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Geographic Variation in Virginia Pine

Results of the First Trial in Pennsylvania, Maryland and Tennessee[1]

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1. Introduction

Virginia pine *(Pinus virginiana* Mill.), distributed over a large range in the eastern United States, is highly valued for pulpwood. Therefore, it is worth consideration for planting and more intensive study.

As a pioneer species on a variety of sites, Virginia pine occurs from sea level to elevations of 2,500 feet in the Appalachian Mountains *(Fig. 1)*. It grows naturally in 16 states from Long Island (New York) and central Pennsylvania to northern Mississippi, Alabama and South Carolina but is not found on the Coastal Plain south of Virginia. The western range consists of isolated stands in southeastern Indiana and western Tennessee.

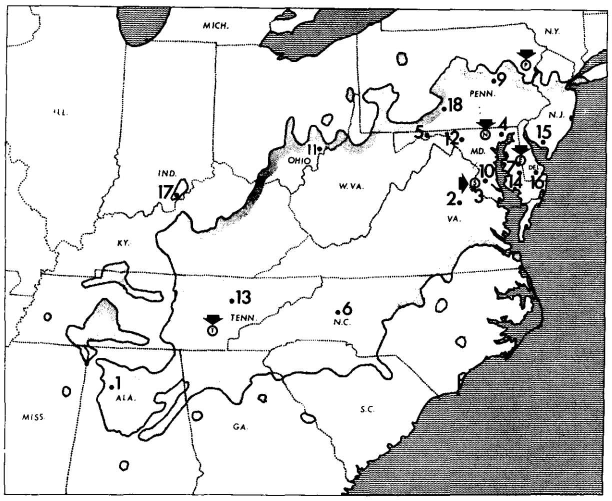

Figure 1. — Natural distribution of Virginia pine, locations of collection areas (numbered dots) and locations of test areas (letters in circles, devoted by arrows).

Virginia pine is placed in the series *Insignes*. It has two (sometimes three) needles per fascicle which are 1.5 to 3.5 inches long, pale green, usually twisted, rigid, and sharp-pointed. Cones are two to three inches long, reddish brown at maturity, conic-ovoid to oblong, symmetrical, persistent and are found in all portions of crown. Cone scales are thin, flat, terminating in a prickle.

The bark is dark brown. Under forestry conditions Virginia pine reaches heights of 80 feet and more, but open-grown trees are stunted and scrubby.

This species has only recently become a commercially important tree with the growth of the southern pulp industry. Consequently, there is no large backlog of silvicultural, growth and genetic information for Virginia pine as exists for many other species in the region (Nelson ***et al.***, 1951; Genys *et* al., 1964). Several attempts have been made to cross Virginia pine with other species (especially of *Insignes*), but only the cross of P. *virginiana* X P. *clausa* was a certain success. Some superior tree selection has been made followed by grafting and establishment of seed orchards but there are no published data on individual tree inheritance. Thor (1964) studied the phenotypic range in wood properties of Virginia pine in Kentucky and Tennessee. He found variations of .49 to .55 in specific gravity and 3.5 to 4.2 millimeters in tracheid lengths.

2. Objectives, Materials and Methods

This study was started in 1955 by Craig D. Whitesell, then employed by the Maryland Department of Research and Education (Whitesell, 1958). The objectives were to (1) determine the range and pattern of genetic diversity, (2) provide practical information on the best seed sources for immediate reforestation needs, and (3) provide basic information for future, more intensive improvement programs.

Two trials were started. This is a report on Trial No. 1, which includes data on a total of 17 provenances from 10 states, grown in permanent test plantations in three states *(Fig.* 1). Two plantations in Maryland were nearly complete

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Table 1. — Origin data for the 17 provenances of Virginia pine *(Pinus virginiana* MILL.).

