The presented results indicate a remarkable deviation in frequencies between $B_3B_3$ and $B_2B_3$ (13 : 44 that is 1 : 3.4) which cannot yet be explained satisfactory. Doubling their portions means evaluating a lower limit of the rate of self-fertilization if it can be assumed that both heterozygotes are equally frequent and that the non-detectable homozygote $B_2B_2$ is at least as frequent as $B_3B_3$.

In this case the rate of self-fertilization can be expected to be at least 11.6% (2 X (13 + 44) = 114 selfed seeds out of 987). Having in mind that the deviation in frequencies may be caused by the rare allele $B_3$, all genotypes which are not homozygous with respect to B, can be assumed to be at least equally viable. In this case the given value can be calculated more precise so that the rate of self-fertilization increases to 14.7% (13 + (3 X 44) = 145 selfed seeds out of 987).

### Further aspects

The application of the described method will be extended to estimate rates of self-fertilization and other fertilization probabilities of and between individual trees in stands as well as in seed orchards.

If more investigations are performed, possible uncertainties have to be dealt with such as occurrance of distinct isozyme patterns of the same allele in endosperm and embryo or deviations in the frequencies of the two detectable LAP phenotypes. In addition the estimations of rates of self-fertilization have to be improved, if cross-fertilization by gametes of other marker trees has to be taken in account.

### Acknowledgments

### Summary

Analysing isozymes in endosperm and embryo tissue it is possible to estimate rates of self-fertilization of individual trees. Comparing for example leucin-aminopeptidase isozyme patterns of embryo and endosperm tissue of individual seeds of a certain "marker tree", two out of totally four genotypes originating from self-fertilization can be identified definitely. Preliminary results are given within a stand of Norway spruce: the rate of self-fertilization of one spruce tree was estimated to be 14.7%.

*Key words:* Self-fertilization, Leucin-aminopeptidase (LAP), seed analysis, Norway spruce.

### Zusammenfassung

Anhand der Analyse von Isoenzymen in Endosperm- und Embryogewebe ist es möglich, eine Abschätzung der Selbstbefruchtungsraten von Einzelbäumen vorzunehmen. Vergleicht man z. B. Leucinaminopeptidase-Isoenzymmuster aus dem Embryo- und Endospermgewebe einzelner Samen eines bestimmten Genotyps, so lassen sich zwei von insgesamt vier aus Selbstbefruchtung stammende Typen präzise identifizieren. Ein vorläufiges Ergebnis wird aus einem Fichtenbestand mitgeteilt: Die Selbstbefruchtungsrate einer Fichte wird auf 14,7% geschätzt.

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# Variance components and gains in volume growth of Virginia Pine (Pinus virginiana Mill.)

By G. Rink and E. Thor[1]

## Introduction

Since most estimates of additive genetic variance components in forest tree breeding are based on experiments in only one environment, these estimates may be inflated by the presence of a genotype-environment interaction (Namkoong, Snyder and Stonecypher, 1966; Stonecypher, 1966; Evans and Thor, 1971). These interactions usually are low (King, 1965, Wells and Wakely, 1966; Wright, 1973). However, if it is assumed that most forest trees are hetero-

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zygous for most characteristics, seed collected from random trees in a provenance will probably most closely resemble a "hybrid" blend with considerable genetic diversity. Crop breeders generally recognize that genetic diversity contributes to phenotypically consistent performance (Allard, 1961; Reich and Atkins, 1970).

One objective of this paper is to evaluate and compare the genotype-environment interaction at the provenance and open-pollinated progeny levels in Virginia pine (*Pinus virginiana* Mill.). Another objective is to obtain estimates of heritability and gain in volume growth of this species.

## Materials and Methods

Plantations were established in 1967 from open-pollinated seed collected from 13 stands, four in Kentucky and

nine in Tennessee, selected from the Coastal Plain, Cumberland Plateau and Mountains, and Great Valley physiographic regions *(Figure 1)*. All were even-aged natural stands of average or better than average quality established on abandoned fields with 50-year site indices ranging from 60 to 87 feet (THOR, 1964). With one exception (stand 10), they had received no silvicultural treatment or management; stand 10 was a United States Forest Service seed production area which had been heavily thinned to remove undesirable trees. The stands ranged in age from 28 to 53 years.

between rows. Two border rows were planted around each plantation; these consisted of a mixture of half-sib progenies.

