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DYNAMICS OF IMPROVED LOBLOLLY PINE PLANTATIONS AND THE
IMPLICATIONS FOR MODELING GROWTH OF IMPROVED STANDS

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Abstract.--A study was initiated to examine the dynamics
of genetically improved loblolly pine plantations and to
develop guidelines for incorporating the effects of genetic
improvement into various types of growth and yield models for
loblolly pine plantations. The limited data base from stands
of improved stock dictated that any modeling effort concentrate
on the synthesis of fragmented information from many types of
studies rather than the usual data fitting procedures.

A series of hypotheses concerning stand dynamics and
growth patterns in stands of improved stock relative to stands
of unimproved stock were developed and tested. Results of
these tests indicate: 1) at the seed source and family
levels, the shape of the height-age curve is dictated by the
site, but the level of the height-age curve is dictated by the
seed source or family; 2) at the seed source and family levels,
the shape of the height-diameter relationship at a given age is
determined by site and initial density while the level of the
height-diameter relationship is determined by the seed source
or family and is directly related to the dominant height of
the seed source or family at that age; and 3) given that
silvicultural treatments are the same and are equally intense
and successful, variances of height and diameter in stands
originating from selected genotypes are not different from
those in genetically unimproved stands.

Implications for modeling growth of stands originating
from selected genotypes are: 1) genetic improvement affects
the rate at which stands develop, but does not fundamentally
alter the pattern of stand development from that of unimproved
stands; 2) changes in genetic material on a given site will
likely affect the level, but not the shape, of such basic
relationships as the height-age and height-diameter relation-
ships; and 3) correctly characterizing the height-age profile
will be very important.

Additional keywords: Pinus taeda L., height-age relationship,
height-diameter relationship, stand-level variance.

In modeling the growth and yield of forest stands, we seek to mathematically interpret the biological relationships that underlie and drive stand development. The logical way to approach the problem of modeling the growth and yield of genetically improved stands of loblolly pine (Pinus taede L.) is by studying the dynamics of such stands. An understanding of the growth and dynamics of genetically improved stands relative to unimproved stands is important for decisions regarding selection and breeding as well as forest management.

Certain basic relationships are key components of stand dynamics. They are: 1) the development of dominant height through time or the height-age relationship; 2) the development of the height and diameter distributions through time; 3) the relationship of the mean height by diameter class across the range of diameters at a given age, or the height-diameter relationship; and 4) the mortality-time relationship. Hypotheses concerning the similarities and differences between stands of improved and unimproved stock were developed and tested for the first three relationships listed above. This paper details the hypotheses tested, the test results and the implications of the results for modeling growth of stands of genetically improved stock.

DATA

The data available to this study were diverse types and not, by study design or plot structure, the kind usually used for growth and yield analysis. This dictated that the hypotheses be tested and the implications be proposed by the synthesis of fragmented information rather than the usual modeling techniques.

The data base used is comprised of three components: 1) the Loblolly Phase of the Southwide Pine Seed Source Study up to age 25 (Wells and Wakeley 1966); 2) a 15 year-old block-plot half-sib progeny test planted near Bogalusa, Louisiana, belonging to Crown Zellerbach Corporation; and 3) three 16 year-old, ten-tree row-plot progeny tests located in eastern Virginia, eastern South Carolina and north-central Alabama released to this project by the North Carolina State University-Industry Tree Improvement Cooperative. The row-plot progeny test data were grouped into half-sib families on the male parent thereby combining rows from different locations within a rep in an attempt to overcome the environmental artificiality of the row-plot design. The row-plot tests were then analyzed at the half-sib level.

The block-plot progeny test is replicated 4 times at the same location with each rep containing twelve 121 tree plots (11 x 11 trees) with the inner 49 trees as measurement trees. Spacing is 8 x 8 feet. Each rep contains 11 plots of selected genotypes and 1 plot of local woodsrun origin as a control.

A complete description of the Southwide Pine Seed Source Study design is given in Wells and Wakeley (1966).

Analysis of the Seed Source Study allowed hypotheses to be tested regarding similarity or difference of growth pattern of different seed

sources at the same location and at different locations. Analysis of the half-sib block-plot progeny test allowed hypotheses to be tested regarding growth patterns of half-sib families at the same location. The row-plot progeny test data were used to further test hypotheses accepted using the Seed Source Study and the half-sib block-plot progeny test data.

