Shoot Elongation in Provenance and Progeny Tests of Red Pine[1])

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The possibility that progeny testing to some extent can be combined with the praduction of genetically improved seed in seedling seed orchards places great emphasis on the evaluation of progeny performance at a young age. Customarily progeny development is followed by periodic measurements and analyses which reveal the summation of several years of responses to environment. The completeness of the picture of progeny development, however, is determined largely by the length of time between measurements. Total height at plantation age 10 for example reveals little of what might be expected at age 15, while total heights at ages 2, 5, and 10 serve to suggest how the magnitude of progeny differences may be expected to change as the test develops. Of further interest is progeny performance under the different environments existing before and after crown closure within the test. A more dynamic examination of the course of early progeny Performance may thus be of value in understanding juvenile-mature correlations and in increasing the efficiency of identification of the genetic components of progeny development.

The present study is an investigation of early progeny performance of red pine (Pinus resinosa Ait.) to provide information of value in progeny test evaluation. This species is well suited for studies of progeny development because it produces only one flush af shoot elongation annually. Shoot elongation is thus delimited by branch clusters, and a record of annual shoot elongation is maintained for many years. Conclusions of general applicability to progeny evaluation of other species may be questionable because red pine as a species is characterized by relatively limited variation (Fowler, 1963; Lester and Barr, 1965) and possibly by maternal effects (Fowler, 1963).

Materials and Methods

Data were taken from two 11-year-old plantations containing the same seed sources. The plantation locations and origins of seed are shown in *Fig.* 1. Each planting contained twenty open-pollinated, one-parent progenies, 7 seed collections from stands in Canada, and control stock of uncertain origin from northern Wisconsin or central Minnesota. The experimental design was a modification of the triple rectangular lattice in that incomplete blocks were not randomized within replicates. For this study the design was treated as a randomized complete block design with three replicates. Both plantings were established with 2-2 nursery stock on sandy soils which had been formerly farmed. Each plot was planted as a square of 36 trees spaced 6 feet apart. Survival in both plantings was high, with no plot containing less than 60% of the planted trees and most plots containing 90 to 100%. Sample trees were identified as the tallest undamaged tree in each row of each plot. Means for each seed source thus included data from 18 trees. The sampling method was based on the assumption that because only a small percentage of the number of trees planted make up the major portion of the harvest from a plantation, the growth potential of only the larger trees is of interest. The sampling fairly clasely approximated performance of the seed sources as a whole as indicated by a correlation of 0.89 between plot means calculated from the sampling of tallest trees and a random sampling of 20 to 25 trees per plot (Lester and Barr, 1965). Annual shoot elongation was measured to the nearest centimeter as the stem length from the top of one branch cluster to the top of the next highest branch cluster, or to the base of the terminal bud when the current year's choot elongation was measured.

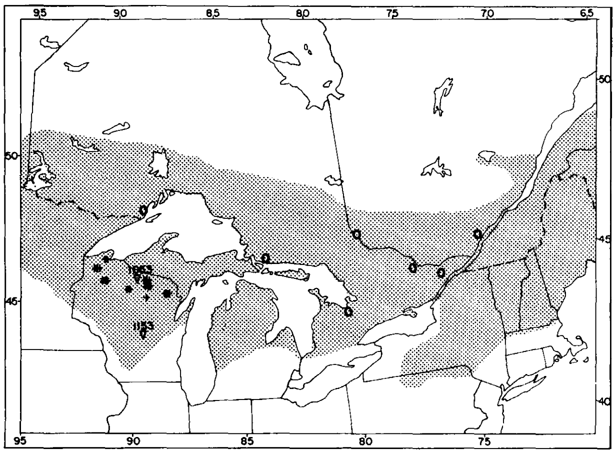

Figure 1. — Location of seed origins (○ = Canadian provenances, + = parent trees for open-pollinated, one-parent progenies) and experimental plantations (V). Stipled background represents the natural range of red pine.

