ANALYSIS OF GENETIC VARIATION FOR HEIGHT GROWTH AND SURVIVAL IN OPEN-POLLINATED PROGENIES OF EASTERN WHITE PINE[1]

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ABSTRACT.--Open-pollinated progenies of eighteen clones, from two seed years (1971 and 1973) in the University of New Hampshire eastern white pine (Pinus strobus L.) clone bank, were measured for height growth and survival after three growing seasons in the nursery. Family variation, for both traits, was significant each year and heritability estimates were moderately high, being much larger in 1973 than 1971. Correlations of family seed weights with family means of each trait were large and significantly different from zero in 1973, and smaller and non-significant in 1971, suggesting that seed size effects were primarily responsible for the higher heritability estimates in 1973. When data for both years were combined in one analysis, the variance due to genotype x environment interaction effects was found to be of nearly equal magnitude to the family variance component, for both traits. The genetic correlation between seedling height and survival is small and positive, indicating that selection for increased rates of survival will also result in slight gains in height growth.

While there have been many studies dealing with patterns of geographic variation in eastern white pine (Pinus strobus L.) (e.g., see Demeritt and Kettlewood 1976 and Wright 1970), few genetic studies in this species dealing with inheritance

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patterns of individual traits have been reported (Kriebel et al. 1972; Wright 1970). Information on the relative magnitudes of various genetic and non-genetic sources of variation, heritabilities, and genetic correlations among different traits, is necessary so that efficiency in breeding can be maximized.

In this paper, we report on the analysis of genetic variation for height growth and survival in open-pollinated progenies of eastern white pine, after three growing seasons in the nursery. Two experiments, involving the same set of open-pollinated clones, pollinated in two different years and planted at different times in separate parts of the nursery, are compared. It was of interest to determine the degree to which estimates of variance components, heritability and genetic correlation might differ under such varying conditions.

MATERIALS AND METHODS

Experimental Design and Materials

The plant materials analyzed in this study are open-pollinated progenies of 18 eastern white pine clones from two pollen years (1970 and 1972). Seed for these progenies was collected from open-pollinated cones of grafted trees in the University of New Hampshire White Pine Clone Bank, in 1971 and 1973. At the time of the pollinations, the clone bank contained ramets of 46 trees from widely scattered localities throughout the state of New Hampshire. Most of these trees were grafted into the clone bank from 1962 to 1966. The majority of the clones, including the 18 used in this study, are from trees selected for superior volume growth and form. The clone bank is bordered by a natural stand of white pine. Since there has been little production of pollen among the clones, it is assumed that the majority of pollen came from the natural stand.

Following collection of cones in both years, seeds were extracted and stored by families. They were than planted in plastic tubes, stratified for 65 days at 43°F, germinated in a greenhouse and then transplanted early the following summer to the New Hampshire Forest Nursery. The seedlings were placed into standard four foot nursery beds and subjected to normal nursery practices during the three years prior to measurement.

The nursery design for the 1971 seed crop consisted of four randomized complete blocks. The number of seedlings planted per family plot within each block ranged from 10 to 70, with a mean of 53. Seedlings were spaced at 10 x 10 cm within plots with 30.5 cm between plots. The design for the 1973 seed crop was identical, except that the families were planted in the same order in each block, rather than randomized. In addition, the number of seedlings per plot ranged from 9 to 100 with a mean of 44.

Height and survival data were collected for each experiment after the third growing season. A random sample of six trees per plot, with the exception of a few plots in 1973 having only 5 trees, were measured for height. Seedlings on the outside edges of the plots were excluded from height measurement, unless no other seedlings were available. All trees transplanted into the nursery were scored for survival.

Statistical Procedures

The data for each seed year was subjected to analyses of variance and covariance for a randomized complete block design. One of the four blocks in 1973 was discarded because damage to part of a seed bed resulted in heavy mortality and stunting of trees in part of that block. Tests of significance of the various mean squares involving 1973 data must be interpreted with caution because of the lack of randomization of plots within blocks. Analyses of variance of the combined data for both years follow the methods for combining experiments of unequal size, given in Cochran and Cox (1957, Chapter 12).

