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Precocious Flowering in Some Pines of the Lariciones Group[1])

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One obstacle to genetic work with forest trees is the length of the period between generations (breeding cycle) of many tree species. Numerous experiments in the induction of flowering in young tree seedlings by various treatments of the plants and by modification of their environment have been carried out during the last 25 years, but thus far the results have not been promising. Another possible method of shortening the breeding cycle of at least some forest trees is to achieve this by genetic means. Precocious flowering has in many cases been found to be inherited. The following review of literature presents some of the better known cases of precocious flowering in Scots pine (Pinus silvestris L.) and some other species of the Lariciones group.

LÖFFLER (1923) in his outline for proposed breeding work with Scots pine and Norway spruce Picea abies [L.] KARST.) recommended the use of precocious trees, flowering at age 6–8. They were to be used for the purpose of rapidly obtaining information on the inheritance of silviculturally important characteristics. Within a span of 20–30 years it should have been possible to obtain information applicable to the breeding of materials with longer breeding cycles for direct use in forestry.

MÜLLER (1937) found Scots pine bearing cones at age 5–8 and staminate strobili at age 10 in plantations and natural stands in north Germany. The interval between first ovulate and staminate flowering usually exceeded five years. In three plantations of different ages in Saxony the proportion of trees with ovulate strobili was 2.7% at age six, 6.7% at age eight, and 20.4% at age 10. In all three plantations the average heights of the trees with ovulate strobili were greater than of the non-flowering trees. Several examples are given where abundant supply of light and nutrients were conducive to precocious female flowering while the opposite seems to hold true for the early production of male catkins. In a progeny test, after open pollination, with single tree plots, one progeny of an 8-year-old tree contained 47% trees with ovulate strobili at age six while another progeny of a 12-year-old tree had 12%. The same progenies had 78% and 50% trees respectively, with ovulate strobili at age nine. In another series an 8-year-old tree had a progeny containing 50% trees with ovulate strobili at age six while a progeny of a 27-year-old tree contained only 9%. Also in these tests trees with precocious flowering continued to show superior height growth as compared with non-flowering trees, at least during early life. A breeding plan is proposed, based on single plant selection and progeny testing. With 10-year breeding cycles, four generations of selected trees, including the original parents, should become available for final evaluation in about 22—25 years and the best lines could then be selected for use in forestry. Relatively wide spacing is recommended for individual evaluation. This is estimated to require a total of about 700,000 plants to be tested on an area of about 500 acres.

Based on observations for 55 species and varieties of pines growing at Placerville, Calif. RICHTER (1939) reported an average minimum age of ovulate strobili production to be 5.2 years. The average minimum age of male catkin production of 39 species and varieties was 4.4 years. The minimum age for flowering of 14 species and varieties of the Lariciones group was reported to be 5.1 years for strobili of both sexes. Scots pine could flower, both male and female, at age five, its variety rigensis LOUD. at age four and P. densiflora SIEB. & ZUCC. at age two. The latter species produced good seeds after female flowering at three years of age. The climatic conditions at Placerville are considered to be quite favourable to reproductive precocity.

SCHRÖCK (1949) found precocious trees in progeny test plantations of Scots pine near Berlin, Germany. Several progenies of young trees contained greater proportions of precocious seedlings than progenies of older trees, indicating that the precocious flowering habit is inherited. Also in this case, precocious flowering could be found combined with good growth rate and growth form. The author believed that the tendency to precocious flowering was dominant and was introduced into native Scots pine materials through cross pollination from plantings of foreign origin. Some progenies of trees flowering at age 13 contained up to 89% precocious seedlings of which 7% were males, 55% females and 38% monoecious. It is pointed out that the dioecious flowering habit is valuable in seed orchards if it is persistent and under strong genetic control.

MORRISON-BELL (1950) reported a Scots pine transplant (2/2) planted in 1948 near Oxford, England and photographed with mature cones early in 1950. This plant must have produced functional ovulate strobili at age four and was seemingly normal in other respects.

HERRMANN (1951) and MERGEN and CUTTING (1957) reported a rare occurrence of male catkins on mugo pine (Pinus mugo TURRA) at an age of 16 and 12 months respectively. HERRMANN found male catkins on one seedling which he had micrografted on Norway spruce. MERGEN and CUTTING found three out of 330 seedlings to have male catkins. In

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both cases secondary needles started to form right above the catkins.