## Measurements

Five-year measurements were obtained from all plantations at the end of the 1971 growing season. Measurements included:

1. Total height to the nearest foot (1 ft = 0.3048 m).
2. Stem diameter at the midpoint of the total height of each tree (half-height) to the nearest 0.1 inch.
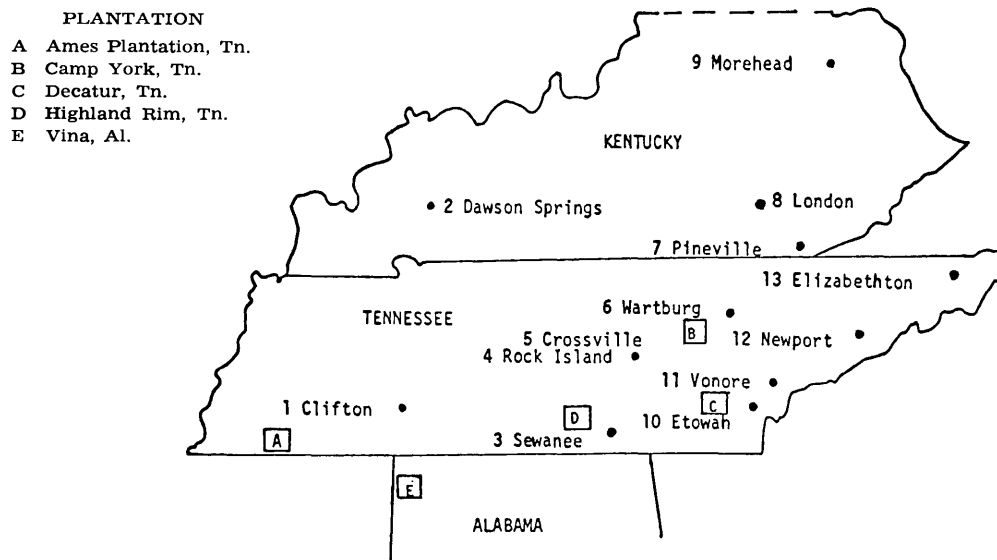


Figure 1. — Location of parent stands and plantation sites in Kentucky, Tennessee, and Alabama.

Within each stand 15 trees were selected as potential parent trees from which seed could be collected. Criteria for selection were that trees be dominants or codominants and that they could be climbed safely. Although poor, average, and excellent phenotypes were included, these criteria may have resulted in a slight sampling bias toward taller and sturdier trees. Abundant cone production was not a selection criterion.

Replicated plantings of open-pollinated progeny were installed at each of five planting locations. Of the original 195 trees selected as parents, only 128 yielded enough seedlings to be included in the experiment. Unfortunately, the number of progeny produced by parent trees varied so much that only the Highland Rim plantation included all 128 families. Ninety families were represented at the other four locations.

At each location seedlings were outplanted in 10-tree row plots arranged in a randomized complete block design in which families nested in stands were randomized in blocks. Each plot contained half-sib progeny of a single parent tree.

All plantations consisted of 10 replications with the exception of Vina which had nine replications. Spacing between trees was 4 feet within family-row plots and 8 feet

Individual tree volumes were computed from total height and stem diameter measurements by a volume prediction equation for young loblolly pine (PERRY and ROBERTS, 1964):

$$V = (10.62D^2H)/1728$$

where

$V$ = volume in cubic feet (ft³).
$D$ = stem diameter at half-height in inches.
$H$ = total height in feet.

### Statistical Analysis

Expected mean squares for the model used for the analysis of variance, combined across all locations, are presented in *Table 1*. All effects were assumed to be random except location, which was fixed. The linear model for this analysis is:

$$Y_{LR(F/P)W} = M + L_L + R/L_{R/L} + P_P + PL_{PL} + F/P_{F/P} + (FL)/P_{(FL)/P} + E_{LR(F/P)} + W_{LR(F/P)W}$$

where

$Y_{LR(F/P)W}$ = individual observation.
$M$ = mean
$L_L$ = location effect $L = 1,\ldots,q$, where $q$ = number of locations.
$R/L_{R/L}$ = effect of replications whithin locations, $R/L$ =

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1,...,j, where j = number of replications at a given location.

$P_P$ = stand effect, P = 1,...,i, where i = number of stands.

$PL_{PL}$ =·effect of interaction of stand with location.

$F/P_{F/P}$ = family-within-stand effect, F/P = 1,...,t, where t = number of families in a given stand.

$(FL)/P_{(FL)/P}$ = effect of wihtin-stand interaction of location with family.

