DIFFERENCES IN GROWTH RATE AND IN ACCELERATION OF GROWTH RATE AMONG LOBLOLLY PINE RANGEWIDE SEED SOURCES CONFIRMED

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Abstract.--Loblolly pine *(Pinus teada* L.) from 15 rangewide seed sources were planted in 15 widely separated plantations. Height growths at 3, 5, 10, 15, 20 and 25 years of age indicated that differences in growth rate and in acceleration of growth rate existed and should be useful for selection. The average growth rate for the study was 20 percent, but for the best seed sources (No. 329 and NO. 317), it was 25 percent per year. While seed sources No. 305 and No. 319 had fast growing rates only before age 15, seed source 321 was a slow starter, but had the best growth rate in the later years. Selection from fast growth rate would result in simultaneous selection for slow "incremental relative rate of relative growth rate".

Additional Keywords: Pinus teada; growth curves, provenance testing

INTRODUCTION

When the size of a tree or a forest is plotted over its age, the curve s defined is commonly called the growth curve. The cumulative growth curves are usually sigmoid-shaped, and therefore can be recognized in three or four phases of growth development (Husch et al., 1972; Switzer and Shelton, 1981). The phenotypic variance, genetic variance and heritability related to these growing periods, has been revealed (Namkoong et al., 1972; Franklin, 1979). During the juvenile acceleration phase, a period of comparatively free growth, seedlings that are genetically superior in the non-competitive condition grow faster than those that are less well adapted. The result is that in the plantation, the genetic variance among populations is low, but increasing. On the other hand, the environmental error increases logarithmically, so there may be a juvenile genetic culmination in this phase as the acceleration of error variance overtakes that of the genetic variance. As the more slowly growing seedlings also capture their site, inter-tree competition is intensified. During the maturing linear growth phase, trees that are genetically superior in the competitive condition have a greater constant growth rate than those that are less competitive. Populational differences strongly emerge, but the error variance is restricted. Therefore, another genotypic culmination can be observed at this phase. During the third period (senescent deceleration phase) growth rate is reduced, but the decreasing rate may be different for different trees. When the rapidly developing phenotypes are slowing down

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faster than the less rapidly developing phenotypes, heritability starts to fall. Finally, when the carrying capacity is reached, the over-mature forest enters the phase of constancy. Therefore, it is natural for tree breeders to assume that growth rate and acceleration of growth rate is different among different seed sources at different phases of stand development. The first objective of this paper is to test whether or not such a hypothesis is true for the loblolly pine. In economic analysis of tree improvement program, it is also important to know the cumulative growth curve and the annual increment growth curve. When a forest is under sustained yield management, the rotation age is set at the maximum mean annual increment. It can be determined by drawing a tangent from the origin to the growth curve. The rotation age is logically inside the senescent deceleration phase. Therefore, we should consider both growth rate and deceleration of growth rate in a tree improvement program.

In this paper, the Loblolly pine south-wide study is used to illustrate the racial difference in growth rate and in growth rate of growth rate (acceleration or deceleration), as well as the relationship between the first and the second derivatives of the growth curve.

SOUTH-WIDE LOBLOLLY PINE SEED SOURCE STUDY

Complete details of the Loblolly pine experiment are given by Wells and Wakeley (1966). Fifteen seed sources are represented and 15 plantings survived after 25 years in the field.

Measurements of total height were made on each tree at various ages from 1 to 27 years. We used all available trees measured in 3, 5, 10, 15, 20, and 25 years to calculate the mean height growth for each seed source. The average number of trees in each seed source was about 500 for the range-wide study. Means of the 15 seed sources are listed in Table 1. The mean standard deviation and the coefficient of variation are also presented.

ACCELERATION MODEL FOR GROWTH

Most growth models describing size at age data are associated with growth to (actural increment) or relative growth rate (increment relative to size). For example, when an essential factor for growth is limiting and conserved at a constant value, the actural increment is constant and the growth model is a linear model. Without limiting factors and with a constant relative growth rate, it is an exponential model. With limiting factors acting on the growth rate itself, the model is monomolecular. If the limiting factor is affecting the relative growth rate, the model becomes a logistic model. Finally, the Bertalanfly model related growth rate to both catabolism and anabolism (Savageau, 1979).

Because growing is a dynamic process, one may consider the seemingly abstract question: "What is the relative growth rate of the relative growth rate?"

Table 1.--South-wide regional means of height growth among loblolly pine seed sources.

