SEED PRODUCTION IN THE FIRST EIGHT YEARS AND FREQUENCY OF NATURAL SELFING IN A SIMULATED JACK PINE SEEDLING SEED ORCHARD

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ABSTRACT.-- Seed production and percent of natural selfing were determined in an 8 x 8-foot, 1200-tree plantation. Actual seed production was determined through age 6; production through age 8 was projected based on first-year cone counts at age 7. The percent of natural self-pollination, production of seedlings from natural selfing, and percent of selfs that were lethal were determined by marker seedlings. Ovulate strobili production began at 17 months of age; by age 4 a few trees produced small quantities of mature cones and seed. By age 8 years most trees produced an average of 39 mature cones per tree, 26,200 cones per acre, or 655,000 filled seed per acre. Total filled seed per acre produced through age 8 years was 1,159,000. The overall average of open-pollinated seedlings resulting from natural selfing was about 7 percent. The frequency of natural self-pollination, determined from carriers of selected seedling marker types, ranged up to 34 percent; on the average more than half of these were lethal. Removing trees showing high selfing percentages and careful culling of poorer seedlings grown from orchard seed before field planting should reduce the impact of natural selfing on wood yield in such plantations to a minimum.

Three important considerations for managing pine seed orchards are: how early do they produce seed, how much seed do they produce, and how much seed results from selfing?

Jack pine (Pinus banksiana Lamb.) begins to produce ovulate strobili in the third and fourth year when grown under standard nursery conditions (Righter 1939, Wright 1964, Rudolph 1966b), but as early as 17 months if started in the greenhouse under near-optimum conditions (Rudolph 1966b,

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Jeffers and Nienstaedt 1972). Once cone production begins it is fairly regular (Godman and Mattson 1976) and increases until crown competition becomes a factor (Roe 1963).

Jeffers (1976), using well-substantiated seed yields per cone (Schantz-Hansen 1941, Rudolf 1958, Roe 1963, Rudolph 1966b, 1967, Jeffers 1972), and actual female strobili per tree at age 5, predicted a yield of 267,000 full seed per hectare of jack pine seed orchard at age 6.

Most wind-pollinated seed produced on jack pine results from cross-fertilization but up to 25 percent naturally selfed seed has been reported in progenies of individual trees (Fowler 1965a, 1965b, Rudolph 1966a, Teich 1970, Sittmann and Tyson 1971). Hadders and Koski (1975) have reviewed the factors affecting the proportion of natural selfing in relation to production of seed in pine seed orchards. Selfing can result in reduced cone set, lower filled seed yield, poorer seed germination, lower survival of seedlings, depressed growth rate, and increased frequency of deviant types (Fowler 1965b, Rudolph 1966a, 1967, 1976), all undesirable features in seed orchard management.

In this paper I report the actual seed production in a simulated seedling seed orchard through age 6 from seed, the projected yields through age 8 based on first-year cone counts at age 7, and I estimate the frequency of natural selfing based on the proportion of various marker seedling types in open- and controlled self-pollinated progenies. I also recommend the means to reduce the effect of natural selfing on future wood yields.

MATERIAL AND METHODS

Trees for this study were grown from seed collected in August, 1960 from approximately 50 jack pine trees in an extensive stand near Rhinelander, Wisconsin. Variable quantities of seed per tree comprised the bulk lot. The primary objective of the study was to determine the effects of gamma irradiation of the seed at various exposure levels on the long-term survival and reproductive capacity. However, the design of the study, particularly of the field test, lends itself well for consideration as a simulated seed orchard. The radiation effects, which will be reported elsewhere, do not invalidate the seed production results to be presented here but do make the estimates slightly more conservative than could be expected without irradiation due to slightly lower production in the highly irradiated lots. The slight impact of irradiation noted on seed yield and self-ability will be discussed in the results section. Design details relating to radiation treatments will only be presented to put the total experiment into perspective.