$E_{LR(FP)}$ = term resulting from pooling effects for interaction of stand with replication in location and of family with replication-within-location-and-stand (Error A).

$W_{LR(FP)W}$ = within-plot effect.

The "Harvey Procedure", (Maximum Likelihood General Purpose Program) computes least-squares estimates of variance components for all effects (in other words, for the terminal variance component and "k" coefficient on each main effect component in the expected mean square) except interaction effects. However, since the program provides inverse elements of segments of the inverse matrix for each effect, "k" coefficients were computed for these interactions using the "direct method" of Harvey (1960):

$$k = \frac{1}{m}\left[ \sum_i Z^{ii} - \frac{1}{d.f.} \sum_{ij} \sum Z^{ij} \right]$$

where

d.f. = number of degrees of freedom for the effect in the sample of data.

m = number of subclasses.

$\sum_i Z^{ii}$ = sum of diagonal elements of the appropriate segments of the matrix.

$\sum_i \sum_j Z^{ij}$ = sum of off-diagonal elements of that matrix.

The resulting "k" coefficient is divided into the difference between the two appropriate mean squares to obtain an estimate of the variance component.

An analysis of variance was computed across all locations following a combination of Henderson's (1953) Method 1 and Method 3. To avoid negative sums of squares and obtain least squares estimates of mean squares, the analysis was partitioned into three models.[2]

latter three were computed separately for each stand. Sums of squares from these models were then combined into an overall analysis of variance.

### Combined Location Analysis

Mean squares, degrees of freedom, and levels of significance are presented in *Table 2*. The predominance of statistical significance for all sources tested is a reflection of the sensitivity of the experimental design.

*Table 2.* — Analysis of variance for volume per tree.

| Source of Variation | d.f. | Mean Squares |
|---|---|---|
| Locations | 4 | 584.1694 |
| Replications in locations | 44 | 26.1942** |
| Stands | 10 | 50.6665** |
| Stands × locations | 37 | 1.9936** |
| Families in stands | 93 | 5.9909** |
| (Locations × families)/stands | 318 | 0.9550** |
| Error A[a] | 3917 | 0.6010** |
| Residual (within plot) | 29749 | 0.2974 |

a Sums of squares for the interaction of stand with replication within location and for the interaction of families with replication within location and stand were pooled to obtain sums of squares for Error A.

** P < 0.01.

Estimates of variance components are presented in *Table 3*. No variance component was computed for replications within locations or for the interaction of stand with replication in locations; therefore, their percent contributions to total variance were not computed. Since locations were assumed to be fixed, no variance component was available corresponding to this effect.

The within-plot component accounts for 80 percent of phenotypic variance and is the single largest source. Variance components for parent stands and for families within stands each contributed approximately 4.6 percent to phenotypic variance.

The components for the two interactions, $S^2_{L \times P}$ and $S^2_{(L \times F)/P}$ are so small that for practical purposes they

*Table 1.* — Analysis of variance and expected mean squares for analysis combined across locations.

| Line Number | Source of Variation | d.f. | Expected Mean Squares |
|---|---|---|---|
| 1 | Locations | L-1 | $\sigma^2_W + k_{13}\sigma^2_E + k_{14}\sigma^2_{R/L} + k_{15}\sigma^2_{L \times P} + k_{16}\sigma^2_{(L \times F)/P} + k_{17}\Theta^2_L$ |
| 2 | Replications within locations | (R-1)L | $\sigma^2_W + k_{11}\sigma^2_E + k_{12}\sigma^2_{R/L}$ |
| 3 | Stands | (P-1) | $\sigma^2_W + k_9\sigma^2_E + k_{10}\sigma^2_P$ |
| 4 | Stands × Locations | (P-1)(L-1) | $\sigma^2_W + k_7\sigma^2 + k_8\sigma^2_{L \times P}$ |
| 5 | Families within stands | (F-1)P | $\sigma_W + k_4\sigma^2_E + k_5\sigma^2_{(L \times F)/P} + k_6\sigma^2_{F/P}$ |
| 6 | (Locations × families) within stands | (L-1)(F-1)P | $\sigma^2_W + k_2\sigma^2_E + k_3\sigma^2_{(L \times F)/P}$ |
| 7 | Error A | L[(F-1)(R-1)P + (P-1)(R-1)] | $\sigma^2_W + k_1\sigma^2_E$ |
| 8 | Residual (within plot) | (W-1)RF(P)L | $\sigma^2_W$ |

Sums of squares for the effects of locations, stands and their interaction were computed independent of the complete model *(Table 1)* as were the effects for families, locations and their interaction; sums of squares for the

can be disregarded; their combined total accounts for only one percent or less of the phenotypic variance.