Seed Source	Regional Mean at Age 3	5	10	15	20	25
	- - - - - - -	- - - - - - -	0.01 ft.	- - - - - - -	- - - - - - -	- - - - - - -
301	451	1089	2872	4174	5270	6092
303	455	1092	2907	4283	5388	6339
305	479	1137	3021	4440	5582	6410
307	391	948	2566	3907	5078	5907
309	481	1120	2866	4166	5331	6305
311	388	940	2599	3955	5146	5964
315	432	1043	2716	4085	5133	6007
317	381	926	2518	3821	4928	5865
319	457	1057	2790	4113	5243	6069
321	377	903	2545	3898	4976	6028
323	433	1079	2897	4244	5317	6162
325	438	1048	2793	4020	5006	5849
327	412	992	2654	3782	4843	5681
329	393	934	2608	3779	4831	5643
331	346	905	2585	3915	4912	5949
Mean	421	1014	2729	4039	5132	6018
St. Dev.	40	82	159	197	220	222
C.V. %	9.5	8.1	5.8	4.9	4.3	3.7

To illustrate, let us assume that the size of a tree at age t is Y(t); then the growth rate is the difference between two sizes for a given time period, dY/dt. Dividing the increment by its size, the relative growth rate is obtained. For example, in Table 2, the sizes (column 2) at age 1 and age 2 are respectively 100 and 200, hence the growth rate (column 3) is 100, and the relative growth rate (column 4) is unity. Furthermore, let us denote the relative growth rate by Z, the difference between two Z's is dZ, then, dZ/dt is called acceleration in column 5 of Table 2. Dividing acceleration by its relative growth rate in column 6 we have a term called the relative acceleration rate or "the relative growth rate of the relative growth rate (dZ/Z)." If we denote the relative acceleration rate by X, then we have the following relationship:

$$Z = dY/(Ydt)$$
$$\text{and} \quad X = dZ/(Zdt)$$

Thus, the acceleration model concerns the modeling of X.

The simplest model for the relative acceleration rate X is to decompose it into two components: a constant (BO) and an incremental relative acceleration (B1) * Z:

$$X = -(BO + BI * Z)$$

where BO and B1 are regression coefficients. For convenience, the model is written with a minus sign on the right-hand side because decceleration is more common than acceleration. For example, the value of X in the 5th column of Table 2 can be expressed as X = -(.1 + .1Z).

Table 2.--Simulated example to illustrate the relationship among growth rates and acceleration of growth rates.

(1)	(2)	(3)	(4)	(5)	(6)
		Growth Rate		Acceleration Rate	
Age t	Size Y	Actual dY/dt	Relative Z=dY/(Ydt)	Actual dZ/dt	Relative X=dZ/(Zdt)
1	100.00				
		100.00	1.0000		
2	200.00			-0.2000	-.2000
		160.00	0.8000		
3	360.00			-0.1440	-.1800
		236.16	0.6560		
4	596.16			-0.1086	-.1656
		326.32	0.5474		
5	922.48			-0.0847	-.1547
		426.80	0.4627		
6	1349.28			-0.0677	-.1463
		532.96	0.3950		
7	1882.24			-0.0551	-.1395
		639.76	0.3399		
8	2522.00			-0.0455	-.1340
		742.36	0.2944		
9	3264.36			-0.0381	-.1294
		836.50	0.2563		
10	4100.86				

Given the model as above, what would be the model for the size Y(t) and the relative growth rate Z(t) at a given time at T?

To simplify calculation in modelling, let us use * for multiplication and ** for power function and denote the following terms:

Y1B = Y1 ** B1
Y2B = Y2 ** B1
E1N = EXP {-BO * (T - T1)}
E1P = EXP { BO * (T - T1)}
E21 = EXP {-BO * (T2 - T1)}
E2T = EXP {-BO * (T2 - T)}

Here, T1 and T2 are the ages at the beginning and at the end of the growth model. Y1 and Y2 are the expected sizes at the beginning and at the end of the growth model. Yl, Y2, BO, and B1 are four parameters to be estimated in the nonlinear regression model for total growth Y(t):

$$Y(t) = \{Y1B + (Y2B - Y1B) * (1 - E1N)/(1 - E21)\} ** (1/B1)$$

The input data points are observed sizes and ages (Y(t) and T).