Average annual shoot elongation was calculated as the average for the 18 trees in each seed source for each year. Weather data for the correlation af annual shoot elongation with climatic variables from the previous year were obtained from measurements compiled at the state weather station nearest to each planting. The nearest weather station for planting 1053 was 3 to 4 miles west, and for 1153 was 10 miles north. Weather data must thus be considered as only estimates of rainfall and temperature at the plantation. For estimates of repeatability each datum was transformed to its percentage of the plot mean in an attempt to remove the effects of increasing annual shoot elongation during the earlier years and to provide a form of adjustment for site dififerences between replicates of each seed source. Data for correlations of total height were obtained by adding measurements for annual shoot elongation to measurements of the distance between the ground and the branch cluster formed at the plantation age 2. Field data were used directly in the calculation of correlations between measurments of annual shoot elongation. For both groups of correlations the sums of squares and cross products were corrected for replicate effects before the correlation coefficient was calculated.

Results

Pattern of Total Shoot Elongation

Initial interest in the data concerned possible differences in the pattern of total shoot elongation in (different seed

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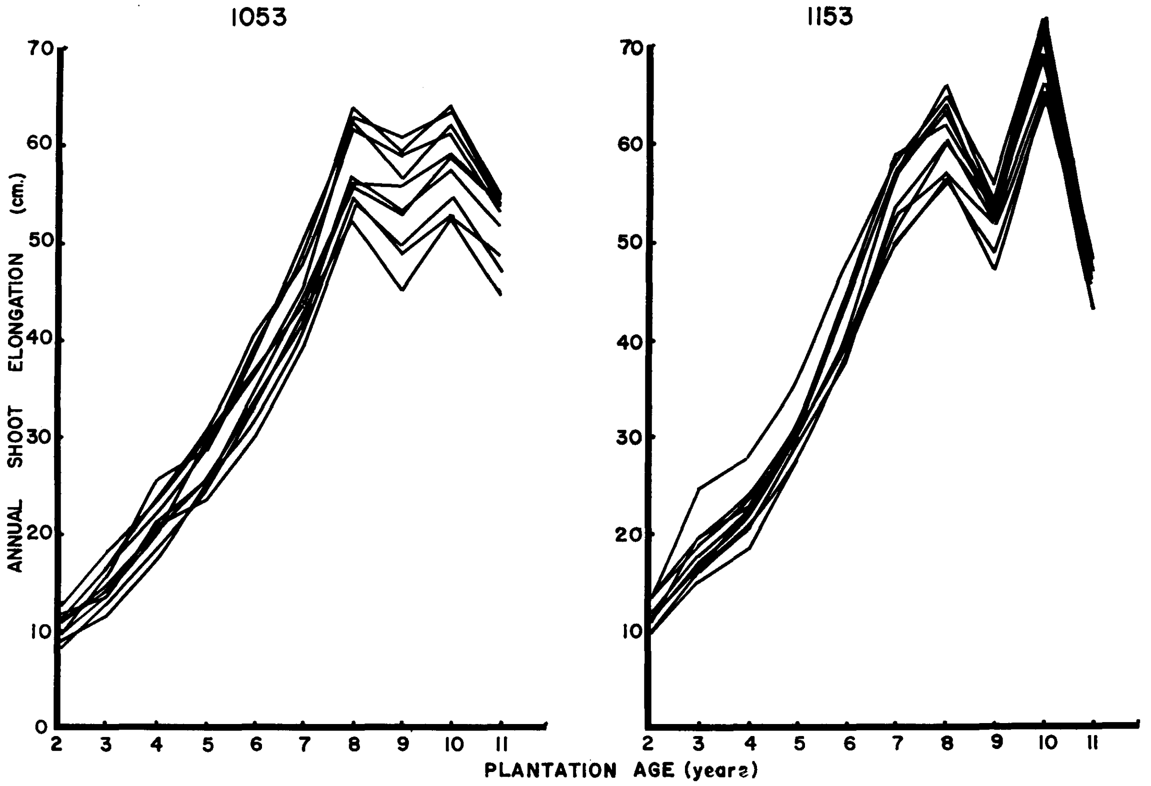

Figure 2. — Patterns of total shoot elongation for the five fastest growing and five slowest growing seed sources in two plantations over a period of ten years.

sources. The plantations differed by about 1.5 feet in mean height, while differences of 2.5 to 3 feet existed between seed sources within plantations. In both plantations, crowns of all seed sources had closed by age 11 but plantation 1153 was markedly more dense than 1053. As indicated in *Fig. 2* apparent differences in competition had no marked effect on the pattern of annual shoot elongation in different seed sources in either plantation although there were consistent quantitative differences between the seed sources (see LESTER and BARR, 1965 for a detailed discussion).