In December, 1966, thirteen samples of 300 seeds each were fully imbibed in water. They were then gamma irradiated at one of thirteen exposures ranging to 19,200 R. The irradiated seedlots were divided into three replications of 100 seeds each and sown in sand in a greenhouse. At 1 month of age, 125 seedlings per exposure randomly chosen from the combined three replications were transplanted into 2½ in. x 2½ in. x 3 in. veneer plant bands, and randomly assigned to five replications of 25 seedlings each. The seedlings were grown in the greenhouse until May 1967 when they were transplanted to the Hugo Sauer Nursery near Rhinelander, Wisconsin. The same design as in the greenhouse was followed in the nursery but with a 7 in. x 7 in. spacing between plants. Incidence of flowering was scored on the nursery-grown seedlings in the spring, 1968 and percent of trees flowering and ovulate conelets per tree determined.

Approximately 1200 seedlings survived and were field planted near Lake Tomahawk, Wisconsin on June 10, 1969 at an 8 ft. x 8 ft. spacing inthe same randomized block design as was used in the nursery with 5 x 5 tree plots.

All open-pollinated cones produced in 1970, 1971, and 1972 (ages 4, 5, and 6 years) were collected separately from each tree each year. Seed was extracted by shaking the cones in a sieve with 1/4 in. x 1/4 in. openings following a brief dip in boiling water to open the cone scales. The seed was counted and X-rayed to determine percent filled. Percent of trees with mature cones and seed yields were determined.

In the spring, 1973, when the trees were in their seventh growing season, the total number of ovulate conelets per tree was scored on the center nine trees of each plot to facilitate estimation of cone production in 1974 or at age eight. Also in the spring, 1973, two trees that had relatively abundant male and female strobili production were selected in each plot for controlled self-pollinations. Whenever possible, trees in the same position within plots were selected to provide for a relatively uniform but representative selection of trees throughout the planting. Thus, a total of ten trees per each of the twelve radiation treatment levels (no trees survived in the 19,200 R treatment) or 120 trees were selected for the self-pollinations. Five isolation bags were placed on each tree and the female strobili in each of the 600 bags were self-pollinated on June 1 and 2, 1973. Mature cones from the self-pollinations were collected in late September, 1974, keeping those from each pollination bag separate. Five open-pollinated cones from each of the bagged trees were collected at the same time. Of the 120 trees self-pollinated, 106 produced a total of 1200 cones.

The selfed seed together with the sample of open-pollinated 1973 seed from five cones on the same trees was extracted by hand by removing the cone scales, counted, X-rayed to determine percent filled, and germinated in sand in the greenhouse. The seedlings were examined at frequent intervals for 3 months to search for characteristics with potential as genetic markers. Frequency of markers within individual tree progenies was expressed as a percent of total seedlings germinated.

A similar procedure for screening for marker seedlings was used to screen open-pollinated seed from all trees producing cones in 1972. Whenever possible, 200 filled seed from each of the 1178 trees producing cones was sown; however, fewer filled seeds were available from some trees. A "damping-off" fungus problem in one greenhouse bench during germination reduced the number of open-pollinated families that could be effectively screened to 848.

Percent of open-pollinated seedlings resulting from natural self-fertilization was determined for all families that were segregating for the various types of marker seedlings. It was assumed for simplicity, that the markers were recessive and that they segregated in a 3:1 ratio upon selfing; that is, the frequency of marker seedlings in the open-pollinated progenies was multiplied by four. The simplistic 3:1 ratio was assumed in this study because a genetic explanation for apparent deviations from this ratio observed in some families is not known.

Percent of natural self-pollination was calculated as the ratio:

$$\frac{\text{percent of marker seedlings in open-pollinated progenies}}{\text{percent of marker seedlings in controlled self-pollinated progenies}}$$

Application of this ratio assumes that self-pollen is as viable and active as cross-pollen and that one embryo occurs per ovule. It must be recognized that the percent of natural self-pollination determined in this manner may be over-estimated to an unknown degree due to possible mating between carriers of common markers.