Schröck (1957) investigated the offspring resulting from open pollination of a markedly cone-sick, 19-year-old Scots pine found in a plantation in East Germany. The tree in question was also crooked and had several forks on the main stem; its cone production was normal during the eight years following its discovery, but the growth rate was below the average of the plantation. The seed yield was below normal, as well as the survival of the resulting seedlings in the nursery and plantation. Their first flowering occurred at age four mostly on cone-sick trees. At age seven the flowering trees were smaller than the non-flowering ones. The following segregation was then observed:

		Growth form		Total	
		abnormal	normal		
flowering	cone sick	136	16	152	
					345
	normal cone distribution.	123	70	193	
not flowering		236	136	372	
		495	222	717	

Two independent dominant genes were postulated on the basis of this segregation. One determines precocious flowering (up to age seven) and the other cone-sickness. Most of the trees of normal growth form did not flower while there was a slight preponderance of precocious trees with abnormal growth form.

Mergen (1961) observed the precocious Mugo pine seedlings mentioned previously (1957) for two consecutive years and in each year male catkins were produced. A check was made of the relationship between the first flowering and flowering in the succeeding year on 14 different species and pine hybrids in his progeny test plantations. A regression analysis indicated a highly significant relationship. Approximately half of the trees flowered in the year succeeding their initial flowering. This is an indication that the so-called non-sexual cycle of these trees had been completed and they were able to continue flower production. He also observed that interspecific pine hybrids occasionally flower at an earlier age than seedlings of their parents. This is interpreted as possibly being determined by complementary genes of the parental species shortening the juvenile phase of the hybrids.

Wright (1964) stated that most of the *P. densiflora* and *P. thunbergii* Parl. seedlings grown under good nursery conditions in Michigan will bear small crops of female and male strobili by their 4th or 5th year. Under field conditions good seed crops can be expected by the 6th or 7th year and it is not unusual to find natural reproduction around trees less than 10 feet tall.

Gerhold (1966) found several precocious Scots pine seedlings of Christmas tree plantation origin in 34 open-pollinated families set out in three plantings in Pennsylvania. Out of 3150 trees, two produced ovulate strobili at age three, 71 at age four, 311 at age five and 370 at age six. One seedling produced male catkins at age four and another at age five. At age seven, 65 seedlings had male catkins. Another strain, also of Christmas tree plantation origin, a commercial variety "Nye Branch", had three to five times as many flowering trees as an average family of the above and 1.25 to 1.50 times as many as the most prolific family. The number of trees with conelets at one of the localities, where the trees also were tallest, was over twice as great as at either of the two other localities.

In a recent paper Polk (1967) further describes the "Nye Branch" precocious strain of Scots pine and discusses its use in seed orchards. He comes to the conclusion that precocity is undesirable in commercial stocks but may be of some use in the development of special experimental materials.

Materials and Methods

The Ontario Department of Lands and Forests has been actively engaged in hard pine breeding work since 1956. In the course of this work many species and hybrids of the *Lariciones* group of pines have been raised at the Southern Research Station, Maple, Ontario. During the period 1964—66, observations on flowering and counts of male and female strobili were made on some of these.

Most of these materials were raised in the following manner: The seeds were germinated in petri dishes in early January. The germinated seeds were planted individually in two-inch plastic cups in a greenhouse, where they were raised under an extended photoperiod. The long day was obtained through additional illumination of the seedlings with low intensity light (50 f. c.) for 4—8 hours. A soil mixture consisting of one part pine humus (F-layer) and one part granitic sand was used as a growing medium. The seedlings were transplanted into beds in a nursery when 6—7 months of age. At this time most terminal buds were developed and height growth had ceased. The seedlings remained in the beds until the beginning of the third growth cycle (age 27 months) when they were transplanted into test plantations or observations plots. Observations on flowering were made when the seedlings were 17 months and 29 months of age. The results are presented in *Table 1.*

Table 1. — First ovulate strobili production of some *Lariciones* pines at Maple, Ontario.

Age	Species and hybrids
17 months (beginning of second growth cycle)	*P. densiflora* *P. silvestris* *P. nigra* Arnold × *(nigra × densiflora)* *P. (nigra × densiflora) × nigra* *P. (nigra × densiflora) × densiflora* *P. (nigra × densiflora) × (nigra × densiflora)*
29 months (beginning of third growth cycle)	*P. densiflora × silvestris* *P. (densiflora × nigra) × silvestris* *P. silvestris × (densiflora ×nigra)* *P. (densiflora × silvestris) × (silvestris × mugo)* *P. (densiflora × nigra) × (densiflora × nigra)*

In addition to the above observations, one experiment was initiated to determine to what extent within-species variation in age at first flowering was under genetic control. In the spring of 1960, 87 precocious Scots pine were selected from beds containing approximately two million 2/1 seedlings in the Provincial forest nursery at St. Williams, Ontario. The sole criterion for selection was the presence of one-year-old cones on these seedlings. The seedlings thus must have produced ovulate strobili at age two.