For several years following planting, the growth pattern of red pine is characterized by systematic increases in the amount of annual shoot elongation. As noted by WILDE (1964), only extreme environmental conditions result in a qualitative modification of the early growth pattern of red pine. Simple correlations of total shoot elongation with various combinations of monthly rainfall and temperature for the previous year were calculated to indicate whether fluctuation in shoot elongation could be largely attributed to climatic variation *(Table 1)*. Table 1 suggests an increased importance of variation in rainfall and temperature in closed plantations for the correlation coefficients are generally higher during the 1961—63 period than the 1954—60 period. However, more precise climatic data, measurements from several more years of shoot elongation in closed plantations, and further knowledge of the time (s) at which climate exerts its major influence on shoot elongation would be needed to establish the relative importance of climatic variables on shoot elongation in the open and closed plantation environments.

Table 1. — Simple correlation coefficients (r) for mean annual shoot elongation of all measured trees with mean rainfall or temperature for various periods.

Period of Measurements	Climatic Variables						$r_{.05}$
	Rainfall			Temperature			
	Annual	Apr.-Oct.	Jul.-Aug.	Annual	Apr.-Oct.	Jul.-Aug.	
Plantation 1053							
1954—63	0.29	0.11	0.21	—0.65	—0.12	—0.03	0.63
1954—60	0.18	0.18	0.36	—0.24	0.03	0.08	0.75
1961—63	0.58	0.36	0.75	0.85	—0.61	0.88	1.00
Plantation 1153							
1954—63	0.23	0.17	0.36	0.42	—0.19	—0.35	0.63
1954—60	0.25	0.24	0.67	—0.73	—0.11	—0.01	0.75
1961—63	0.49	—0.91	—0.14	0.90	0.47	0.83	1.00

Repeatability

Analogous to the desirability of visualizing progeny testing as a developmental process is the need for understanding the changes in components of variance which may accompany a changing test environment. Analyses of variance on a series of annual measurements from pedigreed progenies would be a reliable means of obtaining such information. In the present study uncertainty of genetic relationships between open-pollinated, one-parent progenies and the presumed absence of genetic relationships between individuals from the general seed collections suggested that the approximate methods of estimating the effects of different environments on variance would be appropriate.

For these estimates the statistic "repeatability" was calculated. Repeatability (r_I) is the intraclass correlation of repeated measurements on the same individual. The statistic is calculated as $\frac{\sigma_B^2}{\sigma_B^2 + \sigma_W^2}$, where σ_B^2 is the component of variance attributable to differences between individuals and σ_W^2 is the component attributable to variation of repeated measurements within individuals. The σ^2_B contains environmental variance resulting from permanent differences between the environments of each tree in addition to genetic differences between trees. Repeatability estimates the upper limit of heritability and can thus serve as a measure of the possible magnitude of genetic control for a characteristic which is expressed repeatedly. As noted by FALCONER (1960) r_I is generally easier to determine than heritability, and may often be known while heritability is unknown.

Repeatabilities were calculated, as illustrated in *Table 2,* for plantation ages 4 to 6 and 9 to 11 for each seed source in each plantation. The values ranged from -0.12 to $+0.82$.

Confidence limits were calculated for the 5% and 1% levels of probability to test whether each r_I differed significantly from zero. Each r_I was transformed to z where $z = \frac{1}{2} \log_e \frac{(1 + [k-1]\, r_I)}{(1 - r_I)}$, $\sigma_z = \sqrt{\frac{k}{2\,(k-1)\,(n-2)}}$, and k = the coefficient of σ^2_B, r_I = repeatability, and n = number of individuals measured (LEGAULT and TOUCHBERRY, 1962). This test was more conservative than a test of the variance ratio (STEEL and TORRIE, 1960) although both tests supported the same conclusion.

