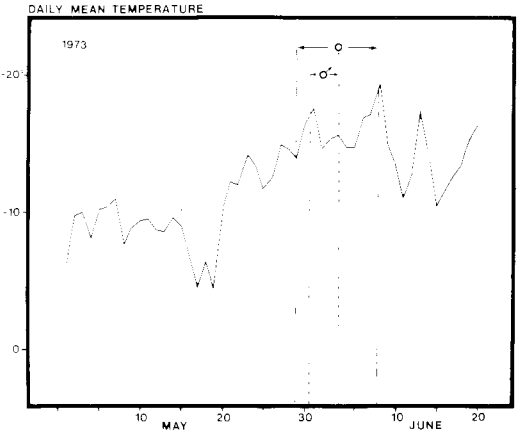


Figure 19. The daily mean temperature from May 1 to June 20, 1973 at Ultuna approximately 30 kilometres east north-east of Långtora. The arrows indicate the duration of the receptivity and the pollen dispersal measured as the difference between the ascending and descending parts at the 20 per cent level of the curves showing the mean values for all clones in Figures 14 and 26, respectively.

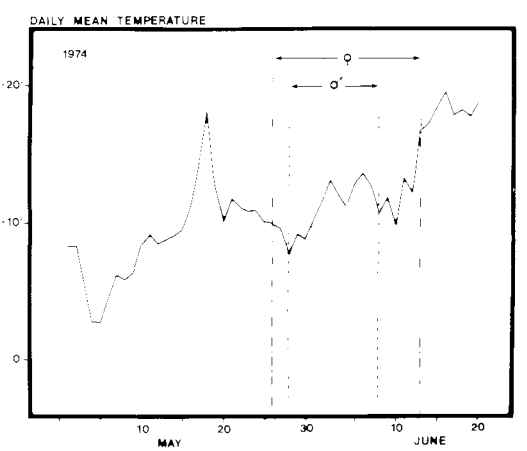


Figure 20. The daily mean temperature from May 1 to June 20, 1974 at Ultuna approximately 30 kilometres east north-east of Långtora. The arrows indicate the duration of the receptivity and the pollen dispersal measured as the difference between the ascending and descending parts at the 20 per cent level of the curves showing the mean values for all clones in Figures 15 and 27, respectively.

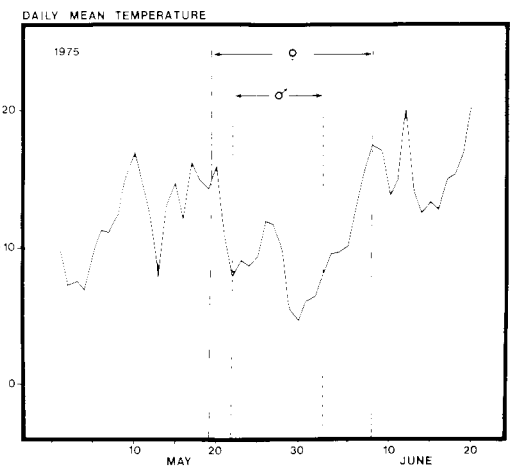


Figure 21. The daily mean temperature from May 1 to June 20, 1975 at Ultuna approximately 30 kilometres east north-east of Långtora. The arrows indicate the duration of the receptivity and the pollen dispersal measured as the difference between the ascending and descending parts at the 20 per cent level of the curves showing the mean values for all clones in Figures 16 and 28, respectively.

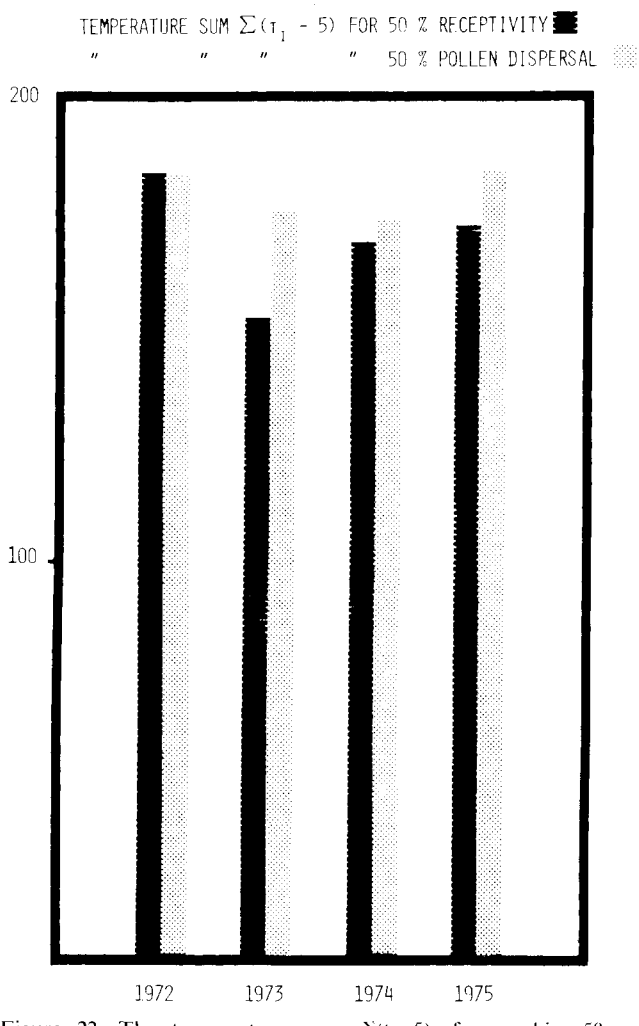


Figure 22. The temperature sum, $\Sigma(t_i-5)$, for reaching 50 per cent receptivity and 50 per cent pollen dispersal.

calculated. The data are compiled in Figure 22. Although the temperature sums vary from one year to another, it is clear that the temperature conditions are of greater importance for the onset and duration of the receptivity than the date. It should also be remembered that the daily mean temperature need not be the best temperature characteristic when relating temperature to a biological developmental process.

The variation in onset and duration of receptivity between individual strobili of the same graft growing in different directions on the crown is exemplified in Figure 23 for a graft of one early and one late clone, respectively. The general pattern of development was that the strobili growing at the southern part of the graft were earlier with a short duration of receptivity whereas the strobili at a northern exposure showed a late onset and a prolonged receptivity. Deviations from the general pattern could be due to the fact that the strobili were growing at different distances from the ground and further that some strobili had a more shaded position near the stem.

As may be seen from Figure 17, no drastic changes between the clones as regards their

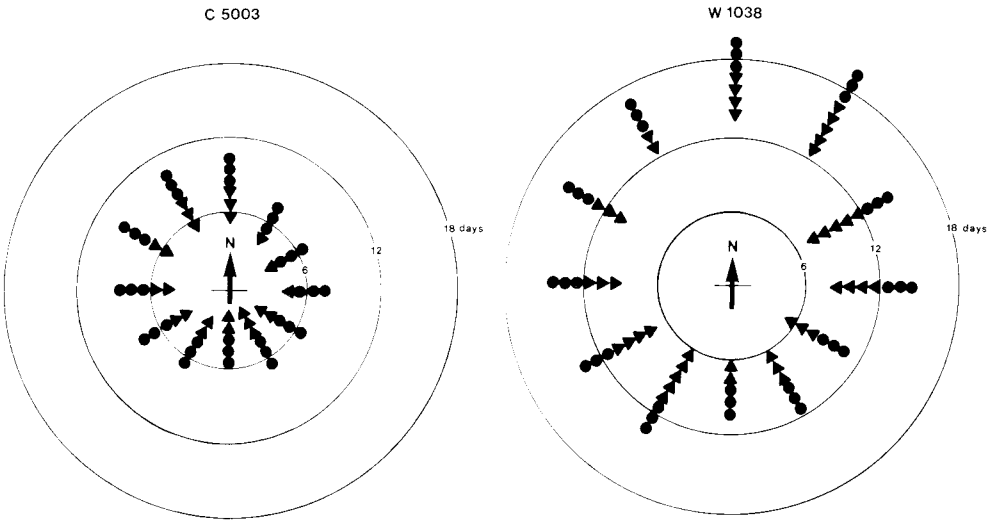


Figure 23. Schematic illustration of a graft from one early (C 5003) and one late (W 1038) clone with 12 female strobili growing in different directions on the crown. For each strobilus, the onset and duration of the stages shown in Figures 7–8 (▲) and 9 (●) are indicated. Each symbol refers to one day of observation.

sequence for the onset of receptivity occurred. The sequence for reaching 25 per cent receptivity in 14 clones investigated phenologically in 1972–1975 was compared by means of a χ^2-test. This test revealed that the ranking of the clones between the four years was non-random ($p<0.1$ per cent). This means that clones which are early one year usually maintain this characteristic and the same holds true for the late clones. Some variation in ranking of the clones between different years was observed which might be due to the fact that the strobili studied phenologically did non occupy exactly the same position on the graft each year. As is clearly seen from Figure 23 the position of the strobili on the crown is of great importance for the onset of receptivity.

No influence of the origin of the clones on the sequence in which the receptivity appeared could be traced in the present investigation. In a similar study of Scots pine provenances Karrfalt *et al.* (1975) reported a difference in the point of time for female strobilus development, the northern provenances being earlier than the southern ones. However, overlapping occurred, which agrees with the observations in the present investigation.

