GROWTH MODELS FOR SLASH PINE FAMILIES

D.L. Rockwood', B. Yang', and H. Gresham'

Abstract:--Height, DBH, and volume growth models in response to density, age, site index, interfamily competition, and genetics were developed for 29 15/16-year-old slash pine families in six progeny tests in Florida. Families significantly influenced the shape, asymptote, and rate parameters of height-age and site index curves. Separate base-age invariant height-age models were developed for each family to account for polymorphism associated with the shape and rate parameters. In Nelder design tests, tree height was not affected by density, but DBH and stand volume-index were negatively related to density as early as age four years. Growth dynamics, based on density, age, site index, competition level, and families, were fit to these data. There were significant differences for the estimated parameters of the equations: -0.0739 to 0.0616 (equivalent to 13% of average total height), -0.0513 to 0.1385 (20% of average DBH) and -0.1598 to 0.3331 (54% of average volume-index) for the poorest to best growing families. Interfamily competition coefficients ranged from -0.0026 to 0.0169 (2% of average height), 0.0206 to 0.0169 (10% of average DBH) and 0.0394 to 0.3758 (42% of average volume-index), and differences between mixed and pure plantings were not significant.

Keywords: Growth models, Pinus elliottii, Nelder Design, Row plots, Block plots.

INTRODUCTION

Growth models and stand simulators directly relate to management decisions about value and rotation length, and they are alternatives to traditional selection and genetic gain prediction systems. Stand growth models can project family differences from young ages to estimate selection differential and percent gain at rotation age (Knowe and Foster 1989). Selection on growth models promises greater flexibility and better maintenance of growth rates than pointwise selections (Magnussen and Kremer 1993). Buford (1986) and Buford and Burkhart (1987) concluded that stand-level gains could be estimated by determining the apparent increase in site index due to genetically improved loblolly pine. Knowe and Foster (1989), Buford and Burkhart (1987), and Nance and Wells (1981) discussed some of the problems related to modeling growth of genetically improved stock. Progeny tests are generally not suitable for developing necessary growth functions. Family plots of less than 10 trees efficiently rank families but provide poor estimates of stand parameters. With larger plots sufficient to construct individual growth trajectories, a functional analysis of growth as a stochastic process would furnish the necessary parameters for construction of a selection index and estimation of genetic progress. Growth model analysis offers the advantage of a succinct presentation of growth results.

This study presents total height (TH), diameter at breast height (DBH), and stand volume-index (SVI) growth models and their relationship to genetic parameters of 15- or 16-year-old trees in 29 slash pine (Pinus elliottii var. elliottii Engelm.) families. The growth patterns associated with families are examined. This study also addresses progeny tests with row plots and operational densities.

'School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611-0420.
'Champion International Corporation-Western Florida Region, 117 Pace Parkway, P.O.Box 875, Cantonment, FL 32533. Journal Series Paper No. N-01094 of the Florida Agricultural Exp. Sta.

MATERIALS AND METHODS

In 1978 and 1979, St. Regis Paper Company established 29 families in six tests near Cantonment, Florida (Table 1, Rockwood 1983). Two 1978 plantings had nine families in 1) a split plot design involving two competition levels (pure = all trees of the same progeny, and maximum = each measurement tree surrounded by trees of the other eight families and 2) Nelder plots (families assigned to spokes) with eight densities. The 1979 plantings included as many as 23 families in pure vs. maximum competition block plots, Nelder's plots, and 10-tree row plots.

TH, DBH, survival, and rust incidence were measured at age 4, 6, 8, 11, and 15 or 16 years. SVI was calculated as DBH^2 x TH x survival. In addition, the absolute growth increment and relative growth rate for each of the growth traits from age 4 to 6, 6 to 8, 8 to 11, and 11 to 15 or 16 were calculated.

Height and Site Index. After comparing various models, the analysis used the more flexible Richards' function (Balocchi et al. 1993) that permits each tree to have its own unique growth function. The height-age relationship of individual families was described by using the growth model:

$$H = A(1 - \exp(-b^{*}age))^{c} + \sigma \qquad (1)$$

where

H = average height

A = asymptotic or maximum height

b = rate coefficient

c = shape coefficient

σ = random error

Equation (1) was fit to the dominant/codominant trees at each age for each family x replication x design combination. A full model expanded in the asymptote, rate and shape coefficients (A, b, and c) compared to the model (1) used for all 29 families was changed to:

$$H_d = b_1(1 - \exp(-b_2 age))^{b}{}_{3} + \sigma \qquad (2)$$

where

$b_1 = a_1 + \Sigma a_{1i}F_i$

$b_2 = a_2 + \Sigma a_{2i}F_i$

$b_3 = a_3 + \Sigma a_{3i}F_i$

a_1 = ave. maximum height

a_2 = ave. rate coefficient

a_3 = ave. shape coefficient

F_i = 1 for the ith family

= 0 otherwise

H_d = average dominant-codominant height

Table 1. Description of slash pine progeny tests established at Cantonment, FL, in 1978 and 1979.