They were transplanted to a nursery at Maple, Ontario where some continued to flower. An abundant crop of male and female strobili was produced by many of these seedlings in the spring of 1963 and the following controlled pollinations were carried out:

Precocious × precocious (same population) RP 309
Precocious × precocious (different populations) RP 310
Precocious × normal (different populations) RP 311

The pollination techniques used were similar to those described by MERGEN, ROSSOL and POMEROY (1955). The selected precocious seedlings belong to a strain of Scots pine from western Europe grown for several generations in southern Ontario under moderate selection pressure for general climatic adaptation, nursery performance and survival in plantations. The other precocious Scots pine is a clone of the same strain; it was selected in a plantation at Maple, Ont. for flowering at age 10. The normal Scots pine is a clone of Czechoslovakia origin selected in a provenance test plantation at the Petawawa Forest Experiment Station and grafted at Maple, Ontario. The results of these pollinations are given in *Table 2.*

Table 2. — Cone and seed sets after pollinations of precocious Scots pine.

	RP 309	RP 310	RP 311
No. ovulate strobili pollinated	232	226	230
No. cones set	205	193	202
No. cones collected	98	94	86
No. trees pollinated	16	23	18
full seeds/cone	6.64	7.23	7.19
empty seeds/cone	1.62	2.45	2.58
empty seeds %	19.63	25.49	26.43

The seedlings resulting from the above pollinations were raised in a replicated experiment under the conditions previously described. The experimental design consisted of randomized rows of 12 seedlings replicated six times. The design was maintained in the nursery planting. When the seedlings were 17 months old (at the beginning of the second growth cycle) they were examined and numbers of strobili recorded. The results of this examination are presented in *Table 3.* At this time 15 plants of RP 309, with ovulate strobili, not included in the replicated and randomized planting, were marked. These were later shipped to the Department of Forestry and Rural Development in Fredericton, N. B. for further observation under different growing conditions. The second examination of the seedlings was made at the end of the second growth cycle, in October 1966. The total and current height growth of the seedlings was measured and they were classified in respect to growth form as normal, multinodal *(Fig. 1),* and with bud prolepsis. The class multinodal comprised plants combining bud prolepsis with strong apical dominance and producing two whorls of side branches during their second growth cycle. The results of this tally are presented in *Table 4.*

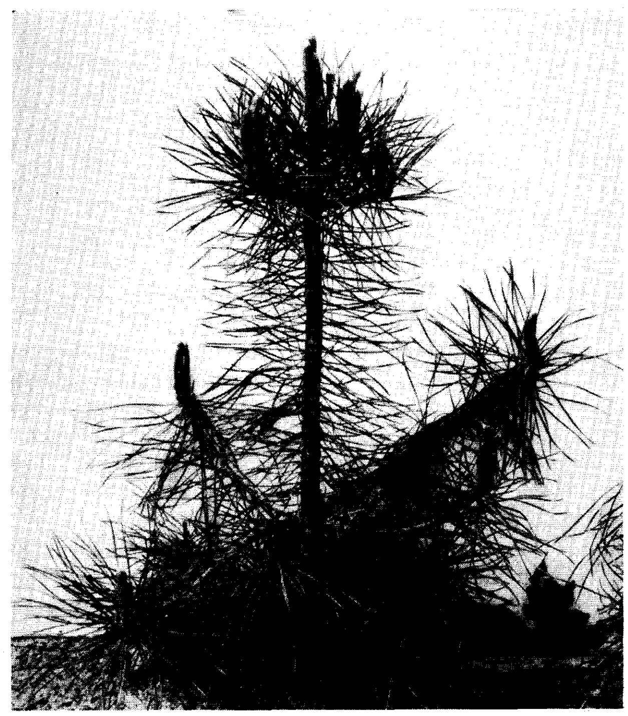

Fig. 1. — A multinodal Scots pine.

Table 3. — Strobili production of 17 month-old and 29 month-old precocious Scots pine.