Components of variance and covariance were estimated using standard procedures of analysis. Expected mean squares for each analysis are given in the appropriate ANOVA tables in the Results section. In order to correctly interpret these components in genetic terms, the assumptions described by Stonecypher et al. (1964) and Dudley and Moll (1969) must be accepted. These assumptions are: 1. The parents are random members of the population, 2. Experimental errors are independent, 3. Inheritance is of a normal diploid type, 4. The progenies are not inbred, 5. There is no epistasis or maternal effects, 6. All seedlings within progenies are half-sibs. Under these conditions, it is then possible to relate the variation due to difference among female parents (o^2_f) to the additive genetic variance (o^2_A) such that $o^2_f = \frac{1}{4} o^2_A$. The family variance component can then be used to estimate narrow sense heritability, which is the ratio of the total additive genetic variance to the total phenotypic variance.

Narrow sense heritabilities were calculated on a family basis (h^2_f) for both height and survival and on an individual basis (h^2_i) for height. Formulas for estimating these heritabilities are:

$$\hat{h}^2_f = \frac{\hat{\sigma}^2_f}{\frac{\hat{\sigma}^2_p}{r} + \hat{\sigma}^2_f} \qquad \text{and} \qquad \hat{h}^2_i = \frac{4\,\hat{\sigma}^2_f}{\hat{\sigma}^2_p + \hat{\sigma}^2_f}$$

where $\hat{\sigma}^2_f$ = estimate of component of variance due to differences among female parents.

$\hat{\sigma}^2_p$ = estimate of component of variance due to interaction of replications and family plot means.

r = number of replications

Since there are subplot measurements for height, $\hat{\sigma}^2_p$ can be further subdivided in this trait, such that

$$\hat{\sigma}^2_p = \frac{\hat{\sigma}^2_\omega}{\kappa} + \sigma^2_{rf},$$

where $\hat{\sigma}^2_\omega$ = estimate of component of variance due to differences among progenies in plots.

$\hat{\sigma}^2_{rf}$ = estimate of component of variance due to interaction of replications and female parents.

κ = harmonic mean of the number of seedlings per plot.

When data is combined over years, the estimators become:

$$\hat{h}^2_f = \frac{\hat{\sigma}^2_f}{\frac{\hat{\sigma}^2_p}{7} + \frac{\hat{\sigma}^2_{fy}}{2} + \hat{\sigma}^2} \qquad \text{and} \qquad \hat{h}^2_i = \frac{4\,\hat{\sigma}_f^2}{\hat{\sigma}^2_p + \hat{\sigma}^2_{fy} + \hat{\sigma}^2_f}$$

where σ^2_{fy} = estimate of component of variance due to interaction of female parents and years. All other components are as defined above.

The genetic correlation of three-year height growth with survival was estimated for each year's data by:

$$r_g = \frac{\hat{\sigma}_{fxy}}{\sqrt{\hat{\sigma}^2_{fx}\,\hat{\sigma}^2_{fy}}}$$

where $\hat{\sigma}_{fxy}$ = estimate of female parent covariance for height and survival.

$\hat{\sigma}^2_{fx}$ and $\hat{\sigma}^2_{fy}$ = estimates of component of variance due to differences among female parents for height (x) and survival (y), respectively.

RESULTS AND DISCUSSION

Seed Years Analyzed Separately

Family height and survival means for the 1971 and 1973 seed years are presented in Table 1. A great deal of variation among families for both traits, is evident each year. Particularly striking is the range of means in 1973, in which height varies from 26.8 to 16.5 cm and survival from 88.3% to 50.6%. Analyses of variance for these traits give further insight into the magnitude of family variation. (Table 2). All family mean squares are significant at the 1% level, indicating that much of the variation among families is due to genetic causes.

Estimates of height and survival heritabilities for each year are given in Table 3. In general, the heritabilities are fairly large, suggesting that rapid gains for each trait are possible through selection programs. There is quite a difference between family and individual height heritability estimates each year. In 1971, heritability based on family height means is almost twice the heritability based on individual seedling heights. This result is not unexpected since within-plot variance (σ^2_w) is by far the largest source of variability in height (Table 4). Kriebel et al. (1972), have pointed out that under these conditions, samples consisting of multi-tree plots can be very effective in reducing the error of estimating family means. If the reduction in error more than compensates for using only one-quarter of the additive variance in the numerator of the heritability, h^2_f will be higher than h^2_i.