Test ID (Co-Year-No.)	Design
8-78-1	Randomized complete block design (RCB), 2 reps; main plots of 454 and 907 trees/acre; subplots of 9 families; sub-sub-plots of pure and maximum competition block plots.
8-78-2	RCB, 6 reps; 9 families; 8 densities: 191, 250, 327, 428, 559, 731, 956, 1250 trees/A.
8-79-3	RCB, 4 reps; 9 families in main plots; sub-plots of pure and maximum competition block plots plus row plots; 545 trees/A.
8-79-4	RCB, 4 reps; 9 families in main plots; sub-plots of pure and maximum competition block plots; 545 trees/A.
8-79-5	RCB, 6 reps; 23 families; 8 densities: 191, 250, 327, 428, 559, 731, 956, 1250 trees/A.
8-79-6	RCB, 6 reps; 18 families in 10-tree row plots; 545 trees/A.

The algebraic difference form of equation (2) (Borders et al. 1984) was selected for the final height-age equation:

$$H_2 = H_1((1 - \exp(-\beta_1 age_2))/(1 - \exp(-\beta_1 age_1)))^{\beta 2} + \sigma \qquad (3)$$

where

H_1 = dominant/co-dominant height at age 1

H_2 = dominant/co-dominant height at age 2

β_1 = rate coefficient

β_2 = shape coefficient

Replacing H_2 with site index (SI) and age_2 with base age (A_b = 15/16) produced an equation for predicting site index:

$$SI = H_d((1 - \exp(-\beta_1 age))/(1 - \exp(-\beta_1 A_b)))^{\beta}{}_2 \qquad (4)$$

Density and Family Effects. Means of densities and families for TH, DBH, and SVI were compared using the Nelder design tests. The phenotypic coefficient of variation was calculated for each density. For TH, DBH and SVI at age 15/16 years, the relationships with density were modelled by the simple linear model:

$$Y(TH, DBH, \text{ or } SVI) = \exp(c_1 + c_2 * \ln(TPA) + c_3 * (\ln(TPA))^2 \qquad (5)$$

where

TPA = trees/acre,

c_1, c_2, ana c_3 are the intercept or the log transformed trait value at one density, me slope or me linear relationship between the log transformed trait value, and the curvature of this relationship, respectively. c_2 is the initial relative growth rate, and c_3 is half the rate at which the relative growth rate declines with density.

Growth and Yield Dynamics. Using data for individual trees at ages 4, 6, 8, 11, and 15/16 years, the growth model included site index, density, family, age, and competition level for TH, DBH, and SVI:

$$Y(TH, DBH, \text{ or } SVI) = \exp(d + d_1 * \ln(TPA) + d_2 * \ln(age) + d_3 * \ln(SI) + \Sigma d_i * F_i + \Sigma d_j * C_j) \qquad (6)$$

where

Age = measurement ages

d, d_1, d_2 and d_3 = intercept, Density, Age, and SI coefficients

d_i = parameter estimate for families $F_1 \ldots F_i$

F_i = 1 if family i,
0 otherwise;

d_j = parameter estimate for competition levels $C_1 .. C_j$

C_j = 1 if competition j,
0 otherwise;

Model (6) was used to predict growth for different families in various designs.

Linear Model Effects. All traits in each test were analyzed by the following linear model:

$$Y_{ijshl} = u + R_i + F_j + RF_{ij} + D_s + RFD_{ijs} + W_{ijsl} \qquad (7)$$

where

Y_{ijsl} is the value of the l_{th} tree in the i_{th} replicate in j_{th} family and s_{th} density, u is the overall mean, R_i is the effect of the i_{th} replicate, F_j is the effect of the j_{th} family, RF_{ij} is the interaction of families with replicates, D_s is the effect of s_{th} density, RFD_{ijs} is the interaction of replicates, families, and densities, and W_{ijsl} is the residual error. All terms in Model (7) were considered to be random effects with variances σ^2r, σ^2f, σ^2rf, σ^2d, σ^2rfd, and σ^2w (within plot), respectively.