The percent of self-pollinations that were lethal was determined from the relationship:

$$\frac{\begin{pmatrix}\text{percent of natural} \\ \text{self-pollination}\end{pmatrix} \text{ minus } \begin{pmatrix}\text{percent of open-pollinated seedlings} \\ \text{from natural self-fertilization}\end{pmatrix}}{\text{percent of natural self-pollination}}$$

RESULTS AND DISCUSSION

Cone and Seed Production

Ovulate strobili production began in the spring, 1968, in the nursery at approximately 17 months of age, on 28 percent of the trees (table 1). Of the total surviving trees, 21 percent had one, 6 percent had two, and less than 1 percent had three or four ovulate strobili per tree.. Percent of trees flowering was significantly lower in some of the highest radiation levels. Thus, the overall average percent of trees flowering was below what might have occurred without irradiation (table 1). However, even with this decrease, the percent of trees producing ovulate strobili in this population is somewhat higher than that previously reported for 17-month-old seedlings (Rudolph 1966b, Jeffers and Nienstaedt 1972). Less than one percent of the trees produced male strobili at this age.

Table 1.--Ovulate strobili production in the nursery in 1968 on 17-month-old jack pine seedlings field planted into a simulated seed orchard the following year

Gamma exposure (R)	Total trees	Trees with: One ovulate strobilus	Two ovulate strobili	Three ovulate strobili	Four ovulate strobili	Total trees flowering:	
	Number	Percent				Number	Percent
0	112	28.6	1.8	2.7		37	33.0
150	117	20.5	12.0	1.7		40	34.2
300	102	23.5	8.8			33	32.4
600	120	25.8	2.5			36	30.0
1200	114	13.2	4.4			20	17.5
1800	96	22.9	4.2	1.0		27	28.1
2400	108	26.8	8.3	1.8		40	37.0
3600	100	15.0	4.0		1.0	20	20.0
4800	107	15.9	4.7			22	20.6
7200	90	23.3	4.4	1.1		26	28.9
9600	84	17.8	2.4	1.2		18	21.4
14400	49	16.3	8.2			12	24.5
Total or Mean	1199	20.8	5.5	0.8	0.1	331	27.6[1/]

1/ Based on total trees flowering divided by total number of trees.

Practically all the cones aborted and no cones were collected in 1969. This was probably due to the transplanting to the field in June, 1969, and to the lack of pollen in the nursery in 1968. Probably for the same reasons, the percent of trees with mature cones at age four years in 1970, less than 16 percent, was only slightly over one-half as many as produced ovulate strobili in 1968 and less than two mature cones per flowering tree were produced (table 2). The ovulate strobili primordia for the 1970 cones were differentiated during the 1968 growing season in the nursery and possibly suffered high abortion from transplanting shock and lack of pollen in 1969. Similarly, only 10 seeds were produced per cone and only 23 percent of these were filled.

In 1971, at age 5, the proportion of trees producing cones increased to about one-half but the number of cones per cone-bearing tree was still only about two (table 2). However, the number of filled seeds per cone, seven, was three times that in 1970 but still far below normal even though more than two-thirds of the total seed was filled. This possibly resulted from a meager supply of pollen in 1970. The number of filled seeds produced per acre in 1971 increased to more than 12 times that in 1970.

A more abundant pollen supply on the orchard trees in 1971 was apparent because in 1972 at age 6, 22 seeds per cone were produced and three-fourths of them were filled (table 2). This, coupled with an increase in percent of trees producing cones to 93, and more than ten cones per tree, increased the yield of filled seeds per acre to more than 113,000. The total yield of filled seed per acre through age six years was more than 119,000.

Actual production per acre was higher than predicted by Jeffers (1976), who used ovulate strobili at age 5 for his prediction of production at age 6, even though there were only 681 trees per acre compared to 3000 in Jeffers' study. This was largely due to more cones per tree than predicted which was only partially offset by a lower yield of filled seed per cone, 16.5, rather than the 25 predicted by Jeffers (1976). As noted earlier, the relatively few filled seeds per cone at age 6 is due at least partially to insufficient pollen. Mass artificial pollination with pollen from selected trees would likely increase substantially the yield of filled seed in such young orchards. By age 7, there was enough pollen to adequately pollinate the ovulate cones that matured at age 8.