METHODS AND RESULTS

Height-age relationship

When modeling stand development, the most important relationship to understand and correctly characterize is the height-age relationship. The analysis of the height-age profiles in the data available was therefore of primary interest.

Nance and Wells (1981) used the Southwide Pine Seed Source Study and a fairly inflexible model for height growth to study differences in site index among different seed sources. One result of their work is that at any given location of the Seed Source Study, the shape of the height-age curve is the same for all seed sources, but the level of the curve is affected by seed source and block. To determine whether or not these results were an artifact of the model used by Nance and Wells (1981) the analysis was repeated using the very flexible Richards' function:

$$H = A(1-exp(-b*age))**c \qquad (1)$$

where: H = height at any given age
A = asymptotic or maximum height
b = rate parameter
c = shape parameter.

Equation (1) was fitted to the tallest seven trees at each age (roughly analogous to the tallest 100 trees per acre) for each seed source x block x location combination. Analysis of variance for A, b, and c and graphical analysis of the resulting curves for each location showed significant seed source and block effects on A, the asymptotic height, but generally no seed source or block effects on b and c, the rate and shape parameters, respectively[2] Differences did occur among all the parameters from location to location. These results support the findings of Nance and Wells (1981) and also indicate that an extremely flexible function is not necessary for this analysis.

Extending the conclusions about height-age patterns in the Seed Source Study to a general hypothesis, patterns of the height-age profiles in the block-plot progeny test were examined. The equation

2. In the interest of space, exhaustive tables of test and fit statistics are not given in this paper. Such tables can be obtained from the senior author on request. All tests of significance were carried out with a = 0.05.

$$\log (H) = a + b(1/age), \qquad\qquad\qquad (2)$$

4)ere: H   = height at any given age
       a   = level or intercept parameter
       b   = slope or shape parameter
       log = logarithm base e,

was fitted to the tallest seven trees at each age for each plot (family x block combination). An analysis of variance for the estimates of the slope parameter, b, was done following the form of Table 1. Results of this. analysis showed that there are no family and no rep effects on the shape parameter. That is, the height-age curves are the same shape for all the families across all the reps. Equation (2) was fitted to the data from each plot again while maintaining a common slope parameter, b, for all plots. An analysis of variance (Table 1) was performed on the estimates of the intercept and the results showed significant family effects on the intercept, but no rep effects on the intercept.

Table 1.--Form of <u>analysis of variance for block (rep) and seed source</u> <u>(family) effects on the parameters of the height-age and height-</u> diameter relationships.

Source of Variation	Degrees of Freedom	Mean Square	F-ratio
Block (Rep)	b-1	MSB	F_B =MSB/MSE
Seed Source (Family)	s-1	MSS	F_S=MSS/MSE
Error	(b-1)(s-1)	MSE	

Extending this analysis to the row-plot progeny tests, equation (2) was fit to the tallest 15% of the trees at each age for each plot (half-sib family x rep combination) for the three progeny tests. An analysis of variance on the estimated slopes was done following Table 1. Results of this analysis showed that there are no family and no rep effects on the slope or shape parameter, b. Equation (2) was fitted to the data from each plot again while maintaining a common slope parameter, b, for all plots within a test. An analysis of variance (Table 1) was performed on the estimated intercepts and the results showed significant family and rep effects on the intercept term in all three tests.

The conclusion of this phase of the study is that at a given location, the shape of the height-age profile is the same among seed sources or families, but the level of the height-age curve differs by seed source or family. This result is consistent from the Southwide Pine Seed Source Study to the block-plot half-sib progeny test to the row-plot progeny tests.

Height-diameter relationship

Height-diameter relationships are used in many growth and yield models to predict the mean height for a given diameter or diameter class.