RESULTS AND DISCUSSION

Height and Site Index. The comparisons of the parameter estimates obtained for Model (1) fit to individual families (Table 2) suggested that polymorphism existed among families in addition to differences in level. The estimate for maximum height A was between 75 to 83' for most families but about 67' for 71-57 and 94' for 89-57 and 95-58. The estimate for b was about 0.12-0.13 for most families but only 0.10-0.11 for 89-57 and 95-58, and about 0.15 for 71-57. In addition, the estimate for shape (c) of 89-57 and 95-58 was conspicuously lower than the other families.

Estimates of the coefficients of model (3) and (4) for different families are given in Table 3. Family parameters ranged from 0.0927 to 0.1263 for ß$_1$ and from 1.2529 to 1.6021 for ß$_2$. Site index (SI) at Base age of 15 years can be calculated for different families using parameters ß$_1$ and .

Density and Family Effects. Density means for tree TH were not significantly different, but DBH and SVI were negatively related to density. Means of DBH versus density by ages indicated that DBH growth differences for densities as early as the fourth year became definite by years of 6, 8, 11, and 15/16. The SVI response was very similar to the DBH response, as would be expected. Applying model (5) to the age 15/16 data gave the overall equations:

$$TH = \exp(1.7403 + 0.5276*\ln(TPA) - 0.04296*\ln^2(TPA)) \qquad R^2=0.554$$

$$DBH = \exp(1.5962 + 0.1598*\ln(TPA) - 0.02795*\ln^2(TPA)) \qquad R^2=0.985$$

$$SVI = \exp(7.9945 + 0.0694*\ln(TPA) - 0.042*\ln^2(TPA)) \qquad R^2=0.985$$

For DBH and SVI between ages 4 and 15 years, the overall R^2 increased significantly, but for TH only increased slightly.

For individual families, the effectiveness of model (5) changed with age, and there were noticeable differences among the families. By 15 years, all families had responded to density for SVI (all $R^2 >0.8$) except 62-57 and 74-57 which still had $R^2 < 0.6$. From 4 to 15 years, density had less effect on TH growth than on other growth traits (all $R^2 < 0.7$). TH usually has higher heritability than other growth traits and is also a good predictor of stand volume at rotation.

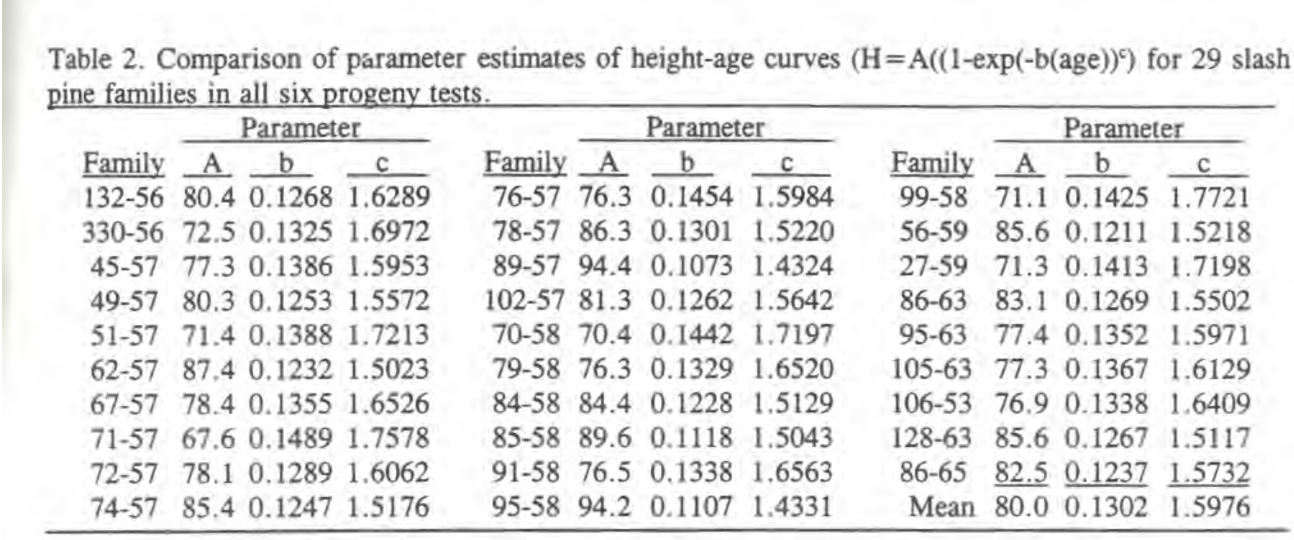

Table 2. Comparison of parameter estimates of height-age curves ($H=A((1-\exp(-b(age))^c)$ for 29 slash pine families in all six progeny tests.