It should be noted that these two interaction components are based on least squares estimates of k values obtained by the "direct method" of Harvey (1960). A common method of verifying the accuracy of estimates of k values is to compare them with harmonic means of subclass frequencies.

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Table 3. — Estimates of variance components ($S^2$) and heritability ($h^2$), and standard errors (S.E.) for volume per tree.

| Source | Estimated variance component × 100 | Standard Error × 100[a] | Percent of estimated Phenotypic variance |
|---|---|---|---|
| $S^2_P$ | 0.0172 | | 4.65 |
| $S^2_{L \times P}$ | 0.0011 | | 0.30 |
| $S^2_{F/P}$ | 0.0171 | ±0.0030[a] | 4.62 |
| $S^2_{(L \times F)/P}$ | 0.0026 | | 0.70 |
| $S^2_{(R \times F)/L,P}$[b] | 0.0348 | | 9.40 |
| $S^2_W$ | 0.2974 | | 80.33 |
| $h^2$[c] | 0.1944 | ±0.0341[d] | |

[a] S.E. $(S^2_{F/P})$ = standard error of family-within-stand variance component

$$\sqrt{\frac{2}{k_6^2} \left[ \frac{M.S.^2_{F/P}}{d.f. + 2} + \frac{M.S.^2_{(L \times F)/P}}{d.f. + 2} \right]}$$

[b] This component obtained by substracting the within-plot mean square in Model A (Table 1) from the mean square for (family × replication)/locations and stands, and dividing the resulting difference by an estimate of k (Model A, Table 1) obtained from the sum and sum of squares of all frequencies of family × replication in stands and locations in the formula:

$$k = \frac{1}{d.f.} (N - \frac{\Sigma n^2}{N}).$$ *

* N = Total number of observations

n = Number of observations in each cell.

The mean square for (family × replication)/location and stands was obtained by subtracting from the sum of residual sum of squares for all stands in Model C (Table 1) the within-plot sum of squares in Model A (Table 1) and dividing by the appropriate degrees of freedom (Table 1).

[c] $$h^2 = \frac{4s^2_{F/P}}{s^2_W + s^2_{(R \times F)/L,P} + s^2_{(L \times F)/P} + s^2_{F/P}}$$

[d] S.E.$(h^2)$ = standard error of heritability

$$\frac{4 \times S.E. (s^2_{(F/P)})}{s^2_W + s^2_{(R \times F)/L,P} + s^2_{(L \times F)/P} + s^2_{F/P}}$$

While estimates of k values for main-effect components are in fairly close agreement with harmonic means, estimated k values used in computing $S^2_{L \times P}$ and $S^2_{(LxF)/P}$ (Table 4) are double the harmonic means in all but one

Table 4. — Estimates of k values used in estimating the interaction variance components $\sigma^2_{(L \times F)/P}$ and $\sigma^2_{L \times P}$ and harmonic means of corresponding subclass frequencies. The arithmetic average of k values of the 11 stands was used in estimating $\sigma^2_{(L \times F)/P}$.

| Stand Number | k Value for $\sigma^2_{(L \times F)}$ | Harmonic Mean |
|---|---|---|
| 1 | 66.07 | 66.78 |
| 2 | 191.82 | 64.31 |
| 3 | 128.37 | 66.73 |
| 4 | 149.30 | 69.79 |
| 6 | 148.19 | 74.40 |
| 7 | 145.34 | 58.75 |
| 8 | 136.18 | 71.55 |
| 9 | 142.00 | 73.64 |
| 10 | 145.71 | 71.27 |
| 11 | 132.41 | 61.52 |
| 13 | 141.19 | 72.68 |
| Average | 138.78 | 68.19 |

| k Value for $\sigma^2_{L \times P}$ | Harmonic Mean |
|---|---|
| 1286.38 | 601.16 |

case. Only for stand 1 is the k value for the interaction of families and locations in close agreement with the harmonic mean. Since stand 1 is the least unbalanced of all

stands and, unlike all other stands, has no missing cells in any replications, it appears that the lack of agreement between k values and harmonic means is the result of confounding due to unbalanced of experimental design. Use of estimates of k values obtained by the "direct method" of HARVEY (1960) in calculation of interaction variance components provides conservative estimates of these components. Use of harmonic means in these calculations would double the estimates of interaction variance components, thus accounting for a maximum of two percent of the phenotypic variance.

