Effects of Inbreeding in Red Pine, Pinus resinosa Ait.

III. Factors Affecting Natural Selfing[1])

By D. P. FOWLER[2])

(Received for publication July 13, 1964)

Introduction

Red pine is a self-fertile species capable of producing normal, healthy seedlings following self-pollination (FOWLER, 1964, 1965 a). A self-fertile species is not necessarily self-fertilized under natural conditions. Natural barriers to selfing may be present which prevent pollen of an individual tree from reaching the female flowers[3]) of that same tree. Even if the pollen does reach the ~female flowers, they may not be receptive or the pollen may be unable to compete successfully with pollens from other trees. Polyembryony, resulting from the fertilization of more than one egg cell per ovule, is common in Pinus (MCWILLIAM, 1959), but usually only one embryo matures (BUCHHOLZ, 1931). Thus proembryos or embryos which may result from fertilization by (different male parents, continue to compete until a single embryo matures.

Many species of plants forego the advantages and disadvantages of sexual reproduction and reproduce apomictically. Other plants, including several tree species, avoid self-pollination and its disadvantages by being completely or partially dioecious.

Several factors that may act as barriers to natural selfing in red pine are here examined. These factors are:

1. Presence or absence of unisexual individuals.
2. Position of male and female strobili.
3. Time of pollen release and receptivity of ovulate strobili.
4. Parthenocarpy and parthenogenesis.
5. Selective fertilization.

In addition to these five factors, the degree of natural selfing in this species was examined. A brief review of the literature is presented for each of the subjects as they occur in the paper.

1. Presence or Absence of Unisexual Individuals

The genus Pinus is composed of monoecious species (SHAW, 1914). Red pine is no exception. Examples of fully mature, genetically unisexual pines are extremely rare.

Young trees of several species of pine may be either male or female and may retain this condition for several years. **WRIGHT** (1953) reported that young Pinus densiflora SIEB. and Zucc., P. *armandi* FRANCH., P. *strobus* L. and P. *griffithii* **MCCELLAND** have a tendency toward femaleness. **SCHRÖCK** (1949) reported many precocious Scots pine, Pinus *silvestris* L., to be exclusively male or female. SYLVEN (1916) reported that it was not uncommon for Scots pine in closed stands of northern Sweden to produce only male flowers for many years while female flowers were found only on open-grown trees with well developed crowns.

HOLST (1962) mentioned a fastigiate type of red pine found occasionally near Bancroft, Ontario that produced exclusively male strobili. This would appear to be the only report of genetically unisexual red pine trees.

In conjunction with pollinations carriad out at Kane, Pennsylvania, Vivian, Ontario, and Lake Abitibi, Ontario (FOWLER, 1965 a) observations were made on the tendency toward maleness or femaleness of over 100 trees.

Results *and* Discussion

The trees on which observations were made at Kane, Penna. were part of a provenance test established in 1937 (HOUGH, 1952). The plantation only recently began to produce cones in quantity and most of the cone production is restricted to edge trees or to a few of the dominant trees within the plantation. Virtually all of the trees in this plantation produced large to fairly large crops of male strobili in 1961. Thus, a large portion of trees in this plantation could be considered to be male or at least exhibiting a tendency toward maleness. No strictly female trees or trees exhibiting a strong tendency toward femaleness were encountered. Invariably, if a tree had female flowers, it also had abundant male flowers.

Observations were made on approximately 40 trees at Vivian, Ontario during the period 1958 to 1961. Many of the trees in this plantation have been flowering abundantly for several years. During the period 1958 to 1961, all the trees examined produced male flowers. In 1958 and 1959 most of the trees examined were predominantly or exclusively male. In 1960, which was a heavy flowering year in this plantation, all except the suppressed trees produced female and male strobili. In 1961 many of these same trees, which produced female strobili in 1960, produced only male strobili.

Observations were made on approximately 20 trees in 1961 at Lake Abitibi, Ontario. Of these trees, nine had an abundant crop of male and female flowers, while the remainder fell in a gradient between exclusively male and monoecious. No exclusively female trees were encountered.

Mature red pine trees are rarely, if ever, exclusively female. A high proportion of the trees in a closed stand or plantation may be functionally (but not genetically) male. This is especially true in poor ~flowering years when only a small portion of trees produce ovulate strobili.

The fact that exclusively female trees are virtually nonexistent in red pine rules out dioecism as a barrier to self-pollination. Self-pollination in stands containing a high proportion of male trees would be approximately the same if all the trees were monoecious. The presence of a large proportion of such trees would maintain a higher level of available cross-pollen than if these trees did not flower.

In a poor flowering year, when only scattered trees produce ovulate strobili, the amount of selfing is likely limited by the quantity of pollen available from functionally male trees.

---

[1]) Contribution 64 — 7. Ontario Department of Lands and Forests. This paper is the third of a series based on a dissertation submitted to the Graduate School of Yale University as partial fulfillment of the requirements of the **PhD** degree.

[2]) Research Scientist, Ontario Department of Lands and Forests, Maple, Ontario, Canada.

[3]) Throughout this paper, the term "flower" is used in its broad meaning — a reproductive organ.

2. *Position of Male and Female Strobili*

In the genus *Pinus* male and female flowers are carried over a large portion of the tree crown (Wright, 1953). The ovulate flowers are concentrated in the upper portion while the male flowers are most plentiful in the lower portion (Sarvas, 1962). Male flowers do not occur in the uppermost whorls of most pine species (Wright, 1953).

Little information is available concerning the position of red pine flowers. Red pine apparently does not differ from the general pattern of the genus in respect to flower position (Wright, 1953). Godman (1962) in his studies of the effects of thinning on the production of cones, reported that at high basal areas (160 sq. ft./acre) almost all the cones were found in the top one-third of the crown. Even at low densities (60 sq. ft. basal area/acre) few cones occurred in the lower third of the living crown.

In the spring of 1961, during the course of pollination work at Kane, Penna., Lake Abitibi, Ont., and Vivian, Ont., records were kept of the position of male and female flowers in the crowns of 45 trees. The position of the flowers was recorded in respect to the terminal growing point. The branches produced in 1961 were designated as whorl one, those produced in 1960 as whorl two and so forth down the tree. The position of the highest and lowest female flowers was recorded as was the whorl with the largest number of female flowers. In the case of two modal whorls, the whorl closest to the mean concentration of female flowers was recorded. The modal whorl, rather than the mean, was taken because it obviated counting all the female flowers on a tree. The position of the highest male flower and the quarter of the crown bearing the most male flowers was also recorded.

In June, 1962, the 45 trees for which records were obtained in 1961, were observed again to determine if any change in the pattern of flowering had occurred. Twenty additional trees with crown types poorly represented in the 1961 records were also observed and the position of the male and female flowers was recorded as in 1961. In total, records were kept for 65 trees of which 45 were observed in two subsequent years.

Results and Discussion

Observations made in 1962 on 45 trees from which data had been obtained in 1961 clearly indicated that the general pattern of female and male strobili position in the crown had not changed during the ensuing year. The data from 1961 and 1962 have, therefore, been combined.

Four distinct crown types were encountered among the trees studied:

1. Open-grown or edge trees with well developed crowns extending almost to the ground. Data from 27 trees.
2. Dominant trees in closed stands on which the lower branches were suppressed. Data from 15 trees.
3. Trees with their lower branches pruned to a height of approximately 18 feet. Data from 15 trees.
4. Trees with the upper portion of their crowns damaged or broken. All the trees of this type were found at Kane, Penna. and resulted from porcupine feeding. Data from eight trees.