Table 3 presents a summation of the statistical significance of r_I values calculated for each seed source in each plantation. Repeatability differs significantly from zero in most of the seed sources. The magnitude of repeatabilities is somewhat lower under a closed plantation environment in 1053 and markedly lower in 1153.

Table 2. — Form of calculations of r_I for each seed source and for pooled data.

Source of Variation	Degrees of Freedom	Expected Mean Square
Each Seed Source		
Between Trees	17	$\sigma^2_W + 3\,\sigma^2_B$
Within Trees	36	σ^2_W
Total	53	
Pooled Data (16 one-parent progenies)		
Progenies	15	
Between Trees	272	$\sigma^2_W + 3\,\sigma^2_B$
Within Trees	576	σ^2_W
Total	863	

Table 3. — Numbers of seed sources with repeatabilities (r_I) in three classes of statistical significance.

Hypothesis	Ages 4—6			Ages 9—11		
	A[1]	B[2]	Total	A[1]	B[2]	Total
Plantation 1053						
$r_I = 0$	3	4	7	1	6	7
$r_I > 0$[3]	1	4	5	2	8	10
$r_I > 0$[4]	4	12	16	5	6	11
Plantation 1153						
$r_I = 0$	2	2	4	6	13	19
$r_I > 0$[3]	0	6	6	2	2	4
$r_I > 0$[4]	6	12	18	0	5	5

[1]) A represents data from 8 general seed collections.

[2]) B represents data from 20 open-pollinated, one-parent progenies.

[3]) at the 5% level of probability.

[4]) at the 1% level of probability.

To examine the relationship of r_I under one environment to r_I in another, a general estimate of r_I was calculated using pooled data. Before pooling, the homogeneity of the r_I values for each type of seed source was tested using z and its confidence limits at the 5% level of probability. For the general collections, r_I values were homogeneous in both plantations. The data were thus pooled for each planting. In planting 1053 the highest and lowest values for r_I for open-pollinated, one-parent progenies differed significantly from each other. The data from those progenies were omitted from the pooled data. Because the progenies with the highest and lowest r_I values were different in the two age groups, the pooled estimate included data from 16 progenies only. In 1153 the highest r_I was markedly greater than the other 19 and the data for that progeny were omitted from the pooled estimate.

Estimates of r_I using pooled data were calculated by the same methods already described. The results are summarized in *Table 4.* A test of significance using the confidence limits of z indicated that the estimates of r_I in 1053 are not significantly different from each other. In 1153 environmental influences had markedly reduced repeatability in each class of seed sources during ages 9 to 11. The repeatabilities under the two conditions of stand environment are highly significantly different from each other.

Because repeatability is a ratio, possible causes for changes in the magnitude of r_I must be sought in the components of variance σ^2_B and σ^2_W rather than in the r_I values themselves. In the present study, both components were markedly reduced under the closed plantation environment *(Table 5).* The reduction, however, was not proportional for both components. In each analysis for σ^2_B decreased more than σ^2_W resulting in a lowering of r_I.

Table 4. — Estimates of repeatability using pooled data.

Number and Type of Seed Sources	Plantation 1053		Plantation 1153	
	Ages 4-6	Ages 9-11	Ages 4-6	Ages 9-11
8 General Collections	.49	.46	.56	.20
16 One-Parent Progenies	.47	.35		
19 One-Parent Progenies			.48	.28

Table 5. — Variance components, σ^2_B and σ^2_W, calculated from measurements of annual shoot elongation in different stand environments.

	General Collections			One-parent Progenies		
Component	Ages 4-6	Ages 9-11	Ratio[1])	Ages 4-6	Ages 9-11	Ratio
Plantation 1053						
σ^2_B	.020383	.005565	.27	.021925	.004160	.19
σ^2_W	.020830	.006478	.31	.025708	.007296	.35
Plantation 1153						
σ^2_B	.011776	.001608	.14	.013059	.002017	.15
σ^2_W	.011510	.003985	.35	.010152	.006642	.65

[1]) Ratio (ages 4-6/ages 9-11) indicates differences in magnitude of change in each component in the two environments.

