CONE SET, SEED YIELD, SEED QUALITY, AND EARLY SEEDLING DEVELOPMENT OF S_2 GENERATION JACK PINE

Thomas D. Rudolph[1]

Abstract.--Self-pollinations were made on 29 S_1 trees and S_1 x S_1-mix crosses were also made on 24 of these she S_1 trees. Open-pollinated progenies from seed on the S_1 trees were also analyzed. Eight of the S_1 self-pollinated trees and 6 of the S_1 x S_1-mix crosses had complete cone abortion. About 69% of the cones in the self-pollinated S1 trees and 58% of cones in the S_1 x S_1-mix crosses aborted by the end of the first. year; by cone maturity abortion reached 75 and 69%, respectively. Number of filled seeds per cone varied between female parent genotypes and some cones had no filled seeds. The S_1 self-pollinations yielded less than half as many filled seeds per cone as the S_1 x S_1-mix crosses and S_1 open pollinations. Germination of filled seed was generally high regardless of degree of inbreeding. Inbreeding depression in seedling height of the S progenies averaged 15% after 10 weeks. The results indicate that jack pine is largely self-compatible even in the second selfed generation. A strong correlation between S_2 and S_1 x S_1-mix progenies in seedling height together with wide within and among progeny variation indicates that selection for growth in inbred lines will be possible for improvement breeding in jack pine.

Additional keywords: *Pinus banksiana*, self-pollinations, inbreeding, outcrossing, inbreeding depression, genetic correlation, genetic variation.

Inbreeding in forest tree species has received the attention of forest geneticists and tree breeders primarily from the viewpoint of the extent and effects of self-pollination in seed orchards (Fowler 1965b, Hadders and Koski 1975). There has been less interest in the use of inbreeding as a tree improvement strategy. Hadders and Koski (1975) have summarized the available information for Pinaceae on the genetic principles of self-fertilization, estimation of the degree of self-fertilization, and the factors affecting the proportion of selfed seeds after open pollination in relation to production of seed in seed orchards. The aim of seed orchard design and management is to maximize cross-pollination between unrelated trees and to minimize inbreeding and especially self-pollination, the most serious degree of inbreeding. Self-pollination has, in general, been found to result in inbreeding depression

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1/ Principal Plant Geneticist, Institute of Forest Genetics, North Central Forest Experiment Station, USDA Forest Service, Rhinelander, Wisconsin.

which manifests itself in reduced seed yields, higher early seedling mortality, reduced vigor, and the appearance of chlorophyll-deficient and other aberrant recessive seedlings.

Self-incompatibility does not appear to be a significant factor in limiting self-fertilization in the Pinaceae (Mergen *et al*. 1965; Hagman and Mikkola 1963; Mikkola 1969, Forshell 1974). Pollen tube growth and syngamy appear to be normal following self-pollinations. Inbreeding depression, therefore, must result from the expression of lethal and other deleterious genes beginning at the zygote stage -- the so-called "genetic load" (Orr-Ewing 1957; Fowler 1965a; Sorenson 1969, 1971; Franklin 1972; Sarvas 1962; Koski 1973). Embryo abortions alone have been reported to account for up to 90% lethality following self-fertilization (Hadders and Koski 1975). Thus, zygotes resulting from self-fertilization are in most cases eliminated in breeding and production populations. Nevertheless, with present-day practices of providing optimum growth conditions in seedling production, many of these inherently weak seedlings survive, find their way into plantations, and decrease the wood yield. It is, therefore, important to know the extent and effects of inbreeding in the production of genetically improved forest trees.

Although it is desirable to avoid or at least minimize inbreeding in *production* populations for reforestation purposes, the use of inbreeding as a strategy for developing *breeding* populations for potential improvement must not be overlooked. Inbreeding schemes have been extremely successful for improving corn, for example, but similar attempts to improve tree species by crosses between inbreds have been limited. Franklin (1969), for example, from self-pollination studies in loblolly pine (*Pinus taeda*), concluded that the potential of inbreeding for improving that species was limited. His conclusion was based partly on the difficulty and high cost of producing inbred material. Snyder (1968) reached a similar conclusion for slash pine (*Pinus elliottii*). Others have suggested the use of inbreeding and outcrossing of inbreds in forest tree breeding (Matthews and McLean 1957; Barker 1966; Bingham 1973; Andersson *et al*. 1974; Lindgren 1975a, 1975b). Among the advantages of using inbreeding are that it provides a large genetic variance for selection, has a potential for large genetic gains from biclonal and multiclonal seed orchards of S_1 clones with high combining ability, and provides for greater potential gains in species in which phenotypic selection is ineffective (Lindgren 1975a, 1.975b). Disadvantages of inbreeding schemes include the long time required to develop and test inbreds, the generally but not invariably later and poorer seed production of inbred trees, and the relative effectiveness of phenotypic selection in many species which makes the use of F1 material more appealing.

In jack pine (*Pinus banksiana* Lamb.), the disadvantages of inbreeding may be less serious because (1) time between generations can be reduced to as little as 3 years (Rudolph 1966h; Jeffers and Nienstaedt 1972), (2) seed yield and quality in inbreds including self-pollinations have been found to be acceptable for breeding purposes (Rudolph 1966a, 1967), and (3) phenotypic selection for growth rate appears to be ineffective (Canavera 1975). Thus, jack pine appears to be a choice species in which to study inbreeding for improvement.

In this study the objectives were to evaluate the feasibility of producing S_2 families of jack pine by comparing seed production and early seedling development in the S_2 generation with S_1 x S_1 crosses, open-pollinations on the S_1 trees, and open-pollinations on the S_o trees.

MATERIAL AND METHODS

Complete details of the origin of the jack pine seed from which the S_o trees were grown were previously described by Rudolph (1966a, 1966b, 1967). Briefly, the seed was collected in 1950 on the Chippewa National Forest in Minnesota, sown in standard nursery beds in 1951, and the seedlings were field planted on the Argonne Experimental Forest in Wisconsin in the spring of 1954.

Self-pollinations to produce the S_1 generation were made in 1962 and 1963. The S_1 seed was sown in sand in greenhouse benches in March, 1965; the seedlings were potted at 3 months and then field planted directly from the pots near Rhinelander, Wisconsin in July, 1966. Seed yield and quality, segregation for various genetic markers, and other details pertaining to the S_1 generation have been previously described (Rudolph, 1966a, 1967).