Family	A	b	c	Family	A	b	c	Family	A	b	c
132-56	80.4	0.1268	1.6289	76-57	76.3	0.1454	1.5984	99-58	71.1	0.1425	1.7721
330-56	72.5	0.1325	1.6972	78-57	86.3	0.1301	1.5220	56-59	85.6	0.1211	1.5218
45-57	77.3	0.1386	1.5953	89-57	94.4	0.1073	1.4324	27-59	71.3	0.1413	1.7198
49-57	80.3	0.1253	1.5572	102-57	81.3	0.1262	1.5642	86-63	83.1	0.1269	1.5502
51-57	71.4	0.1388	1.7213	70-58	70.4	0.1442	1.7197	95-63	77.4	0.1352	1.5971
62-57	87.4	0.1232	1.5023	79-58	76.3	0.1329	1.6520	105-63	77.3	0.1367	1.6129
67-57	78.4	0.1355	1.6526	84-58	84.4	0.1228	1.5129	106-53	76.9	0.1338	1.6409
71-57	67.6	0.1489	1.7578	85-58	89.6	0.1118	1.5043	128-63	85.6	0.1267	1.5117
72-57	78.1	0.1289	1.6062	91-58	76.5	0.1338	1.6563	86-65	82.5	0.1237	1.5732
74-57	85.4	0.1247	1.5176	95-58	94.2	0.1107	1.4331	Mean	80.0	0.1302	1.5976

Table 3. Estimates of the coefficients (β_1, β_2) for models (3) and (4).

	Parameters			Parameters			Parameters	
Family	β_1	β_2	Family	β_1	β_2	Family	β_1	β_2
132-56	0.1045	1.4489	76-57	0.1224	1.4184	99-58	0.1225	1.6021
330-56	0.1134	1.5272	78-57	0.1101	1.3520	27-59	0.1231	1.5411
45-57	0.1196	1.4163	89-57	0.0965	1.2531	56-59	0.1011	1.3417
49-57	0.1062	1.3786	102-57	0.1059	1.4040	86-63	0.1057	1.3712
51-57	0.1168	1.5413	70-58	0.1239	1.5397	95-63	0.1148	1.4169
62-57	0.1016	1.3223	79-58	0.1106	1.4729	105-63	0.1157	1.4331
67-57	0.1137	1.4726	84-58	0.1031	1.3332	106-63	0.1148	1.4612
71-57	0.1263	1.5743	85-58	0.0927	1.3244	128-63	0.1071	1.3321
72-57	0.1076	1.4260	91-58	0.1145	1.4759	86-65	0.1041	1.3928
74-57	0.1023	1.3376	95-58	0.0983	1.2529	Mean	0.1103	1.4194

Growth and Yield Dynamics. Between ages 4 and 15/16 years, the average growth in TH, DBH, and SVI was from 13.9' to 54.9', 2.4" to 9.0", and 84 to 4445, respectively. The Model (6) coefficients for density, age, site index, competition level, and individual family terms for TH, DBH, and SVI are provided in Table 4. If a particular coefficient is negative, the associated term in the model reduces the trait value; if the coefficient is positive, the model term increases the trait value. If a family or competition level is included in the model, then its contribution is equal to the value of the coefficient; otherwise it contributes 0.

Family coefficients ranged from -0.0739 to 0.0616 for TH, -0.0513 to 0.1373 for DBH, and -0.1598 to 0.3331 for SVI (Table 4). A negative coefficient indicates a family with below average growth, and a positive value denotes a better than average family. The differences in family coefficients correspond to 13% of the average total height, 20% of average DBH, and 54% of average SVI from the poorest to the best growing families. Family 95-58, for example, was the most vigorous for TH and SVI, and the low growth families were 71-57 and 27-59. Overall, however, the relative performances of these 29 families, as reflected by their coefficients, were not correlated with their evaluations in traditional progeny tests, but the same lack of correlation existed at ages 4 (Rockwood 1983) and 6 (Rieghard et al. 1985).