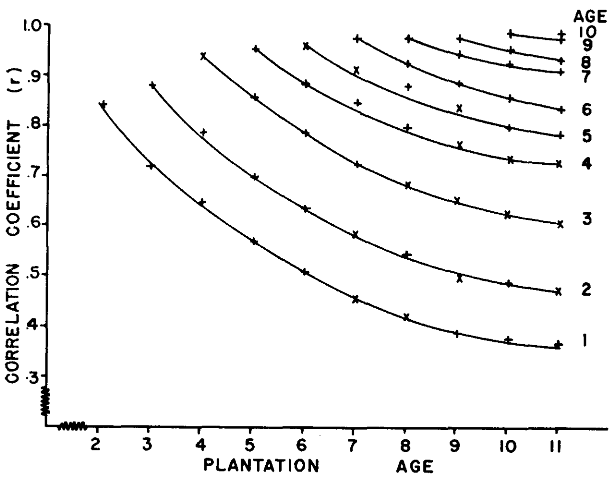

Figure 3. — Simple correlations of total height for 20 open-pollinated, one-parent progenies in plantation 1153 (× represents a pooled estimate of r calculated from non-homogeneous data).

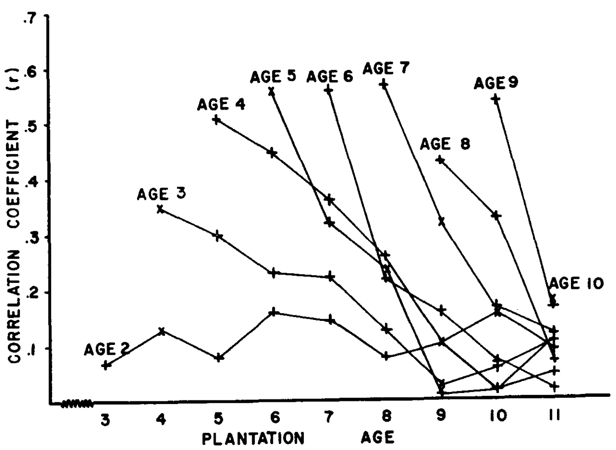

Figure 4. — Simple correlations of annual shoot elongation for 20 open-pollinated, one-parent progenies in plantation 1153 (× represents a pooled estimate of r calculated from non-homogeneous data).

Correlations — Total Height

Matrices of simple correlation (r) were calculated using total height data for each seed source in both plantings. The coefficients in each group, general collections and one-parent progenies, were then tested for homogeneity (Steel and Torrie, 1960) and combined in an average estimate of r for each group. Several of the average coefficients were derived from non-homogeneous data as indicated in *Fig. 3.* A small bias in z was ignored in the calculations. For the present data this bias, $\frac{\rho}{2(n-1)}$, would always be less than 3% of any r value.

Figure 3 is a graphical representation of the correlation matrix for open-pollinated, one-parent progenies in plantation 1153. The general form of the curves in both groups of seed sources was similar. Curves were steeper in 1053 so that the correlation of total height at any age with age 11 was up to 0.14 lower.

As expected, correlations decreased with an increasing number of years between measurements and the rate of decrease was most rapid in the early years of progeny development.

No striking discontinuity marked the end of a period of establishment for the trees although after plantation age 3, the curves were noticeably less steep than at earlier ages in both plantations. Similarly, no major change in curve form identified the transition to a closed plantation environment. In these data the choice of an early age at which to estimate progeny performance at a later age thus appears to be largely a matter of choosing an acceptable level of r.

Correlations — Annual Shoot Elongation

A matrix of simple correlation coefficients for annual shoot elongation of one-parent progenies is graphically represented in *Fig. 4.* Correlation coefficients for the other groups of seed sources were similar in magnitude. The correlation between annual shoot elongation decreased markedly when the measurements were separated by more than one or two years.