All S_1 trees were from different S_o parents except in two instances; two S_1 trees of S parent N-46 and two of S_o parent P-88 were included. Pollinations on the S_1 trees were made in late May and early June, 1974. When possible, 14 isolation bags were placed on each of 29 S_1 trees, but on several trees a lack of female strobili resulted in fewer bags. A single bag on each of 10 trees was included for unpollinated controls. S_1 trees to be pollinated were selected primarily for presence of both male and female strobili. Trees of exceptionally poor growth and form were avoided. Female strobili in half the bags on each S_1 tree were selfed to produce S_2 seed; the other half were pollinated with a mixture of equal amounts of pollen from each of the 29 S1 trees to produce what I will call S_1 x S_1-mix seed. A total of 372 female strobili were self-pollinated and 305 were cross-pollinated. On trees with a limited number of female strobili, preference was given to making self-pollinations. Thus, 5 of the 29 trees had self-pollinations only.

Cone abortion in the controlled pollinations was scored at the end of the growing season following pollination and again at cone maturity. The cones from the controlled pollinations and 5 open-pollinated cones from each S_1 tree were collected in early October, 1975.

The seeds were extracted by removing the cone scales by hand and total seed yields for each lot were determined. Separation of each seedlot into "large" and "small" seed was done with a U.S. Standard No. 18 sieve (1 sq. mm openings). Past experience has shown that only very rarely are seeds passing through this sieve filled. Open-pollinated seed from the S_o trees (parents of the S_1 trees) on the Argonne Experimental Forest was included when available. The S_o tree plots had been previously thinned so seed from some trees was not available for comparison.

All seeds were X-rayed following the procedure previously described for jack pine by Rudolph (1967). The proportion of filled seed was scored on the X-radiographs.

The seed from each lot was placed on moist filter paper in separate petri-dishes to germinate on April 16, 1976. Continuous fluorescent light and room temperature (approximately 22 °C) were provided during germination. The seeds began to germinate within 4 days and a final germination count was taken at 30 days.

As soon as the seed germinated and before the seedcoats were shed, the seedlings were planted into "Jiffy 7" peat pellets in a greenhouse. Ten replications of 4 trees were planted in all lots that had sufficient seedlings. However, seed and seedling yields in some lots were less than the required 40 so not all lots contained all 10 replications. Surplus seedlings in other lots were lined out into bulk plots in greenhouse benches containing peat for replacement of mortality in the replicated design.

Greenhouse temperatures were usually 22° C during the day and 17°C at night, but daytime temperatures occasionally reached 30° C on warm sunny days. A 50% shade screen covered the greenhouse. The seedlings were fertilized with commercial water-soluble 20-10-10 fertilizer as needed to maintain vigorous growth.

Survival and seedling height were measured 10 weeks after sowing and the seedlings were transplanted into nursery beds in late June and early July 1976. The nursery design was the same as in the greenhouse but with a 25 x 25 cm spacing between plants.

In the data analyses, comparisons in cone set were made between the S_1 selfs and S_1 x S_1-mix crosses. Comparisons of total seed yield and yield of filled seed included the S_1 selfs, S_1 x S1-mix crosses, and the Sl open-pollinations. Seed germination and seedling survival and height comparisons were made between and among S_1 self, S_1 x S_1-mix cross, S_1 open-pollination, and S_o open-pollination progenies. The relation between seedling height growth of the various progenies at 10 weeks from sowing to S_1 (parent) tree heights was also determined. It should be noted that comparisons were made only between progeny groups in which seeds and/or seedlings were available in the groups to be compared.

RESULTS AND DISCUSSION

Cone Set

No cones were produced in the 10 unpollinated control isolation bags.

In the S_1 self-pollinations, 31% of the pollinated strobili remained at the end of the growing season following pollination; an average abscissicn and/or abortion rate of 69% (Table 1). In the S_1 x S_1-mix crosses, comparable percentages were 43.5 and 56.5. First year abortion was significantly higher in the S_2 pollinations. Proportion of cones maturing was about 25 and 31% in the S_2 and S_1 x S_1-mix, respectively, but this difference was not statistically significant possibly because more abortion occurred in the S_{11}x S1 -mix crosses during the second year than in the S_1 selfs. A total of 102 cones from 372 pollinated strobili were produced from the S2 pollinations and 101 from 305 in the S1 x S_1-mix pollinations. Whenever available, 5 open-pollinated cones from each of the Sl trees were collected; a total of 87 cones (Table 2).

Table 1.--Number of females pollinated, cone set the first year, and mature cone production on S1 jack pine trees following self-pollination and cross-pollination with other S1 trees

S_1 tree no.	S_1 Selfed (S_2): No. of females pollinated	S_1 Selfed (S_2): Percent of conelets remaining after first season	S_1 Selfed (S_2): Percent of cones matured	S_1 x S_1-Mix: No. of females pollinated	S_1 x S_1-Mix: Percent of conelets remaining after first season	S_1 x S_1-Mix: Percent of cones matured
N2	28	46.4	25.0	16	68.8	56.2
N12	6	33.3	33.3	--[a]	--	--
N15	3	0.0	0.0	--	--	--
N23	11	45.5	45.5	9	11.1	0.0
N36	17	39.3	29.4	17	76.5	76.5
N40	5	0.0	0.0	5	60.0	60.0
N46-1	14	42.9	28.6	18	55.6	38.9
N46-2	10	50.0	50.0	--	--	—
N53	12	0.0	0.0	14	21.4	14.3
N78	35	8.3	0.0	16	75.0	6.2
N82	12	50.0	33.3	8	50.0	50.0
S16	7	0.0	0.0	3	0.0	0.0
S41	11	36.4	36.4	--	--	--
S42	8	75.0	62.5	9	77.8	55.6
S46	6	16.7	0.0	--	--	--
S75	10	60.0	40.0	11	81.8	27.3
S91	4	50.0	50.0	5	80.0	60.0
S100	7	42.9	42.9	6	50.0	50.0
P14	14	7.1	7.1	8	0.0	0.0
P43	21	0.0	0.0	10	0.0	0.0
P49	8	62.5	25.0	12	75.0	66.7
P62	11	18.2	18.2	7	0.0	0.0
P87	8	12.5	12.5	10	60.0	40.0
P88-1	20	60.0	50.0	31	38.7	38.7
P88-2	10	30.0	20.0	15	33.3	20.0
P90	10	20.0	20.0	13	23.1	15.4
P91	16	12.5	12.5	18	11.1	5.6
P92	41	80.5	73.2	30	66.7	60.0
P100	7	0.0	0.0	14	28.6	0.0
Total	372			305		
Mean		31.0[b]	24.7		43.5	30.9
SE		±4.50	±3.87		±5.88	±5.22

a/ No pollinations made.

b/ Comparison by "t" test indicates significant difference at 5% level from S_1 x S_1.