The results are presented in *Figure III — 1.* While it is evident that on undamaged red pine trees there is a more or less distinct separation of a predominantly female portion of the crown and a predominantly male portion, the region where male and female flowers overlap is quite large. Where the normal growth pattern of the tree had been changed, resulting from porcupine damage, the normal separation of male and female flowers is disrupted. All of the trees examined had at least some of their female flowers lower in the crown than the highest male flowers. Even in the absence of any wind or thermal disturbances, some of the female flowers would be in a position to be self-pollinated. In the presence of wind or thermal turbulence, most of the female flowers would receive self-pollen. It is concluded that, while the position of the female flowers in the crown of a red pine tree may be a barrier to self-pollination, it is by no means absolute.

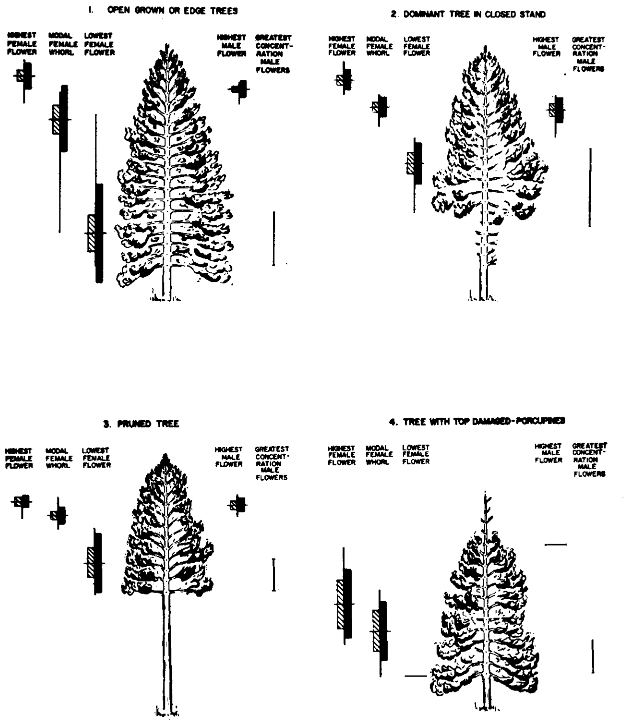

Figure III — 1. — Position of male and female flowers in the crowns of red pine trees of four crown types. — The vertical line represents the sample range; the short horizontal line is the sample mean; the black rectangle to the right of the range line is one standard deviation above and below the mean; and the hatched rectangle to the left of the range line two standard errors above and below the mean.

3. *Time of Pollen Release and Receptivity of Ovulate Strobili*

Bigngham and Squillace (1957) presented an adequate review of the literature on the time of pollen release and receptivity of ovulate strobili in pines. They concluded: "In *Pinus monticola* stands, and apparently in stands of most other pines, little if any phenological cross-sterility could exist." Doyle and O'Leary (1935) and Wettstein (1940) did not consider dichogamy to be of any importance in Scots pine. Wright (1953) found no evidence of dichogamy in red pine. On the other hand, Sarvas (1962) considered that a slight difference in the time of ovulate flower receptivity and the time of pollen shedding might be an important barrier to self-pollination in Scots pine. Sarvas' conclusions are based on the finding that only a certain number of pollen grains can be held in the pollen chamber of an ovulate flower and that only these pollen grains compete in fertilization.

In June, 1961, observations were made on the time of pollen shedding and receptivity of ovulate strobili in 36 trees at Kane, Penna., two trees at Vivian, Ont. and nine trees at Lake Abitibi, Ont. The dates when pollen release began, reached its maximum, and finished were recorded. The criteria used to estimate ovulate flower receptivity were the same as those described by Cummings and Righter (1948) with only slight modifications. They were as follows:

		Cummings and Righter (1948)
Stage 1	strobili visible but enclosed in protective sheath	Stages 1 and 2
Stage 2	ovulate scales pushing through sheath. Scales visible but not receptive	Stage 3
Stage 3	strobili partly open. Scales separating from axis (of strobili)	Stage 4
Stage 4	strobili open. Ovulate scales at right angles to axis (of strobili)	Stage 5
Stage 5	strobili closed. Ovulate scales closed or closing	Stage 6

The ovulate strobili were considered to be receptive from the latter part of stage 3 until the scales are closed in stage 5. Stage 4 represents maximum receptivity.

Results and Discussion

The results are presented in *Figure III — 2.*

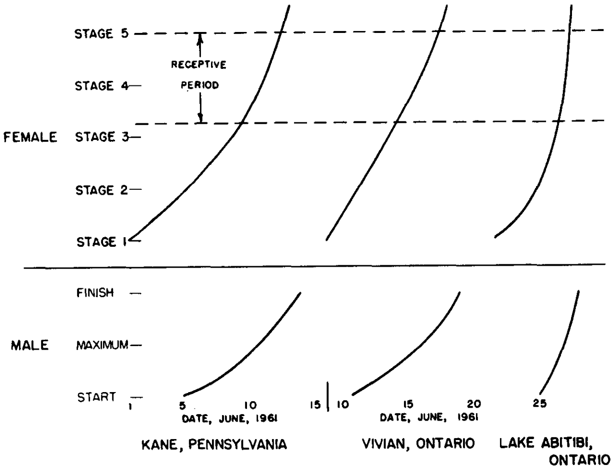

Figure III — 2. — Time of pollen release and ovulate strobili receptivity of red pine trees at Kane, Pennsylvania; Vivian, Ontario; and Lake Abitibi, Ontario.

The flowering period from the time at which the ovulate strobili first became visible to the time when they were no longer receptive, was quite different for the three areas in which the observations were made. At Kane, Penna., the ovulate strobili first became visible on or about June 1st and the flowers completed their receptive stages about June 14th, a period of two weeks. At Vivian, Ont., the dates were June 9th to about June 19th, a period of 11 days, and at Lake Abitibi the dates were June 22nd to approximately June 28th, a period of only seven days.

These considerable differences in the length of the flowering period were most likely caused by differences in climatic conditions in the three areas. Bingham and Squillace (1957) and Wright (1953) reported similar differences in areas of different elevations and latitudes respectively. It is unlikely that this phenomenon is under strong genetic control in red pine, as no differences in this respect were observed between the trees of different origins located at Kane.

In all 47 trees observed (with the possible exception of one tree at Lake Abitibi) the male flowers on the most exposed portion of the tree crowns dehisced a day or two before the female flowers became receptive. This is in contrast to the findings of Wright (1953) who reported that the ovulate strobili were receptive slightly before pollen release began. Pollen discharge continued throughout the receptive period of the ovulate strobili. The periods of maximum pollen discharge and highest receptivity of the ovulate strobili were synchronized, almost to the day, in the trees observed.

It is of interest that, except for one tree (from Cedar, Wisconsin), all the red pines observed at Kane, Penna. were in phase with one another. No more than two days difference in onset and conclusion of pollen dispersal and the stages of ovulate strobili development was observed in the trees representing nine climatic regions. As much variation was noted in strobili development within single trees as between trees of widely differing origins.

Some of the synchronization of flowering time between these trees of differing origins might result from the fact that 1961 was a late flowering year for red pine. The pollination season, as based on the date of maximum ovulate strobili receptivity at Vivian, Ont. was 13 days later in 1961 than the average (June 4th) of the period 1958 through 1960. Telescoping of the flowering season, as discussed by Bingham and Squillace (1957) and by Wright (1953), possibly masked any variation in time of flowering that might have existed among the trees of different origins.