After the four parameters Yl, Y2, BO and B1 are obtained from fitting the total growth model, the relative growth rate at time T can be expressed as:

$$Z(t) = (B0/B1) * (Y2B - Y1B)/\{Y2B * (E1P - 1) + Y1B * (1 - E2T)\}$$

The solutions to Y(t) and Z(t) are due to Schnute (1981).

FITTING THE MODEL

Fitting the acceleration model to data from Table 1 was carried out by PROC NLIN (SAS., 1985). The initial values used for the nonlinear regression fitting were as follows:

Y1 = 420
Y2 = 6020
BO = 0.06
B1 = 0.8

The initial value for Yl and Y2 were obtained from the grand mean of height at age 3 and 25 years, while those for BO and Bl were by experience. With these initial values, the model converged rapidly. It took less than one second of the computer time to complete the NLIN procedure.

The nonlinear regression parameters and their standard error were listed in Table 3. All regression coefficients are significantly different from zero, but not all seed sources have the same coefficients. The coefficients Y1 and Y2 in Table 3 are very close to the regional means at age of 3 and 25 years in Table 1 respectively.

The degree of determination (R-square) for modeling the height growth of the loblolly pine was extremely high. In all 15 cases, the R-square was more than 0.9999. On the other hand the root mean square of fitting error was very low. In no cases would it exceed 0.1 feet.

RESULTS AND DISCUSSION

By inserting the value of Yl, Y2, BO and Bl into the equation for the relative growth rate, and at the same time, entering the value of T from 4 to 24 in step of 2, we have the projected relative growth rates for the 15 seed sources of loblolly pine in Table 4.

Table 3.--Estimates of regression parameters and standard errors for the acceleration model.

Seed Source	Estimate (standard error) of Coefficient			
	Y1	Y2	B0	B1
305	460 (44)	6402 (44)	.0736 (.0124)	.718 (.122)
303	429 (60)	6317 (60)	.0555 (.0167)	.840 (.166)
309	459 (59)	6293 (58)	.0416 (.0167)	.930 (.171)
323	411 (51)	6146 (50)	.0657 (.0143)	.795 (.140)
301	431 (52)	6083 (52)	.0632 (.0150)	.806 (.150)
319	439 (45)	6065 (45)	.0654 (.0138)	.742 (.137)
321	347 (70)	5999 (71)	.0449 (.0212)	.833 (.206)
315	418 (32)	5993 (71)	.0625 (.0098)	.765 (.097)
311	378 (40)	5970 (40)	.0706 (.0128)	.646 (.123)
331	314 (89)	5909 (88)	.0448 (.0254)	.890 (.244)
307	383 (33)	5913 (33)	.0666 (.0107)	.673 (.103)
317	362 (38)	5854 (38)	.0501 (.0121)	.803 (.118)
325	410 (73)	5823 (72)	.0586 (.0213)	.867 (.213)
327	385 (80)	5668 (78)	.0464 (.0238)	.930 (.240)
329	363 (75)	5630 (74)	.0577 (.0232)	.823 (.228)
Combined	396 (59)	6062 (58)	.0498 (0171)	.859 (.170)

Table 4.--Computed relative growth rates of loblolly pine seed sources.

Seed Source	Age 4	6	8	10	12	14	16	18	20	22	24	ave.
305	1.342	.415	.230	.152	.109	.082	.064	.051	.041	.034	.028	.232
303	1.158	.365	.207	.139	.102	.079	.062	.051	.042	.035	.030	.206
309	1.053	.337	.193	.132	.099	.077	.062	.052	.043	.037	.032	.193
323	1.217	.379	.213	.142	.102	.078	.061	.049	.040	.033	.028	.213
301	1.202	.376	.211	.141	.102	.078	.062	.050	.041	.034	.028	.211
319	1.304	.407	.228	.152	.110	.084	.066	.053	.043	.036	.030	.228
321	1.174	.347	.214	.146	.108	.084	.068	.056	.047	.040	.034	.213
315	1.267	.396	.223	.149	.108	.083	.065	.053	.043	.036	.030	.223
311	1.494	.463	.258	.171	.123	.093	.073	.058	.047	.039	.032	.259
331	1.099	.350	.200	.137	.101	.079	.064	.053	.044	.037	.032	.200
307	1.437	.447	.250	.167	.121	.092	.072	.058	.047	.039	.032	.251
317	1.214	.385	.219	.149	.110	.085	.068	.056	.046	.039	.033	.219
325	1.120	.352	.199	.133	.097	.075	.059	.048	.040	.033	.028	.198
327	1.051	.334	.191	.130	.096	.075	.060	.050	.042	.035	.030	.190
329	1.180	.371	.210	.141	.103	.079	.063	.051	.042	.035	.030	.210
All	1.135	.360	.205	.139	.103	.079	.064	.052	.044	.037	.031	.204