The parameters for competition levels ranged from -0.0026 (Mix) to 0.0169 (Row) for TH, 0.0206 (Row) to 0.1122 (mix) for DBH, and 0.0394 (Row) 0.3758 (Mix) for SVI. These differences in interfamily competition coefficients represented 2% of average height, 10% of average DBH, and 42% of average SVI. Differences between mixed and pure plantings were not significant.

Model (6) and the coefficients in Table 4 may be used to estimate the growth of these 29 families under conditions similar to these six progeny tests. To predict TH, DBH, and SVI of family 330-56 in row plot competition at age 10 years on a SI 60 site (base age 15 years) with 400 TPA, for example, the models:

$$TH = \exp(0.9021+0.0072*\ln(TPA)+1.108*\ln(age)+0.0032*\ln(SI)-0.0123*F(330\text{-}56)+0.0169*row)$$

$$DBH=\exp(0.3348-0.1555*\ln(TPA)+0.9664*\ln(age)+0.0015*\ln(SI)+0.0548*F(330\text{-}56)+0.0206*row)$$

$$SVI = \exp(1.5718-0.3037*\ln(TPA)+3.0413*\ln(age)+0.0045*\ln(SI)+0.0972*F(330\text{-}56)+0.0394*row)$$

would estimate TH at 33.6', DBH at 5.5", and SVI at 1002.