The pattern of change in r illustrated by *Fig. 4* further demonstrates points from other analyses. The rapidly increasing rate at which correlations with age 11 approached zero as the trees developed in both plantations illustrates the increased influence of local environment already suggested from calculations of repeatability. The decrease in r for successive years after age 8 also points to changes in local environment as the stand closes in 1153 although a comparable decrease in 1053 was found only at age 10. In addition, one conclusion from the matrix of r values for total height is supplemented by *Fig. 4.* The level of maximum correlation between annual shoot elongation in successive years seems to be reached by age 4 or 5, substantiating the suggestion that if any observable discontinuity of development exists between the time the tree is planted and the time it becomes established in the field, the change in development occurs at about 4 years after planting.

Discussion

Although progeny performance at rotation age is the ultimate criterion in progeny test evaluation for characters of growth, the need for information long before rotation age may be partially satisfied by studies of progeny test development at early ages. The pattern of annual shoot elongation in several successive years suggests the direction of future progeny development and also indicates the influence of changing stand environment on progeny development. In the present study, developmental patterns of shoot elongation for several provenances and open-pollinated, one-parent progenies were similar in form. The data can thus be interpreted as applying rather generally to red pine of similar seed origins and growing on similar sites.

The first 8 years following planting were characterized by shoot elongation which increased annually at an approximately exponential rate. During the early period, annual shoot elongation was apparently little affected by variation in rainfall or temperature. Motley (1949) noted the absence of a marked response in annual shoot elongation of red pine to variation in May-November rainfall of the preceding year during a period of 10 years following planting. The growth pattern of white pine, by comparison, corresponded more closely with variation in rainfall. Friesner and Jones (1952) similarly noted the absence of a correlation between rainfall of one year with the extent of shoot elongation in the next year in young red pines. In red pine, the relatively short period of shoot elongation in late May and early June (Kozlowski and Ward, 1961) probably allows the species to generally escape severe water stresses during shoot elongation. The period of bud differentiation in July and August (Duff and Nolan, 1958) is probably more subject to water stresses which may be reflected in elongation during the following spring. Shoot elongation in red pine at a young age thus appears to be relatively independent of climate. If this is so, the heritability of annual shoot elongation should be relatively high for several years after the seedlings recover from planting.

In both plantations, striking changes in the pattern of shoot elongation occurred at age 9. Weather records for the areas in which the plantations are growing show no major departures from long term averages of precipitation and temperature in the period 1961–1963. Probably the change in the pattern of shoot elongation reflects an increased influence of environment on the endogenous regulation of shoot elongation. The increased influence of environment is presumably attributable to the onset of competition between trees for water.

The apparent restriction of the expression of differences between trees was illustrated by the marked reduction in both components of variance, σ^2_B and σ^2_W, in measurements of shoot elongation at ages 9 to 11. In contrast to the general reduction in variance, the decreases in repeatabilities represented differential effects of a changed environment on the components σ^2_B and σ^2_W. For each pair of r_I values σ^2_B decreased more than σ^2_W. This indicates that the effect of that portion of environment which is temporarily peculiar to each tree had assumed greater importance. In the terminology of Falconer (1960), $r_I = \frac{V_G + V_{EG}}{V_G + V_{EG} + V_{ES}}$, V_G = genetic variance, V_{EG} = environmental variance contributed by permanent differences in environment between individuals, and V_{ES} = variance within individuals arising from temporary differences in the environment of each individual. The observed decreases in r_I thus suggest that under increased competition, V_{ES} increased in relation to $V_G + V_{EG}$.