The diameter and predicted height values are then used in stand volume and value calculations. The wide use of this relationship dictated its investigation. Only data from unthinned studies or unthinned parts of studies were suitable for analysis of the height-diameter relationship as thinning destroys stand structure and, with it, the base line development of the height-diameter relationship. Nine locations of the Seed Source Study unthinned by age 15 were used (see Table 2). The block-plot progeny test was thinned after age 8. Given that the dominant heights ranged from 38 to 50 feet at age 8 in these plots, the height-diameter relationship was well-developed at age 8 and these data were appropriate for the analysis. The three row-plot progeny tests were unthinned and the age 16 data from these studies were used in the analysis.

Table 2.--Location of the nine Southwide Pine Seed Source Study plantations used in the analysis of the height-diameter relationship.

Location	County or Parish	State	Series
C AL (2)	Coosa	Alabama	2
E MD (1)	Worcester	Maryland	1
N MS (2)	Winston	Mississippi	2
S MS (1)	Pearl River	Mississippi	1
S MS (2)	Pearl River	Mississippi	2
SE LA (1)	Washington	Louisiana	1
SE LA (2)	Washington	Louisiana	2
SW GA (1)	Dooly	Georgia	1
W SC (2)	Newberry	South Carolina	2

The function used to model the height-diameter relationship in this analysis was:

$$\log(H) = a + b(1/D) \qquad (3)$$

where: H = mean height for a given diameter, D
         a = level or intercept parameter
         b = slope or shape parameter
         $\log$ = logarithm base e.

Equation (3) has been found to work well for loblolly pine and examination of residual plots showed that it fit the data from all the studies well.

Equation (3) was fitted to all the height-diameter pairs for each seed source x block combination (plot) for each of the nine locations of the Seed Source Study used. An analysis of variance (Table 1) was done on the estimated slope parameters, b, at each location. At 8 of the 9 locations, seed source did not affect the shape of the height-diameter curve. At 8 of the 9 locations, blocks did not affect the shape of the height-diameter curve. Given these results, equation (3) was refitted to each plot while maintaining a common slope within each location. The analysis of variance indicated in Table 1 was performed on the estimates of the intercept, a,

within each location. At 2 of the 9 locations, blocks significantly affected the intercept. At 3 of the 9 locations, seed source significantly affected the intercept, and at 3 of the 9 locations, block and seed source significantly affected the intercept. Recall that there were significant block and seed source effects on the intercept of the height-age relationship. The estimated slopes were significantly different across locations. Simple linear regressions were calculated for the estimated intercepts on dominant eight at age 15 of the appropriate plot. Eight of the 9 regressions had r values greater than 0.79. Using r simply as a measure of association, the intercept, or level, parameter of the height-diameter relationship at age 15 is strongly related to the dominant height at age 15 of that source on that site. The conclusion from this portion of the analysis is that the height-diameter relationships are the same shape across seed sources at any given location at age 15 and the level of the relationship is directly and strongly related to the dominant height of the source at age 15.

Extending this conclusion to a general hypothesis, the same type of analysis was performed on the block-plot progeny test data at age 8. Equation (3) was fitted to the height-diameter pairs for each plot (family x block combination). The analysis of variance indicated in Table 1 was performed on the estimates of the slope, b. The results of the analysis of variance showed no block or family effects on the slope parameter. Using a common slope, b, equation (3) was refitted to the data from each plot. An analysis of variance of the form in Table 1 was carried out on the estimated intercepts. There were no rep effects, but there were significant family effects on the intercept parameter. Recall that there were no rep effects but there were significant family effects on the intercept of the height-age equation for these plots. The simple linear regressi9n of the estimated intercepts on the dominant height of the plots had an r of 0.93. The conclusion from this portion of the analysis is that the height-diameter relationships are the same shape across families at age 8 and the level of the relationship is directly and strongly related to the dominant height of the family at age 8.

Performing the same type of analysis with the row-plot progeny tests, equation (3) was fitted to the height-diameter pairs for each plot (half-sib family x rep) for the three separate tests. For each of the three tests, an analysis of variance (Table 1) was conducted on the estimates of the slope, b. There were no significant rep or family effects on the slope parameter, b, in any of the three row-plot progeny tests. Maintaining a common slope for each test, equation (3) was refitted to the height-diameter pairs for the three tests. An analysis of variance (Table 1) was performed on the resulting estimates of the intercept, a. There were significant family and rep effects on the intercept in all three row-plot progeny tests. Recall the significant rep and family effects on the estimates of the intercept for the height-age relationship for these data. A simple linear regression of the estimated intercepts of the height-diameter relationship on the plot dominant height was calculated for each of the three progeny tests. All had r values greater than 0.88. The slope parameters were different in the three tests. From this analysis of the three row-plot progeny tests, the conclusion is that the height-diameter relationships are the same shape across families within a test at age 16 and the level of the relationship is directly and strongly related

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to the dominant height of the family at age 16.

