The influence of silvicultural practices on genetic improvement: height growth and weevil resistance in eastern white pine

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Summary

When grown in a common environment, the progeny of white pine (Pinus strobus L.) from weeviled stands improved by selection thinning outperformed the progeny of wolfy dominants from untreated stands in both height and weevil resistance. Within families, weevils tended to attack the tallest trees. Among families the relationship was not as strong and actually reversed during the last year of measurement. Therefore, it is possible to select for weevil resistance without sacrificing height growth. The improvement in height was attributed in part to natural and artifical selection for rapid growth, but primarily to a reduction in inbreeding. In unthinned stands inbreeding depression may have resulted from crossing among the codominants and their parents, wolfy dominants of the type removed in selectively thinned stands. The reduction in weevil attack was primarily the result of selective removal of low value, weeviled parents. The data demonstrated that silvicultural operations such as thinning or regeneration cutting can result in genetic improvement if properly applied, or genetic deterioration if silviculturists ignore genetic principles.

Key words: Pinus strobus, timber stand improvement, selective thinning, genetic variation, inbreeding

Zusammenfassung

In natürlicher Umwelt angezogen, übertraf eine Nachkommenschaft der Weymouthskiefer (Pinus strobus L.) aus Beständen mit Rüßler-Befall und selektiver Durchforstung die Nachkommenschaft von Protzen aus unbehandelten Beständen sowohl im Höhenwachstum als auch in der Rüßler-Resistenz.

Innerhalb von Familien griffen die Rüßler die größten Bäume an, zwischen Familien war diese Beziehung nicht so stark, im letzten Jahr der Messung sogar umgekehrt. Daher ist es möglich, auf Rüßler-Resistenz zu selektieren, ohne einen Verlust im Höhenwachstum hinnehmen zu müssen. Eine Verbesserung des Höhenwachstums wurde zum Teil auf natürliche und zum Teil auf künstliche Selektion auf Raschwüchsigkeit zurückgeführt, in erster Linie aber auf eine Reduzierung der Inzucht.

In nicht durchforsteten Beständen mag die Inzuchtdepression aus Kreuzungen zwischen den mitherrschenden Bäumen und ihren Eltern resultieren, in selektiv durchforsteten Beständen aus Kreuzungen zwischen Protzen solchen Typs, wie sie hier entfernt wurden.

Eine Reduzierung des Rüßler-Befalls war in erster Linie eine Folge der selektiven Entfernung befallener Eltern von geringem Wert. Die vorgelegten Daten zeigen, daß forstliche Maßnahmen bei sachgemäßer Anwendung, wie Durchforstung und Zurückschneiden, eine genetische Verbesserung bewirken können, jedoch zu einer Verschlechterung führen, wenn man genetische Prinzipien außer Acht läßt.

Introduction

There is very little information on the potential of silvicultural practices to alter the genetic composition of timber stands. Nevertheless, such information is vitally important because silvicultural systems of natural regeneration still predominate in forestry. Virtually all New England forests are naturally regenerated, so silviculturists must work with populations in situ, and management practices are the key to the health of the genetic resource. All silvicultural actions will affect genetic composition to a greater or lesser extent, by modifying both selection pressures and breeding structure. Avoidance of adverse genetic effects requires a policy of active gene management. Many species are thought to have suffered deterioration in form and growth as a result of overexploitation without concern for genetic effects (e.g. Styles 1972; Keiding and Kemp, 1977), but evidence is anecdotal. In Scots pine (Pinus sylvestris L.) progeny of older stands experienced greater selection pressure for diameter and height growth as a result of selective thinning as well as natural selection (Wilusz and Giertych, 1974).

Our objective was to determine the genetic effects of improvement cutting and selection thinnings on eastern white pine (P. strobus L.). In New England such cuttings in old-field white pine often involve removal of fast-growing, wolfy, weeviled dominants of low value (Fig. 1). It has been common knowledge for over a century that the white pine weevil (Pissodes strobi Peck.) attacks the tallest trees (Fitch, 1858; Belyea and Sullivan, 1956). Therefore, many practicing foresters feared that timber stand improvement to remove weeviled trees might be equivalent to selection against rapid growth. To test the possibility, seed was collected from weeviled dominants in untreated stands and from better stems in treated stands. The seed was germinated and seedlings were compared in a common environment after 9 and 12 years of growth.