## Application of Results

Since Virginia pine is grown primarily for fiber, increased yield of wood per tree is an appropriate primary selection criterion. RINK and THOR (1973) found that gains in weight of wood per tree were at least 10 percent greater when selection was for diameter only than when selection was for a combination of diameter and specific gravity. Although a positive correlation existed for individual trees between diameter growth and wood specific gravity (r = 0.235), this correlation was not present on a stand mean basis; the fastest growing stands had significantly lower wood specific gravity than several slower growing stands. Since individual tree volumes were highly correlated with both diameter and height, volume was chosen as the primary selection criterion.

Low stand × location and family-within-stand × location variance components suggest that by selecting trees from stands and families with high volume growth at all locations, the establishment of one seed orchard to provide improved seed for all localities may be possible. This may involve some sacrifice of local growth potential because families with outstanding growth at only a few locations would be rejected.

Results (Table 3) suggest that a combination of stand, family-within-stand, and within-plot selection may be appropriate for a long term breeding program to increase volume yield. Merits of such a three-stage selection system, as compared to a two-stage scheme without stand selection, and with single-stage mass selection as they may be applied to the five study locations, can be compared on the basis of expected gains.

Expected gains were computed using the variance components method for multistage selection described by NAMKOONG, SNYDER and STONECYPHER (1966) and adapted by EVANS and THOR (1971). These are the gains to be expected at each location if the plantation were rogued of everything except selected trees.

Stand selection, the first stage of the three-stage system, may be based on DUNCAN's New Multiple Range Test. Trees originating from any stand with the poorest growth, or not significantly different from the poorest, at any plantation would be marked for roguing.

Such a selection scheme would result in the selection of four stands: stand 7 from the Cumberland Mountains of south Kentucky, stand 10 from the Great Valley near Etowah, Tennessee, stand 11 from the Great Valley near Vonore, Tennessee, and stand 13 from the Great Valley near Elizabethton, Tennessee. Trees from stand 10 provided the greatest volume growth at all locations except Vina where trees from this stand ranked second. This superiority may be a reflection of the fact that trees from stand 10 are open-pollinated progeny of selected phenotypes; the original stand had been rogued to remove undesirable trees.

Selection of families from these four stands would again

be on the basis of good performance at all locations. Rejecting families ranking in the lower half of families from the four selected stands in more than one location would retain a total of 13 families.

Within-plot selection would result in the retention of the one phenotypically most superior individual in each plot containing trees from the selected families.

Selection intensities for family and within-family selection at each location in the three-stage selection scheme are shown in Table 5, along with mean tree volumes for unselected populations and for the four selected stands. Table 6 presents expected gains from the three-stage and two-stage selection, for each location, together with variance components for analyses of variance of the four stands selected for retention in three-stage selection.

The expected gains resulting from such a three-stage selection scheme are surprisingly high. Percent gain over

mean unselected volume ranges from a low of 23.5 at Decatur to a high of 61.9 percent at Camp York. The high expected gain at Camp York is the result of the relatively great family-within-stand variance component at that location.

Expected gains from stand selection range between 10 and 13 percent. Gains from family and within-family selection are more variable, both ranging among locations from 6 to 20 percent.

Two-stage selection results in greater expected gains than three-stage selection at two plantations, Decatur and Highland Rim; three-stage selection shows higher gains at the other three locations. This result is not unexpected; since only stands with superior performance in all locations were selected, some individual families with superior performance in a specific location would be deleted.

Choice of a selection scheme should depend upon relative

Table 5. — Mean tree volumes, numbers of families and selection intensities for three-stage selection.

| Items | Ames | Camp York | Decatur | Highland Rim | Vina |
|---|---|---|---|---|---|
| Mean tree volume, unselected population, ft³ | 0.081 | 0.089 | 0.090 | 0.151 | 0.114 |
| Mean tree volume, four selected stands, ft³ | 0.091 | 0.101 | 0.100 | 0.166 | 0.126 |
| Families in four selected stands, number | 34 | 34 | 39 | 39 | 36 |
| Families selected from four best stands, number | 12 | 12 | 13 | 13 | 13 |
| Family selection[a] intensity | 1.05 | 1.05 | 1.10 | 1.10 | 1.03 |
| Average number[b] of trees per plot | 7.74 | 6.84 | 6.11 | 9.18 | 9.23 |
| Within-family[a] selection intensity | 1.63 | 1.55 | 1.52 | 1.70 | 1.70 |

[a] NAMKOONG, G., and E. B. SNYDER. 1969. Accurate values for selection intensities. Silvae Genetica 18: 172—173.
[b] Based on average within-plot survival at each location.