	Maple, Ontario						Fredericton, New Brunswick
	RP 309		RP 310		RP 311		RP 309
	17 mo.	29 mo.	17 mo.	29 mo.	17 mo.	29 mo.	29 mo.
No. seedlings examined	203	92	70	39	171	61	15
No. seedlings with ovulate strobili	42	35	0	9	1	5	6
No. ovulate strobili	54	118	0	29	2	7	30
Per cent seedlings with ovulate strobili	20.7	38.0	0.0	23.1	0.6	8.2	40.0
Ovulate strobili per flowering seedling	1.3	3.4	0.0	3.2	2.0	1.4	5.0[1])
Ovulate strobili per seedling	0.3	1.3	0.0	0.7	0.01	0.1	2.0

[1]) One seedling produced 14 ovulate strobili.

At the beginning of the third growth cycle, in the spring of 1967, the seedlings, including those in the nursery outside the experimental design, were set out in a plantation at a spacing of 5 × 10 feet in randomized rows. Only seedlings of normal growth form, i. e. with a single stem and no bud prolepsis in 1966, were retained. At the time of flowering they were tallied for the presence of ovulate and staminate strobili. There were no staminate strobili on any of the trees at that time. The results of this examination are presented in *Table 3.*

At the termination of the third growth cycle, in the autumn of 1967, the total and current height growth of the trees was measured. At this time it was also possible to compare the height growth of trees tallied as having borne ovulate strobili in the spring with the non-flowering trees. The results of these tallies are presented in *Table 4.*

Results

The observations on flowering of the various *Lariciones* pines and hybrids grown at Maple, Ontario are given in

Table 4. — Seedling height growth after 20 months and 32 months in cm.

	Height growth after 20 months (end of second growth cycle)					
	RP 309		RP 310		RP 311	
	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
Total height						
normal	49	36.3	48	31.4	32	34.3
multinodal	2	30.5	2	28.5	5	33.6
proleptic	21	37.0	16	29.1	35	37.0
Current height growth						
normal	49	26.4	48	25.0	32	26.4
multinodal	2	22.5	2	22.5	5	25.6
proleptic	21	27.6	16	23.2	35	28.7

	Height growth after 32 months (end of third growth cycle)					
	RP 309		RP 310		RP 311	
	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
Total height						
normal	70	51.6	28	51.3	42	48.5
top injury	22	42.4	11	50.3	19	49.2
Current height growth						
normal	70	20.1	28	20.3	42	19.6
top injury	22	12.1	11	17.0	19	18.0
Total height						
with ovulate strobili	35	50.7				
without ovulate strobili	57	48.6				
Current height growth						
with ovulate strobili	35	16.0				
without ovulate strobili	57	17.8				

Table 1. With the exception of *Pinus resinosa* Ait. and *Pinus nigra* and varieties, most species and hybrids of the *Lariciones* group produce at least some ovulate strobili at age five. No strobili have been observed on *Pinus resinosa* and *Pinus nigra* varieties up to age eight. Staminate strobili production usually begins 2—3 years after the first ovulate strobili are produced. *Pinus densiflora* and its hybrids often produce ovulate strobili at the beginning of the second or third growth cycles. This is in accord with the observations of Righter (1939) and others and indicates that at least some of the precocious flowering of this species is dominant in crosses with the late-flowering *Pinus nigra* and its varieties and with *P. silvestris.* Of all the seedlings examined only one, a *(P. densiflora* × *nigra)* × *silvestris,* produced staminate strobili by the beginning of the third growth cycle.

The results of the precocious Scots pine experiment are presented in *Tables 2 and 3. Table 2* shows that the seed set of the cross precocious × precocious of the same population (RP 309) is slightly (significantly) lower than the seed set of the other two crosses — precocious × precocious of another population and precocious × normal (RP 310 and RP 311). The extremely precocious flowering is thus accompanied with a slight decrease in fertility, i. e. pollen of the extremely precocious materials is not as successful on ovulate strobili of the same kind as pollen of the other kinds.

The ovulate strobili production at age two *(Table 3)* seems to be inherited as if determined by recessive genes.

Pollination within the extremely precocious materials resulted in 20.7% of the seedlings producing .3 ovulate strobili per seedling (1.3 per flowering seedling) while only one of the seedlings resulting from out-pollination of the extremely precocious materials produced ovulate strobili. No staminate strobili were produced at that time.

The results of the second year's growth of the seedlings in question are presented in *Table 4.* At this time, seedlings of RP 310 (precocious × precocious of a different population) were significantly shorter than seedlings of the other two populations. This applies also, although to a somewhat lesser extent, to their current height growth during 1966. This difference was no longer evident at the end of the third growth cycle. The total height growth of the few multinodal seedlings was slightly, but not significantly, lower than that of normal seedlings.

