SITE INDEX MODELS FOR HEIGHT GROWTH OF PLANTED LOBLOLLY PINE (*Pinus taeda* L.) SEED SOURCES

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Abstract.--The loblolly phase of the Southwide Pine Seed Source Study (Wells and Wakeley 1966) was analysed to assess the effect of seed source on site index variation. Height growth differences among seed sources were evaluated using site index models, and the results presented as coefficients that can be used in existing growth and yield models for loblolly pine. A practical interpretation of the results was based on the time required to achieve a given size.

In most of the plantations, there was a significant effect of seed source on site index at index ages 25 or 27. Differences in site index between seed sources were consistently greater than 5 feet, and occasionally greater than 10 feet in the 15 plantations studied. Except for one plantation in south Mississippi, seed source effects on the form of the site index curves was not large.

Additional keywords: Geographic variation, growth and yield modeling.

In American forestry, site index, or the mean height achieved by dominant and codominant trees by a given index age, is almost universally accepted as the fundamental indicator of site quality. This is clearly an oversimplification in that the site index of a given forest site depends on the potential growth rate of the trees occupying the site. So it is common to name the species for which the site index applies. A fundamental question arises as to whether this refinement should he extended to the point of specifying the site index that applies to each seed source, half-sib family, full-sib family, or any other definable genetic group that could he planted on the site.

The answer is of fundamental importance to both forest geneticists and forest managers. If geneticists have improved the growth potential of improved stock compared with woodsrun stock--and there are many indications that they have--then these gains should be quantifiable in terms familiar to managers. By expressing genetic improvement in terms of site index, geneticists can accomplish this step and perhaps in the process gain a better understanding of the biology of the system they are attempting to change.

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Forest managers need answers to such questions to effectively handle improved planting stock. Just as managers handle better sites differently than they do poor sites, improved stock may require different strategies than woodsrun stock. For example, better sites are managed on shorter rotations, thinned more often, and can be planted with fewer trees. If they are not managed differently, much of the advantage may be lost. In the same way, improved stock may require similar refinement to maximize economic gain.

Unfortunately, much of the existing data on genetic effects on growth rate are based on unsuitable small row plots. However, in certain genetic field tests, large plots of relatively homogeneous material are replicated on different sites. It should be possible in these tests to estimate site index for each plot and, within the limits of the experimental design, assess the effect of genetics on site index.

In this paper we analyse the loblolly phase of the Southwide Pine Seed Source Study (Wells and Wakeley 1966) to assess the effect of seed source on site index variation. Height growth differences among seed sources are evaluated using site index models. The results are presented as coefficients that can be used in existing growth and yield models for loblolly pine. A practical interpretation of the results is based on the time required to achieve a given size.

MATERIAL AND METHODS

The Southwide Pine Seed Source Study is sponsored by the Southern Forest Tree Improvement Committee. It was established in 1952-53 by numerous industrial cooperators under the direction of Philip C. Wakeley, Southern Forest Experiment Station, now retired. The study sought to determine to what degree inherent geographic variation (i.e., genetic variation) in four southern pines is associated with geographic variation in climate and physiography.

Details of the loblolly phase of this study appear in Wells and Wakeley (1966). Fifteen seed collection areas, or seed sources, were selected and bulk seed from at least 20 trees in each area was collected in 1951. The seed sources were grouped into two sets, or series, with nine sources in each series--six unique to a series and three common to both series. Seedlings were placed in 19 test plantations during the winter of 1952-53.

The experimental design of each plantation is a randomized complete block with four blocks--usually of nine seed sources from one series and eight from the other. Each seed source plot contains 121 trees (11 x 11 trees) with 72 outer trees used as borders and the inner 49 as test trees. Spacing was 6 x 6 feet.

Each of the 49 interior test trees in each plot was measured at 1, 3, 5, 10, 15, 20, and 25 years after planting, except for occasional measurements made at 16, 22, or 27 years instead of 15, 20, or 25. Total height, survival, and damage from insects, disease, and other agents were recorded at each measurement age. Diameter at breast height (d.b.h.) was recorded at measurement ages past 5 years.