Table 6. — Variance components, narrow sense heritability, expected volume gains per tree at age 5, and new population means, resulting from three-stage selection, and expected gains from two-stage selection. Numbers in parentheses indicate percent contribution of each stage of selection.

| Component | Ames | Camp York | Decatur | Highland Rim | Vina |
|---|---|---|---|---|---|
| $S^2_W \times 1000$ | 2.488 | 3.347 | 2.555 | 4.140 | 4.039 |
| $S^2_{(F \times R)/P} \times 1000$ | 0.410 | 0.562 | 0.522 | 0.445 | 0.594 |
| $S^2_{F/P} \times 1000$ | 0.110 | 0.350 | 0.065 | 0.291 | 0.300 |
| $h^2$ | 0.15 | 0.33 | 0.08 | 0.24 | 0.24 |
| Gain from stand selection, ft³ | (12.6) | (13.3) | (11.1) | (9.9) | (10.8) |
| | 0.012 | 0.012 | 0.010 | 0.015 | 0.012 |
| Gain from family selection, ft³ | (10.5) | (19.3) | (6.3) | (10.8) | (13.3) |
| | 0.009 | 0.017 | 0.006 | 0.016 | 0.015 |
| Gain from within family selection, ft³ | (12.2) | (29.2) | (6.0) | (14.5) | (19.8) |
| | 0.010 | 0.026 | 0.005 | 0.022 | 0.023 |
| Total gain, ft³ | 0.029 | 0.055 | 0.021 | 0.053 | 0.050 |
| Estimated mean of new population, ft³ | 0.110 | 0.144 | 0.111 | 0.204 | 0.164 |
| Percent gain, three-stage selection | 35.2 | 61.9 | 23.5 | 35.2 | 43.9 |
| Percent gain, two-stage selection | 22.3 | 51.2 | 26.3 | 40.0 | 33.9 |

improvement in volume growth expected in trees from seed produced by the resulting seed orchard. Although three-stage selection provides approximately 10 percent estimated improvement from stand selection, additional progeny testing will be needed to determine the actual magnitude of this gain.

Gains from mass selection consisted of 13 to 27 percent of the gains from two-stage selection. Therefore, mass selection would be a less effective technique for producing improved seed.

Assuming that the Highland Rim plantation were to be converted into a seed orchard by one of the two selection schemes outlined, one more problem arises. Most effective seed orchard spacing is about 30 feet by 30 feet, or between 40 and 48 trees per acre (each replication is approximately one acre). While the selection schemes outlined allow for only 13 trees per acre, if the need for seed is more immediate, selection intensities could be lowered enough to permit retention of the number of trees required for optimum production.

## Summary

Analysis of tree volumes at age five in a progeny test of wind pollinated *Pinus virginiana* MILL. revealed that 80 percent of phenotypic variance was associated with differences between half-sib progeny within plots. Progeny were from randomly selected trees in 13 natural stands in Tennessee and Kentucky, and were outplanted in randomized complete block designs at five locations.

Variance components for the interactions between planting locations and parent stand, and among locations and families within stands together accounted for less than one percent of the total, and could thus be disregarded. A three-stage selection scheme, eliminating progeny from the poorer parent stands, the poorer families and all but the best tree of each family in each replication should result in gains ranging from 23.5 to 61.9 percent at individual planting locations.

*Key words: Pinus virginiana* MILL., Volume growth, Genetic gain, Genotype — environment Interaction.

## Zusammenfassung

In 13 autochthonen Beständen von *Pinus virginiana* MILL. in Kentucky und Tennessee wurden insgesamt 128 Familien aus freier Abblüte zufällig selektiert und auf 5 Versuchsflächen in 10facher Wiederholung in je einem randomisierten, vollständigen Blockversuch ausgepflanzt. Die Untersuchung im Alter 5 ergab, daß 80% der gesamten phaenotypischen Varianz auf Halbgeschwister innerhalb der Parzellen entfielen, während nur weniger als 1% auf die Interaktionen Standort × Bestände und Standort × Familien entfiel. Ein simuliertes 3fach hierarchisches Selektionsschema (Elimination der schlechtesten Bestände und der schlechtesten Familien in verbleibenden Beständen und Auswahl des besten Baumes in verbleibenden Familien) ergab einen Gewinn von 23 bis 62% auf den einzelnen Standorten.

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