Table 2.--Total and filled seed yields per cone in S_1 self, S_1 x S_1 cross, and S_1 open-pollinated jack pine

S_1 tree no.	S_1 Selfed (S_2) No. of cones	Total seeds per cone	Filled seeds per cone	S_1 x S_1-Mix No. of cones	Total seeds per cone	Filled seeds per cone	S_1 Open Pollinated No. of cones	Total seeds per cone	Filled seeds per cone
N2	7	39.6	0.1	9	52.7	37.2	5	65.2	50.6
N12	2	34.0	12.0	--a/	--	--	5	38.4	18.6
N15	0	--	--	--	--	--	0	--	--
N23	5	28.2	15.2	0	--	--	5	54.4	35.0
N36	5	47.2	24.4	13	42.5	23.6	5	55.2	39.6
N40	0	--	--	3	73.0	0.0	5	60.0	0.0
N46-1	4	70.0	16.2	7	55.7	30.3	3	62.3	38.0
N46-2	5	28.6	1.8	--	--	--	1	3.0	1.0
N53	0	--	--	2	44.0	13.0	5	12.6	4.2
N78	0	--	--	1	66.0	0.0	5	45.0	0.0
N82	4	49.0	20.5	4	40.8	31.3	1	39.0	25.0
S16	0	--	--	0	--	--	0	--	--
S41	4	1.8	0.0	--	--	--	0	--	--
S42	5	40.6	13.8	5	45.6	33.0	5	48.2	37.4
S46	0	--	--	--	--	--	0	--	--
S75	4	64.5	1.0	3	35.3	18.7	1	45.0	23.0
S91	2	19.0	7.0	3	15.7	11.7	5	54.2	39.0
S100	3	9.3	0.5	3	21.3	14.7	0	--	--
P14	1	55.0	5.0	0	--	--	0	--	--
P43	0	--	--	0	--	--	5	42.0	16.8
P49	2	46.0	12.5	8	35.9	16.2	5	45.0	29.8
P62	2	58.0	7.5	0	--	--	5	61.0	26.0
P87	1	23.0	2.0	4	35.8	20.8	2	17.5	11.0
P88-1	10	69.5	32.8	12	41.2	32.9	5	75.0	49.0
P88-2	2	40.0	0.5	3	49.7	31.3	2	21.0	21.0
P90	2	29.0	0.5	2	38.0	14.0	2	46.5	16.5
P91	2	37.0	2.5	1	24.0	10.0	5	20.8	8.2
P92	30	51.3	12.0	18	46.3	29.8	5	60.4	35.4
P100	0	--	--	0			0		
Total	102			101			87		
Mean		40.0	8.9b/		42.4	20.5		44.2	23.9
SE		±4.02	±1.96		±3.39	±2.60		±4.00	±3.32

--a/ No pollinations made

b/ Comparison by "t" test indicates significant difference at 1% level from S_1 x S_1 and S_1 open-pollination.

The proportion of pollinated cones remaining after the first season in the S2 and S1 x S_1-mix pollinations was positively correlated (r = 0.592). Also, as could be expected, the proportion of pollinated cones remaining after the first season was highly positively correlated with the proportion reaching maturity in both the S_2 (r = 0.874) and S_1 x S_1-mix pollinations (r = 0.691) although additional cone abortion occurred in the second year. The percent of pollinated strobili reaching cone maturity showed a positive correlation between the S1 self- and Sl x S_1-mix pollinations (Figure 1). Those relations suggest that pollination failures (e.g. due to differences in time of optimum receptivity among female strobili) may be partially responsible for the cone abortions.

Eight of the 29 S_1 trees produced no mature cones following self-pollination (Table 1). In the S_1 x S_1 controlled crosses, 6 of 24 S1 trees or a similar proportion produced no cones. Only 3 S_1 trees (S16, P43, and P100) on which both S_1 self- and S_1 x S1-mix pollinations were made produced no cones from either type of pollination. In other words, some trees produced cones from S1 self-pollinations but not from S x S crosses and vice versa. One would expect that S1 trees producing no cones after cross-pollination with a mixture of S1 pollen would be even less likely to produce cones after self-pollination when pollinated at the same time, but this is apparently not always true. A complete explanation of this result is not possible from the present study but it could be at least partially due to within-tree differences in flowering phenology and female receptivity. Additional, more detailed pollinations would be required to verify this.

Seven of the 29S_1 trees produced no open-pollinated cones. Of these 7, 4 (N15, S16, S46, and P100) also produced no cones from the controlled pollinations. Because all of these trees produced female strobili and an abundant wind-carried pollen supply is available in the planting, it is possible that such trees are reproductively sterile, with failure occurring sometime after pollination. Controlled pollinations for several years would be required to rule out seasonal or other possible environmental effects on cone development in specific genotypes.

<u>Seed Yield</u>

Total seed yield per cone varied from 40.0 in the S self- to 44.2 in the S_1 open-pollinations; the difference was not significant (Table 2). A significant positive correlation for total seed yield per cone occurred between the S_2 and S_1 x S_1-mix groups (Figure 2).

Sifting the seed through a U.S. Standard No. 18 sieve (1 sq. mm openings) showed no significant difference between types of pollinations in the proportion of total seed that was large; approximately three-fourths of the seed in all lots was large (Table 3). However, only one-fourth of the large seed was filled in the S_2 lots as compared to two-thirds in the S1 x S1-mix crosses and S_1 open-pollinations, and more than four-fifths in the S_o open-pollinations. Average number of filled seeds per cone was about 9 in the S_2 pollinations or less than one-half that in the S_1 x S_1-mix and S_1 open-pollinations (Table 2) and represents inbreeding depression for this factor of about 63% when the S_2 is compared to S_1 x S_1-mix and S_1 open-pollinations. The correlation of filled seeds per cone was not significant