Materials

Three pairs of stands, with and without prior treatment by selection-improvement thinning, were chosen for seed collection in a 100-hectare portion of the Yale Forest in Swanzey, New Hampshire, U. S. A., lat. 42.9° N and long. 72.3° W. Two additional stands of scattered trees left standing after the 1938 hurricane were located within the same 100 ha. Stands were between 2 and 8 ha in size except for one, an untreated plot of 0.4 ha. Each stand was situated in such manner as to reduce the possibility that westerly winds might blow pollen from one kind of stand (i.e. thinned or untreated) to another. Maximum distance between stands was 1.7 km and the closest were 100 m apart along a north-south line. Maximum difference in elevation was only 40 m. Six of the stands were on soils derived from till and were of the Gloucester and Paxton series with site

indexes of about 21 m at 50 years. Two stands (numbered 1 and 4) were on Merrrimac outwash sand with site index of about 18 m. Major provenance differences were not expected because of the proximity of the stands and similarity in edaphic conditions.

All stands had originated by invasion of old fields abandoned 50 to 100 years earlier. In all cases the original colonizers were known or suspected to be widely scattered trees that had arisen from seeds dispersed from rather distant fence-rows or woodlots. When the colonizers began bearing seed at about age 20, the remaining open areas were seeded with their progeny. In one of the three thinned stands so much time had elapsed since thinning that this scenario of two-stage colonization could not be verified. But it is certain that two-stage colonization of old fields was common in the locality and that the trees from which seed was collected in all the untreated stands and the hurricane residuals were original colonizers, of an older age class than the surrounding stems. Because they developed with little competition, the first-stage colonizers became large-limbed, stocky, "wolf" trees or "cabbage pines", deformed by repeated weevil attacks. In the timber stand improvement cuts, these super-dominants were removed and the remaining stems were subjected to selection thinnings to remove badly weeviled dominants or codominants, to release straighter codominants, and to adjust spacing. The three improved stands had been thinned 5, 9, and 12 years, respectively, before we collected seed, and some of the released trees had begun to produce cones.

In the stands that were nearly destroyed by the 1938 hurricane, the cabbage pines, or original colonizers, had been the only trees strong enough to withstand the wind, so the effect was the reverse of an improvement cutting. By the time seed was collected, the progeny of the cabbage pine, which were seeded after the hurricane, had begun to produce pollen. In both the hurricane-decimated stands and the untreated stands, the trees from which we gathered seed could have been pollinated either by their progeny or by other original colonizers.

Seed was collected in 1959, a good seed year, by gathering cones dropped by red squirrels *(Tamiasciurus hudsonicus)*. In stands which had been subjected to improvement cutting cones were collected beneath three of the best-formed, tallest trees available in the stand. In stands which had received no treatment, cones were collected from three of the badly-weeviled dominants, the type that had been removed in the treated stands. In the two stands damaged by the 1938 hurricane, cones were collected from the surviving dominants. Care was taken to collect cones only when there was no ambiguity regarding their origin. Therefore, each collection should be the offspring of a single seed parent and approaches a half-sib family if pollination was random. Most stands were represented by three families, but because of inadequate numbers of seed, two stands had only two families apiece.

Methods

Seed was cold-stored until sown at the Pachaug State Forest Nursery, Connecticut in December 1965. Seedlings were lifted in April 1969 as 3—0 stock and transplanted to the field. The field site at the Yale Forest, Eastford, Connecticut (lat. 41.9⁰ N, long. 72.1⁰ W) had been in agricultural use (i.e., mown for hay) up to 2 years before planting. The site was a drumlin top with soils of the Paxton series.
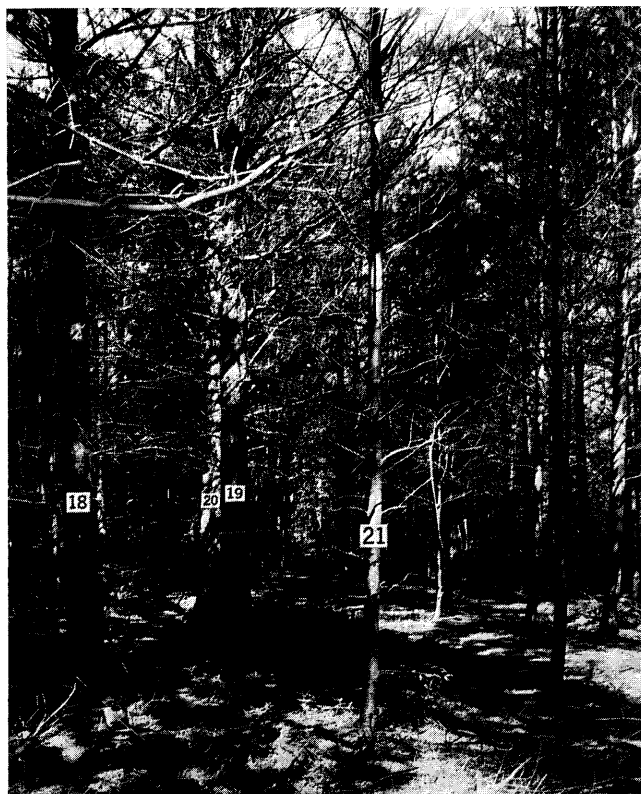