Although telescoping of the flowering seasons probably accounts for much of the lack of variation in time of flowering among the trees of different origins at Kane, it is doubtful if it can account for all of it. It has been noted by the writer that little variation exists between the time of flowering of individual red pine trees, even in normal flowering years at Maple and Vivian, Ontario. Virtually all red pine pollinations can be made on the same day in any one season. In contrast to this, a considerable difference in time of flowering in different clones of *Pinus monticola* (7 days), *P. strobus* (6 days) and *P. silvestris* (6 days) has been observed at Maple, Ontario in normal flowering years.

Even when one considers the possible importance of slight differences in time of pollen shedding and receptivity of ovulate strobili as suggested by Sarvas (1962), it is unlikely that dichogamy can be a strong barrier to self-pollination in red pine.

4. *Parthenocarpy and Parthenogenesis*

Fowler (1965 a) reported that significant differences in size exist among red pine seedlings produced by different female parents regardless of the male parent. This fairly strong maternal effect on seedling size might suggest development from apomictic seeds, such as occurs in *Crataegus* and *Citrus* spp. (Stebbins, 1950).

Allen (1942) and Orr-Ewing (1957) report that Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, is occasionally parthenocarpic and suggest that it might also be parthenogenic. Both authors obtained some seeds with normal embryos from unpollinated cones. Orr-Ewing (1957) reported that these seeds produced normal diploid seedlings which showed little variation in either height or form. Langner (1959) obtained 11 seeds from 12 unpollinated cones of *Picea Omórika* (Pančić) Purkyne. Although these seeds failed to germinate, he considered apomixis to be a distinct possibility in this species.

Parthenocarpy is common in *Larix* (Plym Forshell, 1953; Piatnitsky, 1934, and Larsen, 1956), in *Abies* (MacGillivray, 1957) and probably in most other coniferous species that mature their cones in a single year.

The presence or absence of parthenocarpy in *Pinus* is a much more debatable question. Ehrenberg and Simak (1957) report that in Scots Pine, isolated but unpollinated strobili occasionally develop cones, mostly without seeds or with empty seeds. On the other hand, Plym Forshell (1953) reported that most unpollinated Scots pine strobili fail to produce cones. The few cones and seeds that she obtained from unpollinated strobili were attributed to contamination. Sarvas (1962) supports the finding that in Scots pine pollination is necessary for cone development.

McWilliam (1959) obtained fully developed cones with only hollow seeds on *Pinus nigra* Arnold after pollination with red pine pollen. No fertilization had taken place in these cones. The formation of normal cones containing empty seeds is common when interspecific crosses are attempted with red pine[4]).

In conjunction with the pollinations carried out in 1958, 1959 and 1961 (Fowler, 1965 a) a number of isolated ovulate strobili were left unpollinated to check on the effectiveness of the isolation procedure.

Results and Discussion

The results obtained from the isolated but unpollinated ovulate strobili are presented in *Table III — 1*.

Five of the 395 isolated, but unpollinated, female strobili developed into cones. All five of these cones matured on a single tree located in Algonquin Park, Ontario. None of the 107 seeds obtained from these cones contained any living gametophyte tissue. It is doubtful if these five cones resulted from contamination before or during the isolation period.

It is concluded that pollination is usually required for cones to mature and that fertilization is necessary for the production of full seed in red pine.

5. Selective Fertilization

In an earlier paper (Fowler, 1965 a), it was shown that self-pollination and cross-pollination were equally successful in producing normal seedlings. In these studies the female flowers were pollinated with either self- or cross-pollen but not with both in mixture as would occur under natural conditions. The question is whether or not there is any preferential selection in favour of self-pollen or cross-pollen.

The subject of selective fertilization has been reviewed by Squillace and Bingham (1958). One obvious feature of this review is the scarcity of studies of selective fertilization in coniferous species. Only one serious attempt to study selective fertilization in conifers has been reported. Squillace and Bingham (1958) and Barnes, Bingham and Squillace (1962) carried out a series of selective fertilization experiments with *Pinus monticola*. In their study, pollinations were made between two trees, A and B, as follows: A × A, A × B and A × (A + B). Equal volumes of A and B pollens were used in the mixed pollination. Three such series of crosses were reported in their 1958 paper. Differences in growth rate among the one-year-old progenies were used to estimate the degree of selective fertilization. It was concluded that in one tree, a moderately self-fertile one, selection was in favour of crossing. In another tree, a highly self-fertile one, the result of selfing was superior to crossing with one male parent, but the reverse was true with another.

In their studies, reported in 1962, two "completely self-fertile" and two "partially self-fertile" trees were used as female parents. Differences in epicotyl length and average time to germinate were used as independent criteria to estimate the degree of selfing. In the completely self-fertile trees there was, in general, no discrimination against selfing. In the partially self-fertile trees, cross-pollination yielded more germinable seeds than self-pollination. An albino marker gene, occurring in a 1 : 3 ratio of white to normal in the selfed progeny of one partially self-fertile tree, was also utilized to give an evaluation of selective fertilization. Pollination of this tree with a mixture of self- and cross-pollen from two other trees, as well as with a mixture of self- and cross-pollen from a number of other trees combined, showed that in each case outcross pollen was five times more effective than self-pollen in yielding germinable seed.

During the course of the inbreeding study in red pine, (Fowler, 1965 a) a tree was located which contained a suitable marker gene for selective fertilization studies. A self-pollinated progeny of Tree 585, located at Vivian, Ontario, contained 93 chlorotic seedlings and 460 normal ones. The deviant seedlings, although not albino, were definitely chlorotic. They exhibited pale pink hypocotyls and light yellow-green cotyledons and were readily distinguishable from their normal sibs. Although these seed-

Table III — 1. — Results from isolated but unpollinated female strobili.

Location	Year	Number of Origins	No. Trees	No. Strobili		Cones Matured	No. Seeds	
				Isolated	Set		Full	Empty
Vivian Forest, Ont.	1958	1	4	12	10	0	0	0
Vivian Forest, Ont.	1959	1	4	15	14	0	0	0
Kane, Pa.	1961	9	28	76	67	0	0	0
Lake Abitibi, Ont.	1961	1	9	45	36	0	0	0
Algonquin Park, Ont.	1961	1	2	76	70	5	0	107
Swastika, Ont.[5])	1961	1	13	130	129	0	0	0
Chalk River, Ont.[5])	1961	1	7	41	32	0	0	0
Totals		15	67	395	358	5	0	107

[5]) Isolations made by the Canada Department of Forestry, Chalk River, Ontario.

---

[4]) Unpublished data, Ontario Department of Lands and Forests, Maple Ontario and Mark Holst, Petawawa Forest Experiment Station, Chalk River, Ontario.

lings occurred in a ratio of 1 deviant to 4.95 normal, the deviant seedlings most likely were homozygous in respect to a single recessive allele and had a lower survival value than their heterozygous or homozygous normal sibs. None of the deviant seedlings lived more than a few months, even under greenhouse conditions.

In the spring of 1961 a number of pollinations were made on tree 585:

585 × 585 (Self-pollination)
585 × (585 + T7) (Self + Cedar, Wisconsin)
585 × (585 + T32) (Self + Cedar, Wisconsin)
585 × (585 + 622) (Self + Vivian, Ontario)
585 × (585 + 1782) (Self + Vivian, Ontario)

The pollen mixtures were obtained by mixing equal volumes of pollen from the two male parents.