5 Estimation of the fraction of receptive ovules

It is quite clear that the number of receptive ovules varies between the strobili shown in Figures 7–9. Moreover, the number of ovules in which the pollen grains had reached the pollen chamber already during a previous stage, is not known. To evaluate this is especially difficult during a protracted developmental process. An estimation of the fraction of ovules still available for pollination had to be carried out. This estimation was based on the hypothesis "first come, first served" which means that the probability of fertilization by a particular pollen grain is low if another pollen grain had already reached the pollen chamber. The relevance of this hypothesis was proved by Franklin (1974) for *Pinus elliottii* and we have assumed that it holds also for *Pinus sylvestris*.

A scheme was constructed (cf. Figure 24) which considers the "first come, first served" hypothesis. As seen from Figure 24 it was presupposed that no stage (▲ or ● cf. above) contributed to future fertilizations for more than 3 days. For each symbol the first day was assumed to contribute 4–5 times more than the second day. The scheme was applied to those days when a pollination was expected to take place. The threshold value for pollen shedding amounted to four per cent. Moreover, it was assumed that the strobili which reached only the stages shown in Figures 7–8 (▲) during the time for pollination contributed 50 per cent less to the transfer of genes to the progeny than the other strobili (cf. Figure 24).

This scheme should be regarded only as an initiated guess. No investigation has been or can ever be carried out to test the scheme. Moreover, it may be stated already here that the differences in the point of time of receptivity influenced the transfer of genes to the next generation to a much lesser extent than the frequency of flowering.

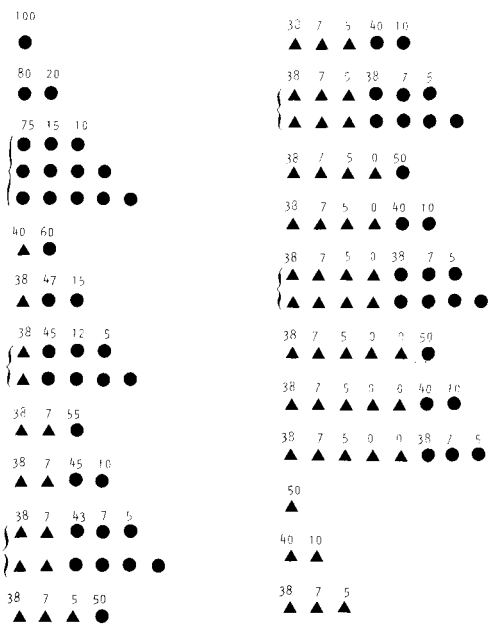


Figure 24. Schematic illustration of how the estimation of the daily percentage of receptive ovules within a strobilus was carried out (cf. the text).

6 Pollen dispersal

Similarly to earlier investigations along this line (Eriksson *et al.* 1973) the pollen dispersal of a single strobilus was examined following a faint vibration of the part of the twig at which the male strobilus was growing. This may, under unfavourable weather conditions, cause a registration of pollen shedding although no natural pollen dispersal took place. It is regrettable that no other technique for the registration of pollen dispersal from single strobili was available.

In Figures 25–28 the data from this part of the investigation are compiled. In these figures the mean percentage of pollen-shedding strobili for each day during the period of pollen dispersal is shown as well as the percentages for the earliest and the latest clone. Early and late refer to the dates for reaching 25 per cent pollen dispersal. Furthermore, for each clone and each year, the extension in time of the period when pollen shedding occurred in at least 20 per cent of the male strobili is summarized in Figure 29. For this phenological characteristic, significant differences between clones were obtained in 1972 and in 1974 (Table 3). There was also a great clonal variation in the point of time for onset of the pollen-shedding period for all years. Moreover, as can be seen from the Figures 25–29 the pattern varies considerably from year to year. Both the onset of pollen dispersal and the duration of the pollen-shedding period vary. This difference between the years is especially pronounced for 1972 and 1974 (Figures 25, 27, 29).

The ranking of the clones with respect to the onset of pollen dispersal did not vary greatly from year to year. The clones belonging to the early group one year usually remained in this group in the following years also, and similarly for the late group. This may partly be seen from Figures 25–29. The observed variation in ranking of the clones between different years might be attributed to the fact that the strobili studied phenologically did not have exactly the same position on the graft each year (cf. below and Figure 31).

It is quite clear from a joint analysis of the temperature diagrams (Figures 18–21) and the pollen-shedding diagrams (Figures 25–28) that the temperature conditions are to a great extent responsible for the variations in pollen dispersal from year to year. The strong influence of temperature may also be seen in Figures 22 and 30.

Table 3. Analysis of variance with respect to phenology of the male flowering.

Year	Source of variation	DF	Point of time for onset of pollen shedding in 20 per cent of the strobili	Time duration of the pollen shedding at the 20 per cent level (see Fig. 26 for an explanation)
1972	Clone	14	5.00***	2.57**
	Replication	3	1.22	3.46*
1973	Clone	16	6.07***	1.69
	Replication	3	0.47	1.38
1974	Clone	19	7.22***	3.07***
	Replication	3	0.31	0.25
1975	Clone	19	9.17***	1.44
	Replication	3	0.56	1.12

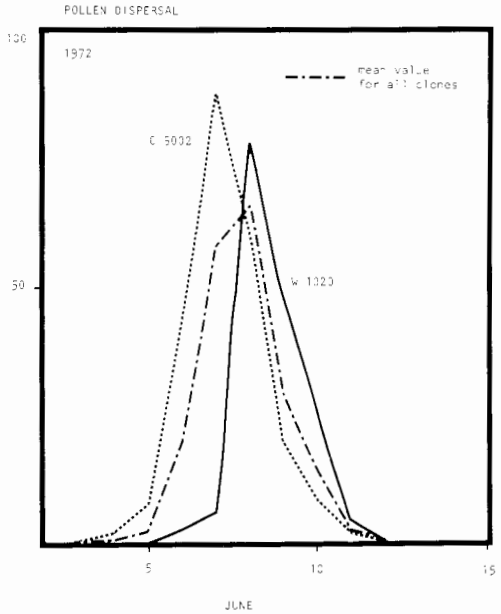


Figure 25. The percentage of pollen-shedding strobili on different days in June 1972 for the earliest and the latest clone as well as the mean values for all clones.

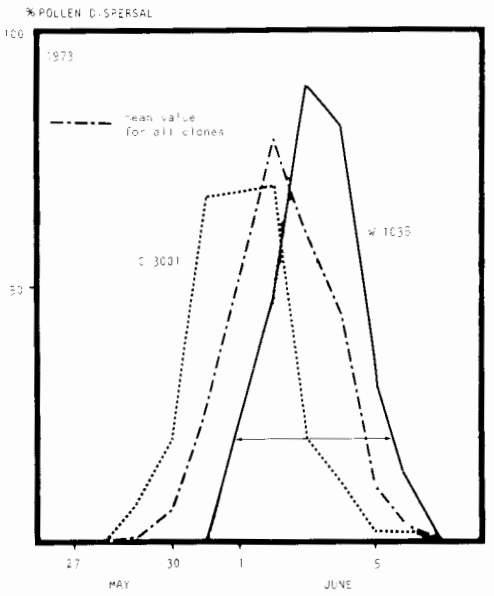


Figure 26. The percentage of pollen-shedding strobili on different days in May and June 1973 for the earliest and the latest clone as well as the mean values for all clones. The arrows on the curve for W 1038 illustrate the time duration of the pollen shedding at the 20 per cent level which was subjected to an analysis of variance presented in Table 3.

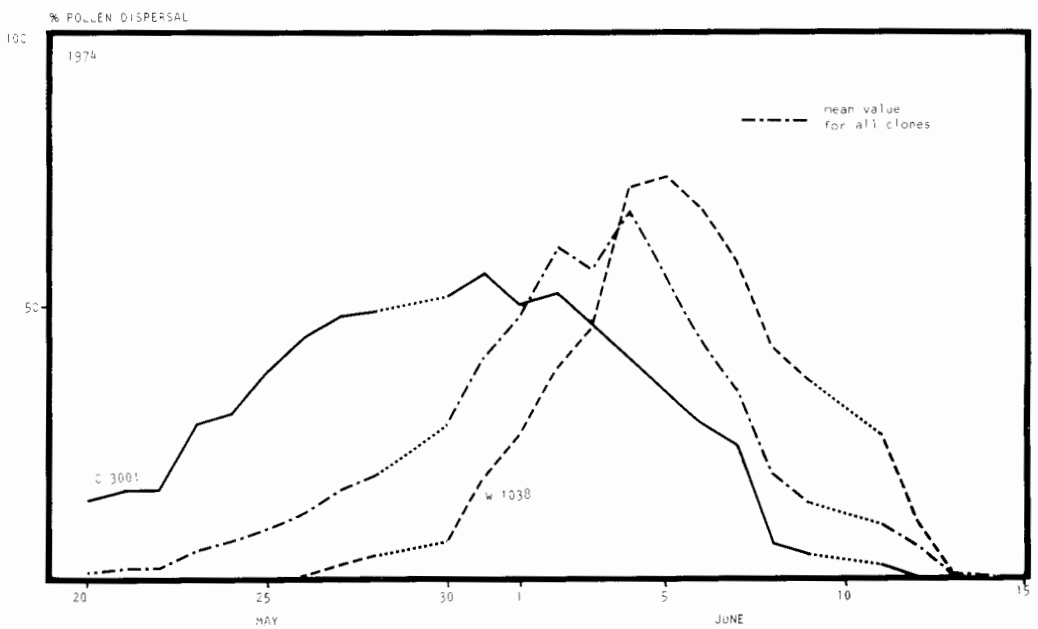


Figure 27. The percentage of pollen-shedding strobili on different days in May and June 1974 for the earliest and the latest clone as well as the mean values for all clones.