Fig. 1. — An old-field stand of eastern white pine at the Yale Forest before (left) and after(right) an improvement-selection thinning. The trees numbered 18, 19, and 20, which happen to be in a clump in this case, were the original colonists of the old field and were 60-years-old. The trees left in the cutting (and number 21) were 35-years-old and progeny of the older age-class. (Yale University photo.)

Seedlings were planted with planting bars at a spacing of 6 × 6 ft.

The design was a compact family block (PANSE and SUKHATME, 1961) with six replications or blocks. The main plots were stand treatments (selectively thinned, untreated, or hurricane), subplots were stands within treatment categories, and sub-subplots were families in stands. There were 6 to 10 trees per family in the interior sub-plots, depending upon whether the stand was represented by two or three families, and these were randomized in two-tree pairs to facilitate systematic thinning at a later date (Fig. 2). There were two border rows around the experiment,

Selectively thinned / Unthinned

10	11	11	10	10	9	9	9	2	2	2	1	1	1	1	3	3
10	9	9	11	11	10	10	9	2	1	1	2	2	2	2	1	1
9	10	10	11	11	11	11	10	1	2	2	1	1	3	3	1	1
9	10	10	11	11	9	9	11	3	1	1	2	2	3	3	3	3
11	9	9	9	9	10	10	11	3	2	2	1	1	3	3	2	2
14	12	12	13	13	14	14	12	6	6	6	6	6	8	8	7	7
13	13	13	12	12	14	14	13	6	6	6	8	8	7	7	8	8
14	12	12	14	14	13	13	12	8	8	8	7	7	7	7	7	7
15	15	15	15	15	15	15	15	4	4	4	5	5	5	5	5	5
15	15	15	16	16	16	16	15	5	5	5	4	4	5	5	4	4
15	16	16	15	15	16	16	16	5	4	4	5	5	4	4	5	5
16	15	15	16	16	16	16	16	4	4	4	5	5	5	5	4	4

(Stand labels within grid: Stand 4, Stand 1, Stand 5, Stand 3, Stand 6, Stand 2)

Fig. 2. — Sample plot layout for an exterior replicate (Block II) of progeny from selectively thinned and untreated stands. Dotted lines separate interior trees from border rows. Each number represents a single seedling and refers to the seed tree parent.

and seedlings in the border rows belonged to the same stand as the adjacent interior plots.

Height was measured in autumn 1974, six growing seasons after plantation establishment when the seedlings were 9-years-old, and in autumn 1977 when they were 12-years-old. At both times death of the terminal due to weevil attack was recorded. In 1977 number of attacks since 1974 was counted as well as current attack. In some cases we noted that the weevil had not fully penetrated the shoot, but had meandered near the surface leaving the terminal scarred but alive. The larvae had not formed a chamber to pupate. This apparent ability to throw-off attack was also recorded.

For weevil attack, we included border rows in the analysis to increase precision. Rate of attack was approximately the same in the border rows as in the interior plots, and results of analyses with or without border rows were similar. However, border rows were shorter than interior plots because of brush competition and shading from surrounding forest on two sides, so only interior trees were analyzed for height. Some deer browse occurred and browsed seedlings were excluded from analysis. In one block, browse virtually eliminated the plot representing hurricane survivors. Because of loss of the plot and because the main comparison was between selectively thinned and untreated stands, the hurricane type was excluded from analysis of variance for main effects. For analysis of stands within the hurricane type and for analysis of variation among families within stands, the block was omitted from analysis.

Analysis of variance was run on plot means. For stands within treatments and families within stands a separate

analysis was run for each treatment type and each stand, respectively (PANSE and SUKHATME, 1961). A separate analysis was run to calculate within plot variance. Components of variance were estimated from the expected mean squares.

Results

Nine growing seasons after establishment survival ranged from 76% to 96% among families, averaging 88%. Most mortality was the result of deer browse, largely localized within one block.

Seedlings of parents from selectively thinned stands were taller than those from untreated stands (P < 0.05), and the difference increased from the sixth through the ninth growing season. In fact, there was almost no overlap in height between the two groups; the tallest family from untreated stands barely reached the height of the shortest family from selectively thinned stands (Fig. 3). Mean height of seedlings from hurricane-thinned stands was intermediate, but closer to that of untreated stands.

