INBREEDING DEPRESSION IN EASTERN WHITE PINE

H. B. Kriebel 1/

Abstract.--Inbreeding depression was measured in 3 progeny tests of eastern white pine derived from crosses in a native stand. Nine Si progenies were compared with outcross progenies from the same trees. Values for progenies of individual trees, based on all check crosses, varied from -.12 to -.44, and for locations from -.15 to -.38. More precise comparisons, based on check crosses of several females with the same males, indicated that (1) an estimate based on an open-pollinated check progeny sometimes differed widely from an estimate based on a group of outcross means; (2) individual trees usually did not vary widely in inbreeding depression within experiments; (3) there was a large effect of planting site on inbreeding depression.

Additional keywords: Inbreeding, selfing, white pine, *Pinus strobus*.

Estimates of inbreeding depression in pines have varied from 0 to 39% depending on both the species and the families involved (Franklin 1970). Inbreeding depression is relative, not absolute, based on mean performance of one or more progenies from selfing in comparison with mean performance of control- or open-pollinated cross progenies from the same female parent or parents. Data are usually limited and the accuracy of estimates is, therefore, generally low.

Most published estimates have been made on nursery-age trees. In eastern white pine (*Pinus strobus* L.), a 14% reduction in height at age 1 and a 22% reduction at age 4 were reported by Fowler (1965) and Johnson (1945) respectively. Both of these estimates were based on one Si progeny.

Three progeny tests of eastern white pine in Ohio include some families obtained from selfing in addition to outcrosses and open-pollinated material. All progenies came from parents in a small natural old-field stand occupying about 2 hectares (5 acres) in northern Ohio near the western range limits of the species. The stand is surrounded by a predominantly hardwood forest. Its probable parents are a group of about 8 nearby old trees. A moderate level of inbreeding is therefore assumed in the parents of the progenies in the experiments.

Of the 3 progeny tests, two (AC-14 and AC-15) are side by side with similar site and environmental conditions. The third (AC-18) is 3 kilometers away and has site conditions similar to the others except for better soil drainage. All three are randomized block experiments including 40 to 50 families.

1/ Professor, Department of Forestry, Ohio Agricultural Research and Development Center, Wooster, Ohio 44691.

METHODS

Total height was measured at age 5 in Experiment AC-15, at age 6 in AC-14 and AC-18, and at age 10 in AC-14. Numbers of families and of trees per family are shown in Table 1.

Inbreeding depression of a tree was calculated from progeny means by the formula:

$$I.D. = \frac{\bar{x}_o - \bar{x}_s}{\bar{x}_o}$$

where x_o is the mean of one or more outcross progeny means for the female tree and x_s is the mean of the progeny derived from selfing.

An overall estimate of inbreeding depression was obtained for each of the 3 experiments at the ages indicated, based on all outcross family means. Estimates for individual female parents were then averaged within experiments.

More precise estimates of inbreeding depression included (1) comparative estimates from control-pollinated versus open-pollinated check progenies, (2) estimates for trees with the same group of male parents in check crosses, (3) a small test of progeny location effect provided by 2 separate S1 progenies of one tree, each with the same 2 males in the check crosses and (4) comparative estimates in one experiment at ages 6 and 10.

RESULTS

Average inbreeding depression for each female parent and means for the 3 experiments are shown in Table 1.

A comparison of estimates of inbreeding depression derived from controlled- and open-pollination is shown in Table 2. Overall, there was no difference in mean height of control- and open-pollinated progenies and thus in inbreeding depression. For some females, however, there was wide variation in mean height between progenies from the two types of cross-pollination, hence two widely divergent estimates of inbreeding effect were obtained.

Tables 3 and 4 indicate that both male and female parent had an effect on progeny height. Elimination of the male effect by using progenies from the same males gave a large difference in inbreeding depression between the two AC-15 S1 progenies but not among the 4 AC-18 progenies. The outcross means in Table 4 include fewer females than in Table 3 but are based on 4 males instead of 2. They therefore provide better estimates of general outcross performance and hence of inbreeding depression than the lower values for the same 3 trees in Table 3 (b).

Table 1.--Data base and estimates of inbreeding depression (I.D.) 1/ using all check progenies

Location and (Experiment Number)	♀ Tree No.	No. of outcross pollinated families2/	Mean no. of trees per outcross family	No. of trees in selfed family	I.D. age 5-6	I.D. age 10
1	1278	7	28	6	-.18	--
(AC-15)	1280	3	29	20	-.12	--
					$\bar{x}$ = -.15	--
1	689	1	36	36	-.18	-.15
(AC-14)	691	2	35	20	-.15	-.12
	1254	4	38	35	-.30	-.23
					$\bar{x}$ = -.21	-.17
2	683	4	28	8	-.30	--
(AC-18)	1256	5	24	32	-.44	--
	1278	9	36	6	-.42	--
	1281	9	33	24	-.37	--
					$\bar{x}$ = -.38	--

1/ I.D. = proportionate reduction in mean height relative to outcross mean height, in this and succeeding tables (see text).