Figures 5–12. Different developmental stages of the female strobili. Photos Kjell Lännerholm.



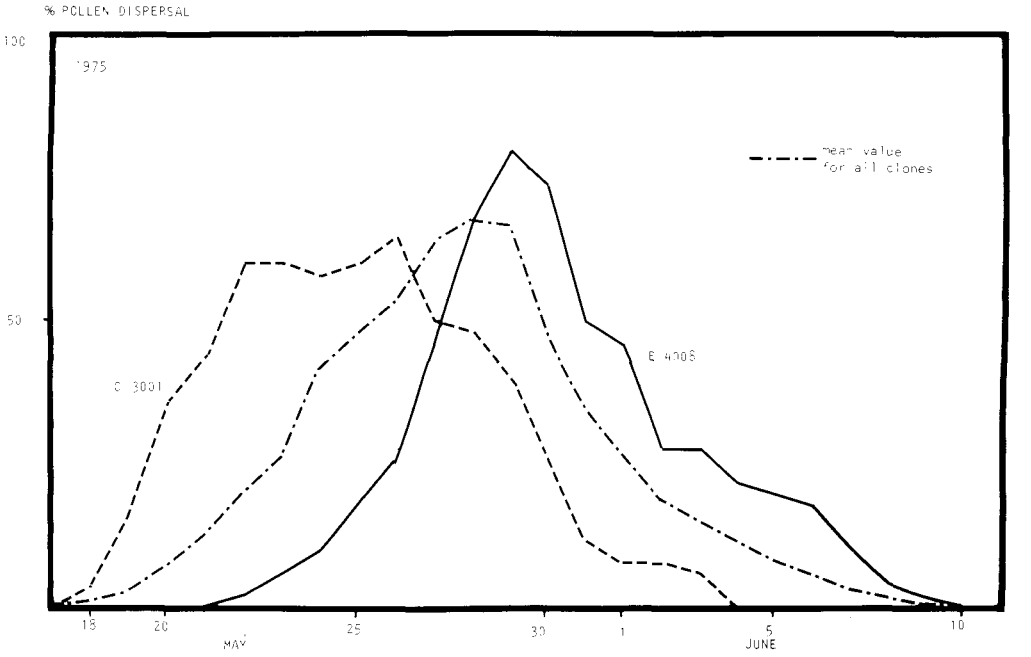



Figure 28. The percentage of pollen-shedding strobili on different days in May and June 1975 for the earliest and the latest clone as well as the mean values for all clones.

As regards the variation within the same graft between individual strobili growing in different directions on the crown, this is illustrated in Figure 31 for an early clone (C 5003) and a late clone (W 1038). The pollen shedding usually starts earlier and is of shorter duration in the southern part of the crown than in the northern part of the crown.

It might have been expected that the origin of the clones would influence the onset of the pollen shedding in such a way that the northernmost ones would be the earliest ones. However, no such trend could be revealed in the present study. Two of the Finnish clones, C 5003 and C 5010, were certainly early but the third Finnish clone investigated, C 5002, was not an early one (cf. Figure 29).

Furthermore, the W-clones, which were the northernmost ones among the Swedish clones showed a great variation with respect to the onset of the pollen dispersal (cf. Figure 29). Since the clones cannot be regarded as representative for the populations (all being plus trees) from which they were selected, they cannot be expected to behave as average trees from those populations.

According to Koski (1975) tens of kilograms of pollen per hectare are required to achieve a satisfactory pollination in a pine seed orchard. In the same paper Koski showed the relationship between pollen production and stem diameter. If the grafts in the Långtora seed orchard behave in the same way as the grafts studied by Koski (1975) it is clear that the pollen production is not yet satisfactory in the seed orchard studied by us. After a few more years the grafts would exceed the critical size, which guarantees that the majority of fertilizations will take place by seed orchard pollen and maximum genetic gain could be obtained.

An estimation of the contamination by pollen from stands close to or far away from the seed orchard is a delicate task. The pine stand closest to the seed orchard of Långtora is situated more than 1.5 kilometres from the orchard, which, according to the investigations by Andersson (1955) should reduce the amount of pollen from outside considerably

compared to the pollen quantity within the stand. The data obtained by Hadders (1973) are disappointing in this respect since a heavy seed crop was obtained from a seed orchard in spite of a complete emasculation of all male strobili within that seed orchard. Nor was there in this case a Scots pine stand in the closest vicinity of the orchard.

The quantitative relationship between seed orchard pollen and pollen from outside as well as the point of time for pollen shedding are of importance for estimating the amount of "illegitime matings" in the seed orchard (matings between seed orchard clones and pollen from any other Scots pine trees). There are no means available to establish this frequency. However, the present investigation may give some indications of the anticipated frequency of "illegitime mating".

In Figures 32–34 the percentage of pollen dispersal within the seed orchard is demonstrated, as well as the amount of the pollen recorded every four hours by the pollen-catcher. The figures were drawn in such a way that the peak frequency of pollen shedding determined by direct examination of the seed orchard clones should be at the same level as the frequency determined in the pollen-catcher the same day. Thereby a visual impression of the pollen contamination may be obtained. The interpretation of the curves is easiest if their peaks do not appear simultaneously. If they coincide it is impossible to reveal any contamination. On the other hand if they do not coincide it suggests that contamination plays a role.

It is necessary to guard against drawing to far reaching conclusions from these figures since the pollen-catcher reveals the actual amount of pollen in the air, whereas the examination of the individual strobili may exaggerate the pollen dispersal on days with

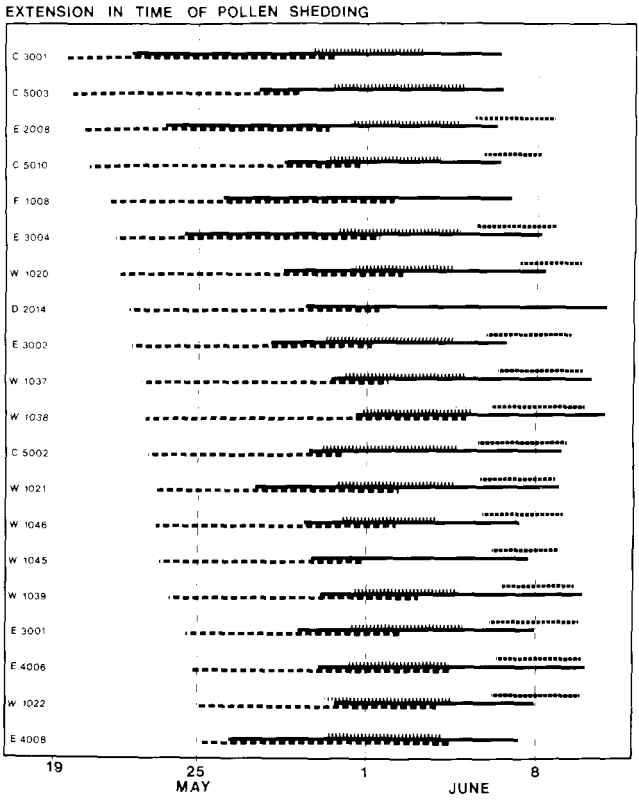


Figure 29. The extension in time of the period when pollen shedding occurred in at least 20 per cent of the male strobili for each clone and each year ▬▬ 1972 ▪▪▪▪ 1973 ▬▬ 1974 ▬ ▬ 1975.

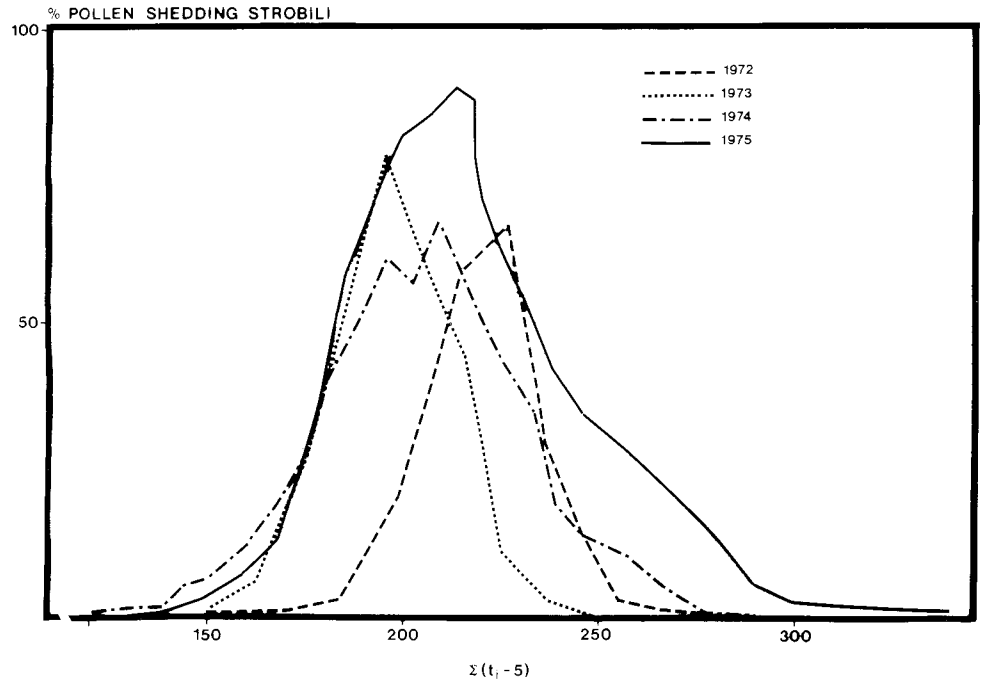


Figure 30. The mean pollen dispersal in the years 1972–1975 plotted against the temperature sum $\Sigma(t_i-5)$.