There were several ways to compare the impact of weeviling. The proportion of trees attacked in 1974 and in 1977 was greater for seedlings from untreated stands than in
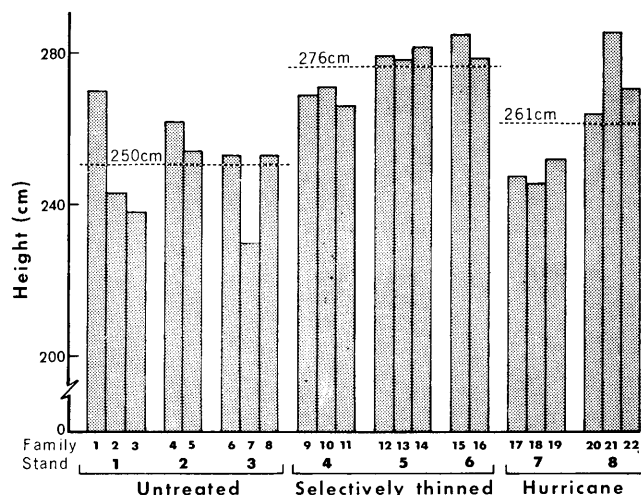

Fig. 3. — Histogram of means for 12-year height of open-pollinated white pine families. Dashed lines are averages for unthinned, selectively thinned, and hurricane-damaged stands, respectively.
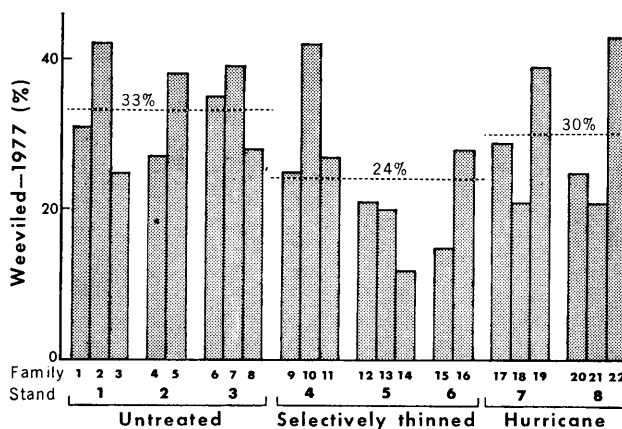

Fig. 4. — Histrogram of means for weevil attack in 1977 on open-pollinated white pine families. Dashed lines are averages for unthinned, selectively thinned, and hurricane damaged stands, respectively.

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those from selectively thinned stands. The difference was not significant in 1974 when many seedlings were just beginning to emerge from the grass and attack was only 8.3%, but was significant at $P < .01$ in 1977 when the proportion attacked was 28.9% *(Fig. 4)*. The proportion of weeviled seedlings from hurricane-thinned stands was closer to the value for untreated stands than to that for selectively thinned stands. Other statistics, (i.e., cumulative number of weevil attacks for the four-year period 1974 through 1977, proportion of terminals that were attacked but not killed, or proportion of trees not weeviled up through 1977) did not vary significantly between stand types. However, in each case values favored seedlings from selectively thinned stands; they produced progeny averaging slightly fewer weevil attacks per tree, a slightly higher proportion of attacked trees in which the terminal survived, and a slightly greater proportion of seedlings never attacked *(Figs. 5—7)*.

Despite the fairly large differences among seedlings representing selectively thinned and untreated stands, differences among stands-within-stand-types and among families-within-stands reached statistical significance in only a few instances *(Table 1)*. Most of these cases could be expected by chance because of the number of tests involved. Only differences among families in stands 2 and 4 for weevil attack in 1977 and between families in stand 6 for ability to throw-off attack seem clearly significant. The lack of consistent patterns of variation are reflected in the components of variance and heritabilities calculated from sums of squares pooled across stands and stand types *(Table 2)*. Though ninth-year height clearly differed between selectively thinned and untreated stands considered as groups, the pooled variance among families was zero. On the other hand, plot-mean heritabilities for weevil attack were substantial.

Discussion

Seed trees from thinned stands were selected for height and form, indicating relative freedom from weevil attack. Badly weeviled stems were removed as potential pollen parents. On the other hand, progeny from untreated stands were the offspring of trees badly deformed by repeated weevil attack, the type of tree removed in selectively thinned stands. Therefore, the tentative superiority of families from selectively thinned stands for all measures of weevil resistance was in the expected direction. Progeny from selectively thinned stands had 27.3% fewer attacks in 1977, 9% fewer attacks per tree over the period 1974 through 1977, and 14.8% more seedlings which had never been weeviled than untreated stands, suggesting that selection was effective in improving weevil resistance.