Results and Discussion

The results are presented in *Table III — 2*. No significant differences between pollens were evident in the resulting number of seed per cone or percent germination. Self-pollination yielded a slightly lower proportion of full seed than mixed pollination. This difference was significant at the five percent level, but as self-pollens also produced slightly more (not significant) seeds per cone, there was no difference between the numbers of full seeds produced.

The ratio of deviant to normal seedlings, as determined from self-pollination of this tree in 1959, was 1 : 4.95. The confirmation of this ratio by the present self-pollinations was considerably better than expected. The ten deviant seedlings and 50 normal ones gave a ratio of 1 : 5. If no selection took place for self- or cross-pollen, the ratio of deviant to normal seedlings from an equal mixture of self- and cross-pollen should be 1 : 4.95 for the selfed half of the progeny, and all the seedlings from the crossed half should be normal. The expected ratio would then be 1 : 10.90. Three of the four pollen mixtures produced fewer mutant seedlings than expected, whereas the other produced more. Chi-square tests of these differences revealed none with a probability of less than .10 (see *Table III — 2*). Chi-square tests of the four pollen mixtures pooled ($\chi^2 = .35$) and for the two Vivian and two Cedar, Wisconsin mixtures ($\chi^2 = .05$ and 1.26 respectively) did not approach significance.

It is concluded that selective fertilization is not a barrier to selfing in the tree studied. It is doubtful if a highly evolved genetic system, controlling selfing or selective fertilization, exists in coniferous species. Selective fertilization in conifers probably takes place in trees heterozygous for recessive genes which, when homozygous, are detrimental during the period between pollination and embryo maturity. BARNES *et al.* (1962) found that highly self-fertile *Pinus monticola* trees did not exhibit selective fertilization to the same degree as partially self-fertile trees.

Red pine is highly self-fertile, homozygous for most alleles and contains few deleterious genes (FOWLER, 1965 a). It is doubtful if selective fertilization is an effective barrier to selfing in this species.

Natural Selfing in Red Pine

The preceding portions of this paper have dealt with five factors that might affect self-pollination and self-fertilization in red pine. Several authors have estimated the amount of natural self-pollination in forest trees. Their opinions as to the importance of selfing in coniferous species differ considerably. By far the majority of workers dealing with this problem believe that the proportion of normal seedlings resulting from self-pollination under natural conditions is low (AUSTIN, 1937; DUFFIELD and STOCKWELL, 1949; DUFFIELD, 1950; RIGHTER, 1958 and others). On the other hand, DOYLE and O'LEARY (1935), working with *Pinus silvestris*, stated: "Under forest conditions, it is probably only in strong wind that cross-pollination takes place to any extent." This statement is based on a study of the pollination mechanism and the phenology of flowering.

SARVAS (1962), working with Scots pine, estimated that self-pollination in stands ranges from 22 to 37 percent but considered that only about seven percent of the viable seeds were produced by selfing. These conclusions were based on percentages of aborted ovules. BARNES *et al.* (1962) used differences in growth rate between selfed and crossed progenies of *Pinus monticola* to study selective fertilization. They found that many trees of this species show a selection for outcross pollen but, when the proportion of self-pollen to outcross pollen is high, as may occur under natural conditions, a high proportion of the seedlings resulted from selfing.

LANGNER (1959) suggested that the self-fertility and high degree of uniformity found in *Picea Omórika* was caused, at least in part, from isolation and inbreeding over many generations.

Isolated trees may produce seeds after self-pollination. JOHNSON (1948) reported obtaining seedlings from an isolated *Pinus nigra* var. *austriaca* (HOESS) ASCHERS. and GRAEBN. which he believed was self-pollinated. AUSTIN (1937) and JOHNSON (1945) have discussed the possibility of obtaining a high proportion of "selfed" seeds from isolated trees.

Most of the estimates of selfing in coniferous species are based on information from studies of one or more of the factors that control self-pollination or self-fertilization. Little work has been carried out to determine what proportion of a tree's progeny actually results from selfing. This is understandable in the light of some of the problems involved. The major problem, of course, is to distinguish seedlings resulting from self-pollination from those resulting from crossing. For this purpose some sort of "marker" is required. LANGNER (1951) utilized a marker gene found

Table III — 2. — Controlled Pollinations — Tree 585.

Pollen Parent	Flowers Number	Flowers Set Number	Cones Number	Damaged Cones Number	Seeds per Undamaged Cone Number	Full Seed Percent	Germ. Percent	Normal Seedlings Number	Mutant Seedlings Number	χ^2	p
585	9	9	5	2	34.7	71.0	86.7	50	10		
585 + T7	9	8	7	0	25.6	72.9	69.0	73	6	.06 >	.75
585 + T32	10	10	6	0	27.7	87.1	74.4	71	3	1.82 >	.10
585 + 622	9	8	5	0	25.4	86.5	87.0	83	10	.66 >	.25
585 + 1782	9	8	7	1	29 0	77.2	69.6	81	6	.26 >	.50
					NS[6]	*[7]	NS	308	25	.35 >	.50

[6] Difference not significant at five percent level.

[7] Difference significant at five percent level.

in an aurea-form of *Picea abies* (L.) Karst. to estimate effective pollination distance in this species, but made no attempt to estimate natural selfing.

Squillace and Bingham (1958), using seedling growth rate as a marker to distinguish the results of selfing from crossing, suggested that, in stands under natural pollination conditions, crossing largely exceeds selfing.

Philp and Sherry (1946) and Moffett (1956) utilized marker genes found in *Acacia decurrens* Willd. and *A. mollissima* Willd. respectively, to estimate the degree of natural selfing in these species. Both these species are self-fertile but, under natural conditions only 5 to 15 percent of the seedlings of *A. decurrens* and an average of about 16 percent of the *A. mollissima* seedlings resulted from self-fertilization. Cram (1960), using an albino marker gene, obtained an estimate of 18 percent for natural selfing in a single *Picea pungens* Engelm.

Squillace and Kraus (1963) utilized albino marker genes to estimate the proportion of natural selfing in *Pinus elliottii* var. *elliottii* Engelm. Estimates of the frequency of albino carriers were made from observations on open-pollinated progenies of 219 trees. A ratio of 3 normal : 1 albino was assumed for progenies of selfed albino carriers and progenies from crosses between albino carriers. The number of albino seedlings that a given carrier produces under open-pollination is equal to one-fourth of its selfed progeny plus one-fourth of the progeny resulting from outcrossing with other carriers. They found natural selfing to vary from 0 to 27 percent in 11 trees. Nine trees showed 5 percent or less selfing while two trees showed 23 and 27 percent.

Material and Methods

Tree 585 is a dominant-codominant tree in a closed plantation at Vivian, Ontario. All except the intermediate or suppressed trees in this plantation are mature and produce male and female flowers in good flowering years. Controlled pollination studies revealed that this tree carried a marker gene. A description of seedlings homozygous in respect to this gene is presented in the preceding section on selective fertilization.

In September, 1960, open-pollinated cones were collected from Tree 585. No records were kept as to the position in the crown from which the cones were collected. The seeds were extracted, full and empty seeds separated and full seeds germinated in Petri dishes. When the seedlings had reached the cotyledon stage, they were evaluated as being either homozygous for the marker or normal.