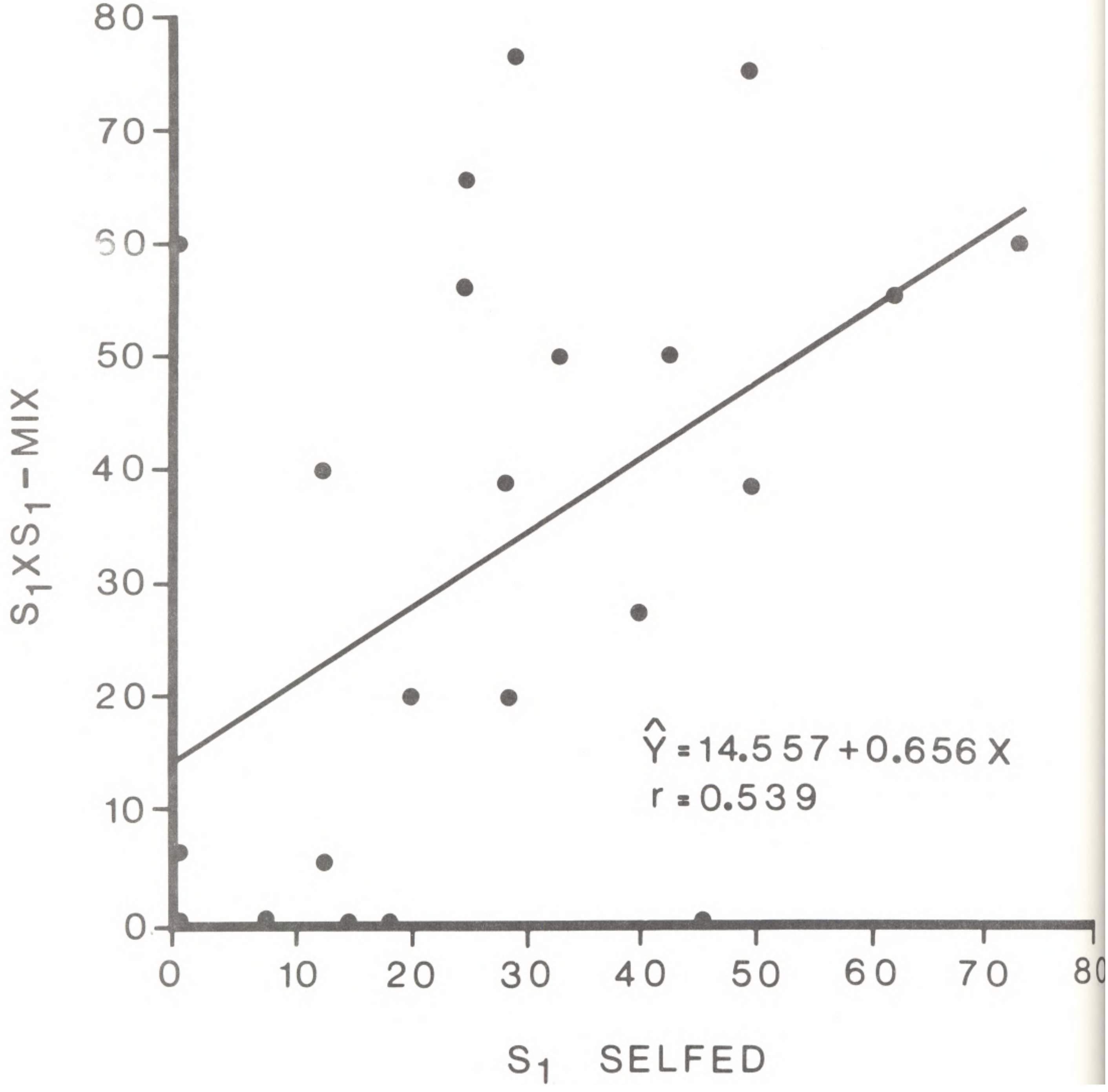

Figure 1.--Relation between S_1 x S_1-mix crosses and S_1 self-pollinations in percent of conelets maturing.

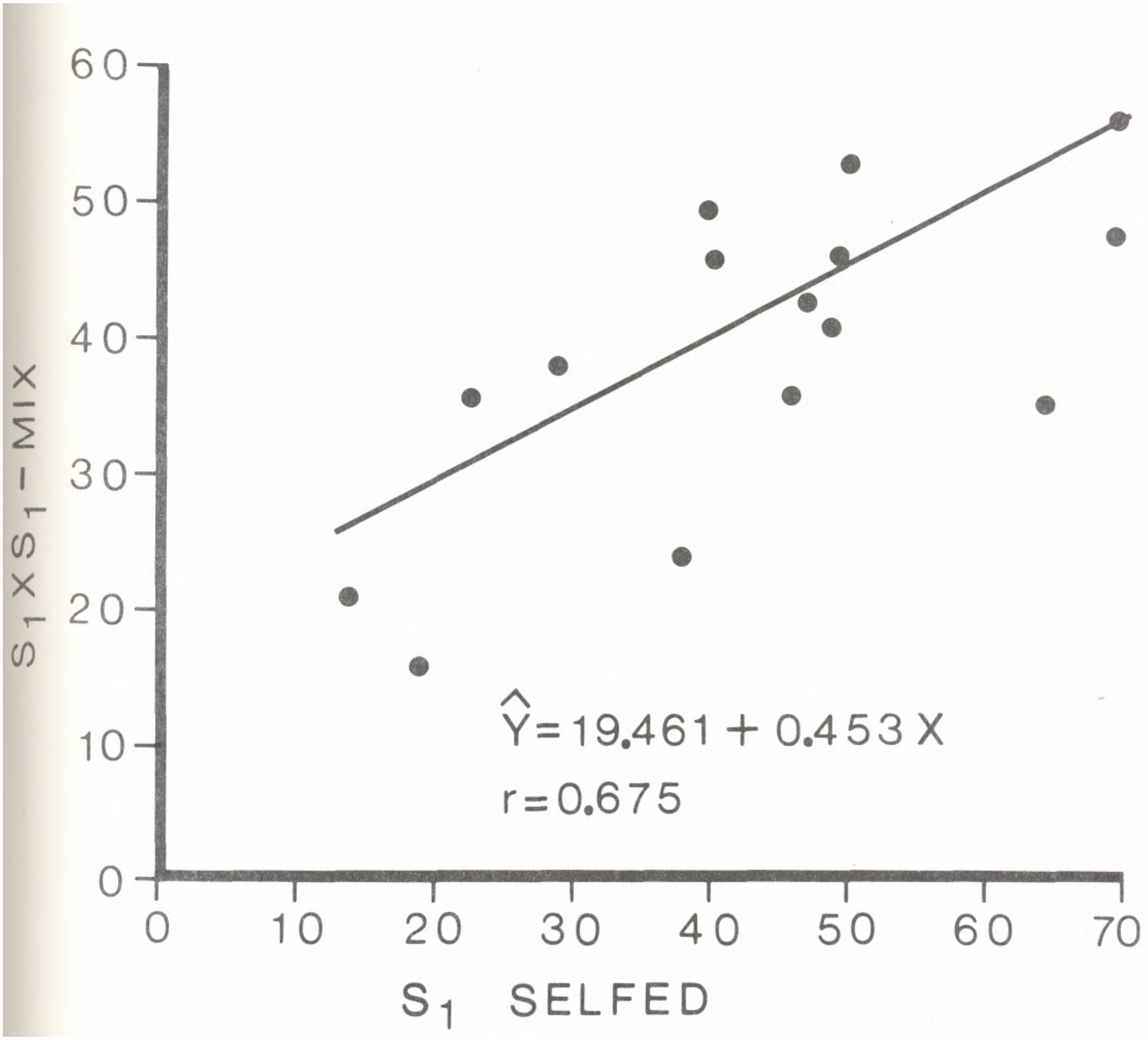

Figure 2.--Relation between S_1 x S_1-mix crosses and S1 self-pollinations in number of seeds per cone.