Yields of filled seed during the first 6 years in this study were also lowered by the choice of transplanting time in June, 1969. Transplantation to the field at this time possibly not only decreased the percent of trees with cones in 1970 but likely had an impact on the production in the next 2 years as well (table 2). If the seedlings had been transplanted in the late summer of 1968 when the primordia

Table 2.--Mature cone and seed production of jack pine trees 4, 5, and 6 years old from seed

Year	Total trees	Trees w/mature cones	Cones per tree		Seed per tree		Filled seed per tree		Seeds per cone	Filled seeds per cone	Total seed filled	Filled seeds per acre at 8 ft x 8 ft spacing
			All trees	Trees with cones	All trees	Trees with cones	All trees	Trees with cones				
	Number	Percent	- - -	- - -	- - -	- - -	Number	- - -	- - -	- - -	Percent	Number
1970	1187	15.6	0.3	1.7	2.8	17.7	0.6	4.1	10.4	2.4	23.3	439
1971	1183	47.0	1.1	2.4	11.6	24.7	8.0	17.0	10.2	7.0	68.6	5,429
1972	1178	93.0	10.1	10.9	221.2	237.8	166.7	179.2	21.9	16.5	75.4	113,513
TOTAL FILLED SEED PER ACRE PRODUCED IN THE FIRST 6 YEARS												119,381

for the 1969 female strobili were already differentiated--but in time to establish the seedlings in the field before winter dormancy--there would have been more 1969 female strobili and more differentiation of 1970 and 1971 strobili. In addition, pollen production could possibly have been greater, resulting in higher seed yields. However, further research is needed to verify the impact of transplanting time on early seed production.

The rapid subsequent rise in cone and seed production beyond age 6 years when the trees were better established in the field and pollen production was more abundant is evident from conelet counts made in 1973 at age 7. Almost 43 conelets per tree were found after natural pollination in the summer, 1973 after early abortion and/or abscission had occurred. Assuming an additional 10 percent cone loss between the first year and cone maturity (Rudolph 1976), about 39 cones per tree could be expected in 1974 at age 8. Using this information and the actual seed yields for the first 6 years the total yields of filled seeds through age 8 may be summarized as follows:

Total filled seed production per acre in 1970 (age 4), 1971 (age 5), and 1972 (age 6), (from table 2)	119,381
Ave. number of conelets per tree in summer, 1973 (age 7)	42.75
Number of cones per tree maturing in 1974 (age 8) assuming additional 10 percent cone loss	38.48
Number of cones per acre in 1974 (age 8) at 8 ft x 8 ft spacing (681 trees)	26,205
Number of filled seeds per tree in 1974 (age 8) assuming 25 filled seeds per cone	962
Number of filled seed per acre in 1974 (age 8) at 8 ft x 8 ft spacing (681 trees)	655,122
Number of filled seed per acre in 1973 (age 7) assuming mid-point between 1972 and 1974	384,317
Total filled seed production per acre through age 8	1,158,820

As pointed out earlier, the yields given above are somewhat lower than may ordinarily be expected with the same cultural methods due to the decreased yields at the higher radiation levels. Nevertheless, they indicate that substantial seed yields in jack pine seedling seed orchards can be expected 8 years from seed. Assuming that at least 90 percent of the filled seed is viable (personal observation), about

1 million seedlings per acre of seed orchard can be produced within 8 years. Higher yields could be expected with improved cultural methods and attention to avoiding transplanting shocks. Selection of trees for serotinous cones would permit storing earlier seed production on the trees until yields are high enough to make collections more economically feasible, perhaps beginning at age 8. Selections and thinning could then be applied to promote maximum cone and seed production on the remaining trees in subsequent years.

Frequency of Natural Selfing

Estimated percent of open-pollinated seedlings from natural self-fertilization averaged about 7 percent assuming the markers were a recessive trait segregating 3:1 upon selfing (table 3). This is based on the evaluation of 24 different markers within 567 open-pollinated families among 848 families screened. The range was from about 2 to 18 percent. Proportion of natural self-pollinations, not all of which would result in successful self-fertilization and selfed seedlings, cannot be estimated from open-pollinated progenies.