In September, 1961, cones were again collected from this tree. To determine if position in the crown of the tree influenced the amount of self-pollination, cones were collected separately from each of the top 12 whorls of cone-bearing branches. The lower quarter of the crown produced no cones. The seedlings were evaluated for each of five cones from each whorl, except for whorls one and twelve, which had only two and four cones respectively. Cones were also collected from 22 red pines located closest to Tree 585 and the seedlings evaluated.

Open-pollinated seeds obtained in the fall of 1961 and germinated in the spring of 1962 revealed a second tree containing a suitable marker gene. This tree, number 1010, is one of approximately 12 mature red pine trees located on a small island in Lake Abitibi, Ontario. This island is isolated by approximately two miles from other red pines which occur as scattered trees or in small stands in the Lake Abitibi area.

Some of the seedlings among the progeny of this tree were chlorotic, while others were quite normal in appearance. The deviant seedlings differed from those of Tree 585 in that, within a month of germination, they developed normal pigmentation.

In October, 1962, open-pollinated cones were again collected from Tree 1010. The cones were kept separate from each quarter of the living crown and the resulting seedlings scored as normal or deviant.

In October, 1962, an isolated red pine tree was located in Barrie, Ontario. An intensive search of the vicinity revealed no other mature red pine trees within a mile radius of this tree. The nearest known red pines were located about three miles away. Cones were collected from this tree in the same manner as for Tree 1010.

Results

The open-pollinated cones collected in 1960 from Tree 585 yielded 905 full seeds, which produced 903 seedlings of which 15 were chlorotic. The seeds obtained in 1961 from

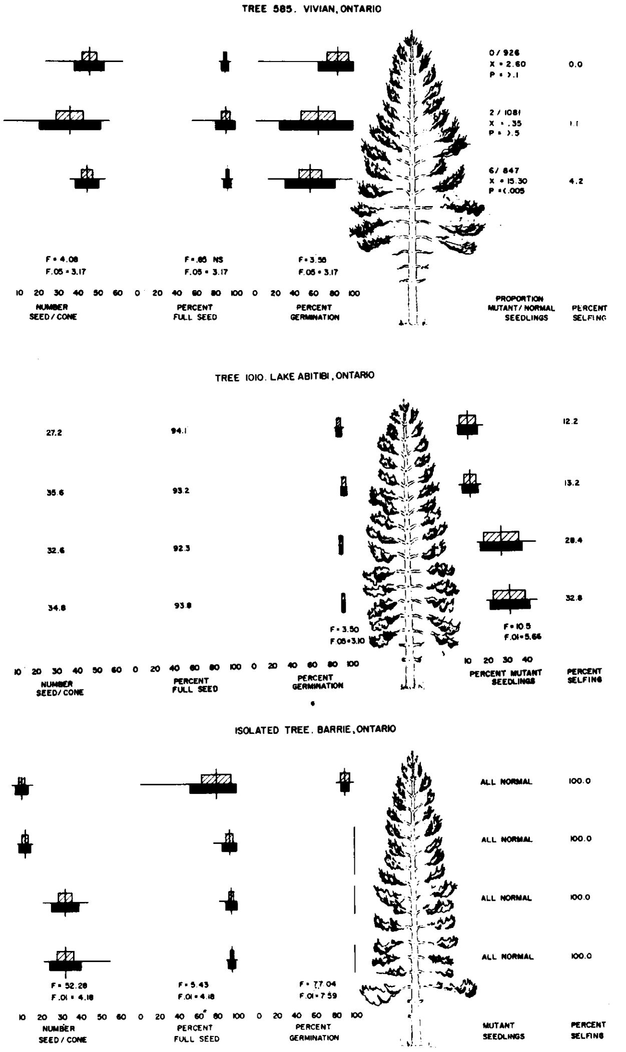

Figure III — 3. — Natural Selfing. — The horizontal lines represent the sample range; the short vertical lines the sample mean; the blackened rectangles below the range lines one standard deviation above and below the mean; and the hatched rectangles above the range lines two standard errors above and below the mean.

this tree produced only eight deviant seedlings from 2,862 full seeds.

The data from the 1961 collection were grouped by quarters of the living crown for analysis and presentation (*Figure III — 3*). A slight, but significant, difference was found between the number of seeds produced per cone from the different crown positions. Cones from the second quarter of the living crown produced somewhat fewer seeds than those from the top and third quarters. Approximately 90 percent of all the seeds on this tree were full regardless of the position in the crown from which they were obtained. Seed germination decreased from the top quarter of the crown to the third quarter, the averages being 83.7 percent, 63.9 percent and 56.6 percent. These differences were significant at the five percent level.

The cones from the top quarter of the crown produced 926 seedlings which were all normal. Two deviants were found among the 1081 seedlings from the second quarter and six deviants among the 847 seedlings from the third quarter. A chi-square test indicated a probability of less than .005 that the occurrence of these six deviant seedlings in the third quarter was due to chance. None of the seeds from the 22 trees surrounding Tree 585 produced any abnormal seedlings.

Of 100 seeds sown from Tree 1010 in 1961, 92 produced seedlings which survived to the cotyledon stage. Of these, 77 were normal and 15 were chlorotic. As the cones collected in 1962 began to open in transit to the Southern Research Station, only average values for seeds per cone and percentage full seed were obtained. The number of seeds per cone was slightly lower in the top quarter of the crown while the percentage of full seed showed little, if any, difference among crown positions. Seed germination was over 90 percent from all four crown quarters. Cones from the top and second quarter of the crown produced 12.2 percent and 13.2 percent deviant seedlings respectively, while those from the third and fourth quarters produced 28.4 percent and 32.2 percent deviant seedlings.

A highly significant difference in the number of seeds per cone was found between the crown positions in the isolated tree in Barrie. Cones from the top and second crown quarters produced 9.9 and 11.4 seeds per cone, respectively, while those from the third and fourth quarters produced 31.9 and 32.1. The percentage of full seed and seed germination were lower for seeds from the top quarter than for seeds from the other quarters.

Discussion

It is evident that position in the crown of the tree, from which cones are collected, has a large influence on the degree of selfing. Large differences are also evident among the three trees studied.

Tree 585, which under normal conditions would receive an abundant supply of pollen from surrounding trees, showed small differences in the number of seeds per cone from different crown positions. The upper half of the crown of the isolated tree, which would receive no cross-pollen, showed a sizeable reduction in number of seeds produced per cone. The percentage of full seeds from Trees 585 and 1010 showed no differences caused by crown position, while the completely isolated tree in Barrie produced a smaller percentage of full seed in the top quarter of its crown. Pollination is usually required to produce seed in red pine. It is probable that the flowers in the top quarter of the crown of the Barrie tree were sparsely pollinated. Whereas under normal pollination conditions (non-isolated trees) several pollen grains are received by the micropyle (SARVAS, 1962), this tree probably received very few grains per micropyle. As there were fewer pollen grains from which to select, non-viable pollen, though supplying stimulus to produce seeds, would fail to fertilize the ovule and hollow seeds would result.

Germination of full seeds was good from the isolated Barrie tree and Tree 1010. Tree 585 showed a great deal of variation in seeds germinated from individual cones, as well as a decrease in percent germination from the top to the third quarter of the crown. At first glance it appears that this decrease in germination might be correlated with an increase in selfing in the lower part of the crown. This is unlikely, as seeds resulting from self-pollination of this tree in 1960 and 1962, germinated well (100 percent and 87 percent respectively). Germination was actually slightly (but not significantly) higher in seeds resulting from self-pollination than in those from cross-pollination.