Table 3.--Percent of total seed that is large, percent filled, germination and seedling production per cone

S_1 Tree no.	S_1 Selfed (S_2): Percent of total seed large	S_1 Selfed (S_2): Percent of large seed filled	S_1 Selfed (S_2): Percent of large seed germ.	S_1 Selfed (S_2): No. of seedlings per cone	S_1 x S_1-Mix: Percent of total seed large	S_1 x S_1-Mix: Percent of large seed filled	S_1 x S_1-Mix: Percent of large seed germ.	S_1 x S_1-Mix: No. of seedlings per cone	S_1 Open-pollinated: Percent of total seed large	S_1 Open-pollinated: Percent of large seed filled	S_1 Open-pollinated: Percent of large seed germ.	S_1 Open-pollinated: No. of seedlings per cone	S_0 Open-pollinated[b]: Percent of large seed filled	S_0 Open-pollinated[b]: Percent of large seed germ.
N2	72.9	0.5	0.0	0.0	79.5	88.9	84.9	35.6	85.9	90.4	88.9	49.8	87.0	76.0
N12	85.3	41.4	37.9	11.0	--	--	--	--	80.7	60.0	60.0	18.6	88.0	41.0
N15	--[a]	--	--	--	--	--	--	--	--	--	--	--	--	--
N23	91.5	58.9	57.4	14.8	--	--	--	--	86.0	74.8	74.8	35.0	79.0	79.0
N36	83.5	61.9	61.4	24.2	63.3	87.7	86.9	23.4	78.3	91.7	90.7	39.2	--	--
N40	--	--	--	--	2.7	0.0	0.0	0.0	--	--	--	--	--	--
N46-1	68.6	33.8	32.8	15.8	72.8	74.6	68.7	27.9	70.0	87.0	80.9	35.3	93.0	90.0
N46-2	60.1	10.5	10.5	1.8	--	--	--	--	100.0	33.3	33.3	1.0	93.0	90.0
N53	--	--	--	--	84.1	35.1	29.7	11.0	41.3	80.8	73.1	3.8	92.0	86.0
N78	--	--	--	--	3.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	--	--
N82	91.3	45.8	45.2	20.2	85.9	89.3	86.4	30.2	87.2	73.5	70.6	24.0	89.0	86.0
S16	--	--	--	--	--	--	--	--	--	--	--	--	--	--
S41	57.1	0.0	0.0	0.0	--	--	--	--	--	--	--	--	--	--
S42	86.7	39.2	35.8	12.6	82.5	87.8	86.7	32.6	86.7	89.5	89.5	37.4	74.0	9.0
S46	--	--	--	--	--	--	--	--	--	--	--	--	--	--
S75	72.1	2.2	2.2	1.0	71.7	73.7	69.7	17.7	71.1	71.9	66.7	20.0	72.0	69.0
S91	92.1	40.0	40.0	7.0	89.3	83.3	69.0	9.7	87.8	81.9	81.9	32.0	72.0	68.0
S100	67.9	5.3	5.3	0.3	79.7	86.3	84.3	14.3	--	--	--	--	62.0	35.0
P14	100.0	9.1	9.1	5.0	--	--	--	--	--	--	--	--	76.0	50.0
P43	--	--	--	--	--	--	--	--	71.9	55.6	55.6	16.8	94.0	75.0
P49	63.0	43.1	43.1	12.5	82.2	55.1	54.2	16.0	80.9	81.9	81.9	29.8	91.0	81.0
P62	63.8	20.3	20.3	7.5	--	--	--	--	60.7	70.3	69.2	25.6	88.0	14.0
P87	100.0	8.7	8.7	2.0	95.1	61.0	61.0	20.8	91.4	68.8	65.6	10.5	73.0	72.0
P88-1	91.4	51.6	51.6	32.8	85.2	86.0	85.8	30.1	82.1	79.6	78.2	48.2	89.0	0.0
P88-2	62.5	2.0	2.0	0.5	79.9	79.0	75.6	30.0	57.5	91.3	87.0	10.0	89.0	0.0
P90	81.0	2.1	2.1	0.5	82.9	44.4	44.4	14.0	87.1	40.7	40.7	16.5	96.0	67.0
P91	23.0	29.4	17.6	1.5	83.3	50.0	45.0	9.0	85.6	46.1	28.1	5.0	85.0	43.0
P92	73.9	32.7	32.2	11.8	73.0	88.2	85.0	28.7	82.4	71.9	71.9	35.8	--	--
P100	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Mean	75.6	25.6[c]	24.5[c]	8.7[d]	72.0	65.0[e]	62.1	19.5	75.0	68.6[e]	66.1	23.5	84.1	56.6
S.E.	±3.83	±4.46	±4.38	±1.94	±5.99	±6.67	±6.50	±2.52	±4.59	±4.88	±4.96	±3.21	±2.07	±6.68

a/ Indicates no seed available.

b/ 100 S_0 seed were taken from stored seedlots that had previously been size-graded. Therefore data on total seed and seedlings per cone is not available.

c/ Comparison by "t" test indicates significant difference at 1% level from S_1 x S_1, S_1 O.P., and S_0 O. P.

d/ Comparison by "t" test indicates significant difference at 1% level from S_1 x S_1 and S_1 O.P.

e/ Comparison by "t" test indicates significant difference at 1% level from S_0 O.P.

between the S_2 and S_1 x S_1-mix groups (r = 0.413) from the same S_1 trees, but that for the S1 x S_1-mix and S_1 open-pollinations was highly positively correlated (Figure 3). The S_2 filled seed yield per cone is very similar to that obtained in controlled self-pollinations on the S_o trees to produce the S_1 trees for this study (Rudolph 1967).

Of the 290 cones from the 29 S_1 trees included in this study, 31 (10.7%) from 10 trees contained no filled seeds. Within pollination types 16% of the cones in the S_2 groups, 5% in the S_1 x S_1-mix crosses, and 11% in the S_1 open pollinations had no filled seeds. In many thousands of controlled pollinations of jack pine in the past, we have not observed cones without any filled seeds. The general assumption has been that if fertilization was completely absent within a developing cone, it would abort. In the present case, because cone development was normal, and large, normal-appearing but empty seeds were produced, it is likely that at least some fertilization occurred in such cones. Subsequent embryo abortion was probably due to lethal recessive genes in the inbred genotypes as discussed by Hadders and Koski (1975). Cytological and anatomical studies following pollination and through the time of fertilization and embryo development would be required to quantify the decrease or complete failure of filled seed production resulting from incompatibility or lack of fertilization as contrasted to that resulting from embryo abortion. Such an analysis in *Pinus sylvestris* L. by Forshell (1974) showed that most empty seeds following self-pollination resulted from embryo abortion.