Heritability estimates are very different in 1973. First of all, the 1973 estimates are much larger than those of 1971. Secondly, the relationship between the individual and family heritabilities is opposite to that found in 1971, i.e., $\hat{h}^2_i$ is _greater_ than $\hat{h}^2_f$. Finally, $\hat{h}^2_i$ is greater than one in 1973, a theoretically impossible result, but one that is statistically probable, especially if any of the assumptions concerning the genetic interpretation of variance components are sufficiently violated. Referring to the heritability formulas given earlier, it is evident that the greater heritability in 1973 can be due either to a decrease in the environmental variation component(s) or an increase in the family variation component, or both. There is no evidence for a reduction of environmental variation in 1973 (Table 4). Survival plot error (o^$^{2}_{p}$) remains almost identical both years and plot error for height (o^$^{2}_{rf}$) is almost 1½ times greater in 1973 than 1971, a difference that is significant at the five percent level. On the other hand, a comparison of the family component of variance in each year shows that o^$^{2}_{f}$ is almost two times greater for survival, and nearly six times greater for height, in 1973 than in 1971.

Table 1: Mean height, survival and seed eightfor open-pollinated eastern white pine progenies.[a]

Clone	Height (cm)		Survival (%)		Seed Wt. (g/100 seed)	
	1971	1973	1971	1973	1971	1973
Bl	16.8	18.9	61.8	54.0	1.552	1.592
B2	19.0	26.5	80.0	88.3	1.888	2.401
B3	19.8	26.8	69.5	81.0	2.416	2.482
C3	18.6	18.9	85.8	79.0	2.169	2.085
El	20.0	22.5	77.9	86.7	1.980	2.184
E3	22.2	26.2	84.5	88.0	2.006	2.220
F2	19.0	26.1	62.8	61.3	1.742	2.229
F4	21.7	27.1	63.6	84.7	2.205	2.995
F7	19.3	24.5	71.2	63.3	2.147	2.380
F10	19.5	24.3	59.6	84.0	2.843	2.804
G3	18.2	25.7	53.6	70.7	2.093	1.915
H2	17.2	16.5	70.0	50.6	2.005	1.450
H4	17.6	19.4	80.6	75.0	1.503	2.112
H6	20.1	20.2	76.0	73.3	1.701	2.138
M2	17.8	23.9	70.9	73.3	2.054	2.742
M3	19.6	23.0	72.1	76.7	1.855	2.165
MS	16.6	21.9	77.1	72.7	1.441	1.856
R3	19.5	23.4	72.4	83.7	1.904	2.165
Mean	19.0	23.1	71.6	74.7	1.972	2.218