Seedlot Number	Seedlot Origin			
	State	County	Town or Forest (F.)	Elevation
				feet
1-MD.	Alabama	Winston	—	—
2-VA.	Virginia	Spotsylvania	Fredericksburg	75
3-MD.	Maryland	Charles	Doncaster State F.	120
4-MD.	Maryland	Harford	Broadcreek Scout Camp	480
5-MD.	Maryland	Allegany	Green Ridge State F.	300
6-N.C.	North Carolina	Alexander	Hiddeite	1500
7-MD.	Maryland	Caroline	S. E. of Denton	50
9-PA.	Pennsylvania	Columbia	McCauley Station	750
10 MD.	Maryland	Charles	Cedarville State F.	200
11-OHIO	Ohio	Washington	East of Reno	300
12-MD.	Maryland	Frederick	N. E. of Frederick	620
13-TENN.	Tennessee	Anderson	Island Home Church	960
14-MD.	Maryland	Carolina	Federalsburg	20
15-N.J.	New Jeresy	Cumberland	Millville	80
16-DEL.	Delaware	Sussex	Hollyville	30
17-IND.	Indiana	Clark	—	—
18-PA.	Pennsylvania	Huntingdon	Standing Stone Exp. F.	850

failures and were therefore abandoned. Five permanent plantations are now available for measurement. Each individual plantation includes only 16 different provenances.

In 1955 cooperators were asked to collect cones from 10 "average" native trees in their vicinity. The seed from each collection area was combined to provide one sample representative of that locality. Pertinent origin data are presented in *Table 1.*

The seeds were sown in spring 1956 at the Maryland State Forest Tree Nursery at Harmans, south of Baltimore. Each seedlot was grown in an unreplicated rectangular plot.

The plantations were established in 1957, 1958, and 1959, using one, two, or three years old stock *(Table 2).* A randomized complete block design was used with 4-tree plots in one plantation and 1-tree plots in 4 other plantations, with in 13 to 25 replications per plantation.

THOMAS G. ZARGER of the Tennessee Valley Authority measured the Tennessee plantation. In other plantations, Mr. WHITESELL made the earlier measurements and later ones were made by the author. The Southern Maryland plantation S was the only plantation with four trees per plot (16 provenances in 13 blocks). There were no missing plots but some plots included only two or three trees. The plot averages were used in the analysis of variance, with the degrees of freedom as follows:

Source of Variation	Degrees of Freedom
Total	207
Blocks	12
Provenances	15
Blocks × Provenances (Error)	180

In other plantations, the 1-tree plots resulted in many missing plots as some individual trees died. Data from these test areas were analysed as a completely randomized experiment with unequal numbers of observations per class with the following degrees of freedom (example from the Maryland plantation N)

Source of Variation	Degrees of Freedom
Total	360
Provenances	15
Error	345

Multiple range tests, using special protection levels (based on degrees of freedom) were applied to determine the significance of differences among specific provenances within a plantation (DUNCAN, 1955). Multi-plantation analysis of variance was performed by summing the sums of squares applicable to the individual plantations. Varietal means were used as items in computing the correlation coefficients.

Table 2. — Description of the five test sites and of the details of experimental design and establishment.

	Location and description	Details of design and establishment
P	Pennsylvania, Monroe Co., Dilldown Exper. For., near Pimple Hill in Pocono Mtns.; stony, elev. 2.000 feet. Owner: Penna. Dept. of Forests & Parks.	1957; 1—0; 16 provenances in 24 blocks; 1 tree per plot; spaced at 10 × 10 feet; brush removed by bulldozer before planting.
N	Northern Maryland, Baltimore Co., Pretty Boy Reservior, Piedmont Plateau, about $8^{0}/_{0}$ north slope; elev. 800 feet. Owner: Baltimore Dept. of Public Works.	1957; 1—0; 16 provenances in 25 blocks; 1 tree per plot; spaced at 10 × 6 feet. Seedlings planted after scalping 1.5 feet squares; first-year mortaly replaced.
E	Eastern Maryland, Caroline Co., near Burrsville, coastal plain of the Eastern Shore, high ground water level, elev. 50 feet. Owner: Glatfelter Pulp Wood Company.	1957; 1—0; 16 provenances in 15 blocks; 1 tree per plot; spaced at 10 × 6 feet.
S	Southern Maryland, Charles Co., Smallwood State Park, coastal plain; elev. about 120 feet. Owner: Md. Dept. of Forests & Parks.	1959; 3—0; 16 provenances in 13 blocks; a 4-tree row per plot; trees spaced at 10 × 6 feet.
T	Tennessee, Hamilton Co., Friendship Exper. Area near Chickamauga Reservoir, formerly farm land. Owner: Tennessee Valley Authority.	1958; 2—0; 16 provenances in 24 blocks; 1 tree per plot; spaced at 10 × 10 feet; first-year mortality replaced.