Most of the plantations were thinned by cooperators some time after the 10th year. The thinning rules were designed to eliminate diseased or suppressed trees and improve the internal spacing of plots. Thinning to a prescribed density (25 test trees per plot, or 617 trees per acre) was the goal rather than a prescribed residual basal area. Throughout the 25-year period, and despite efforts to avoid it, wide variations in density from plot to plot still occurred because of disease, insects, and other uncontrollable factors.

Fortunately, the failure to control density does not preclude a realistic assessment of the effect of seed source on growth potential. The primary measure of growth potential, height growth of dominant-codominant trees, is essentially independent of density except for extremely high or low densities (Smith 1962). Other measures of growth rate, such as diameter, volume growth, basal area, and biomass are sensitive to density and not as useful in comparing growth potential. The almost universal acceptance of site index (the mean height of dominant-codominant trees at a given index age) as a measure of the productivity, or potential productivity, of forest land attests to the utility of this method.

We designated the tallest two-thirds of the surviving trees at age 25 (or 27) as dominant-codominants at all measurement ages. In plots with fewer than nine surviving trees at the last measurement age, we designated the tallest five as dominant-codominants.

A two-way plot of mean dominant-codominant height over age provides a site index guide curve. Mathematical models of such curves play a central role in growth and yield prediction systems. Also, site index models provide a convenient method of summarizing large amounts of height growth data using only a few statistics. This allows statistical comparisons of site index curves from different data sets. For these reasons, we chose the site index curve as the basic unit of observation for growth analysis.

Basically, variation between site index curves reflects fundamental differences in growth rate due to biotic and abiotic factors. Variation associated with seed source reflects genetic differences in growth rate, whereas variation related to blocks or plantations reflects environmental effects and possibly genetic by environmental interaction effects on growth rate. Our approach to the statistical analysis of variation between site index curves consists of (1) characterizing the site index curves with an appropriate mathematical model, (2) partitioning the variation in model coefficients according to the controlled factors in the experimental design (seed source and blocks), and (3) performing statistical tests to judge whether the variation attributable to controlled factors can be considered significant in light of the experimental error variation between model coefficients.

We chose a mathematical model for site index curves proposed by Smalley and Bower (1971) for loblolly pine:

$$H_D = (S_I)\cdot 10^{B_1\cdot(1/\sqrt{A} - 1/\sqrt{I})} \qquad (1)$$

where

H_D = mean height of dominant-codominant trees
A = age in years since planting
I = index age in years
S_I = site index, or the value of H at age I
B_1 = model coefficient

The model is linear when expressed in logarithmic form:

$$LOG_{10}(H_D) = B_0 + B_1 \cdot (1/\sqrt{A}) \qquad (2)$$

where

LOG_{10} = logarithm to the base 10

$$B_0 = [LOG_{10}(S_I) - B_1 \cdot (1/\sqrt{I})]$$

When expressed in this form, it is clear that a graph with $LOG_{10}(H_D)$ as ordinate and $1/\sqrt{A}$ as abscicca should linearize the site index curve if the model is a good representation of the data. We did this for the data from each plot in the data base and found that the transformation linearized all height data beyond 5 years, but in general did not linearize height data at ages 1, 3, and 5. For this reason, we eliminated the first three height measurements from further analyses and used only the height data beyond age 5 to represent the site index curve. This seems justifiable in light of the fact that nursery effects, planting shock, and other short-term effects influence early height growth, even though they are not related to long-term site productivity.

The logarithmic form, equation (2), expresses the general relationship between height and age for a set of data that are uniform in the sense that each site index curve has the same slope (B1) but not necessarily the same intercept (B_0). In growth and yield terminology, such data "follow the same guide curve." Hence, defining B1 is equivalent to defining a guide curve that may be used to generate a site index curve for any site index at any index age simply by setting B_0 to the desired value. For example, the site index curve for site index 60 feet at age 25 can be generated by:

$$LOG_{10}(H_D) = [LOG_{10}(60) - B_1(1/\sqrt{25}] + B_1(1/\sqrt{A})$$

or

$$H_D = (60)10^{B_1(1/\sqrt{A} - 1/\sqrt{25})}$$

We fit each plot to equation (2) separately, using simple unweighted linear regression methods. The lack of fit for each plot was measured by first generating a predicted site index curve for the plot using the plot's site index and B_1 coefficient. Deviations from prediction, in feet, were then taken and their average squared deviation computed. Finally, the square root of this value was used as a measure of lack of fit.