It has long been known (FITCH, 1858) that weevils prefer the tallest trees, perhaps because they have more crown and are more likely to visually or physically intercept the
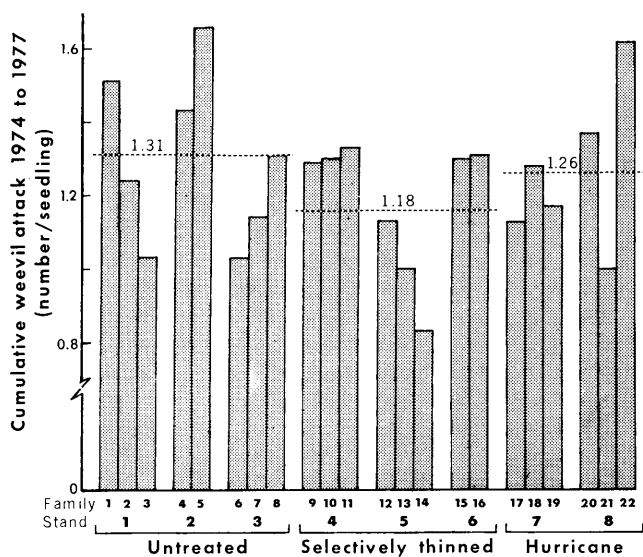

Fig. 5. — Histogram of means for per capita weevil attacks over life of the plantation in open-pollinated white pine families. Dashed lines are averages for unthinned, selectively thinned, and hurricane damaged stands, respectively.

Fig. 6. — Histogram of means for trees which resisted weevil attack in open-pollinated white pine families. Dashed lines are averages for unthinned, selectively thinned, and hurricane damaged stands, respectively.

Fig. 7. — Histogram of means for trees never attacked by weevil over life of plantation in open-pollinated white pine families. Dashed lines are averages for unthinned, selectively thinned, and hurricane damaged stands, respectively.
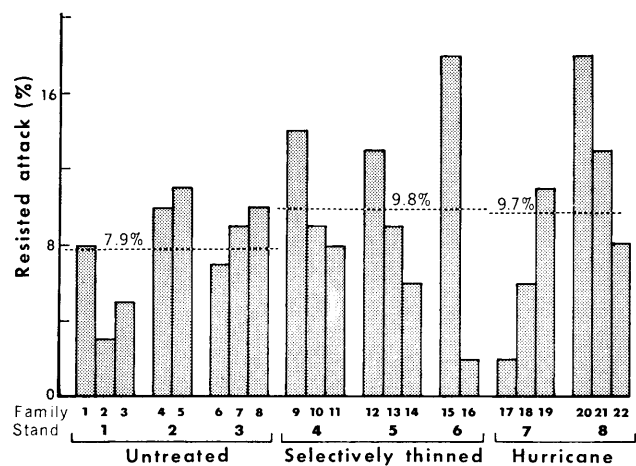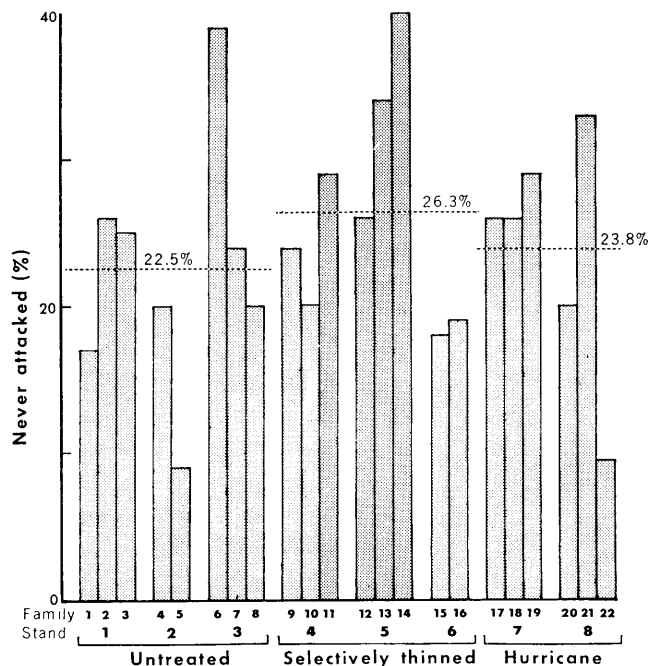
Table 1. — Results of analyses of variance for differences among stands (A) and differences among open-pollinated families within stands (B) for height and weeviling in eastern white pine.