Genetic inferences from the results are clouded by the unknown degree to which the repeatability estimate contains permanent non-random environmental variance. Repeatabilities have been frequently calculated for characteristics of yield in dairy cows. With data from which calculations of heritability in the narrow sense were also possible, heritabilities have ranged from 35% (Van Vleck and Henderson, 1961) to 65% (Lush and Arnold, 1937) of repeatability. Campbell (1960) has suggested that heritability in the narrow sense may seldom exceed 50% of repeatability in forest stands. Assuming that heritability in the narrow sense represents 40 to 50% of repeatability in the present results, a moderate genetic influence on height growth under the open plantation environment is indicated. The substantial components of variance for family means calculated from total height measurements on the same one-parent progenies also suggested a moderate genetic influence on height growth in red pine (Lester and Barr, 1965). On the other hand, marked sensitivity to variation in the soil surrounding each root system or to variation in the degree of competition from vegetation before the plantation closed could result in genetic variance being only a small or negligible part of repeatability. The composition of variance in progeny tests of red pine thus remains in question. Unfortunately, no pedigreed progenies are currently available with which to further explore the genetics of this species.

The correlation analyses for total height may be of considerable value in indicating the expected course of progeny development in the immediate future. Presuming that the slopes of curves in *Fig. 3* continue to decrease, it would appear that under similar experimental conditions, total height, at least up to age 20, would be fairly closely related to the total height at plantation age 8 or 9. Some support for this observation may be derived from a comparison of r values at comparable ages with data on ponderosa pine from Callaham and Duffield (1962). From *Table 6*, red pine in the Wisconsin tests appears to have correlations of a magnitude comparable to those for ponderosa pine. Callaham and Duffield reported correlations ranging from less than .02 to .75 for total height at age 5 with total height at age 20, while the correlations between the ages 12 and age 20 were above 0.8. Therefore, the age at which total height measurements of red pine reflect at least 60% of the variation of total height at age 20 seems to lie between ages 5 and 11.

Table 6. — Correlation coefficients for total height of trees from open-pollinated, one-parent progenies in red pine and ponderosa pine.[1])

Age	Age 5				Age 11		Age 12	
	Red Pine		Ponderosa Pine		Red Pine		Ponderos.Pine	
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
2	.462**	.490**	.328**	.410**	.144**	.250[2])	.089	.053
5					.578[2])	.624**	.559**	.416**

[1]) Data for ponderosa pine are from Callaham and Duffield (1962).

[2]) Coefficients are from pooled data which is not statistically homogenous.

(1) Plantation 1053.

(2) Plantation 1153.

(3) "End" trees in "Institute" plantation.

(4) "End" trees in "Pyramid" plantation.

** Correlation coefficients differ significantly from zero at the 1% level of probability.

One interpretation of the results as a whole, suggests that on sites similar to those studied, plantation spacing which would assure an open stand environment up to about plantation age 10 might be adequate to allow reliable estimates of progeny performance at age 20. The rate of decline in correlations between total height at age 10 and total height at ages older than age 20, would indicate how much further data from 10-year-old progeny tests might be reliably extended.

Acknowledgements

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Summary

Measurements of annual shoot elongation for 9 successive years were made in two 11-year-old provenance and progeny tests of red pine. The pattern of annual shoot elongation exhibited two distinct phases. In the first phase, elongation appeared limited only by the growth potential of each tree. Repeatability of annual shoot elongation was relatively high. The second phase was characterized by annual fluctuation in shoot elongation and a decrease in repeatablity resulting presumably from the increased influence of that portion of environment which contributes

to variation within each tree. Correlation matrices for total height and for annual shoot elongation were presented. Correlation of total height with age 11 exceeded 0.8 after age 5. Correlations of measurements of annual shoot elongation were generally low. The implications of the results for early progeny test evaluation were discussed.

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Vollständige Varianzen und Kovarianzen in Pflanzenbeständen

II. Phänotypische Korrelationen zwischen Bäumen in gleichaltrigen Kiefern- und Fichtenbeständen und den sie umgebenden Gruppen von Konkurrenten

Von K. STERN, Schmalenbeck

(Eingegangen am 15. 4. 1965)