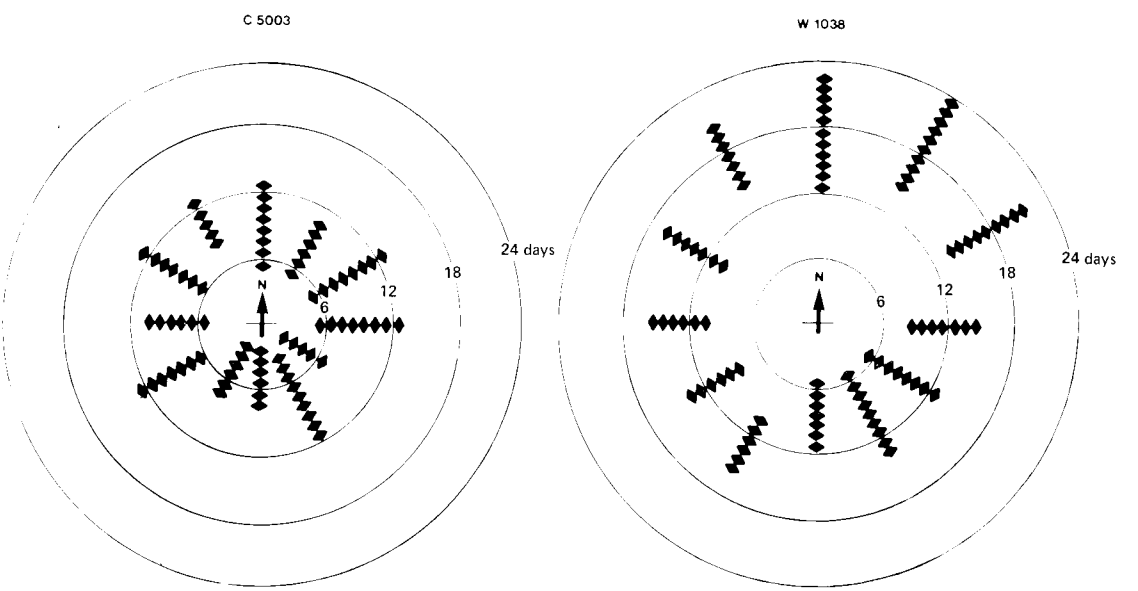


Figure 31. Schematic illustration of a graft from one early (C 5003) and one late (W 1038) clone with 12 male strobili growing in different directions on the crown. For each strobilus, the onset and duration of the pollen shedding are indicated. The symbol –◆– refers to one day of observation.

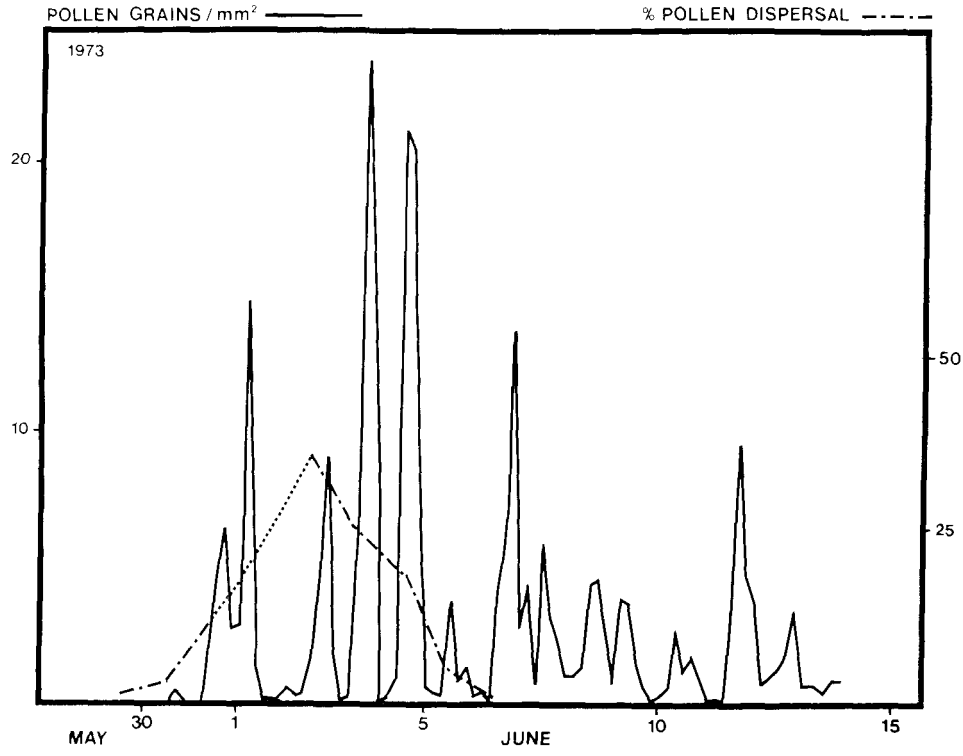


Figure 32. The number of pollen grains per mm² recorded in the pollen-catcher and the pollen dispersal determined by direct observation of the 17 investigated clones in 1973. The dotted part of the curve illustrates one missing value on June 1.

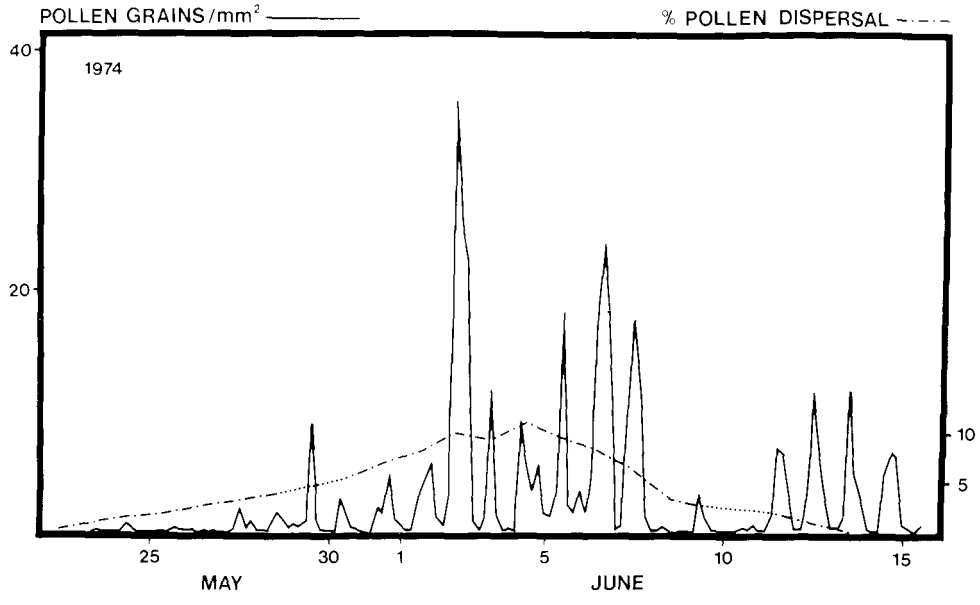


Figure 33. The number of pollen grains per mm² recorded in the pollen-catcher and the pollen dispersal determined by direct observation of the 20 investigated clones in 1974. The dotted parts of the curve illustrate two missing values on May 29 and June 10 respectively.

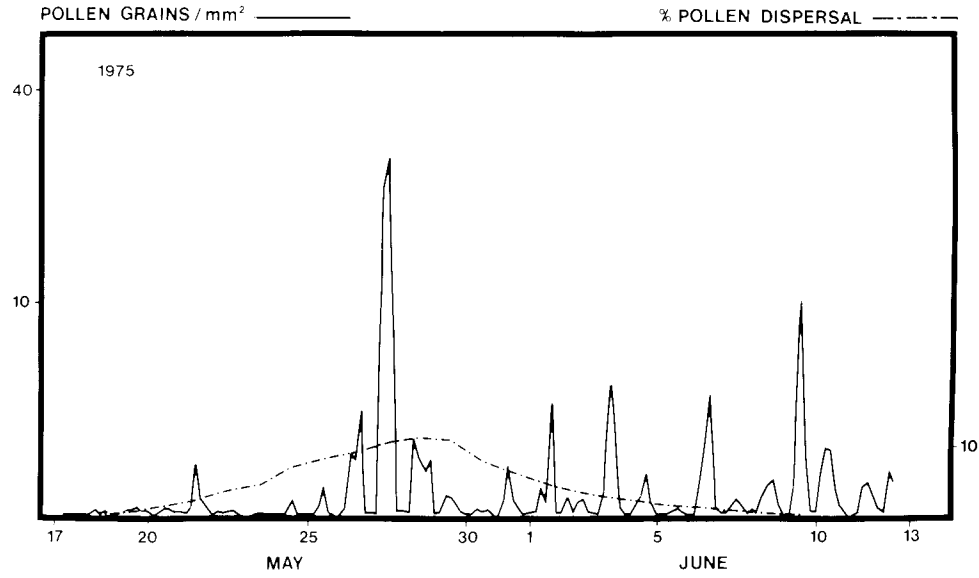


Figure 34. The number of pollen grains per mm² recorded in the pollen-catcher and the pollen dispersal determined by direct observation of the 20 investigated clones in 1975.

low temperature. Sarvas (1955) showed that pollen dispersal occurred mainly on days with a high temperature.