3. Condition of Plantations in 1963

The research plots in the Pennsylvania plantation P had been cleared of brush by bulldozer but the brush rapidly reinvaded. Other plantations remained relatively clean. At the time of measurement, trees had wide crowns but the canopy was still open.

All five research plantations were attacked by the Nantucket pine tip moth *(Rhyacionia frustrana* [COMST.]), disturbing the course of growth. Therefore, branch sizes and some other traits were not studied. In Maryland plantations, a less important damage on foliage was caused by the Virginia pine sawfly *(Neodiprion pratti pratti* [DYAR.]).

Field mice *(Microtus pennsylvanicus* [ORD.]) were the worst pests in Maryland. They girdled and practically destroyed one research plantation in Howard County, Maryland, and two blocks of the plantations in southern Maryland, necessitating elimination of these blocks when calculating comparative growth rates.

4. Mortality

Of the five test plantations, the Pennsylvania plantation P suffered the highest mortality *(Table 3)*. It is on a rocky site outside the natural range of Virginia pine. The same site has had previous failures with other species. In the Virginia pine plantation about 18 per cent of the trees were dead in 1960 (first year); about 33 per cent at the end of 1963.

There were differences among origins at the Pennsylvania site. The four southern origins from Alabama, Virginia, North Carolina, and Tennessee accounted for 62 per cent of the dead trees in 1960 (first year) and for 55 per cent in 1963. The remainder of the mortality was scattered among the 12 northern origins. Analysis showed that the differences in the mortality by 1963 were significant (F value due to origin was 10.51; 2.09 needed for significance at the 1 per cent level; the approximate difference in mortality needed for significance was 9).

Table 3 also contains mortality data for the other four plantations. The apparent decrease in the dead-tree count for some provenances in 1963 was due to replacement of dead trees at the start of the second growing season (in N and T plantations). The first-year mortality differences between origins were significant at the 5 per cent level. This was due to the high mortality of the Alabama provenance (F value = 2.11 with 16/44 degrees of freedom). By the end of 1963, however, there were no discernible between-provenance differences (F = 0.84). For these four plantations the average percentages of dead trees were:

Table 3. — Mortality of the 17 provenances of Virginia pine at five different plantations.

Seedlot No.	Mortality in Plantations			
	P Pennsylvania		N, E, S, T Maryland and Tennessee[1]	
	First year	1963	First year	1963
	number of dead trees			
1-ALA.	21	21	22	16
2-VA.	7	13	3	5
3-MD.	4	8	3	7
4-MD.	0	5	3	6
5-MD.	0	0	0	4
6-N.C.	8	16	5	9
7-MD.	4	7	5	11
9-PA.	2	5	6	9
10-MD.	2	5	3	5
11-OHIO	2	6	2	8
12-MD.	0	1	9	11
13-TENN.	13	20	3	6
14-MD.	3	7	7	10
15-MF.	0	2	3	9
16-DEL.	2	8	1	3
17-IND.	—	—	2	5
18-PA.	1	3	4	12
Total dead	69	127	81	136
Numbers of tree planted				
Per Origin	24		126	
Total	384		2016	

[1] In Plantations N (Maryland) and T (Tennessee), dead trees were replaced before the second growing season.