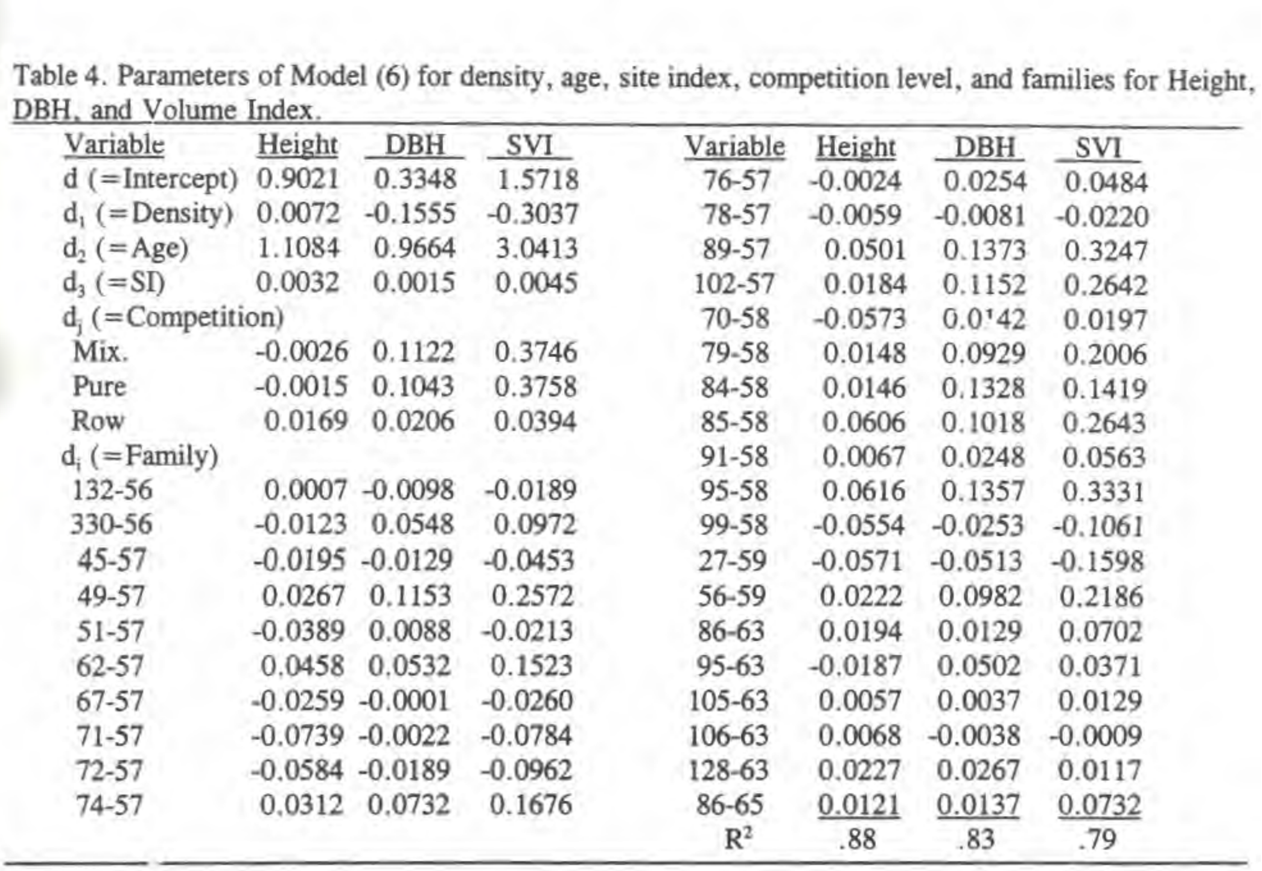

Table 4. Parameters of Model (6) for density, age, site index, competition level, and families for Height, DBH, and Volume Index.

Variable	Height	DBH	SVI
d (=Intercept)	0.9021	0.3348	1.5718
d_1 (=Density)	0.0072	-0.1555	-0.3037
d_2 (=Age)	1.1084	0.9664	3.0413
d_3 (=SI)	0.0032	0.0015	0.0045
d_j (=Competition)			
Mix.	-0.0026	0.1122	0.3746
Pure	-0.0015	0.1043	0.3758
Row	0.0169	0.0206	0.0394
d_i (=Family)			
132-56	0.0007	-0.0098	-0.0189
330-56	-0.0123	0.0548	0.0972
45-57	-0.0195	-0.0129	-0.0453
49-57	0.0267	0.1153	0.2572
51-57	-0.0389	0.0088	-0.0213
62-57	0.0458	0.0532	0.1523
67-57	-0.0259	-0.0001	-0.0260
71-57	-0.0739	-0.0022	-0.0784
72-57	-0.0584	-0.0189	-0.0962
74-57	0.0312	0.0732	0.1676
76-57	-0.0024	0.0254	0.0484
78-57	-0.0059	-0.0081	-0.0220
89-57	0.0501	0.1373	0.3247
102-57	0.0184	0.1152	0.2642
70-58	-0.0573	0.0142	0.0197
79-58	0.0148	0.0929	0.2006
84-58	0.0146	0.1328	0.1419
85-58	0.0606	0.1018	0.2643
91-58	0.0067	0.0248	0.0563
95-58	0.0616	0.1357	0.3331
99-58	-0.0554	-0.0253	-0.1061
27-59	-0.0571	-0.0513	-0.1598
56-59	0.0222	0.0982	0.2186
86-63	0.0194	0.0129	0.0702
95-63	-0.0187	0.0502	0.0371
105-63	0.0057	0.0037	0.0129
106-63	0.0068	-0.0038	-0.0009
128-63	0.0227	0.0267	0.0117
86-65	0.0121	0.0137	0.0732
R^2	.88	.83	.79

Linear Model Effects. Age trends in the contribution of variance components to total TH, DBH, and SVI variances are provided in Figure 1. A linear increase in the total TH variance with age was evident through age 15. Most of the TH variance (1/2) was due to trees within plots. Family, density, replication, and competition contributed comparable amounts of variance (8 - 17%) to the total. As with TH, total variation in DBH increased with age. Density accounted for most of the variation in DBH, especially from age 8 years (Figure 1). Replication was the second largest source of variation at about 20%. Family and competition variances each contributed about 10%. Variation in SVI also increased substantially with age. The largest variance component for SVI after 11 years was due to density (about 1/3). Some 20% was typically due to families. Competition contributed about 15%.

These results have ramifications concerning progeny test design, deployment of genetically improved trees, differential growth patterns, and genetic selection in slash pine. No growth differences in TH or DBH were noted at age 6 due to intergenotypic competition (Rieghard et al. 1985). Based on the overall similarity of the Model (6) coefficients for mixed (i. e., maximum intergenotypic competition) and pure family blocks through 15/16 years, family evaluation and overall yields are not influenced by these extremes of test design. The relatively small influence of competition variance further supports this conclusion. However, only three of the 29 families in these six tests are as genetically elite as what is now typical of advanced generation trees. The observed difference between growth in row plots compared tc block plots must also be considered preliminary because the two types of plots did not occur in the same test and Test 8-79-6 was located slightly apart from the other 1979 tests.