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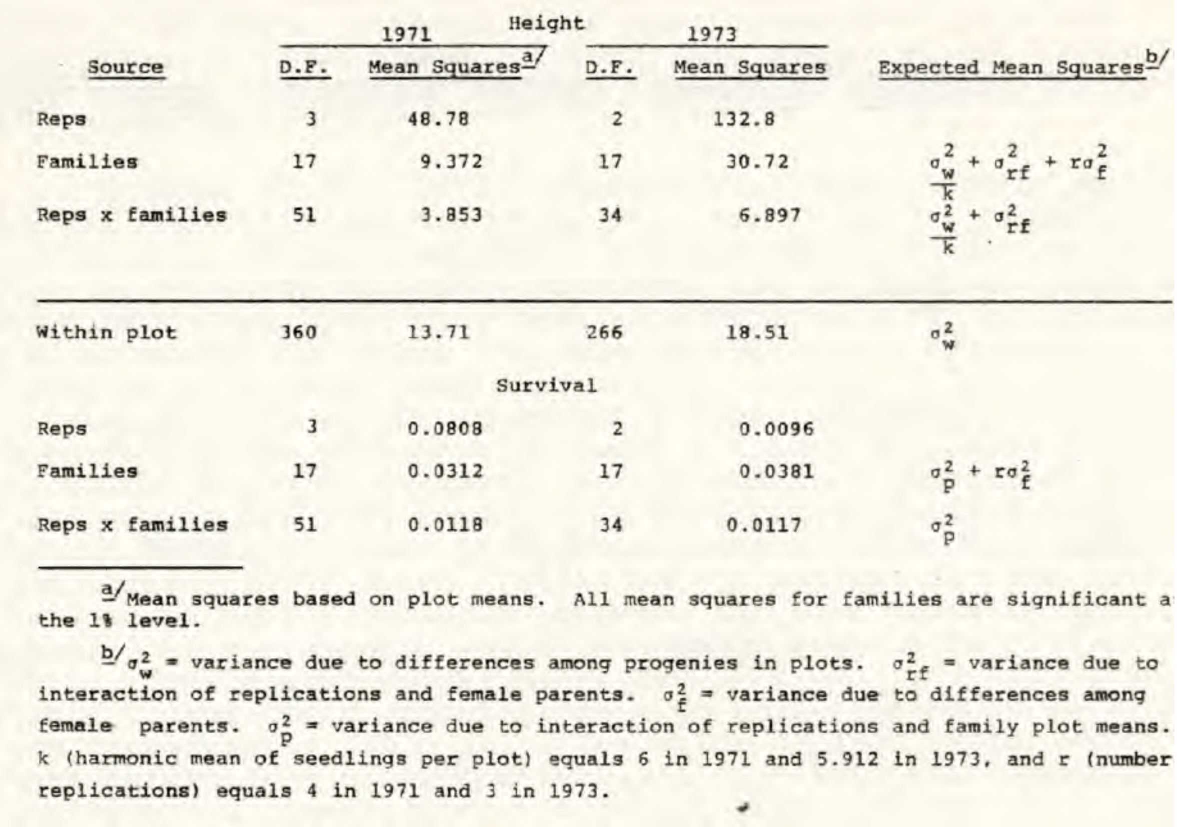
[a] Height and survival family means are based on 4 plotE in 1971 and 3 in 1973. Seed weight is based on the total weight of the seed extracted for each family, from which, a random sample was drawn for sowing in these experiments.

Table 2. Analysis of variance for height and survival for each seed year.



	Height				
	1971		1973		
Source	D.F.	Mean Squares[a]	D.F.	Mean Squares	Expected Mean Squares[b]
Reps	3	48.78	2	132.8	
Families	17	9.372	17	30.72	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2 + r\sigma_f^2$
Reps x families	51	3.853	34	6.897	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2$.
Within plot	360	13.71	266	18.51	σ_w^2
		Survival			
Reps	3	0.0808	2	0.0096	
Families	17	0.0312	17	0.0381	$\sigma_p^2 + r\sigma_f^2$
Reps x families	51	0.0118	34	0.0117	σ_p^2

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[a] Mean squares based on plot means. All mean squares for families are significant a the 1% level.

[b] σ_w^2 = variance due to differences among progenies in plots. σ_{rf}^2 = variance due to interaction of replications and female parents. σ_f^2 = variance due to differences among female parents. σ_p^2 = variance due to interaction of replications and family plot means. k (harmonic mean of seedlings per plot) equals 6 in 1971 and 5.912 in 1973, and r (number replications) equals 4 in 1971 and 3 in 1973.

Table 3. Estimates of narrow sense heritability and the genetic correlation of height and survival.

	Height		Survival	
Seed Year	Family	Indiv	Family	Genetic Correlation
1971	0.59	0.33	0.62	0.16
1973	0.78	1.05	0.69	0.76
Mean	0.68	0.69	0.66	
Combined analysis	0.58	0.42	0.53	

Table 4. Components of variance and covariance for both seed years.