A. Significance levels for variation among stands within treatment types.[1)]

Trait	Stand Types		
	Untreated	Selectively Thinned	Hurricane
9-year height	ns	ns	ns
12-year height	ns	ns	ns
1974 weevil attack	ns	0.10	ns
1977 weevil attack	ns	0.05	ns
cummulative weevil attack	ns	0.10	ns
resisted/attacked	ns	ns	ns
non-weeviled	0.10	0.10	ns

B. Significance levels for variation among families within stands.

Trait	Stand No.							
	1	2	3	4	5	6	7	8
1974 height	0.05	ns	0.05	ns	ns	ns	ns	ns
1977 height	0.10	ns	0.10	ns	ns	ns	ns	ns
1974 weevil attack	ns	ns	ns	ns	ns	ns	ns	ns
1977 Weevil attack	ns	0.05	ns	0.01	ns	ns	ns	0.10
cumulative weevil attack	ns	ns	ns	ns	ns	ns	ns	0.05
resisted/attack	ns	ns	ns	ns	ns	0.01	ns	ns
non-weeviled	ns	ns	ns	ns	ns	ns	ns	0.10

[1)]Values refer to standard probability levels; ns indicates non-significant at the 10% level of probability.

weevil in its flight over the stand than shorter trees, or perhaps because the weevil prefers a stout terminal and

taller trees are more vigorous (CONNOLA, 1973). In our plantation the relationship between height and weevil attack was highly consistent within families. Considering only seedlings that were not attacked by weevil in 1974, we compared the mean height of those subsequently attacked to those not attacked. In 21 of the 22 families it was the tallest trees in 1974 that were attacked in the next three years (Table 3). However, that cannot be the explanation for the observed differences in weevil attack between progeny of selectively thinned and untreated stands, because progeny of selectively thinned stands suffered less weevil damage even though they were already taller than progeny of untreated stands in 1974. Family mean height and weevil attack in 1977 were weakly, but negatively, correlated (r = −0.50). Thus, despite the well-known correlation between height and weevil attack, the tallest families in this study were most weevil resistant.

The height superiority of progeny from selectively thinned stands was not expected. Knowing that height and weevil attack were positively related in other studies (e.g. CONNOLA, 1973) led to the hypothesis that stands selectively thinned to remove weeviled trees would constitute selection against rapid growth. One possible explanation for the deviation from expectation is that selective thinning increased vigor of treated stands and resulted in larger seed which produced larger seedlings. Unfortunately we have no data on seed weight, but the explanation seems unlikely for two reasons. First, seed from untreated stands came from dominants that suffered little competition, so we expect that vigor and seed weight would be similar to that of trees from selectively thinned stands. Second, it would be unusual for the effects of seed weight to be maintained through 12 years. Correlations between growth and seed weight usually disappear during the first two growing seasons. Although maternal effects have been detected up

Table 2. — Pooled components of variance (A) and heritabilities (B) for height and weevil attack estimated from a compact family block experiment of open-pollinated families in eastern white pine.

		Height		Weevil Attack			Resisted :	
A.	Component	9-years	12-years	1974	1977	Cumulative	Attacked	Unweeviled
	Stand Type (σ_t^2)[1/]	16.48857	168.96953	0[2/]	0.00107	0	0	0
	Stands in type (σ_s^2)	0	0	0.00104	0.00119	0.02414	0	0.00360
	Families in stand (σ_f^2)	2.84469	0	0.00169	0.00400	0.00256	0.00006	0.00010
	Plot-to-Plot (σ_e^2)	94.57671	147.17100	0.00662	0.01668	0.01916	0.01112	0.02935
	Within Plot (σ_w^2)	919.59965	2914.23387	[3/]	[3/]	0.90979	[3/]	[3/]
B.	Heritabilities							
	Individual[4/]	0.01	0	–	–	0.01	–	–
	Plot[5/]	0.06	0	0.61	0.60	0.08	0.03	0.02

[1] Groups of stands receiving 1) no silvicultural treatment, 2) selective thinning, or 3) felled by hurricane.

[2] Zero values substituted for negative components.

[3] Within plot analysis not possible for all-or-none traits.

[4] Narrow sense or individual heritability based on assumption of half-sib relationships among progeny within family, no relationship among families, and all genetic variance additive:

$$h^2 = 4\sigma_f^2 / (\sigma_f^2 + \sigma_e^2 + \sigma_w^2)$$

[5] Plot mean heritabilities for a test with 6 replications and 6 individuals per plot for height and cumulative weevil attack: $h^2 = \sigma_f^2 / [\sigma_f^2 + 1/6(\sigma_w^2 / K + \sigma_e^2)]$.