Both Trees 585 and 1010 showed significantly higher proportions of deviant seedlings from cones collected from the lower portion of the tree crowns.

In 1961 natural selfing in Tree 585 was estimated to be 0 percent in the top quarter of the crown, 1.1 percent in the second and 4.2 percent in the third quarter. Average natural selfing for the whole tree was 1.7 percent. This estimate was made assuming a 1 : 4.9 ratio of deviant to normal seedlings after self-pollination and assuming that all the deviant seedlings found on this tree resulted from self-pollination. The first assumption is well substantiated by the results of controlled self-pollinations described earlier. The second assumption is based on the finding that none of the 22 trees surrounding Tree 585 produced deviant seedlings.

Table III — 3. — Estimates of natural selfing, disregarding crown position.

Tree	Percent Self-fertilized Seedlings		
	1960	1961	1962
Tree number 585, closed stand	9.8	1.7	
Tree number 1010, small isolated stand		16.9	21.5
Barrie isolated tree			100.0

On this same basis natural selfing of this tree in 1960 was estimated to be 9.8 percent. The estimates of natural selfing, disregarding crown position, are presented in *Table III — 3*. The large difference between the 1960 and 1961 estimates for Tree 585 may result from differences in pollen available to this tree in these years. 1959 (the year in which 1960 seeds were pollinated) was a normal to poor flowering year for red pine in the Vivian area. Few of the trees had abundant female flowers, although all the dominant or codominant trees had some male flowers. In relation to the other trees in this stand, Tree 585 produced a good crop of female flowers (100 or more) and a heavy crop of male flowers. 1960 (pollination year of 1961 seed) was a heavy flowering year for red pine in this area. Virtually all the dominant and codominant trees produced a good crop of female flowers and an abundant crop of male flowers. In relation to the other trees in the stand, in 1960, Tree 585 was much closer to the average.

It is quite conceivable then that in 1959 the relative amount of self-pollen available to Tree 585 was greater than in 1960. This probably is the cause of the higher percentage of seedlings resulting from selfing produced by the 1960 (1959 pollinated) cones.

The high percentage of deviant seedlings obtained from the lower whorls of Tree 1010 in 1962 indicates that this tree must be homozygous in respect to the recessive allele in question. This is in agreement with the finding that, within a month after germination, the deviant seedlings were indistinguishable from their normal sibs. Assuming that this tree is homozygous for this deviant character and that all the deviants are the result of self-pollination, the estimates of natural self-pollination are the same as the percentages of deviant seedlings obtained. The first assumption is reliable as no other assumption can account for more than 25 percent deviant seedlings. The second assumption is open to question. The stand in which Tree 1010 occurs contains approximately 12 mature trees, of which only three other trees have been tested and found to be free of this deviant allele. In favour of this assumption is the fact that the proportion of seeds resulting from selfing is much lower in the upper half of the crown than in the lower half. The pattern is similar to that of the number of seeds per cone produced by the completely isolated Barrie tree. If one or more of the untested trees in this small stand were contributing deviant-carrying pollen to Tree 1010, this pattern would likely be disrupted.

Virtually all the seeds from the single isolated tree from Barrie, Ontario are considered to be self-fertilized. This is supported by studies of effective pollen dispersal (WRIGHT, 1952; SILEN, 1962). Though 100 percent of the seeds on this tree were self-fertilized, the productive capacity was by no means fully utilized. LYONS (1956) reported the seed production capacity of red pine to be between 30 and 110 per cone and that this number was usually reduced by 50 to 60 percent through normal ovule abortion. Using this as a basis, seed production in the lower half of this tree was well within the range of normal red pine trees (approximately 30 full seeds/cone). Production of full seed in the upper half of the crown (approximately 9 seeds/cone) was well below the established norm.

Discussion and Conclusions

Of the five possible barriers to natural selfing which were studied, dichogamy, parthenogenesis and selective fertilization would appear to be of little or no importance in red pine. The presence of a high proportion of functionally male trees and the relative position of male and female flowers in the tree crowns appear to be of considerable importance.

Functionally male trees are of little importance as a barrier to selfing in good flowering years when most red pines are monoecious. On the other hand, in poor flowering years, when only a few trees are producing female flowers, the presence of a high proportion of pollen-bearing trees would maintain a high level of cross-pollen and thus afford competition to self-pollen. One tree produced 9.8 percent viable selfed seed in 1960. In 1959, when the flowers which produced these seedlings were pollinated, approximately 10 percent of the trees in this plantation produced female flowers. If these same trees had been the only ones to produce male flowers, rather than virtually all the trees, a considerably higher proportion of seeds resulting from selfing could have been expected.

In 1961 only 1.7 percent of the seeds produced by this tree resulted from selfing in the heavy flowering year, 1960. This indicates that, although the presence of a large number of pollen producing trees probably lowers the proportion of selfing that takes place in a poor flowering year, it does not reduce it to the level of a heavy flowering year.

The relative position of the male and female flowers in the tree crowns is probably the most effective barrier to selfing in red pine. In most of the trees examined, there was a more or less distinct separation of the sexes into a predominantly female upper and a predominantly male lower crown. The degreee of overlap of flowers of the two sexes was considerable but could by no means eliminate selfing. It is difficult to assess the effectiveness of flower position as a barrier to selfing without detailed studies of pollen dispersal within individual trees, but it is obvious from the three trees in which natural selfing was studied that self-pollination is not common in the upper part of the tree crowns.

In closed stands, the separation of male and female flowers is more distinct than in open-grown trees or in trees which have had their normal growth pattern disrupted. Selfing in red pine trees in closed stands probably does not exceed 10 percent even in poor flowering years.

Separation of flowers of the two sexes in trees with long, well-developed crowns or in trees which have been disturbed, *e. g.* by porcupine damage, is often rather indistinct. Cones from the lower half of the crowns of such trees can be expected to contain a high proportion of seeds resulting from selfing. Cultural treatments, *e. g.* manipulation of crown size or shape in seed orchards, which change the relative position of the male and female flowers, can be expected to increase selfing.

Cones from the lower portions of the crowns of isolated trees or isolated small stands of trees can be expected to contain a high percentage of self-fertilized seeds.

Acknowledgments

The writer wishes to acknowledge the counsel of Dr. C. HEIMBURGER of the Ontario Department of Lands and Forests and Dr. F. MERGEN of the Yale School of Forestry.

Grateful acknowledgment is made to Mr. O. ROOS, Miss. J. ROBINSON and Mr. N. MCLEOD for assistance with preparation of the illustrations. Thanks are also due to Mrs. E. CREED, Mr. T. GRISEZ, Mr. H. HUNTZINGER, Mr. M. HOLST and Mr. G. BROWN for assistance with various aspects of the study.

Summary

Five factors which might act as barriers to the natural production of self-pollinated progenies have been examined: presence or absence of unisexual trees, position of male and female strobili, time of pollen release and receptivity of ovulate strobili, parthenocarpy and parthenogenesis, and selective fertilization.

Natural self-pollination was also examined with the aid of marker genes in two trees and in an isolated single tree.

Of the five factors examined, the presence of a high proportion of functionally male trees, especially in poor flowering years, and the relative position of male and female flowers were found to be important. Natural selfing is considerably higher in the lower part of the tree crown than in the upper part.