Note that the proposed markers from open-pollinated progenies were scored on seedlings 3 months or less old. Therefore, some of the supposed markers, particularly certain of the dwarf types such as the "typical" green dwarf (table 3), need to be verified when the seedlings are considerably older. This classification included all seedlings that showed greatly reduced growth at this young age; some of these slow-growers probably exhibited temporary non-genetic effects such as differences in seed size. Additional development will need to be observed and will undoubtedly result in a reduced number of carrier trees for dwarfism. Other characteristics now classified as markers may similarly prove to be temporary physiological effects with age.

Our previous experience has shown that two marker types, yellow-green cotyledons and light green cotyledons, are under rigid genetic control. And since both open- and controlled self-pollinated progenies were available with these markers, they were chosen for more detailed analysis of natural self-pollination frequency in open-pollination and lethality following self pollination (tables 4 and 5).

The average percentages of marker seedlings in open-pollinated progenies of trees carrying these two types of markers and used in the detailed analysis--3 and 5+ percent for the yellow-green and light green cotyledon types, respectively--were slightly higher than the average for all trees carrying these markers (compare table 3 with tables 4 and 5). An average of about 12 and 8 percent of the open-pollinated seedlings in progenies with the two marker types resulted from natural selfing (tables 4 and 5). The lower than expected estimates (assuming 3:1 segregation) of the percent of open-pollinated seedlings resulting from natural selfing in the light green cotyledon

Table 3.--Estimation of proportion of open-pollinated seedlings resulting from natural selfing from frequency of marker seedlings in 1972 open-pollinated progenies

Marker type	Carrier trees 1/	Marker seedlings within family	Open-pollinated seedlings from natural selfing 2/
	Number	Average percent	Percent
White cotyledons	4	2.0	8.0
Yellow-green cotyledons	28	2.6	10.4
Greenish-yellow cotyledons	9	1.2	4.8
Whitish-green cotyledons	6	4.2	16.8
Greenish-white cotyledons	4	1.7	6.8
Light green cotyledons	13	1.2	4.8
Yellow-green primary leaves	4	2.6	10.4
Bluish-green dwarf (typical)	75	1.3	5.2
Green dwarf (typical)	258	2.0	8.0
Bluish-green dwarf(extremely small)	5	1.1	4.4
Green dwarf (extremely small)	9	0.8	3.2
Short, fine primary leaves	1	1.2	4.8
Bluish-green dwarf w/early bud set	21	1.7	6.8
Thin, fine, short primary leaves	3	1.1	4.4
Bluish-green dwarf with thick, stiff primary leaves	7	1.3	5.2
Stem forked immediately	2	4.5	18.0
No apical meristem	8	1.8	7.2
Cotyledons emerge through seedcoat	72	2.2	8.8
Double embryo	18	1.5	6.0
Tightly fused cotyledons	2	3.0	12.0
Kinky stem	6	0.6	2.4
Reverse germination	9	1.8	7.2
Possible chimera (two shoot types)	2	0.7	2.8
Twisted and deformed primary leaves	1	0.6	2.4
Total	567 3/		
Mean		1.78	7.12

1/ Based on 848 parent trees screened.
2/ Assuming marker is a recessive trait segregating 3:1 upon selfing.
3/ 132 trees are carriers of more than one marker type.

marker type are at least partially due to three factors: (1) unexplainable large deviations from a 3:1 segregation ratio such as in tree 4-150-14 (table 5); (2) similar or higher percentages of marker seedlings in open- and self-pollinated progenies of some trees such as tree 4-7200-18 (table 5); and (3) possible differences in linkages of the marker in different trees with different lethal factors. Sorenson (1969, 1971) has found such distorted ratios due to embryonic lethals.

Estimates of the average proportion of natural self-pollination are over 34 percent as determined from the yellow-green cotyledon marker type (table 4) and over 20 percent as determined from the light green cotyledon type (table 5). However, in both cases, if a 3:1 segregation ratio for the markers is assumed, the average percent of lethals resulting from self-pollination is more than 50. This results in an average production of open-pollinated seedlings from successful self-fertilizations of from 8 to 12 percent and is sligthly higher than natural selfing in slash pine reported by Kraus (1975). The probability is that only one-fourth of these are homozygous recessive for any given deleterious gene. Thus, only 2 to 3 percent of the open-pollinated seedlings in a seed orchard as described here should be deleteriously affected by self-pollination and successful self-fertilization, even though the percentages of seedlings from selfing would be 4 times more. The percentages of natural selfing, as estimated in this study by the use of marker seedlings, may be slightly inflated in that marker seedlings resulting from possible crosses between carriers of common alleles are indistinguishable from selfed seedlings. The occurrence of trees with common marker alleles cannot be verified without controlled cross-breeding.