The situation seems to be quite simple in 1973 when there was a pronounced peak in the pollen dispersal of the seed orchard clones (Figure 32). Both before and after this peak the pollen-catcher revealed high pollen density. This suggests that the pollen contamination during this year was considerable. It has to be added that the maximum temperature was high (>20°C) from May 27 to June 4 and then high again from June 6 on. Since the temperature was more or less constant during the time around June 2 it can be concluded that temperature fluctuations cannot explain the occurrence of several peaks in the pollen dispersal as registered by the pollen-catcher.

The interpretation of the data from 1974 is difficult owing to the extended maximum for the curve of pollen dispersal of the seed orchard clones (Figure 33). The relationship between the curves would have been quite different if the maximum had appeared on June 2 instead of June 4. As the curves are drawn in Figure 33 the pollen contamination from outside is considerable. On the other hand, if the true peak appeared on June 2 the pollen contamination would have been regarded as moderate to negligible. The temperature conditions suggest that the contamination of pollen is somewhat smaller than a comparison of the two curves indicates. Thus, on June 2 the maximum temperature was 20.0°C while it amounted to 18.5°C and 16.5°C on June 3 and 4, respectively.

Regarding the data from 1975, the curve for the pollen-catcher suggests that there should be a greater pollen contamination on May 27 (Figure 34). However, the maximum temperature observed on May 27 was 18.2°C, whereas the corresponding figure for May 28 was 14.6°C, which means that the amount of pollen in the pollen-catcher is expected to be lower on May 28 than on May 27. A pollen contamination cannot be ruled out completely but the size of this contamination may be considerably less than may be expected from the curves in Figure 34.

Summarizing the discussion it may be stated that there was probably a pollen contamination in 1973, whereas a contamination could not be definitely proved for 1974 and 1975.

7 Estimation of the genetic composition of the progeny

The calculations below refer to an imaginary seed orchard comprising all clones studied phenologically. Therefore, the imaginary seed orchard consisted of 17 clones in 1973 and 20 clones in 1974–1975.

The composition of the pollen cloud for each day during the period of pollen dispersal was obtained by multiplying the percentage of male flowering by the percentage of strobili shedding pollen for each clone for that particular day. For each day the percentage of female flowering was multiplied by the percentage of receptive ovules to get the proportion of receptive ovules from each clone on the different days. The percentage for female and male gametes, thus obtained, were multiplied to obtain the proportion of all possible crosses for every day during receptivity. Days, when the pollen shedding was calculated to be less than four per cent of the total pollen shedding (based on the examination of individual strobili and the frequency of flowering) were not included in the calculations. The total sum for all possible crosses (including selfing) were calculated separately for each clone. After that the gene contributions of a clone to the progeny could be calculated. This was done

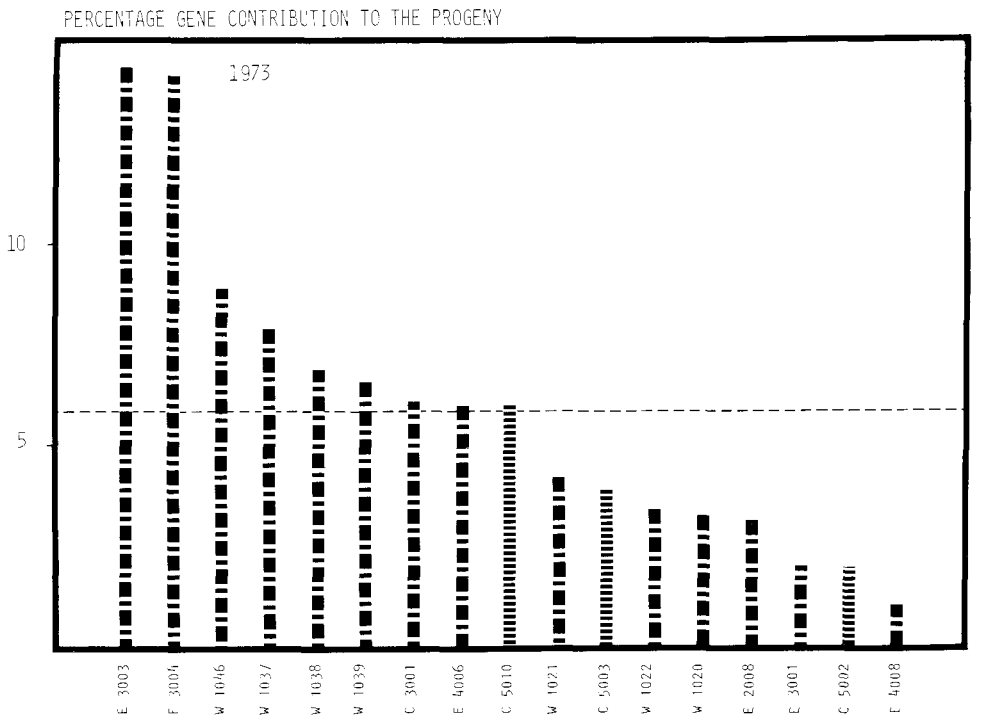


Figure 35. The percentage gene contribution to the progeny of individual clones estimated on the basis both of the frequency of flowering and the point of time for pollen dispersal and receptivity in 1973. The dashed line illustrates the anticipated percentage if all prerequisites for random mating between the 17 clones were fulfilled.

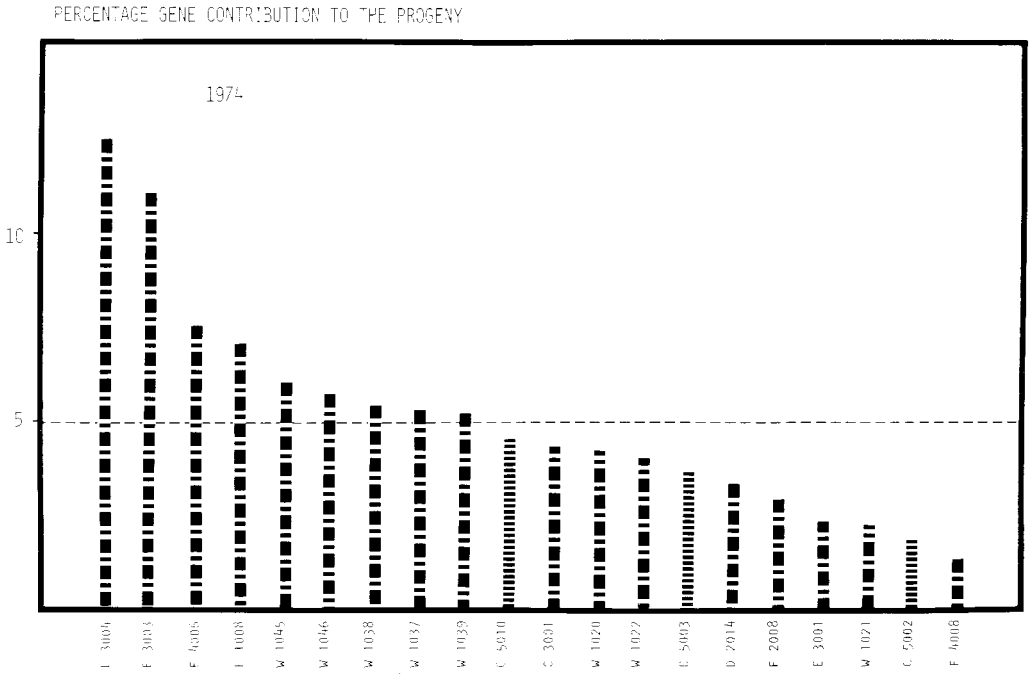


Figure 36. The percentage gene contribution to the progeny of individual clones estimated on the basis both of the frequency of flowering and the point of time for pollen dispersal and receptivity in 1974. The dashed line illustrates the anticipated percentage if all prerequisites for random mating between the 20 clones were fulfilled.

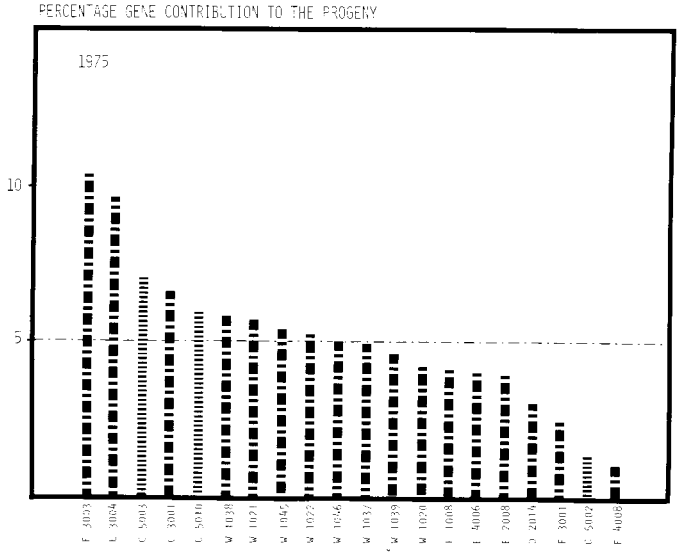


Figure 37. The percentage gene contribution to the progeny of individual clones estimated on the basis both of the frequency of flowering and the point of time for pollen dispersal and receptivity in 1975. The dashed line illustrates the anticipated percentage if all prerequisites for random mating between the 20 clones were fulfilled.