	1971		1973		Combined	
	Height	Survival	Height	Survival	Height	Survival
$\hat{\sigma}^2_{fy}$					1.918	0.0030
$\hat{\sigma}^2_{f}$	1.380	0.0048	7.940	0.0088	2.340	0.0035
$\hat{\sigma}^2_{rf}$	1.569		3.767		2.517	
$\hat{\sigma}^2_{w}$	13.71		18.51		15.75	
$\hat{\sigma}^2_{p}$		0.0118		0.0117		0.0118
$\hat{\sigma}^2_{fxy}$	0.0129		0.2002			
$\hat{\sigma}^2_{pxy}$	0.0280		-0.0300			

Several factors may have contributed to the increase in family variance in 1973. Since different pollen years are involved, different mixes of male parents and/or different patterns of crosses might be expected for each year. Non-random fertilizations resulting in related matings within families tend to inflate family variance and cause an overestimate of the true additive genetic variance (Namkoong 1966). Such deviations fron the assumed half-sib relationship of progeny members might have been substantially greater in 1973 than 1971. An increase in the genetic relationship among family members is expected to also result in decreased variance among seedlings within family plots. This does not happen in 1973; in fact, c is greater in 1973 than in 1971. However, greater environmental variation within plots in 1973, leading to an overall greater within-plot variance in that year, cannot be ruled out.

Another factor, possibly leading to inflated family variance, is inter-genotypic competition, resulting from the systematic planting of family plots in 1973. Interfamily competition can be strong in seedlings of conifers (Adams et al. 1973) and can result in a great deal of non-additive family variance. However, wide spacing between plots and the normally large number of seedlings within plots, probably make strong competition between members of different family plots unlikely.

Kriebel et al. (1972), studied the inheritance of seedling height growth in eastern white pine using diallel cross experiments. Because reciprocal crosses were included, they were able to estimate variance components due to maternal (seed size) effects. They found that seed size effects were fairly large and accounted for about the same percentage of the total variance as general combining ability effects. Thus, the influence of seed weight on growth can be substantial and, in open-pollinated progenies, becomes a hidden component of family variance, which is inseparable from additive genetic effects. Seed weight has been shown to be strongly correlated with height growth in other studies of eastern white pine (Demeritt and Hooker 1975; Spurr 1944), but to account for the difference in family variation between the seed years in this study, the correlation would have to be greater in 1973 than 1971. Family seed weight means for 1971 and 1973 are given in Table 1, and their correlations with family means of each trait are presented in Table 5. Correlation of seed weight with both height (r = 0.70) and survival (r = 0.61) are strongly positive and significantly different from zero in 1973. Neither correlation is significant in 1971 and additionally, the correlation of seed weight with survival is negative. Therefore, seed weight seems to have a strong influence on family means in 1973, but probably has little if any, influence in 1971. This suggests that in 1973, seed weight was the primary factor responsible for the higher family variances and heritability estimates of that year.

Table 5. Matrix of correlations of family means.[a/]

	1971 Height	1973 Surv.	1973 Height	1971 Seed Wt.
1971 Surv.	0.14	0.38	-	-0.30
1971 Height	1.00	-	0.59	0.42
1973 Height	0.59	0.52	1.00	-
1973 Seed Wt.	-	0.61	0.70	0.58

[a/] Correlations were calculated using the family means given in Table 1. All correlations greater than ± 0.47 are significantly different from zero, at the five percent level.

The reason for the different correlations in each year is probably associated with the overall mean difference in seed weight between years. Sayward (1975), reporting on seed crop data for the entire clone bank from which the seed for this study was obtained, found that on the average, seed weighed 17% more in 1973 than 1971. This is reflected in the mean seed weights shown in Table 1, in which 14 out of the 18 families had higher mean seed weights in 1973 than 1971. Perhaps there is a threshold, above which seed weight will have a strong and detectable influence on seedling growth, but below which, other factors affecting growth will have the dominating influence.