Plantation	Mortality at end of	
	First Year	1963
	— per cent —	
N	3	10
E	0.2	4
S	5	8
T	6	4

5. Height Growth

The plantations may be divided into two groups with regard to 7-year height growth. P tells one story and the four other plantations tell a different story. This is apparent from either the comparative growth rates in *Table 4* or the between-plantation correlations in *Table 5*. Performance at the Pennsylvania plantation P was negatively correlated with that at every other site. On the other hand there were

Table 4. — Comparative growth rates of the Virginia pine provenances at the 5 test plantations arranged in decreasing order of growth rate at Maryland and Tennessee plantations.

Seedlot No.	Heights at Plantations					
	P Pennsylvania	N	E	S	T Tennessee	Average 7-year height, Plantations N, E, S, T
		Maryland				
	per cent of plantation mean					*per cent of mean*
3-MD.	89	108	103	110	110	108
10-MD.	94	105	107	107	110	107
13-TENN.	123*	105	101	108	113	107
14-MD.	97	108	112	102	100	106
16-DEL.	95	106	105	105	107	106
7-MD.	98	114	100	105	100	105
4-MD.	106	98	104	100	98	100
2-VA.	86	105	100	98	98	100
11-OHIO	103	100	103	103	93	99
6-N.C.	86*	97	96	102	100	99
17-IND.	—	—	—	95	94	95
9-PA.	105	97	95	97	92	95
12-MD.	95	98	96	93	94	95
1-ALA.	108*	86	91	102	101	95
15-N.J.	97	89	99	93	90	92
18-PA.	110	89	89	90	95	91
5-MD.	95	86	91	—	—	88
Approx. Diff. needed for significance at 5 per cent level	17	12	15	10	12	7
	feet					
Plantation mean	6.32	6.46	7.47	5.92	8.38	7.06

*) based on less than 10 surviving trees, and of doubtful reliability.

Table 5. — Correlations between 7-year heights of Virginia pine provenances at 5 different planting sites.

Correlation coefficients (r) between the heights in				
Plantation (below) and	*Plantations* N	E	S	T
P	—.206	—.293	—.042	—.008
N	1.000	.783	.690	.407
E		1.000	.560	.386
S			1.000	.908

more or less strong correlations among performance at each of the other sites.

In the Pennsylvania plantation P four of the most northerly origins grew best. Two were from Pennsylvania, one from near Baltimore, Maryland, and one from southeastern Ohio. Presumably winter damage at the rather cold test site prevented expression of the inherently more rapid growth of the more southern types.

There were pronounced and statistically significant differences in 7-year height among the remaining four plantations. In the Tennessee plantation T average height was 8.4 feet; in Maryland's eastern shore plantation E it was 7.5 feet; near Baltimore (plantation N) it was 6.5 feet; and in southern Maryland (plantation S) it was only 5.9 feet. Such growth rates correspond to the known productivity of the various regions.

On the Tennessee and four Maryland test sites there was no discernible interaction between provenance and test site indicating that particular seedlots grow well at all sites. Possible significance of the interactions was tested by the standard error of a difference ignoring number of trees because the samples were of similar size, expressed as a plantation mean. None of the interactions approached significance at the 5 per cent level.

6. Effect of Plot Size

Four-tree plots for each seed source, planted in 13 blocks, were used in the Southern Maryland plantation S; 832 trees in total. The other plantations contained 400 trees where each seedlot was represented by 25 one-tree plots.

Actually, the Southern Maryland plantation S was more precise as it offered the smallest least significant differences (L. S. D.) for interpretation of growth rates *(Table 4)*. Theoretically, with the double number of trees the size of the standard error should have been reduced to $1/\sqrt{2} = .707$. However, the least significant difference for the plantation S in comparison to those of the plantations N and T was reduced to only .833.