The seed sources in Table 3 and in Table 4 were ordered according to their heights at the age of 25 years. There seems to be no correlation between heights at any given age and the average relative growth rate. For example, seed source No. 311 which had the greatest average rate of .259 was ranked below average in height. On the other hand, seed source No. 309 which was ranked in the top 20th percentile in height growth would be in the lower 20th percentile of average growth rate. The reason for this lack of consistency may be due to the fact that seed source No. 309 was the tallest one at age 3. Therefore, even with the below average growth rate it continued to have better than average performance. On the other hand, seed source No. 311 which were 10% below average at the beginning would take a long time to overcome the initial slow start even with a superior rate of growth increment.

Another interesting contrast was found between seed sources No. 305 and 309. The initial heights at age 3 for these two seed sources were the same and the final heights at age 25 differed by less than 2%. However, the relative growth rate curves for these two seed sources were quite different. Before age 17, seed source No. 305 had a faster rate than seed source No. 309, but the growth trend reversed itself after that point in time. It can be seen in Table 3 that seed sources No. 305 and No. 309 have different constant acceleration rates (BO) and different incremental relative acceleration rates (B1). The constant acceleration rate is smaller, but the incremental acceleration rate is greater for seed source No. 309 than seed source No. 305.

Differences in the relative growth rates among seed sources through the age periods probably reflect different competition abilities. Seed sources No. 311 and No. 307 were good competitors and seed source 325, 327 and 329 were poor competitors throughout the study period of 4-24 years. Seed source No. 305 and No. 319 were good only before age 15 and seed source 321 had the best growth rate in the later years.

Differences in the acceleration parameter BO and B1 indicate differences in the shape of growth curve among 15 seed sources of loblolly pine. Past studies of growth curves were seldom able to detect the shape differences. For example, in fitting the Weibull function to five half-sib progeny tests, site had no significant effect on the shape parameter. Significance was found in the check-vs.-selection, but not among selections (Spirek et al., 1981). Failure to find significant differences in the shape parameter of the Richard's nonlinear function among populations of Douglas-fir had been reported (Namkoong et al., 1972). The success of detecting shape difference in this study possibly is due to the solid data base and the versatile growth model. First, the regional means with a large sample size over a broad planting area were used. This effectively removed the sensitivity to outlying trees. Secondly the Schnute's model is versatile and with statistically stable parameters (Schnute, 1981).

The average relative growth rate was found to be positively correlated with the acceleration rate (r = .74), but negatively correlated with the incremental relative acceleration rate (r = -.98). The coefficient of acceleration rate (BO) and of incremental rate (B1) were also negatively correlated (r = -.85). Thus, selection for fast growth rate would likely result in simultaneous selection for high decreasing rate of the relative growth rate. The "constant relative rate of relative growth rate" and the "incremental relative rate of relative growth rate" are in check-and-balance.

LITERATURE CITED

Franklin, E.C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genet. 28: 207-212.

Husch, B., C.I. Miller, and T.W. Beers. 1972. Forest Mensuration, 2nd ed. Ronald Press. New York. 410 pp.

Namkoong, G., R.A. Usanis and R.R. Silen. 1972. Age-related variation in genetic control of height growth in Douglas-fir. Theo. Appl. Genet. 42 :151-159.

SAS. 1985. SAS User's Guide: Statistics Version 5 ed. SAS Inst. Inc. Cary, NC. 957 pp.

Savageau, M.A. 1979. Growth equations: A general equation and a survey of special cases. Math. Biosciences. 48: 267-278.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38: 1128-1140.

Spirek, F.J., L.G. Arvanitis, D.L. Rockwood and R.C. Littel. 1981. Modeling diameters and heights of improved slash pine (*pinus elliottii* Engelm. var. *elliottii*) using Weibull distributions. South. For. Tree. Improv. Conf. 16: 47-54.

Switzer, G.L. and M.G. Shelton. 1981. Stand productivity: Some considerations in evaluating genetic improvement. South. For. Tree Improv. Conf. 16: 18-32.

Wells, O.O. and P.C. Wakeley. 1996. Geographic variation in survival, growth and fusiform-rust infection of planted loblolly pine. For. Sci. Monogr. 11:40.