Combined Analysis

Combining the two years of data in one analysis makes it possible to determine the degree to which family performance varies over years. The lack of estimation of genotype x environment interaction variance has been cited as a frequent weakness of inheritance studies in forest trees (Namkoong et al. 1966). When genotypes are tested in only one environment, the interaction of genotypes and environments cannot be separated from genetic effects, resulting both in inflated heritability estimates and reduced accuracy in appraising genotypes. The combined analyses of variance for height and survival are presented in Table 6. For both traits, the family x year mean square is around twice the plot error mean square (Reps x Families/Years), and in each case is significant at the five percent. level. Thus, family x environment interaction effects are strong for both traits, with $o^{\wedge 2}_{fy}$, only slightly smaller than the family variance component ($o^{\wedge 2}_{f}$).' It should be noted that possibly different pollen sources in the two years, or the different planting designs (i.e., random in 1971 vs. systematic in 1973), leads to additional interaction which could contribute to the family x environment interaction component. When the interaction variance is taken into account, heritability estimat are much lower than expected from the mean of the individual year estimates (Table 3).

Despite the significant interaction, the correlation of family height means of 1971 with those of 1973 is fairly large (r = 0.59) and significantly different from zero, at the five percent level (Table 5). Spearman's rank correlation (Steel and Tcrrie 1960) for the same trait, is also significant and of about equal magnitude ($r_s = 0.54$). The correlations for survival means are also positive ($r = 0.44$, $r_s = 0.38$), but neither is significant. An inspection of the five top and bottom ranked families, for each year, gives further insight into the relative performance of families over years. For height, a comparison of the top five ranked families in 1971 and 1973 shows three families are in common. Similarly, for

Table 6. Analysis of variance for height and survival combined over years.

Height

Source	D.F.	Mean Squares[a]	Expected Mean Squares[b]
Years	1	509.8	
Reps/Years	5	82.41	
Families	17	28.39	$\frac{\sigma^2_w}{5.962} + \sigma^2_{rf} + 3.571\sigma^2_{fy} + 7\sigma^2_f$
Families x years	17	11.74	$\frac{\sigma^2_w}{5.962} + \sigma^2_{rf} + 3.429\sigma^2_{fy}$
Reps x families/years	85	5.158	$\frac{\sigma^2_w}{5.962} + \sigma^2_{rf}$
Within plot	626	15.75	σ^2_w
		Survival	
Years	1	0.0296	
Reps/years	5	0.0523	
Families	17	0.0472	$\sigma^2_p + 3.572\ \sigma^2_{fy} + 7\sigma^2_f$
Families x years	17	0.0221	$\sigma^2_p + 3.429\sigma^2_{fy}$
Reps x families/years	85	0.0118	σ^2_p

[a] Mean squares based on plot means. Family x years mean square is significant at the five percent level for both traits.

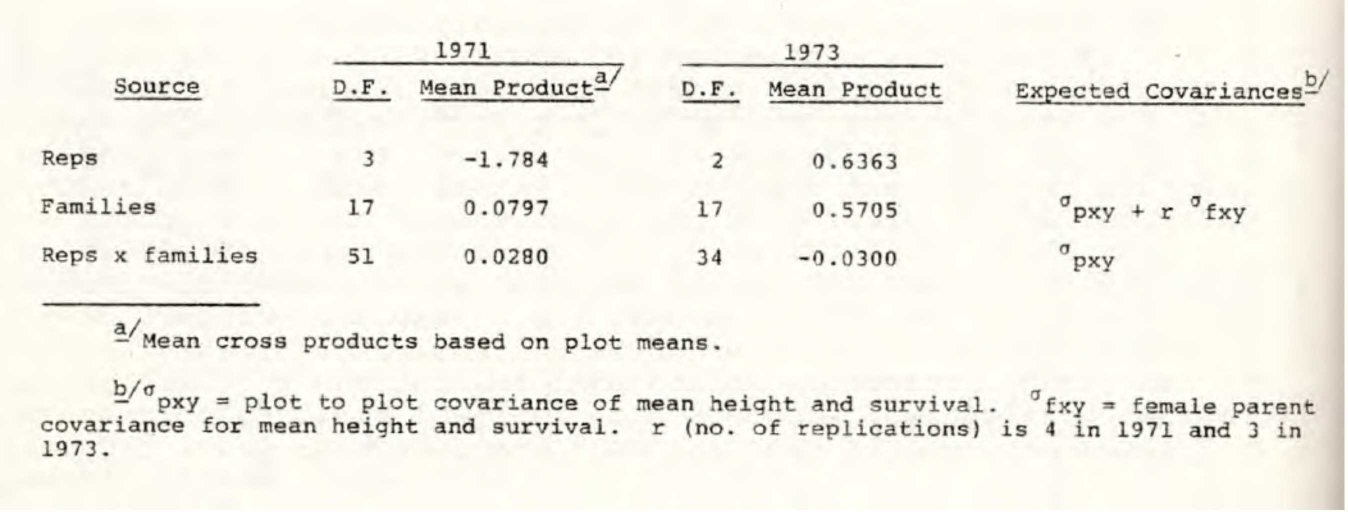
[b] σ^2_w = variance due to difference among progenies in plots. σ^2_{rf} = variance due to interaction of replications and female parents. σ^2_{fy} = variance due to interaction of female parents and years. σ^2_f = variance due to differences among female parents. σ^2_p = variance due to interaction of replications and family plot means.