2/ Includes an open-pollinated family in AC-14 and AC-18.

Table 2.--Comparison of estimates of inbreeding depression at age 6 based on controlled- and open pollination.

♀ Tree No.	Mean Progeny Height (cm) and Inbreeding Depression (I.D.)				
	$\bar{x}$ Control-pollinated progenies	$\bar{x}$ Open-pollinated progeny	$\bar{x}$ For S_1 progeny	I.D. based on cont.-poll. families	I.D. based on open-poll. families
683	24.5	25.2	17.4	-.29	-.31
691	43.6	36.2	33.5	-.23	-.07
1254	36.9	47.2	27.7	-.25	-.41
1256	24.7	20.8	13.4	-.46	-.36
1278	20.7	20.6	12.1	-.42	-.41
1281	19.3	17.4	12.1	-.37	-.30
$\bar{x}$	28.3	27.9	19.4	-.31	-.30

Table 3.--Inbreeding depression in (a) progeny of 2 trees in experiment AC-15 and (b) 4 trees in experiment AC-18 based on the mean of crosses with the same 2 males within experiments.

Experiment	♀ Tree	Mean Progeny Height (cm) and Inbreeding Depression (I.D.)				
	♂	1275	1279	$\bar{x}$	S_1	I.D.
(a) AC-15 (Age 5)	1278	31.6	29.8	30.7	21.1	-.31
	1280	26.1	22.5	24.3	21.5	-.12
	$\bar{x}$	28.8	26.2	27.5	21.3	-.22
		687	1291	$\bar{x}$	S_1	I.D.
(b) AC-18 (Age 6)	683	22.8	29.1	26.0	17.4	-.33
	1256	17.8	24.8	21.3	13.4	-.37
	1278	19.7	22.3	21.0	12.1	-.42
	1281	18.0	19.0	18.5	12.1	-.35
	$\bar{x}$	19.6	23.8	21.7	13.8	-.37

Table 4.--Inbreeding depression in progeny of 3 trees, based on the mean of crosses with the same 4 males. Experiment AC-18, age 6.

♀ Tree	Mean Progeny Height (cm) and Inbreeding Depression (I.D.)						
♂	680	685	687	1291	$\bar{x}$	S_1	I.D.
1256	31.6	24.7	17.8	24.8	24.7	13.4	-.46
1278	26.2	23.3	19.7	22.3	22.9	12.1	-.47
1281	25.4	20.0	18.0	19.0	20.6	12.1	-.41
$\bar{x}$	27.7	22.7	18.5	22.0	22.7	12.5	-.45

Table 5.--Inbreeding depression in relation to progeny environment; one tree selfed and crossed with the same 2 males in 2 field experiments. Experiment AD-15 (age 5) and experiment AC-18 (age 6).

Experiment	♀ Tree	Mean Progeny Height (cm) and Inbreeding Depression (I.D.)				
	♂	1256	1281	$\bar{x}$	S_1	I.D.
AC-15	1278	26.5	17.5	22.0	21.1	-.04
AC-18	1278	20.4	15.1	17.5	12.1	-.31
	$\bar{x}$	23.4	16.3	19.8	16.6	-.16

Inbreeding depression was higher in Experiment AC-18 than in Experiment AC-15 (Tables 1 and 3) but the suggested location effect is inconclusive on this information alone because of differences in cross combinations in the two experiments. Even in the case of tree 1278, which was selfed in both experiments, different males were involved in the crosses in AC-15 than in AC-18. Two other crosses with tree 1278 were, however, included in both experiments (Table 5). Results of this one-tree comparison showed a higher inbreeding depression in tree 1278 S1 progeny in the AC-18 experiment than in the AC-15 experiment, strengthening the otherwise inconclusive evidence of a location effect.

In the 3 Si progenies measured at ages 6 and 10, inbreeding depression was consistently lower at age 10 than at age 6 (Table 6).

Table 6.--Inbreeding depression at ages 6 and 10 based on the same self and outcross progenies. Experiment AC-14.

		Mean Progeny Height (cm) and Inbreeding Depression (I.D.)					
♀ Tree	No. of outcross families	$\bar{x}$ Outcrosses, age 6	$\bar{x}$ Self, age 6	$\bar{x}$ Outcrosses, age 10	$\bar{x}$ Self, age 10	I.D. at age 6	I.D. at age 10
689	1	49.1	40.2	301.8	256.0	-.18	-.15
691	2	39.8	33.5	246.9	216.4	-.16	-.12
1254	4	39.5	27.7	262.9	201.2	-.30	-.23
$\bar{x}$		42.8	33.8	270.5	224.5	-.21	-.17

DISCUSSION

Several points can be made from these analyses of inbreeding depression in eastern white pine.