The conclusion of this phase of the study is that at a given location, the shape of the height-diameter relationship at any age is the same among seed sources or families, but the level of the height-diameter curve at that age differs by seed source or family. In addition, the level of the height-diameter curve is directly and strongly related to the dominant height of that seed source or family at that age. These results are consistent for the Southwide Pine Seed Source Study, the block-plot half-sib progeny test, and the row-plot progeny tests.

Stand-level variance

The shape or spread of the diameter and height distributions, as well as their relative location, determine the ultimate value of a stand. Accordingly, the variances of the height and diameter distributions are of interest in modeling the growth and yield of loblolly pine stands. It has been conjectured that while increasing the mean tree size, genetic selection could reduce the stand value by reduction of the stand-level variance and possible production of fewer large trees (Nance and Bey 1979, Thurmes 1980).

To test this proposal, data from unthinned family block plots were needed. Because the block-planted half-sib progeny test had been thinned after age 8, the data at age 8 were used, since given the initial spacing of 8 x 8 feet and the dominant heights ranging from 38 to 50 feet, the distributions of height and diameter were well developed.

Simple variances of height and diameter were calculated for each plot (family x rep combination) of the block-plot half-sib progeny test. Bartlett's test for homogeneity of variance was performed for both diameter and height in each rep; that is, the variances of the 12 families within a rep were compared. The hypothesis of homogeneity of variance was accepted for the variance of diameter in each of the four reps. The hypothesis of homogeneity of variance was accepted for the variance of height in three of the four reps. These results indicate that the variances of height and diameter generally did not differ among the families within a rep.

An observational analysis was done to determine the relative sizes and ranks of the variances of height and diameter of the twelve families within each rep. For each rep, the variances of height and diameter were ordered from largest to smallest. There were no consistent family rankings across the reps for diameter or height. The variance of diameter for the woodsrun control family ranked largest in one rep, third largest in one rep, and seventh largest in two reps. The variance of height for the woodsrun control family ranked fourth largest in one rep, sixth largest in one rep, seventh largest in one rep, and tenth largest in one rep. It is clear that the height and diameter variances of the woodsrun control family arq not consistently larger than those of the eleven selected genotypes.

The general conclusion to be drawn is that given that silvicultural treatments are equally intense and successful, the variances of height and diameter in stands originating from selected genotypes are not different or consistently smaller than those in stands originating from genetically

unimproved stock.

CONCLUSIONS AND IMPLICATIONS

The major conclusions to be drawn from the work presented here are: 1) given that silvicultural treatments are the same and are equally intense and successful, variances of diameter and height in stands originating from selected genotypes are not different or consistently smaller than those in stands originating from genetically unimproved stock; 2) at the seed source and family levels, the shape of the height-diameter relationship at a given age is determined by the site and initial density while the level of the height-diameter relationship is determined by the seed source or family and is directly related to the dominant height of the seed source or family at that age; and 3) at the seed source and family levels the shape of the height-age curve is dictated by the site, but the level of the height-age curve is dictated by the seed source or family. A very important result of this work is the consistency of the results concerning the height-diameter relationship and height-age relationship from the Southwide Pine Seed Source Study to the block-planted half-sib progeny test to the row-plot progeny test. This consistency suggests implications for growth and yield modeling.

Implications for modeling growth of stands originating from selected genotypes are: 1) genetic improvement affects the rate at which stands develop, but does not fundamentally alter the pattern of stand development from that of stands of unimproved stock; 2) changes in genetic material on a given site will likely affect the level, but not the shape, of such basic relationships as the height-age and height-diameter relationships; 3) from the analysis of the height-diameter relationship, it is likely that the development of the height and diameter distributions will follow from the development of dominant height; and 4) correctly characterizing the height-age profile for a given site will be of primary importance.

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