seedling survival, two out of the top five families are in common for the two years. Further, for each trait, three out of the bottom five ranked families are held in common for 1971 and 1973. However, one of the top five families for height in 1971 is among the bottom group in 1973, and two families exchange rankings between the top and bottom groups for survival. Thus, while rankings are fairly similar for many families in each year, there are also some major shifts which no doubt bring about much of the interaction variance.

Genetic Correlation of Height Growth and Survival

Analyses of covariance for height and survival each year are found in Table 7, and genetic correlations are given in Table 3. Genetic correlation is the degree to which the additive genetic effects of these two traits are related. Both estimates are positive, but the 1973 correlation is much larger. The higher correlation in 1973 is most likely an artifact of the strong seed size effect in that year.

Table 7. Analysis of covariance for height and survival by seed years.



	1971		1973		
Source	D.F.	Mean Product[a]	D.F.	Mean Product	Expected Covariances[b]
Reps	3	-1.784	2	0.6363	
Families	17	0.0797	17	0.5705	$\sigma_{pxy} + r\,\sigma_{fxy}$
Reps x families	51	0.0280	34	-0.0300	σ_{pxy}

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[a] Mean cross products based on plot means.

[b] σ_{pxy} = plot to plot covariance of mean height and survival. σ_{fxy} = female parent covariance for mean height and survival. r (no. of replications) is 4 in 1971 and 3 in 1973.

CONCLUSIONS

1. Much genetic variation, both in three-year height growth and seedling survival, is present among the 18 eastern white pine progenies included in this study.

2. Seed size effects can vary in different years and have considerable influence on the estimation and interpretation of heritability and genetic correlation.

3. The estimates of heritability for 1971 are probably the most reliable in this study, but they may still be over-estimates of the true values. We have shown that genotype x environment interaction can be fairly large, even in the relative uniformity of a nursery environment. Therefore, heritabilities estimated from only one planting in the nursery underestimate the heritabilities that can be expected when several plantings, in different years, are involved. We have also been assuming throughout the analyses that the female parents are random members of the population with regards to both traits (Assumption 1, Statistical Procedures). This may not be true, because the parents used in this study were selected for their vigorous growth in relation to other trees in mature stands. Non-randomness among the parents will, on the average, tend to exaggerate heritability (Squillace and Bengtson 1961), but the bias is probably very slight, since the correlation between adult vigor (measured in natural stands) and nursery height growth is likely to be very small.

4. Selection for height growth on a family basis appears to be a desirable alternative to individual selection in the nursery as long as the additional costs associated with family comparisons, and loss in selection differential, are small. The extent to which selection for height at the nursery stage is worthwhile will depend upon the degree of correlation of seedling height with that of height growth in mature trees. While some results show that this correlation may be fairly strong for individual trees, even up to ten years (Zarger 1965; Synder 1976), the extent of the correlation with crop-age trees and the desirability of this practice in terms of other mature traits, such as disease resistance, form, etc., are not known and await further analysis. Certainly, the high estimates for survival heritability are encouraging, since selection for increased nursery survival is of clear economic importance, especially when valuable, genetically improved stock is involved.

5. The genetic correlation between survival and height is positive. Thus, selection for improved seedling survival, should also lead to a slight increase in juvenile height growth.

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