Seed Germination and Early Seedling Survival

Germination of filled seed was high, therefore, large seed germination percent was similar to percent of large seed filled (Table 3) and was again significantly lower for the S_2 seed.

A more complete measure of the effects of inbreeding depression on seed yield and viability is the number of seedlings produced per cone. In the S2 pollinations an average of only 8.7 seedlings per cone were produced compared to 19.5 and 23.5 in the S_1 x S_1-mix and S_1 open-pollinated groups, respectively (Table 3). The S2 seedling yield is significantly lower than the other 2 groups at the 1% level and gives an inbreeding depression value similar to that for filled seeds per cone. Wide variation in seedling yield per cone was present among S trees ranging from 0 to 50 and suggesting genotypic differences in selfability and in inbreeding depression measured in terms of viable seed production.

Seedling survival scored at 10 weeks after relatively favorable germination and greenhouse growing conditions was high in all seedlots ranging from an average of 81% in the S_2 seedlot to 93.5% in the S_1 open-pollinated lot. The differences between pollination groups were not significant. Thus, under the near-optimum conditions provided, inbreeding depression, expressed as early seedling mortality, does not appear to be a significant factor in the S_2 generation. However, testing of the seedlots under commercial nursery conditions with additional environmental stresses would probably result in greater differentiation between pollination types and manifestation of more severe inbreeding depression expressed as reduced survival in the S_2 generation.

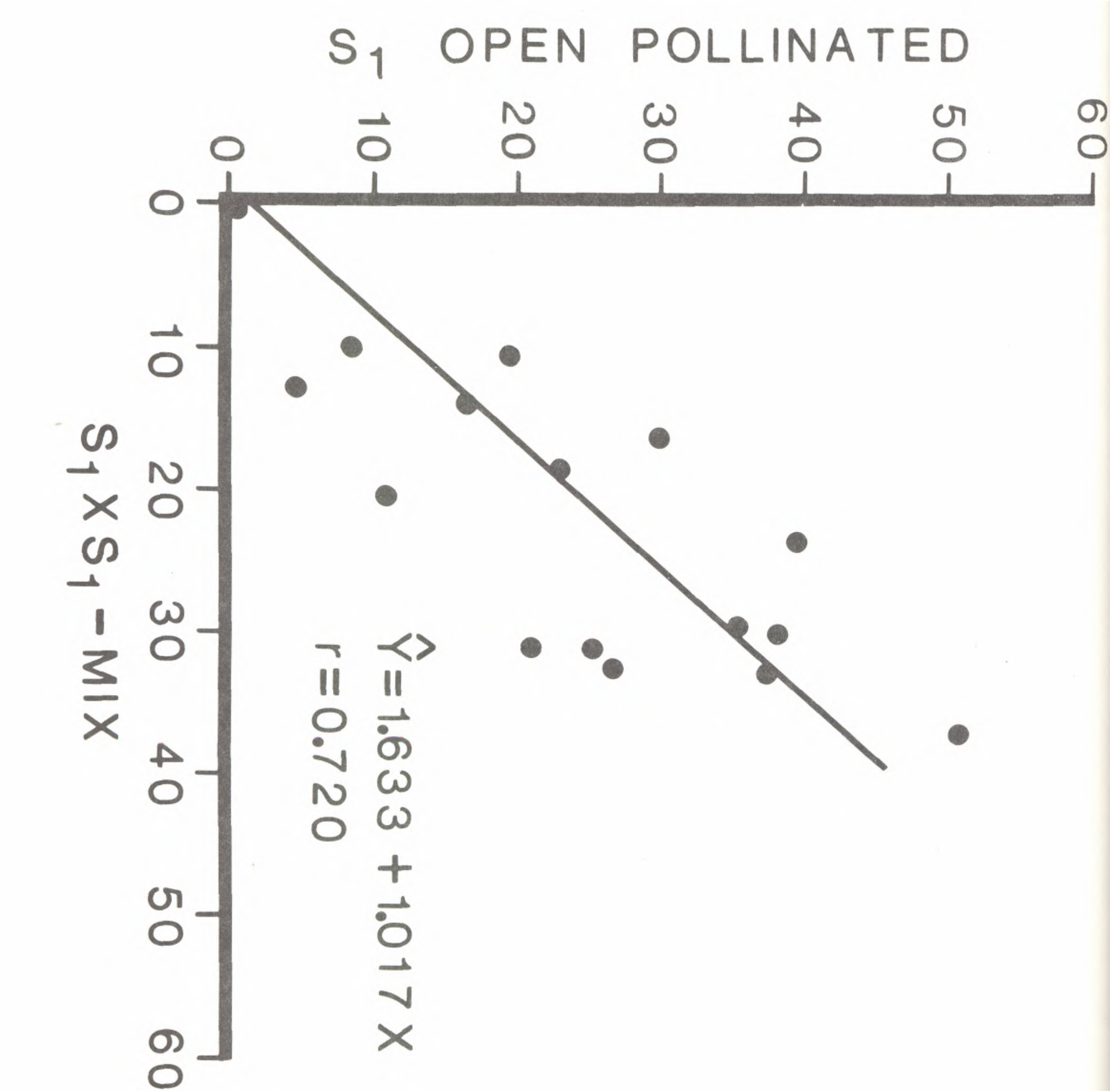

Figure 3.--Relation between S_1 open-pollinations and S_1 x S_1-mix crosses in number of filled seeds per cone.

Seedling Heights

Height of the S_2 seedlings at 10 weeks was significantly less at the 1% level from that of the S_1 x S_1-mix, S_1 open-pollinated, and S_o open-pollinated groups (Table 4). Average height of the S_2 seedlings was 14.2 cm as compared to an average of 16.9 cm for the tallest S1 open-pollinated group or an inbreeding depression of about 15% in the S2 seedlings compared to the S_1 open-pollinations. Height of the S_1 x S_1, and S1 open-pollinated seedlings was not significantly different from the S_o open-pollinated seedlings, which indicates that on the average no inbreeding depression for height was evident at this age in cross-pollinated progenies from inbred lines.

Variation in seedling height, as indicated by coefficients of variation (Table 4), was wide both within and among progenies. This suggests some possibilities for selection among and within inbred families for future breeding involving additional inbreeding and outcrossing of inbred lines. Noteworthy is that the S_2 progeny of S_1 tree number N46-2 was the tallest of all progenies in the study.

Some possible positive trends relating S2, S_1 x S_1-mix, and S_1 open-pollinated seedling progeny height to S1 parent height were evident, but none of the correlations were statistically significant at this young seedling age. It is possible that these relations will become more definitive as the seedling progenies continue to develop under nursery and field conditions and temporary differences such as may be related to seed size become less influential factors. However, it must be pointed out that no selection for height was made within the S_1 families containing the trees used in this study.