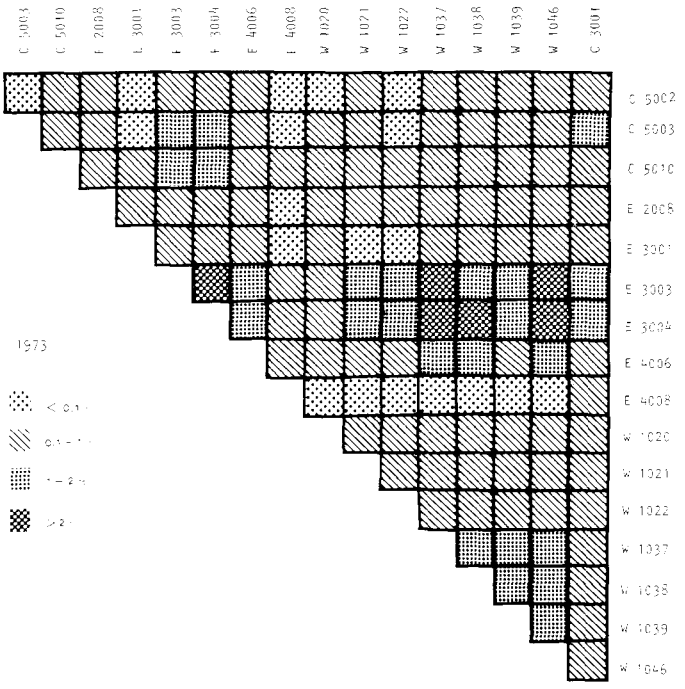


Figure 38. The percentage of the different crosses between the 17 clones examined in 1973, selfing being excluded.

following exclusion of selfing. The main reason for excluding selfing from these calculations is that selfing is undesirable owing to the inbreeding depression it causes (cf. Franklin 1970 and Eriksson *et al.* 1973). Moreover, the high genetic load of many conifers means that most of the self-fertilizations will not give rise to viable seeds (cf. Hadders and Koski 1975).

In Figures 35–37 the percentage of gene contribution to the progeny of individual clones for the years 1973–1975 is illustrated. These diagrams reveal that the clones E 3003 and E 3004 are the two dominating clones in all three years. In contrast to them E 4008, C 5002 and E 3001 contributed least to the progeny in all three years. Although there are slight changes in the ranking among the intermediate clones, the consistency from year to year is large.

The Figures 35–37 also reveal that there is a great difference in magnitude as regards the gene contribution of the clones. The amplitude between the best and the poorest decreased from 1973 to 1975. This change may be due to a levelling-off of the frequency of flowering from 1973 to 1975 or to the weather conditions in the different years. In 1973 the period of receptivity and pollen dispersal was of short duration compared to the situation in 1974 and 1975 when the period was protracted.

The estimated frequency of individual crosses was classified into four groups as may be seen from Figures 38–40. The percentage distribution to the classes was as follows:

	<0.1	0.1–1	1–2	>2 per cent
1973	14.0	63.2	18.2	4.4
1974	12.1	74.2	13.2	0.5
1975	9.5	81.0	9.0	0.5

The expected percentage of each combination amounted to 0.74 per cent (1973, 17 clones) and 0.53 per cent (1974, 1975, 20

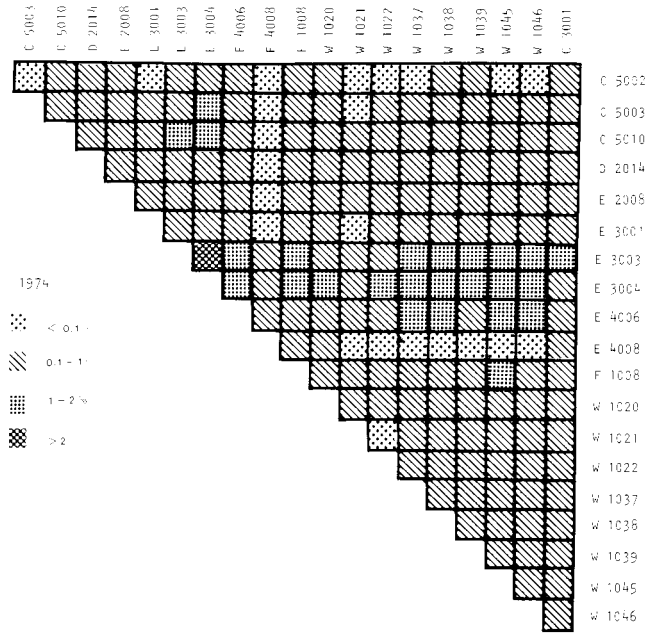


Figure 39. The percentage of the different crosses between the 20 clones examined in 1974, selfing being excluded.

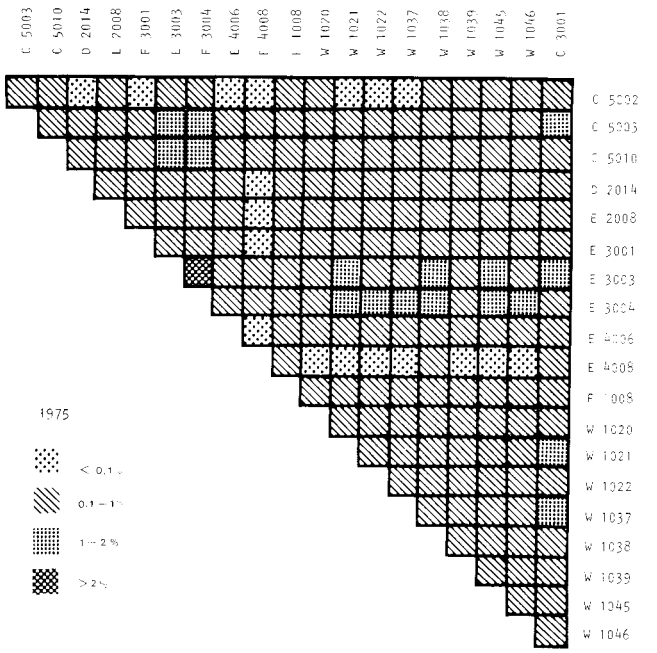


Figure 40. The percentage of the different crosses between the 20 clones examined in 1975, selfing being excluded.

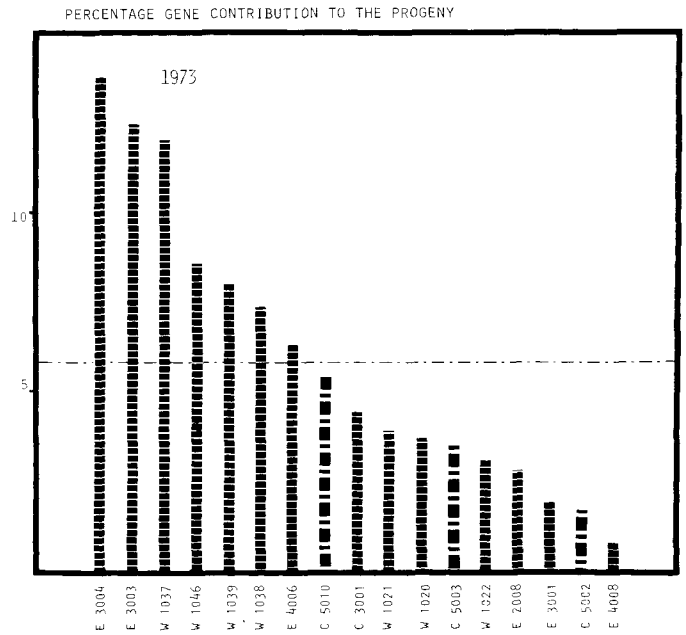


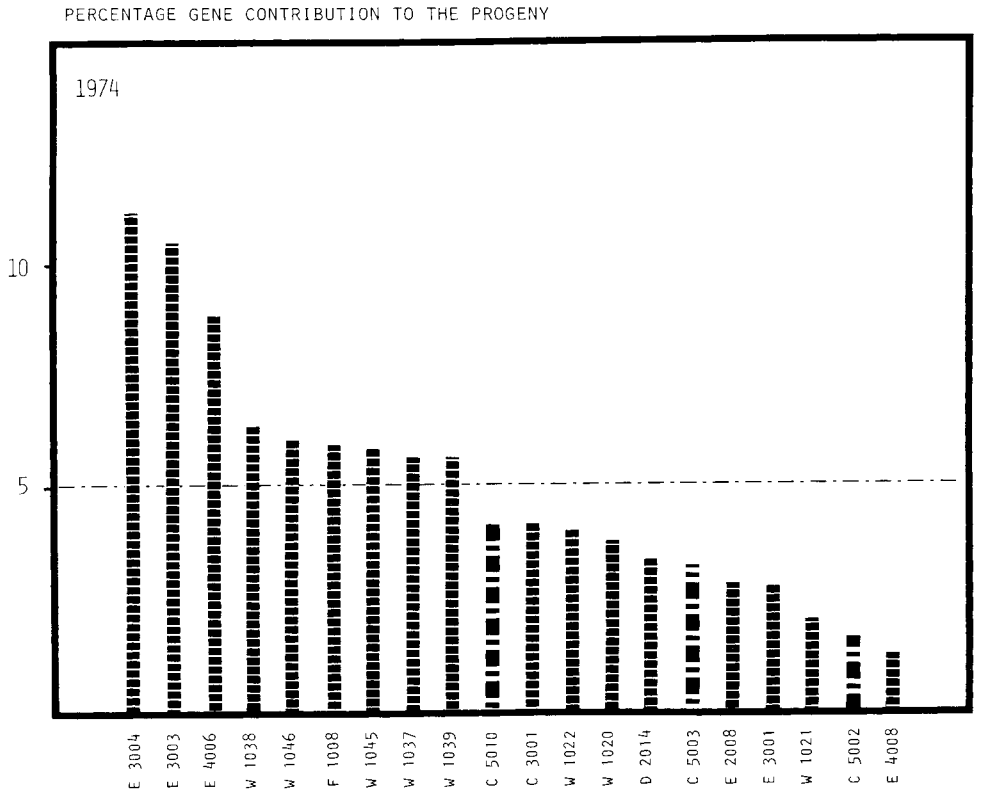
Figure 41. The percentage of gene contribution to the progeny of individual clones in 1973 estimated on the basis of the frequency of flowering only. The dashed line refers to the mean value if the frequency of flowering were the same in all 17 clones.