Plot Mean heritabilities for this experiment for 1974 and 1977 weevil attack, proportion never attacked up to 1977:

$$h^2 = \frac{2}{f} / (\frac{2}{f} + \frac{2}{e} / 6)$$

Last line: It schould read $\sigma_f^2 \ \sigma_f^2 \ \sigma_e^2$

Table 3. — Means by family of nine-year heights (1974) for trees subsequently weeviled in the next 3 years compared to those not wceviled during the period (only trees not weeviled in 1974 included).

Family	Height in 1974 (cm)	
	Weeviled by 1977	Not weeviled by 1977
1	113.6	93.5
2	88.5	68.9
3	85.4	55.3
4	101.5	65.9
5	98.1	64.5
6	103.9	72.4
7	90.1	53.9
8	100.0	44.1
9	105.0	60.9
10	110.3	49.4
11	110.2	80.5
12	111.9	77.4
13	122.7	87.2
14	106.5	95.8
15	111.0	83.1
16	109.3	68.4
17	95.8	75.5
18	98.9	58.1
19	109.2	79.1
20	97.2	85.3
21	109.0	86.4
22	108.0	133.3

to six years of age in white pine (KRIEBEL et al., 1972) and longer in Scots pine (GIERTYCH, 1974), correlations of height with seed weight were non-significant by year two in a recent white pine provenance test (MATHESON, 1977).

Another explanation for the height superiority of progeny from selectively thinned stands might be that weeviling causes reduction in tree height, and progeny from untreated stands were more heavily weeviled. Weevils kill the terminal shoots of the previous one or two years, and side branches, which are typically shorter than the terminals of the same years, turn up to form new terminals. The high incidence of weevil attack in the progeny of untreated stands might thus contribute to their poor performance in height growth. However, family mean height in 1977 was not correlated with cumulative weevil score. Weevil attack may have contributed to differences in height, but was not the complete explanation. Our results, in fact, suggest that the height superiority of progeny from the treated stands was achieved in spite of the well-documented observation that weevils are most likely to attack the tallest white pine.

Our explanation is that susceptibility to weevil damage is not solely related to height and vigor. KRIEBEL (1954) showed, for example, that pines with a low ratio of bark thickness to stem diameter suffered reduced weevil damage. Variation in oleoresin composition may also be implicated (SANTAMOUR, 1965). Trees not weeviled in one year achieve some superiority in height and may thus become more likely candidates for attack in subsequent years.

Since the weevil almost never kills trees, there is very little likelihood of natural selection in favor of resistance to attack. The incidence of attack in white pines growing in unshaded stands is very high. In the case of our open-grown test plantations, only 25% of the trees had escaped

during the first nine years. It is remarkable that so many of the progeny of treated stands were undamaged even though they were among the tallest trees.

In Scots pine genetic gain in diameter growth was attributed to selective thinning. Seed was collected from Polish stands varying in age from 16 to 170 years. Other than sampling error, stands were expected to differ only because older stands had been exposed to more cycles of selective thinning and a greater reduction in numbers because of natural selection than younger stands. Intensive silviculture had been practiced in western Poland for over two centuries, and the oldest stands had probably been thinned several times. In 59-year-old progeny tests there was a trend in diameter and basal area ha^{-1}, increasing from progeny of younger to older stands. A gain of 12.6% could be explained on the basis of putative selection intensity resulting from natural attrition and selective thinning (WILUSZ and GIERTYCH, 1974).

It is possible that the height superiority of progeny from thinned stands of white pine may reflect both natural and artificial selection. The parent trees of the untreated stands and those "thinned" by hurricane developed in the absence of competition. The parents from thinned stands developed in denser natural regeneration where competition was intense, and it may be assumed natural selection placed a premium on height growth. The limited degree of artificial selection involved in the improvement cuts tended to retain trees with the best available combination of high vigor and low incidence of weevil attack.

However, it seems most unlikely that natural or artificial selection of parent trees could have caused the major part of the 10.4% improvement in height growth of progeny from thinned stands over that from unthinned. Given the low heritabilities observed for height, the selection intensity would have had to be immense to produce the 10.4% gain of 26 cm in height. Even if heritability was 0.10, a liberal estimate for natural stands, the selection intensity would have to be 4.5 standard deviations, or one tree saved in 150,000, which is higher than that possible in selective thinning. Even assuming selection in both directions, negative in unthinned and positive in thinned stands, the intensity of selection to produce a deviation of only 13 cm or 4.9% from the mean would be very large.