Seedling height of the S_2 progenies at 10 weeks was highly positively correlated with that of S_1 x S_1 progenies from the same S_1 trees (Figure 4). Thus, S_1 parents that produce the tallest seedlings upon crossing with other inbreds, on the average, also produce taller seedlings in the S2 generation. This suggests that general combining ability can be evaluated by comparing the performance of inbred progenies and that S_1 genotypes showing the best general combining ability in crosses with other inbreds may also produce less inbreeding depression with additional selfing. Such a relation, if it persists, indicates that selection for growth will be feasible in inbred lines of jack pine for crosses between inbreds in improvement breeding.

In jack pine, which has a relatively short time between generations, selection among inbreds need not be restricted to the S1 or S2 generations as suggested by Lindgren (1975a, 1975b). Instead, it could be continued into later selfed generations where homozygosity in the inbreds would be increased and the potential for greater hybrid vigor in crosses between the inbreds improved. A decrease in viable seed yield may be expected following inbreeding because of the accumulation of homozygous recessive lethal genes as was found in this study and by others (e.g., Forshell 1974; Hadders and Koski 1975; Lindgren 1975a, 1975b), but the decrease would not preclude an inbreeding program although some potential progenies may be lost. However, with continued selfing, most lethal genes would he eliminated so that high yields of viable seeds would be expected following crosses between such inbred lines and in double-crosses.

Table 4.--Seedling survival at 10 years

S_1 tree no.	S_1 Selfed (S_2) Percent Survival	S_1 x S_1-Mix Percent Survival	S_1 O.P. Percent Survival	S_o O.P. Percent Survival
N2	--[a/]	96.2	94.8	89.5
N12	100.0	--	92.5	100.0
N15	--	--	--	--
N23	91.9	--	79.4	89.9
N36	88.4	90.8	91.8	--
N40	--	--	--	--
N46-1	84.1	97.4	99.1	44.4
N46-2	77.8	--	100.0	44.4
N53	--	95.4	94.7	97.7
N70	--	--	--	--
N82	93.8	100.0	100.0	97.7
S16	--	--	--	--
S41	--	--	--	--
S42	66.7	11.7[b/]	18.7[b/]	100.0
S46	--	--	--	--
S75	100.0	92.4	75.0	84.1
S91	100.0	93.1	97.4	89.7
S100	--	48.8	--	94.3
P14	20.0	--	--	90.0
P43	--	--	89.3	92.0
P49	92.0	95.3	97.3	86.4
P62	86.7	--	92.2	100.0
P87	0.0	97.6	95.2	94.4
P88-1	86.6	39.9	90.5	--
P88-2	100.0	96.7	100.0	--
P90	100.0	100.0	93.9	67.2
P91	100.0	88.9	100.0	96.0
P92	70.1	68.1	3.35[b/]	--
P100	--	--	--	--
Mean	81.0	86.7	93.5	86.5
S.E.	±6.4	±4.7	±1.6	±3.9

a/ Indicates no seed and/or seedlings available.

b/ Seedlots were infected with a fungus that caused high mortality after germination so were not included in the mean.

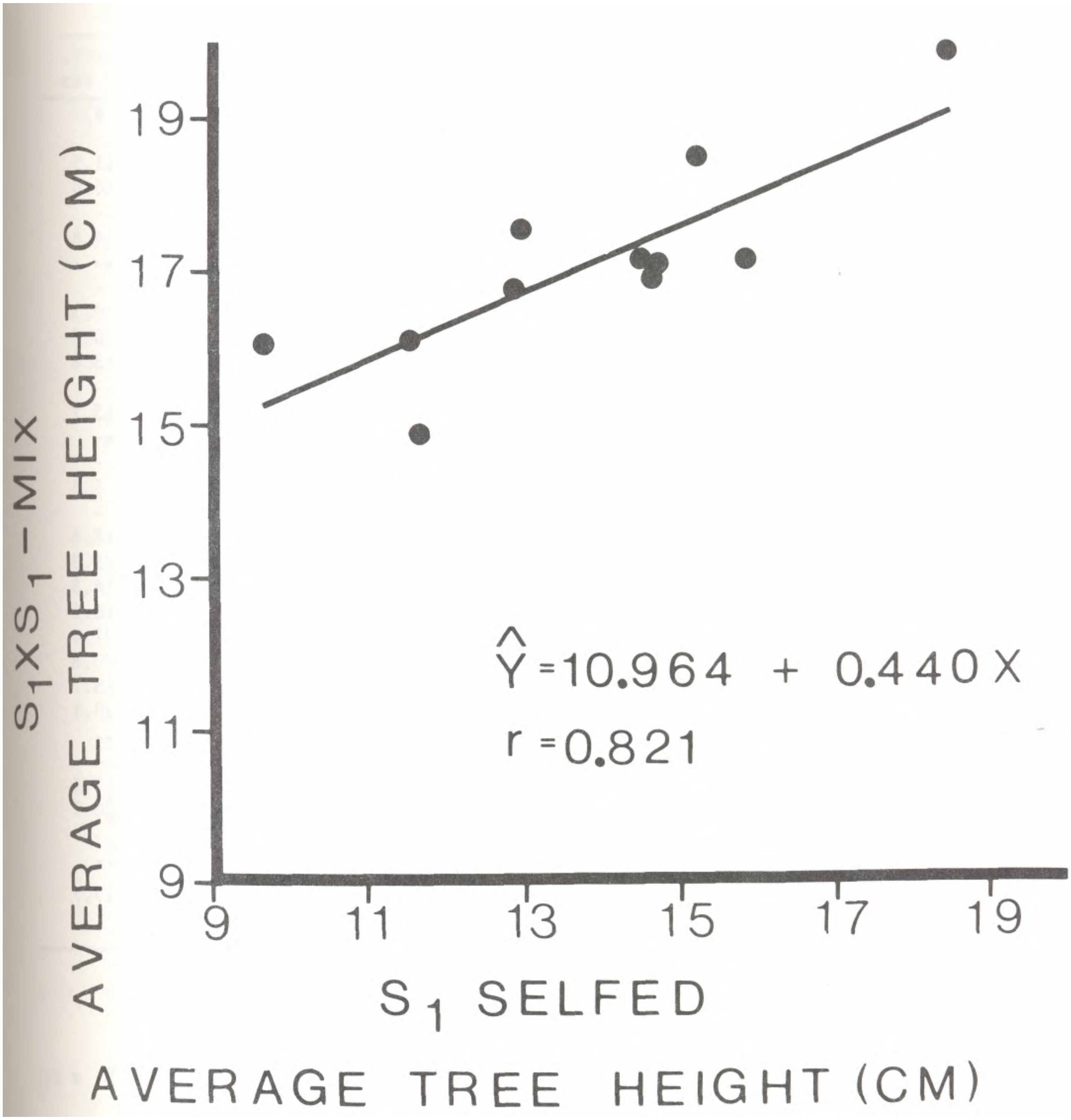

Figure 4 --Relation between S1 x S1-mix crosses and S1 self-pollinations in seedling heights at 10 weeks.