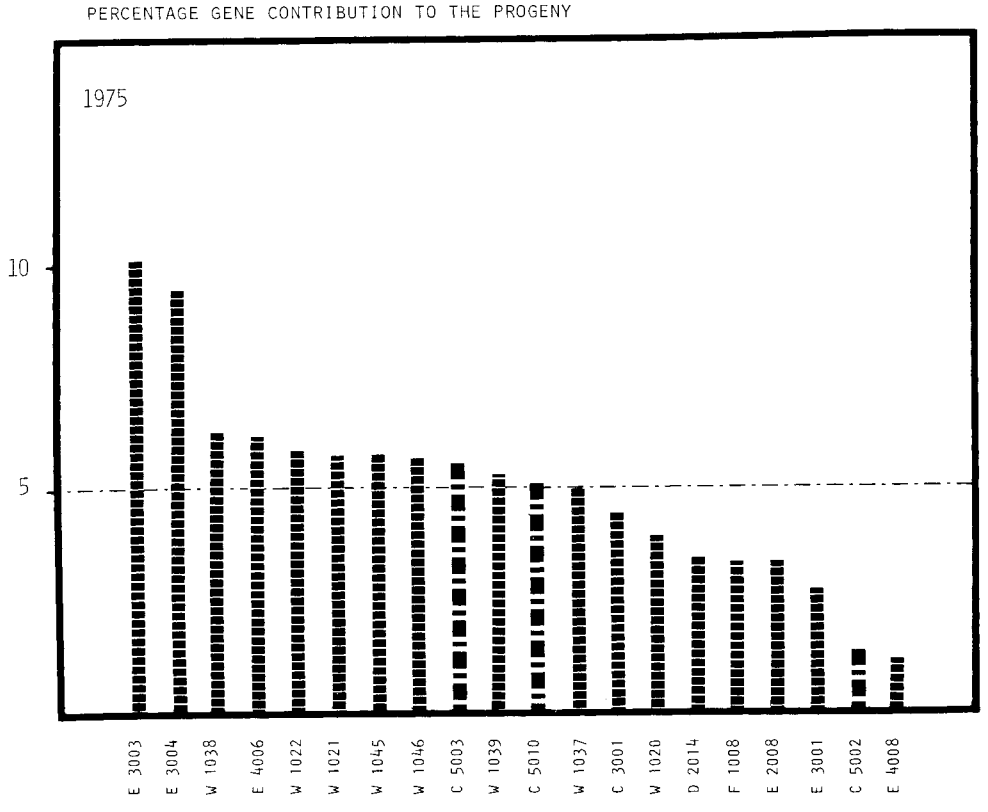
clones). As may be seen from the compilation above, the class 0.1–1.0 per cent which is the category that contains the ideal percentage *i.e.* the mean value if complete random mating had occurred, is the largest. The levelling-off of flowering frequency from 1973 to 1975 is to a great extent responsible for the trends of more and more crosses in the category 0.1–1.0 per cent. The protracted process of receptivity and pollen dispersal may also have contributed to the increase of number of combinations within the "average class". Against this speaks the fact that when phenology alone was considered, the data from 1975 showed the greatest differences between clones as regards their gene contribution to the progeny. It must be regarded as positive that only one combination E 3003×E 3004 exceeds the 2.0 per cent level in 1974 and 1975.

A comparison of the data in Figures 35–37 and 41–43 suggested a great influence of the frequency of flowering on the genetic composition of the offspring. Therefore, we found it worthwhile to calculate the gene contribution to the progeny, as if this was dependent on the frequency of flowering alone, ignoring the phenology completely (Figures 41–43). This calculation revealed good agreement with those including the phenological aspects. The agreement was tested by a correlation analysis. The correlation

Figure 42. The percentage of gene contribution to the progeny of individual clones in 1974 estimated on the basis of the frequency of flowering only. The dashed line refers to the mean value if the frequency of flowering were the same in all 20 clones.

Figure 43. The percentage of gene contribution to the progeny of individual clones in 1975 estimated on the basis of the frequency of flowering only. The dashed line refers to the mean value if the frequency of flowering were the same in all 20 clones.


PERCENTAGE GENE CONTRIBUTION TO THE PROGENY
1974
10
5
E 3004
E 3003
E 4006
W 1038
W 1046
F 1008
W 1045
W 1037
W 1039
C 5010
C 3001
W 1022
W 1020
D 2014
C 5003
E 2008
E 3001
W 1021
C 5002
E 4008


PERCENTAGE GENE CONTRIBUTION TO THE PROGENY
1975
10
5
E 3003
E 3004
W 1038
E 4006
W 1022
W 1021
W 1045
W 1046
C 5003
W 1039
C 5010
W 1037
C 3001
W 1020
D 2014
F 1008
E 2008
E 3001
C 5002
E 4008

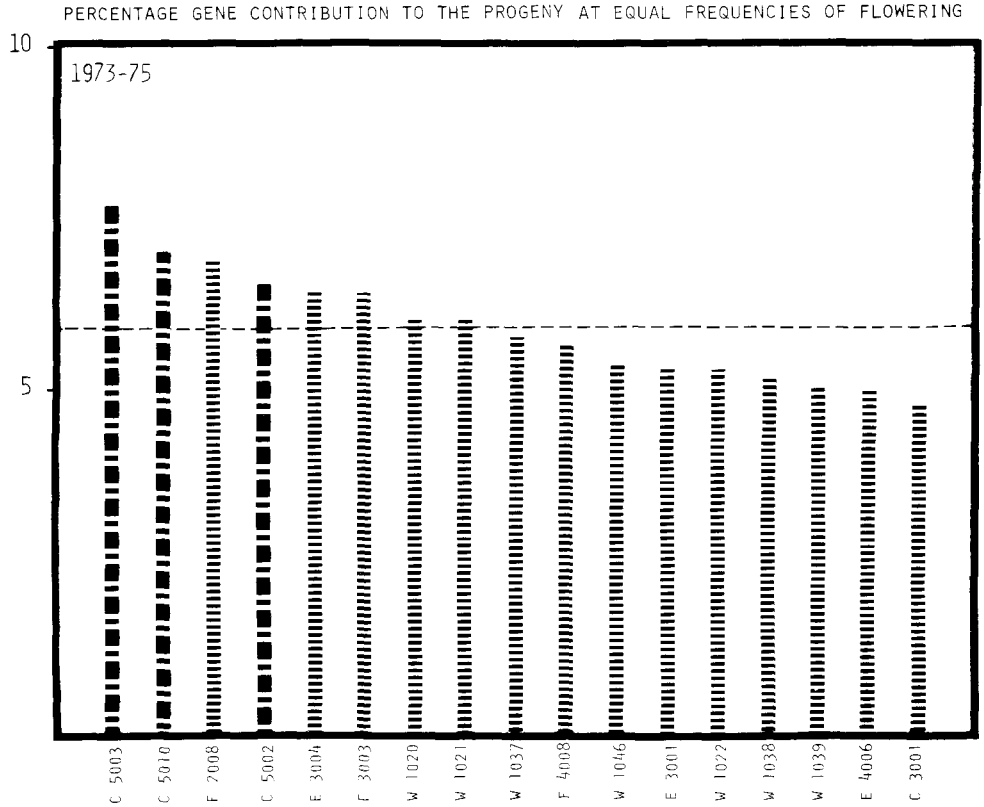


Figure 44. The mean percentage of gene contribution to the progeny for the period 1973–1975 considering only the variation in the point of time for receptivity and pollen dispersal. The frequency of flowering was assumed to be the same in all clones. The dashed line refers to the expected clonal contribution if no variation in phenological characteristics existed.

coefficients for the different years are listed below.

	r
1973	0.945***
1974	0.977***
1975	0.922***

These figures seem to indicate that the phenology could be neglected. Certainly it could be for the actual situation but the conditions may change drastically as the grafts grow and the frequencies of flowering possibly level off. Therefore, the gene contribution to the progeny was calculated assuming that the frequency of male and female strobili was the same for all clones. In this way the importance of the different points of time for receptivity and pollen dispersal could be revealed. The variation between years was limited. Therefore, the mean values for the three years of the individual clones are shown in Figure 44. Compared to the situation described in Figures 35–37 and 41–43 the clonal variation is limited. It is worth mentioning that the clones of Finnish origin occupied a prominent ranking. Although the clone C 3001 was regarded as a male flowering clone only, it ranked high in 1975. However, in 1973 and 1974 it occupied the last position.