The plantations arranged by one-tree plots resulted in a large number of missing plots. However, the portion of these dead trees was relatively small. The data from remaining trees, considered as data from a completely randomized experiment, offered quite satisfactory statistical efficiency to separate the significant differences between the provenances, but no data on differences between the replicates.

7. Reliability of Early Height Measurements

Correlations were calculated between previous and the 7-year height measurements. The 2-year heights had been measured shortly after planting and depended strongly on depth of planting. Because of this lack of precision in determining the actual 2-year heights, the 2−7-year correlatons were low ($r = .48$, .28 and .36 for plantations P, N and E, respectively).

On the other hand an age 5−7 correlation for plantation P was high ($r = .90$). An age 4−7 correlation was strong ($r = .69$) for plantation S. An age 3−7 correlation was low but significant ($r = .50$) for plantation T. The first two were signficant at the 1 per cent level (with 14 degrees of freedom); the last mentioned at the 5 per cent level.

8. Practical Implications

There was generally a difference of about 20 per cent between the slowest and the fastest growing seedlots. That would be the height growth difference between planting the best and poorest seedlots. The volume differential would be considerably greater.

More refined improvement techniques are now in order. These may be either more detailed provenance studies (some are already in progress) or plus-tree selection followed by seed orchard establishment or selective breeding. If a selective breeding program were aimed at a better type for central and eastern Maryland, the present data indicate that the selections might be made over a relatively large area of the Delaware-Maryland coastal plain. The areas in the Allegheny Mountains and the Piedmont Plateau are less promising.

Acknowledgements

As in other provenance studies, this experiment is a result of contribution by a large number of cooperators. Craig D. Whitesell, now with the U. S. Forest Service, initiated this experiment and made a series of early measurements. Mr. S. Sines of the Maryland Department of Forests and Parks grew the seedlings in the nursery. Foresters from the Kingston Research Center (N. E. F. E. S.) assisted in planting the experiment in Pennsylvania; foresters of the Glatfelter Pulp and Paper Company assisted in management of the experiment on their grounds; W. Sushko of the Baltimore Department of Public Works assisted on insect control; L. W. Moats of the Maryland Department of Forests and Parks cared for the plantation at the Smallwood State Park. T. G. Zarger of the Tennessee Valley Authority and J. S. Kring, of the University of Tennessee established the Tennessee plantation and offered the data for this report. R. Hubbard and C. D. Langley of the Natural Resources Institute assisted in measuring the research plantations in Maryland and Pennsylvania. J. W. Wright of Michigan State University reviewed the statistical work.

Summary

Virginia pine *(Pinus virginiana* Mill.), represented by 17 seedlots from its natural range in eastern United States, was studied in 5 replicated plantations, one in Pennsylvania, three in Maryland and one in Tennessee. Seven year results of this study follow:

1. Southern seedlots from Alabama, Tennessee, South Carolina and Virginia showed a high mortality (over 50 per cent) when planted on a poor site, outside of the species range (Pocono Mountains, Eastern Pennsylvania). In the same plantation some provenances from higher elevations had 90 to 100 per cent survival.

2. In four other plantations, the differences in survival were less significant. The highest mortality rate in the Maryland plantations was among the trees originating from Alabama, the most southern source studied.

3. The height growth difference between the best and the poorest seedlots was 20 to 23 per cent.

4. In the Pennsylvania plantation, some sources of higher elevations in the north showed a more reliable growth rate than the sources from the south.

5. Seedlots from the Atlantic coastal plain and Tennessee showed a better growth potential in the Maryland and Tennessee plantations than those from the northern and more mountainous areas. However, the most southern source from Alabama showed only an intermediate growth.

6. Experiments replicated by "one-tree plots" were less precise to determine the trend of variation, than the experiment arranged by "4-tree plots". However, the latter experiment included twice as many trees and its precision on a per-tree basis was about the same.

7. Significant correlations were found between the heights of different seed sources at the age of 7 years and the heights at age 3, 4, and 5 years.