Longer-term field evaluation appears necessary to assess volume related traits such as DBH and SVI. High densities affected DBH as early as four years (Rockwood 1983), and some density x family interactions were detected for TH at 6 years of age (Rieghard 1985). Density became increasingly

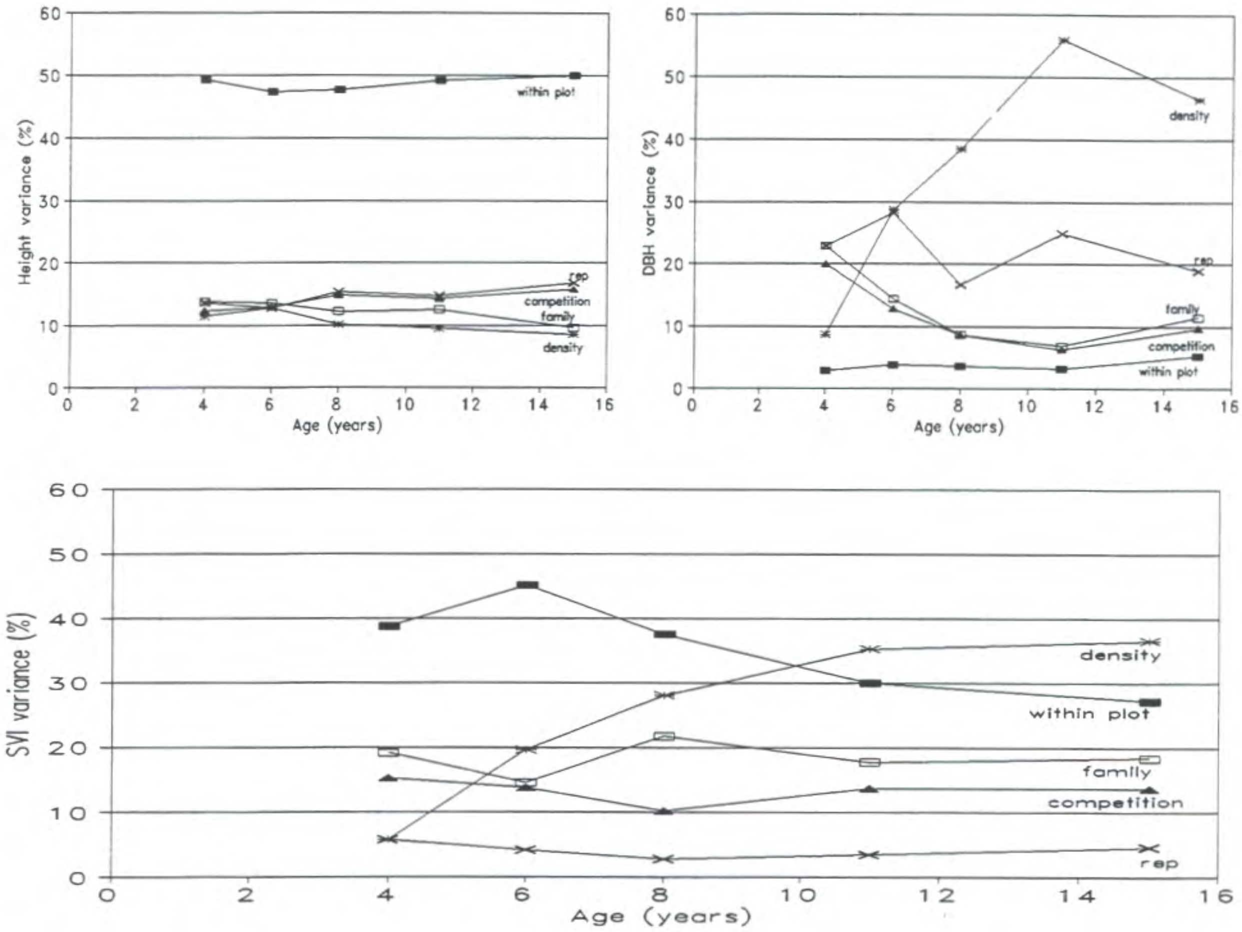

Figure 1. Age trends in contribution of replication, family, density, competition, and within-plot variance components to total variation in height (top left), DBH (top right), and volume index (bottom).

important on DBH after six years. Family variation in these tests, however, seems to remain steady for DBH and SVI after eight years. For these traits, under the moderate levels of fusiform rust incurred in these tests, evaluation periods of up to 10 years may be needed.