8 The estimation of the occurrence of selfing

This estimation is based on less solid basis than the estimation of cross fertilizations since little is known about the self-fertility. It should only be added that a high occurrence of selfing was anticipated for clones E 3003 and E 3004 for all three years. Plym Forshell (1974) studied the seed development after self-pollination and open pollination in Scots pine clones. She observed that for clone E 3003 the frequency of well developed seeds obtained after selfing amounted to 43 per cent. A figure which was well above the mean value for all clones studied. As for clone E 3004 the corresponding figure was just below the average. However, for this clone the percentage of well developed seeds after open pollination was low, amounting to about 60 per cent, which suggests a high frequency of self-pollinations. Since plants from controlled selfings as well as from open pollination and different crossings have been obtained from these clones, the growth performance of these three types of progeny will be studied. Such a study will give further information on the fraction of selfing within the open pollinated progeny. A still better way to test the occurrence of self-fertilization in the open pollinated progeny is to test the isozyme pattern of the offspring. Such an investigation is under progress in cooperation with Dr Dag Rudin.

9 Concluding remarks

As regards the frequency of flowering a great clonal variation has once more been proved (cf. Sweet 1975 for a summary). It was also shown that the willingness to flower remained relatively stable from year to year during the three year period studied. A small levelling-off of the differences in flowering frequency between clones took place during the period 1973–1975.

The point of time for receptivity as well as for pollen shedding varied considerably between the clones. Similar investigations of the flowering phenology in Scots pine and in other pines as well, have shown that there exists a great clonal variation in this respect (cf. Stern and Roche 1974 p. 42–44 for a summary). No relationship between the onset of receptivity or pollen dispersal and the origin of the clones could be traced. As a matter of fact, it is difficult to trace such relationships when studying one or a few selected trees from different populations. The selected trees may deviate randomly from their population means. The yearly variations in onset of receptivity and pollen dispersal was shown to be due to the temperature conditions of different years. The same was true for the duration of the receptivity and pollen shedding.

A theoretical calculation of the genetic composition of the progeny was made. This revealed that the gene contribution was closely correlated with the frequency of flowering whereas the point of time for flowering did not influence the gene contribution to any great extent. However, it must be remembered that following a levelling-off of the frequency of flowering the phenological aspects may increase in importance. However, the synchronization of anthesis and gynesis was fairly good among the clones examined. Furthermore, differences exist between strobili within the same graft with respect to the point of time for receptivity as well as for pollen dispersal (Figures 23 and 31). These differences within a graft were as large as or larger than the differences in the mean values between clones.

The expected frequency of selfing was for most of the clones low but for two of the clones, E 3003 and E 3004, it was relatively high. However, regarding the bulked seed from this seed orchard these figures do not become alarming. Moreover, they may be reduced further, due to the frequency of self-sterility. Therefore, selfing cannot be regarded as being of any greater importance in the seed orchard studied.

The great variation in gene contribution to the progeny of the 17 (1973) or 20 (1974–1975) clones studied should be analysed a little further. Since the flowering frequency was of decisive importance for the gene contribution to the progeny, the differences would have been still more pronounced if all 36 clones within the seed orchard were considered. From Figures 2–3 it is clear that the gene contribution from such a clone as W 1047 would constitute approximately 0.0001 per cent of the total contribution.

It seems necessary to take measures to provoke a levelling-off of the frequency of flowering in this seed orchard to prevent a too dominating gene contribution to the progeny of some clones: When rogueing, grafts from clones like E 3003 and E 3004 should be cut first. This will probably not be too serious a drawback for the owner of the seed orchards, since the prognosis for seed production is quite optimistic (Hadders and Samuelson 1975).

10 Sammanfattning

I en ideal fröplantage skall samtliga möjliga korsningskombinationer erhållas i lika frekvens. Detta fordrar att alla kloner i plantagen lämnar ett lika stort bidrag till avkomman. Större eller mindre avvikelser från detta ideala förhållande förväntas föreligga beroende på att skillnader förekommer mellan olika kloner vad beträffar:

1. blomningsvillighet
2. blomningsfenologiska egenskaper
   2.1 tidpunkten för receptiviteten och dess utsträckning i tiden hos honblommorna
   2.2 tidpunkten för pollenspridningen och dess utsträckning i tiden

Dylika olikheter mellan kloner förväntas vara särskilt framträdande i en provenienskorsningsplantage sammansatt av kloner från vitt skilda klimatområden.

För att studera i vad mån dylika skillnader mellan klonerna påverkar deras genbidrag till avkomman har studier av blomningsfrekvensen och blomningsfenologi utförts i tallplantage nr 48, Långtora, C-län (lat. 59°43′, long. 17°08′, h. ö. h. 15 m). Plantagen anlades under åren 1962–64. Den omfattar totalt 36 kloner och är sammansatt av såväl svenska (F-län–W-län) som finska kloner (figur 1).

Frekvensen av han- och honblomställningar hos samtliga kloner registrerades under åren 1973–1975. Blomningsfenologiska studier startade i mindre skala 1972 och utvidgades därefter till att omfatta 17 kloner år 1973 samt 20 kloner under 1974 och 1975. Inom varje klon etiketterades 50 han- och 50 honblomställningar och utvecklingsförloppet för pollenspridning resp receptivitet följdes så gott som dagligen under den aktuella tiden från mitten av maj till mitten av juni. Samtidigt registrerades den totala pollenmängden i plantagen med hjälp av en pollenfälla konstruerad av professor Sarvas i Finland.

Rangordningen mellan klonerna beträffande frekvensen hon- och hanblomställningar olika år visade sig i stort sett vara densamma. Däremot förekom stora skillnader i blomningsfrekvens mellan klonerna. Detta var särskilt markant för hanblomningen där 25 % av klonerna svarade för 62 % av hanblomningen i plantagen (figur 3). Motsvarande siffra för honblomningen uppgick till 51 % (figur 2). Med stigande ålder hos plantagen förväntas emellertid att en viss utjämning av dessa skillnader skall inträda. Det kan tilläggas att samtliga honblomställningar inte alltid utvecklas till kottar utan att en förlust av honblomställningar inträffar (jfr figur 4). Denna förlust uppskattas till 23 % under 1973–74 och 33 % under 1974–75 (tabell 1).

De olika utvecklingsstadierna hos en honblomställning (strobilus) har illustrerats med färgfotografier i figur 5–12. De receptiva stadierna, då blommorna är mottagliga för pollen, finns avbildade i figur 7–9.

Markanta klonskillnader registrerades samtliga år beträffande tidpunkten för receptivitetens inträde och dess utsträckning i tiden (figur 13–17). Motsvarande klonskillnader kunde också konstateras för pollenspridningen (figur 25–29). Inget samband tycks föreligga mellan blomningsfenologiska karakteristika hos de enskilda klonerna och deras ursprung.

En jämförelse mellan år beträffande receptivitet och pollenspridning visade en tidig start år 1975 jämfört med åren 1973 och 1974 (figur 17 och 29). Vidare var förloppet mera utdraget under 1974 och 1975 än under 1973. Detta senare får tillskrivas det kyliga väder som var rådande under den aktuella tiden 1974 och 1975 i motsats till 1973 medan perioden före starten var speciellt varm under 1975 (figur 18–21). Temperaturens inflytande på blomningsfenologin har ytter-

ligare illustrerats i figurerna 22 och 30.

Det procentuella genbidraget till avkomman visade stor variation mellan de enskilda klonerna. Detta förhållande gäller såväl när beräkningarna av genbidraget grundades på de olika klonernas blomningsfrekvens och blomningsfenologi (figur 35–37) som när hänsyn enbart togs till blomningsfrekvensen (figur 41–43). Om man endast tar hänsyn till blomningsfenologiska data och det förutsätts att alla kloner blommar lika mycket, tenderar skillnaderna i genbidrag att suddas ut (figur 44). Blomningsfrekvensen har således hittills varit utslagsgivande för storleken av de enskilda klonernas genbidrag. Detta gäller i ännu högre grad om samtliga 36 kloner innefattas i undersökningen eftersom variationen i blomningsintensitet är än större i detta fall. Skillnader i blomningsfenologi kan därför påverka klonernas genbidrag först när variationen i blomningsfrekvens försvinner. Det kan tilläggas att dessa skillnader i blomningsfenologi mellan kloner var mindre än eller lika stora som motsvarande skillnader mellan olika blomställningar inom en ymp (figur 23 och 31).

Skillnader i klonernas genbidrag avspeglas också i den genetiska sammansättningen av avkomman från plantagen på så sätt att vissa korsningskombinationer är överrepresenterade medan andra förekommer i mycket låg frekvens (figur 38–40). En tendens till utjämning kunde dock spåras under 1975 då 81 % av samtliga korsningskombinationer hos 20 kloner föll inom gränserna 0,1–1 %. Det ideala värdet vid lika frekvens av alla korsningskombinationer ligger på 0,53 %.

För att kunna göra en bedömning av risken för inblandning av pollen från bestånd utanför plantagen jämfördes data från de dagliga observationerna av antalet rykande hanblommor med data från pollenfällan, som kontinuerligt registrerade den totala pollenmängden i plantagen (figur 32–34). Det är dock inte möjligt att dra några helt säkra slutsatser från dessa data beträffande eventuell polleninblandning under 1974 och 1975. Däremot är det högst troligt att pollen kom in utifrån under den aktuella tiden 1973.

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