The breeding structure of these stands offers an alternative explanation. The scattered, original colonizers once they began to produce seed, filled-in New England's old fields. In time, their progeny reached reproductive maturity and crossed among themselves and backcrossed to their parents, the original colonizers. Thus, seed collected from the dominants in untreated stands or stands felled by the 1938 hurricane may include a high proportion of parent-offspring backcrosses because pollination between adjacent trees is likely to dominate over wider-ranging crosses. Backcrosses would have an inbreeding coefficient of 1/4. The dominants might themselves include a significant proportion of selfs or inbreds because it is possible they resulted in part from self-pollination of a few parents scattered in a matrix of hardwood forest. Under the reduced competition experienced by the original colonizers, such inbreds have a higher chance of survival than under conditions of intense competition. On the other hand, seed collected from stands selectively thinned would be predominantly crosses among half-sibs (i.e. individuals with one parent in common), because of non-random seed dispersal

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around the parents. Crosses among half-sibs have an inbreeding coefficient of 1/8. Both backcrosses and crosses among half-sibs would be expected to show depressed height growth relative to outcrosses, but growth of backcrosses would be reduced twice as much; for southern pine, respectively 5% and 10% below outcrossed values (FRANKLIN, 1970).

If progeny of parents from selectively thinned stands were the result of matings among half-sibs, resulting in a reduction in height of 5% below outcrosses, then outcrosses are expected to be 276/0.95 = 291 cm. If the progeny of dominants from untreated stands were the result of backcrossing, then a 10% reduction in height below that of outcrosses is expected or 291 × 0.90 = 262 cm compared to 261 cm observed for progeny of wolf-trees left after the 1938 hurricane and 250 cm for progeny of untreated stands. Alternatively, if height of the progeny of dominants from untreated stands represents 90% of the height of outcrosses, then outcrossed height should be 250/0.90 = 278 cm which is only slightly greater than heights of progeny from selectively thinned stands, 276 cm.

Therefore, inbreeding could account for much of the observed difference in height between progeny of selectively thinned and untreated stands if the mating system was perfectly regular (i.e., all crosses of the dominants in untreated stands were backcrosses and all crosses of trees in the selectively thinned stands were crosses between half-sibs). Because such a regular mating system is not likely, it is doubtful that inbreeding accounts for all of the variation in height between selectively thinned and untreated stands; but we feel it accounts for a major portion of the difference.

There seems no reason to fear that removal of heavily weeviled trees from old-field white pine stands constitutes selection against rapid height growth. The data suggest that improvement-selection thinning in old-field stands will actually improve height growth of the progeny, in part as a result of its influence on the mating system. Although weevils preferentially attack the tallest trees within families, the relationship does not necessarily hold among families. The tallest families in this experiment had less weevil damage on the average than the shortest families. In addition, because weevil damage slightly reduces tree height, weeviled trees can be outgrown by unweeviled ones and become less subject to attack in subsequent years. The weevil is relatively ineffective as an agent of selection, so it is unlikely that selective thinning to remove weeviled stems would result in selection against height growth, even in single-aged stands of white pine.

An increase in weevil resistance should be expected as a result of selective thinning. Selection against weeviling is effective because 1) it is easy to read the history of weevil attack throughout the life of the tree, 2) weeviling is so extensive that escapes are uncommon, and 3) there is genetic variation for weevil resistance. Variation among families in weevil resistance in our test plantation was greater than that among provenances in a range-wide test (GARRETT, 1972), but this is not unusual. Variation is frequently greater within stands than among provenances; e.g. isozyme studies in conifers have indicated that 93% to 97% of the total variation is among individuals in the same stand (GURIES and LEDIG, in press). Selective thinning and/or the correct silvicultural choices at regeneration can result in genetic improvements in height and weevil resistance.

Unfortunately, expediency has sometimes dictated that wolfy dominants be left as seed trees. Dominants are often left because they are so badly formed they have little or no commercial value, because they are more windfirm than trees that developed in closed stands, and because their wide crowns make them prolific cone and seed producers so relatively few trees need be left to regenerate the stand. This is poor silviculture and will result in stands no better than those harvested, when in fact improvement is possible. The loss is one of opportunity. Similarly, systematic thinning bypasses an opportunity for genetic gain. Thinnings should be applied to maximize long-term genetic improvement as well as short-term returns.

The results suggest that any sort of forest regeneration from populations of limited size, such as scattered or clumped seed trees, may be a risk to the genetic resource and to site productivity, unless genetic effects are considered and steps taken to prevent genetic deterioration. The results reported here should also cause silviculturists to wonder about the genetic implications of true uneven-aged management by the selection system, in which the opportunity for inbreeding between parents and progeny is high.

Acknowledgements

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