Such low percentages of seedlings showing the depressing effects of self-pollination may not be significant in production of genetically improved seedlings from seed orchards although occasional trees showing high selfing percentages should be removed from the orchard. Culling of this small proportion of poorer seedlings from the progenies before field planting should be easily possible. The small numbers of weak seedlings that remain would likely succumb soon under the more rigorous environmental conditions in present-day tree plantations and would have little influence on ultimate wood yield from such plantations.

ACKNOWLEDGMENT

The technical assistance of Edmund Bauer and Larry Petersen is gratefully acknowledged.

Table 4.--Estimation of proportion of seedlings resulting from natural self-fertilization, frequency of natural self-pollination, and percent of selfs that are lethal from frequency of seedlings with yellow-green cotyledons in open- and controlled self-pollinated progenies

Tree no.	Seedlings that are: Open-pollinated	Seedlings that are: Self-pollinated	Marker seedlings: Open-pollinated	Marker seedlings: Self-pollinated	Open-pollinated seedlings from natural selfing 1/	Natural self-pollination 1/	Selfs that are lethal 1/
	Number		Percent				
1-600-3	229	112	2.6	6.2	10.4	41.9	75.2
2-1200-13	41	156	7.3	24.4	29.2	29.9	2.4
2-2400-13	125	38	2.4	2.6	9.6	92.3	89.6
2-3600-3	237	270	3.4	16.7	13.6	20.4	33.2
3-150-8	250	86	2.4	8.1	9.6	29.6	67.6
3-300-13	159	86	1.9	2.3	7.6	82.6	90.8
3-7200-8	166	76	3.6	15.8	14.4	22.8	36.8
3-7200-13	181	28	2.8	10.7	11.2	26.2	57.2
4-1200-3	197	109	1.0	4.6	4.0	21.7	81.6
4-4800-3	323	75	3.4	20.0	13.6	17.0	20.0
4-4800-18	145	238	2.8	7.1	11.2	39.4	71.6
4-9600-3	195	102	0.5	42.2	2.0	1.2	-- 2/
5-150-3	241	13	3.3	7.7	13.2	42.9	69.2
5-1200-18	172	268	3.5	14.6	14.0	24.0	41.6
5-1800-18	82	62	3.7	14.5	14.8	25.5	42.0
Total	2,743	1,719					
Mean			2.97	13.17	11.89	34.49	55.63

1/ Assuming marker is a recessive trait segregating 3:1 upon selfing.
2/ Cannot be determined on basis of 3:1 ratio.

Table 5.--Estimation of proportion of seedlings resulting from natural sel -fertilization, frequency of natural self-pollination, and percent of selfs that are lethal from frequency of seedlings with light green cotyledons in open- and controlled self-pollinated progenies

Tree no.	Seedlings that are		Marker seedlings		Open-pollinated seedlings from natural selfing 1/	Natural self-pollination 1/	Selfs that are lethal 1/
	Open-pollinated	Self-pollinated	Open-pollinated	Self-pollinated			
	Number		Percent				
1-1200-3	118	127	3.4	22.8	13.6	14.9	8.8
1-2400-3	213	87	1.9	9.2	7.6	20.7	63.2
3-150-18	239	158	0.8	5.1	3.2	15.7	79.6
3-300-13	159	86	2.5	8.1	10.0	30.9	67.6
4-150-14	214	192	1.9	55.4	7.6	3.4 2/	-- 3/
4-7200-18	153	43	21.6	14.0	-- 3/	-- 3/	44.0
Total	1,096	693					
Mean			5.35	19.10	8.40	20.55	52.64

1/ Assuming marker is a recessive trait segregating 3:1 upon selfing.

2/ Not included in mean due to large deviation from 3:1 ratio.

3/ Cannot be determined on basis of 3:1 ratio.

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