First, inbreeding depression depends on the particular combination or combinations of check progenies used in the calculations. If these progenies are a representative sample of the stand progenies, a good general estimate of the effects of selfing a particular tree will be obtained. If, in turn, a group of selfed trees thus outcrossed accurately samples the general response to selfing in the stand, a reliable general estimate of inbreeding depression is obtained for the stand as a whole. The stand, in turn, may or may not typify the species.

In this stand, restricted population size suggested that a moderate level of inbreeding existed at the parental level. But wide variation nevertheless existed in outcross progeny performance, as shown in these results and those previously reported (Kriebel, Namkoong and Usanis 1972; Kriebel, Roberds and Cox 1974). Estimates of inbreeding depression based on a single S1 progeny, or on check crosses consisting of only one or two outcross progenies per female parent could therefore be atypical.

Likewise, an estimate based on a comparison with an open-pollinated progeny, or on the mean of a few of these, could be atypical. Rather than panmixis, open pollination of a white pine is likely to be mainly crossing with one or a very few nearby trees to the windward.

Table 2 shows that some control-pollinated progenies were taller than their corresponding open-pollinated progeny. In one case, the relationship was reversed. Averaging 6 females together, however, there was no difference between height of control- and open-pollinated progenies and therefore in inbreeding depression. Evidently, the overall estimate from open-pollinated checks was not atypical. It should be noted that the parent trees tested were scattered throughout the stand, providing a variety of pollen sources for open pollination.

With one exception (tree 1280) the females compared in Tables 3 and 4 differed little in the inbreeding depression of their Sl progenies. The Table 3 estimates are not based on enough check crosses per female to be indicators of general inbreeding depression (compare tree 1278 in Table 3 with the same tree in Tables 1 and 5 with different check crosses). They are, nevertheless, indicative of tree-to-tree variation in Sl performance, considering (1) the fairly large number of trees on which outcross means were based and (2) additivity, i.e. absence of a dominance interaction. The earlier analyses cited have shown that dominance is a non-significant component of variance in these progenies.

The higher level of inbreeding depression in one location than another could be the result of factors other than environment. The crosses made in the two experiments were made in two different years and there was one year's difference in the age at which they were measured. It seems more likely, however, that selfs and outcrosses from a tree do not show the same growth rate differential in differential environments, i.e. the response to homozygosity varies with environment. Barnes (1964) found a similar interaction between site and inbreeding depression in western white pine (<u>Pinus monticola</u> Dougl.).

In comparison with cited earlier estimates of inbreeding depression in eastern white pine, the AC-18 figures are high. They are, in fact, higher than most estimates for pines. This may be the result of environmental differences, but it could also be an effect of a higher-than-usual level of inbreeding in the parent trees.

There is insufficient data to conclude that inbreeding depression declines with age in eastern white pine, although the decline was consistent and of approximately equal magnitude in all 3 S1 progenies measured at ages 6 and 10. Subsequent measurements of all 9 S1 progenies should show whether such a trend exists. The decline could be the result of an unknown environmental influence occurring between ages 6 and 10 and having the largest effect on the most vigorous trees.

CONCLUSIONS

In eastern white pine, an adequate estimate of a tree's general outcross performance is necessary for a meaningful estimate of its Si inbreeding depression. An open-pollinated progeny is not a reliable check on the growth of a selfed progeny from the same tree, nor are one or two outcross progenies. Several are required.

Comparisons of female parents based on common male testers for the check progenies indicate that they vary in inbreeding depression. But in these experiments, differences were small, with one exception.

Site can have a large effect on inbreeding depression. The general level of inbreeding depression at one location was much higher than at another location. Also, two S1 progenies of the same tree in different areas, with comparable groups of check crosses, varied widely in inbreeding depression.

An apparent decline in inbreeding depression with age may be the result of some recently-introduced environmental factor affecting outcrosses more than self s. Further study of the trend should indicate its relation, if any, to inbreeding.

LITERATURE CITED

Barnes, B. V. 1964. Self- and cross-pollination of western white pine: a comparison of height growth of progeny. USDA Forest Serv. Res. Note INT-22, 3 pp.

Fowler, D. P. 1965. Effects of inbreeding in red pine, *Pinus resinosa* Ait. IV. Comparison with other northeastern *Pinus* species. Silvae Genetica 14:76-81.

Franklin, E. C. 1970. Survey of mutant forms and inbreeding depression in species of the family Pinaceae. Southeast. Forest Expt. Sta., USDA Forest Serv. Res. Pap. SE-61, 21 pp.

Johnson, L.P.V. 1945. Reduced vigor, chlorophyll deficiency, and other effects of self-fertilization in *Pinus*. Can. J. Res.

Kriebel, H. B., G. Namkoong and R. A. Usanis. 1972. Analysis of genetic variation in 1-, 2-, and 3-year old eastern white pine in incomplete diallel cross experiments. Silvae Genetica 21:44-48.

Kriebel, H. B., J. H. Roberds and R. V. Cox. 1974. Genetic variation in vigor in a white pine incomplete diallel cross experiment at age 6. Proc. 8th Cent. States Forest Tree Impr. Conf. (in press).