Models (4) and (6) are practical ways to incorporate genetic variation into growth and yield projections. Family specific coefficients may account for polymorphic height growth due to genetic differences. SI estimates reflecting these differences, i. e., applying coefficients such as in Table 3 to Model (4), can adjust for family differences. In turn, these SI estimates can be input into DBH and SVI models to accommodate genetic ranges in stand growth.

Model (6), however, is a whole stand growth and yield model and does not offer the potential of diameter distribution models or individual tree models (Burkhart and Matney 1981). Model (6) can only provide mean TH, mean DBH, and, assuming application of a tree content equation in place of the tree volume-index used here, a stand volume or weight. More useful would be a diameter distribution model that predicts the number of trees by DBH class, so that any genetic influences on the diameter distribution and the number of trees by DBH class in the stand can be depicted.

As shown by Spirek et al. (1981), genetic variation in slash pine may be expected to lead to varying diameter distributions and hence timber values. Improved families, for example, tended to have Weibull

DBH distributions with a higher shape coefficient. These positively skewed distributions consequently would have a larger proportion of large DBH trees than unimproved slash pine, and a stand of improved trees would potentially have more value.

Other aspects of stand development may be influenced by the use of improved families. As outlined by Burkhart and Matney (1981), any genetic influences on slash pine disease resistance, stem form, and wood density need to be represented in an operational growth and yield model for improved slash pine. The preliminary results reported here will be extended to other slash pine tests specifically designed for

CONCLUSIONS

The shape, asymptote, and rate parameters of height-age models differed with families, and site index curves were developed for each family using parameters ß

index is appropriately specified for individual families and the appropriate height-age curve is used, the TH, DBH and SVI models can directly use them at the family level. Tree TH was not significantly affected by density, but DBH and SVI were negatively related to density as early as age four, becoming definite by years of 6, 8, 11, and 15/16. At the family level, DBH-Density or SVI-Density curves were related to age, but the levels of the DBH or SVI-density curves were influenced by individual families. For growth models based on the age, site index, density, and competition levels (row and block), 29 families had significant differences for the estimated parameters of the equations, on the order of -0.0739 to 0.0616 (TH), -0.0513 to 0.1385 (DBH), and -0.1598 to 0.3331 (SVI), by the poorest and best growing families. For the Mix, Pure, and Row design plots, corresponding coefficients were -0.0026, -0.0015 and 0.0169 for TH, 0.1122, 0.1043, and 0.0206 for DBH, and 0.3746, 0.3758, and 0.0394 for SVI. Growth differences between mixed and pure plantings were not significant.

LITERATURE CITED

Balocchi,C.E., F.E.Bridgwater, B.J.Zobel, and S.Jahromi. 1993. Age trends in genetic parameters for tree height in a nonselected population of loblolly pine. For. Sci. 39:231-251.

Borders,B.E., R.L.Bailey, and K.D.Ware. 1984. Slash pine site index from a polymorphic model by joining (splining) nonpolynomial segments with an algebraic difference method. For.Sci. 30:411-423.

Buford,M.A. 1986. Height-diameter relationships at 15 in loblolly pine seed sources. For. Sci. 32:812-818.

Buford,M.A., and H.E.Burkhart. 1987. Genetic improvement effects on growth and yield of loblolly plantations. For. Sci. 33:707-724.

Burkhart,H.E., and T.G.Matney. 1981. Growth and yield modeling -- a place for genetic improvement effects. P.6-17 in Proc. 16th South For. Tree Improve. Conf.

Knowe,S.A., and G.S.Foster. 1989. Application of growth models for simulating genetic gain of loblolly pine. For. Sci. 35:211-228.

Nance,W.L., and O.O.Wells. 1981. Estimating volume potential in genetic tests using growth and yield models. P.39-46 in Proc. 16th South For. Tree Improve. Conf.

Magnussen,S., and T.Kremer. 1993. Growth differentiation in white spruce crop tree progenies. Silvae Genetica 42: 258-265.

Reighard,G. L., and D.L.Rockwood. 1985. Genetic and cultural factors affecting growth performance of slash pine. Proc. 18th S. For. Tree Imp. Conf.: 100-106.

Rockwood,D.L. 1983. Alternative designs for progeny testing slash pine. Proc. 17th. S. Tree Imp. Conf.: 179-185.

Spirek,F.J., L.G.Arvanitis, and D.L.Rockwood. 1981. Modeling diameters and heights of improved slash pine using Weibull distributions. Proc. 16th S. For. Tree Imp. Conf.: 47-54.