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Heritability and Gain Concepts for Evaluating Breeding Systems such as Seedling Orchards[1]

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Introduction

Unbiased estimates of the gains and the time it takes to achieve them are required to weigh costs against benefits for various selection and mating systems. Methods for computing genetic gain are numerous, and various and sometimes contradictory concepts have been published (e. g., Wright, 1960; Hattemer, 1963; Hanson, 1963). As a guide for the tree breeder the anatomy of heritability is here examined, procedures for estimating gain are simplified by a method of accumulating the gains from the various selection stages, and comparisons are made of expected progress for several methods.

The statistical basis for the concept of genetic gain is simple linear regression $(Y - \overline{Y}) = b(X - \overline{X})$, or $y = bx$. Let us assume that the independent variable (X) is the yield or value measured on selected units of a large population: trees within a macrosite, replicated families in a plantation, or any natural unit of trees. It is more convenient to use (x), the difference between the mean of the original unselected population and the mean of the selected individuals (i. e. the selection differential). If (y) is the predicted gain, then the regression coefficient (b) represents the expected rate of response between the selection attempted and the magnitude of the genetic gain expected. This is heritability in the sense of Hanson (1963). The regression coefficient is, by standard definition, $\frac{\mathrm{Cov}\,(x, y)}{\mathrm{Var}\,(x)}$, i. e. the ratio of the covariance between the predictor variable (x) and the predicted variable (y) in the numerator to the variance of the predictor in the denominator. No discussion will be presented on methods for obtaining estimates of the components of variance and covariance except when the method of estimation affects the meaning and use of the component. Rather, it is assumed that proper estimation experiments will supply precise values for the components, and that the principal problem addressed is that of using the components appropriately for specific ways of obtaining genetic gain.

First consider the *denominator* (variance of x). It is commonly regarded as being composed of two distinct parts, i. e. genetic differences and sampling error, either experimental or genetic. The sampling error can be reduced by more extensive sampling of effects that cause errors in properly rating a selection unit with respect to the other units:

1) The genotype-macrosite error variance. Since most programs specify selection only when gross environmental or macrosite effects are comparable, these effects contribute little to error. However, the interaction between macrosite effects and genotypes, independent of the macrosite effects themselves, may be large. In at least some environments, the genotypes depart from their relative average behavior, the size of the departure being measured by the interaction variance (σ^2_{ge}). The interaction will cause an error in evaluating relative merit.
2) The error variance of large plots. This is the failure of the genotypes to behave relatively the same between the blocks or environmental replications within a macrosite (σ^2_p).
3) The error variance of the small plot or microsite. This error (σ^2_t) is due to within-plot differences, i. e., microsite differences (σ^2_w) plus the remaining genetic variability among individuals within plots.

For instance, if unrelated trees are scattered at random within a macrosite class, the variance among them will be: $V(x) = \sigma^2_w + \sigma^2_p + \sigma^2_{ge} + \sigma^2_G$ (the total genetic variance).

If the trees are in families with n to a plot and with r blocks on e macrosites, the variance among family means will be: $V(x) = \sigma^2_t/nre + \sigma^2_p/re + \sigma^2_{ge}/e + \sigma^2_f$ (genetic variance among families). An optimum allocation of n, r, and e in properly designed experiments can minimize this sampling error portion of the variance for a given cost, or can minimize cost for a given variance. By the definition of heritability, the denominator cannot be smaller than the numerator.

In some cases, sampling errors of genetic nature must be considered. For example, when the predicted (y) populations are half sibs but the predictor (x) population estimates are based on a finite sample of full-sib families, the covariance is based on general combining ability but the variance includes specific combining ability. The contribution of this sampling error to the denominator is the specific combining ability variance divided by the number of males.

Secondly, the *numerator* of the regression coefficient Cov (x, y) can be similarly examined once it is known which selection units are being used, the degree to which they vary, and how samplng errors can be reduced. This numerator is the genetic covariance between the material measured in tests, such as those designed to assess the value of the wild-tree selections or progeny mean, and the future

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