I. Problemstellung

In einer früheren Untersuchung (STERN 1965) war versucht worden, die Grundlagen für Versuche über Konkurrenz zwischen verschiedenen Genotypen in Waldbeständen abzuleiten. Dabei hatten sich recht komplexe Verhältnisse abgezeichnet, die nichtsdestoweniger die Konstruktion der Fragestellung gerecht werdender Versuchspläne zulassen. In der vorliegenden Arbeit sind nun erste Versuche zusammengefaßt, die aus Konkurrenz zwischen Bäumen in gleichaltrigen Reinbeständen entstehenden Verteilungsmuster zu beschreiben. Hierfür steht Material der schwedischen forstlichen Versuchsanstalt und der hessischen forstl. Versuchsanstalt zur Verfügung, das uns liebenswürdigerweise von Herrn Prof. CH. CARBONNIER, Stockholm, und Herrn Oberforstrat Dr. R. SCHMITT, Gießen, überlassen wurde. Die umfangreichen Rechenarbeiten wurden beim Rechenzentrum der Universität Hamburg auf dessen „Telefunkenrechner 4“ ausgeführt.

Das Ziel dieser Untersuchung ist es einmal, die Veränderung des Verteilungsmusters der Bäume in gleichaltrigen Beständen in Abhängigkeit vom Alter zu beschreiben. Daneben kann aber auch der Einfluß der Durchforstung auf das Verteilungsmuster aus den Ergebnissen abgelesen werden, da in jedem der 6 Versuchsbestände Parallelflächen mit mindestens 3 verschiedenen Durchforstungsarten bzw. -graden vorlagen, wenn auch nicht überall die gleichen. Weiter ist es möglich, die Verhältnisse bei zwei biologisch so verschiedenen Baumarten wie Kiefer und Fichte zu vergleichen. Die forstgenetische Zielsetzung ist es schließlich, eine erste Schätzung des Anteils der Konkurrenzvarianz an der phänotypischen Varianz der Massenleistung der Bäume (hier gemessen durch Stammgrundfläche oder Durchmesser in Brusthöhe) zu gewinnen. Diese Fragestellung wird auch in anderen zur Zeit laufenden Versuchen mit einer verbesserten Methode untersucht. Das Interesse der Forstgenetik an gerade dieser Frage resultiert aus der Tatsache, daß Konkurrenzvarianz ebenso zu behandeln ist wie „Fehlervarianz“. Das heißt, sie verschleiert die genetisch bedingten Leistungsdifferenzen zwischen den Bäumen und erschwert so die Einschätzung des Zuchtwertes o. dgl. der vom Züchter auszulesenden „besten“ Bäume.

Zum besseren Verständnis der angewandten Methode und der mit ihrer Hilfe gewonnenen Ergebnisse sei zuvor erklärt, was unter einem „Bestand“ verstanden werden soll. Wir gehen davon aus, daß ein Pflanzenbestand nicht eine Ansammlung in ihrer Entwicklung unabhängiger Individuen ist, sondern daß zumindest benachbart aufwachsende Pflanzen sich gegenseitig beeinflussen. Das ist in vielen Versuchen nachgewiesen worden und bedarf keiner weiteren Erläuterung. Zur Kennzeichnung eines solchen Bestandes benötigt man dann mindestens die folgenden statistischen Maßzahlen (es sind erheblich mehr, wenn man auch ökonomische Gesichtspunkte berücksichtigen will):

1. die mittlere Leistung des Individuums, $\bar{y}$,
2. die Standardabweichung der Verteilung der y, σ_y, unter der Voraussetzung normaler Verteilung der y, andernfalls müssen weitere, die Verteilung charakterisierende Statistiken eingeführt werden,
3. die Zahl der Individuen je Flächeneinheit, n,
4. den mittleren Abstand zwischen Nachbarn, d,
5. die Standardabweichung der Verteilung dieser Abstände, σ_d,
6. die Korrelation zwischen benachbarten Individuen und zwar
   - a) deren positiven Teil, der aus Variation der Bodengüte auf der Fläche resultiert (benachbarte Pflanzen haben im Durchschnitt mehr ähnliche Bodenverhältnisse) und
   - b) ihren negativen Anteil, der aus Konkurrenz zwischen benachbarten Bäumen um irgendwelche Nährstoffe, um Licht, Wasser o. dgl. resultiert.

Daneben mag es eine gegenseitige positive Beeinflussung der Nachbarn geben, die wir jedoch nicht getrennt einschätzen können. Auch die Trennung der beiden obenge-