During their third year of growth none of the seedlings produced male catkins. The results of ovulate strobili production are given in *Table 3.* RP 309 had a greater proportion of seedlings with strobili than either of the other two populations. Only in comparison with RP 311 was this difference significant. The materials of RP 309 shipped to New Brunswick contained about as many (40%) seedlings with ovulate strobili as those at Maple, Ontario (38%). RP 311 had significantly fewer strobili per seedling than the other two populations, i. e. the number of strobili per seedling of the two populations having precocious trees as both parents was at this time significantly greater than within the outcrossed population. RP 311 also produced fewer strobili per flowering seedling than the other two populations. Only the difference between RP 311 and RP 310 was significant.

The 15 seedlings of RP 309 moved to New Brunswick in 1966 were similar in respect to flowering in 1967 to those grown in Ontario, indicating that precocious flowering of this population may not be effected by large differences in environment. One of the New Brunswick seedlings produced 14 ovulate strobili. This accounts for the considerable greater number of strobili per seedling in this material.

The results of the third year's growth are presented in *Table 4*. As the differences in total and current height growth of normal trees and of those with top injury, etc. are significant within RP 309, only the height growth averages of normal trees of the different populations are compared at this time. The total height growth of RP 309 is greater than that of the other two populations, reaching a level of significance in comparison with RP 311. The latter also has (not significantly) lower average current height growth than the other populations. Neither total nor current height growth of trees producing ovulate strobili in 1967, within RP 309, differed significantly from tose without strobili, as shown in *Table 4*.

Discussion

There is thus abundant evidence that precocious flowering in Scots pine, and probably in other *Lariciones* pines, is under strong genetic control. Several undesirable characters, such as decrease in seed set, prolonged interval between female and male flowering, cone sickness, poor growth form, and in our case possibly bud prolepsis, appear in progenies selected for precocious flowering. These are probably the result of high selection pressure on small populations which does not allow new balanced gene combinations to be formed at adequate rates (ALLARD, 1960). However, with a wider basis of selection, including some of our recent interspecific hybrids, and with continued rigid selection against such characters, it should be possible to obtain several strains of precocious *Lariciones* pines with good growth form and growth rate, at least in early life. Such strains could be used in pilot breeding projects, to accumulate useful genes showing additive inheritance in such traits as pest resistance, nutrient uptake efficiency, climatic adaptation and wood quality.

The multinodal seedlings listed in *Table 4* deserve special mention. They are plants combining bud prolepsis with strong apical dominance and produce two whorls of side branches during their second growth cycle. It is well known that bud prolepsis in Scots pine and related species is to a high degree dependent on environmental factors and the frequency of this character in any population is subjected to great annual fluctuations. According to FIELDING (1960) the number of whorls of branches on the annual shoot in Monterey pine (*Pinus radiata* D. DON) shows great variation. Uninodal types as well as trees with an excessive number of whorls are undesirable from a forestry standpoint. This character was found to be under rather strong genetic control. The breeding of such moderately multinodal types in the *Lariciones* pines is desirable because of possible gains in wood production and wood quality. Although the multinodal seedlings mentioned above have been destroyed in order to restrict further selection of precocious types to those with normal growth form, there is a good possibility or recovering these from further sowings of the same populations from stored seeds. Multinodal seedlings have also been observed and selected in several other populations of southern Ontario Scots pine and are available for further work. The precocious strain of Scots pine, currently under development, could be used in the breeding of a superior multinodal type with the aid of short breeding cycles.

Summary

After a brief review on the occurence of precocious flowering in *Pinus silvestris* and other *Lariciones* pines in the literature and in the collection of breeding materials and hybrids at the Southern Research Station, Maple, Ontario, of the Ontario Department of Lands and Forests, the results of an experiment with selection for precocious flowering within a strain of Scots pine are given.

In a nursery compartment of about two million 2/1 seedlings, 87 producing ovulate strobili at age two were selected. At age five these flowered abundantly in both sexes and were intercrossed as well as crossed with another tree, selected for flowering at age 10, and with a "normal" clone. The seed set of the cross precocious × precocious within the same population was slightly lower than of the other two crosses. The same population contained 20.7% seedlings producing ovulate strobili at age two, and 38% at age three, while the other two populations contained 0% and .6% seedlings with female strobili at age two and 23% and 8% respectively, at age three. No male catkins have been produced to date. The precocious × precocious materials have thus far shown growth rates slightly superior to those of the other two populations. The height growth of trees with ovulate strobili at age three did not differ significantly from those without strobili. Multinodal seedlings, combining bud prolepsis with strong apical dominance, were observed in all populations at age two. The possible importance of this character in the breeding of *Lariciones* pines is pointed out.

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