It was concluded that natural selfing probably does not exceed ten percent in closed stands but in small isolated stands or in single isolated trees a high proportion of self-fertilized seeds is to be expected.

Zusammenfassung

Titel der Arbeit: *Effekte der Inzüchtung bei Pinus resinosa. III. Faktoren, die eine natürliche Selbstung bewirken.*

Fünf Faktoren wurden untersucht, die als Barrieren für die natürliche Produktion von Selbstungsnachkommenschaften dienen könnten: Vorkommen oder Nichtvorhandensein eingeschlechtlicher Bäume, Position der ♂ und ♀ Blüten, Zeitpunkt des Pollinierens und der Empfängnisbereitschaft der ♀ Zäpfchen, Parthenokarpie und Parthenogenese, und schließlich die selektive Befruchtung.

Die natürliche Selbstung war ferner auch mit Hilfe von Signalfaktoren (marker genes) bei 2 Bäumen und bei einem isolierten Einzelbaum untersucht worden.

Von den 5 geprüften Faktoren waren die Befunde über das Vorkommen einer großen Zahl von ♂ funktionierenden Bäumen, besonders in schlechten Blühjahren, und über die relative Lage der ♂ und ♀ Blüten wichtig. Die natürliche Selbstung ist in den unteren Kronenteilen des Baumes beträchtlich höher als in den oberen.

Es wurde geschlossen, daß die natürliche Selbstung wahrscheinlich 10% in einem geschlossenen Bestand nicht übersteigt, daß aber in kleinen isolierten Beständen oder bei isoliert stehenden Einzelbäumen ein hoher Anteil an selbstbestäubten Samen erwartet werden muß.

Résumé

Titre de l'article: *Effets de l' autofécondation chez Pinus resinosa Ait. — III. Conditions de l'autofécondation naturelle.*

On a étudié 5 facteurs qui pourraient constituer des barrières à la production naturelle de descendances par autofécondation: présence ou absence d'arbres unisexués, position des inflorescences mâles et femelles, époque de la dispersion du pollen et de la réceptivité des fleurs femelles, parthénocarpie et parthénogenèse, fécondation sélective.

On a étudié également l'autofécondation naturelle sur 2 arbres et sur un arbre isolé avec l'aide de gènes marqueurs.

On a pu mettre en évidence l'importance de 2 facteurs sur les 5: présence d'une forte proportion d'arbres essentiellement mâles, spécialement les années de faible floraison; position relative de fleurs mâles et femelles. L'autofécondation naturelle est beaucoup plus forte dans les parties basses de la couronne que dans le sommet.

On peut conclure que l'autofécondation naturelle n'excède pas probablement 10% en peuplements denses, mais que pour les petits peuplements isolés *ou* pour les arbres isolés, on peut s'attendre à une forte proportion de graines autofécondées.

Titre de l'article: *Effets de l'autofécondation chez Pinus resinosa Ait. — II. Etudes sur la pollinisation.*)*

On a étudié les effets de l'autofécondation, en les comparant avec des fécondations croisées, sur les caractères des cônelets, des cônes, des graines et des semis chez 55 *Pinus resinosa.* On a également étudié sur 63 arbres les effets d'une pollinisation croisée avec des sources de pollen très différentes, en comparaison avec la pollinisation par du pollen d'une provenance locale.

L'influence du parent mâle sur les caractères étudiés est négligeable, alors que celle du parent femelle est forte. Cette dernière persiste au cours de la seconde saison de végétation. Cette influence maternelle est attribuée aux facteurs de l'environnement plutôt qu'a des effets génétiques, bien que ne soit pas impossible que l'hérédité cytoplasmique puisse jouer un certain rôle.

Sur les 55 arbres autofécondés, 46 ont produit des semis considérés comme normaux ou mutants. La descendance de l'un de ces arbres comprenait des semis chlorotiques, ce caractère étant dû à un gène récessif homozygote.

On en conclut que *Pinus resinosa,* autant sur le plan individuel que sur le plan de l'espèce, est homozygote pour un grand nombre d'allèles, auto-fertile, auto-compatible et que les semis produits par autofécondation manifestent peu ou pas de réduction de vigueur.

Literature Cited

Allen, G. S.: Parthenocarpy, parthenogenesis and self-sterility of Douglas fir. J. For. 40: 642—644 (1942). — Austin, L.: The Institute of Forest Genetics. Am. Forest Sept. Reprint 6 p. (1937). — Barnes, B. V., Bingham, R. T., and Squillace, A. E.: Selective fertilization in *Pinus monticola* Dougl. — II. Results of additional tests. Silvae Genetica 11: 103—111 (1962). — Bingham, R. T., and Squillace, A. E.: Phenology and other features of flowering of pines, with special reference to *Pinus monticola* Dougl. Intermountain Forest and Range Expt. Sta., U. S. Forest Serv. Res. Paper 53, 26 p. (1957). — Buchholz, J. T.: The pine embryo and the embryos of related genera. Trans. Illionois State Acad. Sci. 23: 117—125 (1931). — Cram, W. H.: Shelterbelt tree breeding. Proc. 7th Meeting Com. For. Tree Breed. Canada II: D 1—5 (1960). — Cummings, W. C., and Righter, F. I.: Methods used to control pollination of pines in the Sierra Nevada of California. U. S. Dept. Agr., Cir. 792, 18 p. (1948). — Doyle, J., and O'Leary, M.: Pollination in pines. Sci. Proc. Roy. Dublin Soc. 21: 181—190 (1935). — Duffield, J. W.: Techniques and possibilities for Douglas fir breeding. J. For. 48: 41—45 (1950). — Duffield, J. W., and Stockwell, P.: Pine breeding in the United States. *In* Trees. U. S. Dept. Agr. Ybk. 1949, 148—153. — Ehrenberg, C. E., and Simak, M.: Flowering and pollination in Scots pine *(Pinus silvestris* L.) Meddel. Statens Skogsforskn. Inst. 46: 1—23 (1957). — Fowler, D. P.: Effects of inbreeding in red pine, *Pinus resinosa* Ait. II. Pollination studies. Silvae Genetica 14, 12—23 (1965 a). — Godman, R. M.: Red pine cone production stimulated by heavy thinning. Lake States Forest Expt. Sta., U. S. Forest Serv., Tech. Note 628, 2 p. (1962). — Holst, M. J.: Forest tree breeding and genetics at the Petawawa Forest Experiment Station. Proc. 8th Meeting Com. For. Tree Breed. Canada II: M 1—25 (1962). — Hough, A. F.: Preliminary results of red pine seed source tests in northwestern Pennsylvania. Northeastern Forest Expt. Sta., U. S. Forest Serv. Sta. Paper 49, 28 p. (1952). — Johnson, A. G.: Albinism in the Austrian pine. J. Hered. 39: 9—10 (1948). — Johnson, L. P. V.: Reduced vigor, chlorophyll deficiency and other effects of self-fertilization in *Pinus.* Canad. J. Res. 23: 145—149 (1945). — Langner, W.: Eine Mendelspaltung bei Aurea-Formen von *Picea abies* (L.) Karst. als Mittel zur Klärung der Befruchtungsverhältnisse im Walde. Z. Forstgenetik 2: 49—51 (1951). — Langner, W.: Selbstfertilität und Inzucht bei *Picea Omórika* (Pančić) Purkyne. Silvae Genetica 8: 84—93 (1959). — Larsen, C. Syrach: Genetics in silviculture. Transl. M. L. Anderson. Oliver and Boyd, Edinburgh, 1956, 224 p. — Lyons, L. A.: The seed production capacity and efficiency of red pine cones *(Pinus resinosa* Ait.). Canad. J. Bot. 34: 27—36 (1956). — MacGillivray, H. G.: Summary report on tree improvement work at the Acadia Forest Expt. Sta. Proc. 5th Meeting Com. For. Tree Breed. Canada II: I 1—14 (1957). — McWilliam, J. R.: Interspecific incompatibility in *Pinus.* Am. J. Botany 46: 425—433 (1959). — Moffett, A. A.: Genetical studies in *Acacia* I. The estimation of natural crossing in black wattle. Heredity 10: 57—67 (1956). — Orr-Ewing, A. L.: Possible occurrence of viable unfertilized seeds in Douglas fir. Forest Sci. 3: 243—248 (1957). — Philp, J., and Sherry, S. P.: The degree of natural crossing in green wattle, *Acacia decurrens* Willd. and its bearing on wattle breeding. J. So. Africa For. Assoc. 14: 1—28 (1946). — Piatnitsky, S. S.: Experiments on self-pollination of *Larix, Acer* and *Quercus.* (In Russian, U. S. Forest Serv. Transl. 290. 22 p.) Trudy Botanicheskogo Inst. Akad. Nauk S. S. S. R. 4: 297—318 (1934). — Plym Forshell, C.: Kottens och fröets utbildning efter själv- och korsbefruktning hos tall *(Pinus silvestris* L.). The development of cones and seeds in the case of self- and cross-pollination in pine *(Pinus silvestris* L.). Meddel. Statens Skogsforskn. Inst. 43: 1—42 (1953.) — Righter, F. I.: Summary of forest tree improvement work in California. Proc. 5th Northeast. For. Tree Imp. Conf., Orono, Me., 1957: 22—24 (1958). — Sarvas, R.: Investigations on the flowering and seed crop of *Pinus silvestris.* Commun. Inst.