Table 5.--S_1 parent tree height at 11 years from seed and seedling height at 10 weeks of S1 self (S2), S1 x S1-mix, S1 open-pollinated, and S_o open-pollinated progenies

S_1 tree no.	S_1 parent tree ht.	S_1 Selfed (S_2) Ave. height	S_1 Selfed (S_2) Coeff. of var.	S_1 x S_1-mix Ave. height	S_1 x S_1-mix Coeff. of var.	S_1 O.P. Ave. height	S_1 O.P. Coeff. of var.	S_o O.P. Ave. height	S_o O.P. Coeff. of var.
	(m)	(cm)	(%)	(cm)	(%)	(cm)	(%)	(cm)	(%)
N2	4.45	-- a/	--	18.0	11.7	17.1	15.8	17.6	11.5
N12	5.47	16.0	23.0	--	--	18.2	17.0	15.3	16.0
N15	3.10	--	--	--	--	--	--	--	--
N23	5.85	13.9	25.8	--	--	16.8	18.8	16.1	14.8
N36	6.35	15.3	25.9	18.5	20.3	18.4	18.3	--	--
N40	5.00	--	--	--	--	--	--	--	--
N46-1	4.12	12.9	24.7	16.8	16.2	14.8	22.3	16.6	20.3
N46-2	3.97	20.1	3.5	--	--	16.5	0.0 b/	17.1	20.4
N53	4.14	--	--	16.2	13.6	16.6	11.3	14.9	13.8
N78	4.70	--	--	--	--	--	--	--	--
N82	5.32	14.5	19.8	17.1	15.8	15.6	21.1	18.4	13.7
S16	3.77	--	--	--	--	--	--	--	--
S41	4.18	--	--	--	--	--	--	--	--
S42	4.97	13.9	32.0	7.3	84.4 c/	13.9	27.4	18.3	5.6
S46	4.87	--	--	--	--	--	--	--	--
S75	5.85	14.6	13.7	16.9	16.9	17.2	8.8	17.3	18.3
S91	3.02	15.9	16.0	17.1	17.7	17.5	18.4	15.1	29.3
S100	4.05	--	--	15.5	44.4	--	--	16.4	14.3
P14	5.32	12.7	16.9	--	--	--	--	17.0	18.2
P43	4.51	--	--	--	--	19.4	13.0	13.2	21.4
P49	6.68	18.5	18.7	19.8	11.5	18.4	17.0	16.1	20.8
P62	4.45	12.4	27.8	--	--	15.2	17.4	17.1	15.7
P87	4.67	--	--	15.1	25.8	17.6	19.3	15.2	20.1
P88-1	4.93	14.8	15.9	17.1	12.8	17.4	15.8	--	--
P88-2	4.12	11.7	0.0 b/	16.1	27.1	19.1	8.9	--	--
P90	4.20	13.0	0.0 b/	17.5	12.9	17.2	13.4	14.7	17.5
P91	3.77	9.7	8.8	16.1	13.0	14.0	26.4	14.8	26.7
P92	5.37	11.7	21.2	14.8	24.6	3.3	85.8 c/	--	--
P100	3.40	--	--	--	--	--	--	--	--
Mean	4.64	14.2 d/	19.6	16.8	19.0	16.9	17.2	16.2	17.7
S.E.	±0.16	±0.60		±0.33		±0.35		±0.32	

a/ No seedlings available.

b/ Single tree.

c/ Trees were attacked by fungi so were not included in the mean.

d/ Comparison by "t" test indicates significant difference at 1% level from S_1 x S_1, S_1 O.P. and S_o O.P.

The possibility of using selected inbred clones in biclonal or multiclonal seed orchards needs to be considered. If high yields of viable seed and hybrid vigor can be expected following crosses between inbreds, then production of further inbreds in such orchards would be minimal and the reduced vigor of the small proportion of inbred seedlings that would be produced should permit simple culling. On the other hand, selection for high combining ability and vigor in the inbred lines should result in large potential genetic gains following outcrossing in the clonal seed orchards.

In discussing the potential use of inbreeding in improvement breeding and orchard seed production based on the results of this study, it must be recognized that the information is from young progenies. Evaluating the progenies as they develop and testing them under field conditions will be necessary to verify the early results. Crosses between selected S_2 parents in this study should be possible within a few years to help further evaluate the potential use of inbreeding in the improvement of jack pine.

SUMMARY AND CONCLUSIONS

Cone set, seed yield, and seed quality were analyzed from self-pollinations (S_2) on 29 S_1 trees and from S_1 x S_1-mix crosses on 24 of the same S_1 trees. Open-pollinated seed yield and quality from the same S_1 trees was also analyzed. Early performance of the progenies from the S_1 self-pollinations, S_1 x S_1-mix crosses, S_1 open-pollinations, and S_0 open-pollinations was compared.

The percent of pollinated strobili maturing into cones did not differ between the S_1 self-pollinations and the S_1 x S_1-mix crosses. Most of the cone abortion occurred the first year. Some flowering trees produced no cones either from open- or controlled-pollinations which suggests reproductive sterility in some S_1 trees.

More than 10% of the cones had no filled seeds. Total seed yield per cone did not differ between S self-, S_1 x S_1-mix and S open-pollinations but yield of filled seed in the S_1 selfs was less than half that in the other two groups. Yield of filled seed per cone was not significantly correlated between S_1 self- and S_1 x S_1-mix and S_1 open-pollinations. Inbreeding depression for yield of filled seeds per cone was about 63% in the S_1 self-compared to S_1 x S_1-mix and S_1 open-pollinations. Germination of filled seed was high and survival at 10 weeks was similar in all lots. Inbreeding depression, measured as number of seedlings produced per cone, was about the same as for filled seeds per cone.

Inbreeding depression in seedling height of the S_2 progenies at 10 weeks averaged 15% compared to S_1 x S_1-mix and S_1 open-pollinated progenies. Correlations relating progeny heights at 10 weeks to S parent height at 11 years were not significant. A strong correlation between S_2 and S_1 x S_1-mix progenies in seedling height plus wide within and among progeny variation indicates that selection for growth in inbred lines will be possible in jack pine for improvement breeding, particularly for production of seed from crosses in orchards of inbred clones.

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