---

*) Appartenant: *Silvae Genetica* 14, 12—23 (1965).

Forestal. Fenn. 53, 198 p. (1962). — Schröck, O.: Die Vererbung der Frühblüte der Kiefer. Züchter 19: 247—254 (1949). — Shaw, G. R.: The genus *Pinus*. Publ. Arnold Arb. 5, Cambridge, 1914, 96 p. — Silén, R. R.: Pollen dispersal considerations for Douglas fir. J. For. 60: 790—795 (1962). — Squillace, A. E., and Bingham, R. T.: Selective fertilization in *Pinus monticola* Dougl. — I. Preliminary results. Silvae Genetica 7: 188—196 (1958). — Squillace, A. E., and Kraus, J. F.: The degree of natural selfing in slash pine as estimated from albino frequencies. Silvae Genetica 12: 46—50 (1963). — Stebbins, G. J.: Variation and evolution in plants. Columbia Univ. Press, 1950, 643 p. — Sylvén, N.: De Svenska Skogsträden. I. Barrträden. Stockholm, 1916, 299 p. — Wettstein, W.: Zur Blütenbiologie von *Pinus silvestris*. Z. Forst- u. Jagdw. 72: 404—409 (1940). — Wright, J. W.: Pollen dispersion of some forest trees. Northeastern Forest Expt. Sta. U. S. Forest Serv., Sta. Paper 46, 42 p. (1952). — Wright, J. W.: Notes on flowering and fruiting of northeastern trees. Northeastern Forest Expt. Sta. U. S. Forest Serv., Sta. Paper 60, 38 p. (1953).

Provenance Differences in Pacific Coast Douglas Fir

1. Seed and Seedling Characteristics

By G. B. Sweet*)

Forest Research Institute, Rotorua, New Zealand

(Received for publication August 19, 1964)

1. Introduction

Many exotic species of value to New Zealand forestry have a wide natural distribution, and consequently provenance trials form an important part of this country's programme for tree improvement research. Next to *Pinus radiata* Douglas fir is New Zealand's most important exotic tree species, and its provenances are being quite intensively investigated. Thulin (14) detailed the existing knowledge of seed sources of New Zealand Douglas fir plantations and described steps which have been taken to establish provenance trials in this species. Among these was the sending, in 1956, of an officer to western North America to collect seed for trial purposes. The collections made included 30 seedlots of Douglas fir which have since been sown, raised in the nursery, and established in field trials. These lots have also been the subject of seed investigations and replicated nursery measurements; it is with the latter trials that this paper is concerned.

The importance of early measurements and observations is twofold. It is obviously important, in examining young trials, to know with some certainty the likelihood of early height relationships changing with age. The literature does not throw much light on this question, and such information can be obtained for any species only if early measurements have been made. Secondly, it is important to be able to verify the origin of seed to be used for commercial establishment, to ensure that large areas are not planted with inferior provenances. Purchasers of seed are very dependent on the honesty of their suppliers, and even where this is of a high order, mistakes are possible. It should be possible, by a combined study of seed and seedling characteristics, to check fairly closely the origin of any provenance, but this can be done only if adequate and reliable data are available on the expected behaviour of provenances.

2. Review of Relevant Literature

Reviewers of European literature on provenance trials of Douglas fir, e. g. Jahn (8), stress the extent to which the growth of this species is influenced by features of climate and site. Many provenances which have proved well suited to the coastal climates in the United States, and which are expected to suit New Zealand conditions, have failed completely in Europe because of spring frost damage and associated infection by the fungus *Rhabdocline pseudotsugae* (e. g. Veen, 16). For this reason current European provenance research in this species is of less interest to New Zealand than that being carried out in North America.

Variations in seed size or seed weight due to provenance have been reported for several species, and these have been correlated with seed source, (e. g. 9, 15): no reference is known to any work correlating seed weight of Douglas fir with seed source, although Allen (1) has been able to separate coastal from interior seed in this species by differences in its gross morphology. Seed-weight differences caused by age, not provenance, have however been reported by J. W. Duffield (1964, pers. comm.) who states that in the Pacific north-west, old trees of Douglas fir have smaller cones and lighter seed than young trees.

Only one reference (3), is known to have been published in which heights of Douglas fir in the nursery were measured in a climate comparable with that of New Zealand. Ching and Bever examined 14 provenances from British Columbia, Washington, and Oregon. They raised seedlings at Corvallis in Oregon and reported significant height differences between provenances, those from higher latitudes being generally taller than those from lower latitudes. No correlation was found between seedling height and altitude of seed source. Munger and Morris (11) reported on the height growth of 13 provenances, 16 years after planting on several sites in Washington and Oregon. Some of these provenances showed a marked interaction with site, thus making difficult any general correlation between height growth and climate of seed source.

The phenology of Douglas fir has been more widely studied. The genetic component was examined by Morris, Silen and Irgens-Moller (10), who showed that the relative order of bud burst remained constant for many years, implying a high degree of genetic control. Silen (12), working with grafted material, also found a high genetic component in time of bud burst, but Walters and Soos (17) found more variation among individual trees in this feature.

Munger and Morris (11), assessing a number of provenances from the Pacific north-west on two sites in Oregon, found that the trees with earliest bud burst in spring came from areas with warm spring days and nights, such as low-altitude plains and wide valleys. Those that flushed next came from high-altitude areas with cold spring days and nights, while the last provenances to flush came from narrow valleys and foothill areas where cold-air drainage gave cold nights following warm spring days. Ching and

---

*) Temporary address: Botany Department, University College of Wales, Aberystwyth, Wales, U. K.