Once estimates of B1 were obtained for each plot within a plantation, we used analysis of variance procedures to partition the plot-to-plot variation between coefficients within a plantation as follows:

Source of variation	Degrees of freedom	Mean square	F-ratio
Blocks	b-1	MSB	FB = MSB/MSE
Seed Source	s-1	MSS	Fs = MSS/MSE
Error	(b-1)(s-1)	MSE	

The same analysis of variance procedures were also applied to the site index of each plot, i.e., the observed value of Hp at the last measurement. For these analyses most plantations were balanced. But whenever there were missing plots, substitution methods as described by Snedecor (1948) were employed. Four of the original 19 plantations suffered excessive damage from fire or other agents and were eliminated.

Overall estimates of B_1 were obtained by simply pooling (H_D,A) pairs for all plots within a plantation and fitting one B_1 coefficient. Estimates of B1 for each seed source in each plantation were obtained by first computing the plantation mean value of H_D for each seed source at each measurement age and then fitting the B1 coefficient to the mean values.

Site index performance can be expressed in terms of time. For example, the following question may be posed: How long would it take a plot to reach a given mean dominant-codominant height assuming the plot grew in accordance with the mathematical model used to represent its site index curve? We answered with the following formula:

$$T_H = [\ B_1/(LOG_{10}(H_D)-LOG_{10}(S_I)+B_1/\sqrt{I})]^2$$

where

T_H = time in years to reach a given height H_D

and B_1 and S_I are specific to the plot in question.

RESULTS AND DISCUSSION

The overall regression coefficients (B_1's) for each planting varied widely (table 1). Differences in climate, soil moisture regime, and site preparation (Wells and Wakeley 1966) probably contributed. The southwestern Georgia plantation exhibited the smallest "error", with only a 0.20 foot average deviation from predicted height. The two southern Mississippi plantations fit worst, with an average deviation of nearly 1 foot.

Table 1.--Analysis of variance of model coefficient (B1) and observed site index (S_T) variation between plots within plantations

Plantation		Overall Fit		ANOVA of S_T			ANOVA of B_1		
Location	Series	B_1	Error 1/	F_B	F_S	MSE 2/	F_B	F_S	MSE
E NC	1	-2.51371	0.84	29.80* 3/	1.41	21.82	14.33*	0.68	0.1088
SW GA	1	-3.04114	0.20	1.41	7.04*	3.61	5.47*	6.16*	0.0177
E NC	1	-2.58167	0.52	5.07*	2.61*	12.28	1.90	0.40	0.0647
W SC	2	-2.36299	0.43	1.81	2.32	20.98	2.71	3.02*	0.0496
N MS	2	-3.78783	0.45	1.95	3.14*	9.63	0.96	1.15	0.0410
N AL	1	-2.87898	0.34	0.00	1.42	17.88	4.63	1.60	0.0126
E NC	2	-2.66222	0.54	6.32*	3.87*	13.59	26.27*	1.69	0.0314
C AL	2	-3.03082	0.81	14.00*	1.65	21.11	11.84*	1.09	0.1399
SW AR	1	-2.68197	0.60	9.18*	4.60*	13.80	0.11	2.70	0.0220
SW AR	1	-2.98396	0.56	14.83*	4.13*	7.88	7.76*	3.00*	0.0391
E MD	1	-3.09563	0.55	3.72*	10.67*	3.68	0.97	0.65	0.1326
SE LA	2	-2.52170	0.62	1.73	4.75*	9.87	3.24	0.63	0.0301
S MS	1	-3.05636	0.98	6.15	1.70	31.86	0.01	8.37*	0.0334
SE LA	1	-2.43230	0.78	1.55	3.65*	13.25	0.84	3.65*	0.0470
S MS	2	-3.17342	0.96	8.00*	9.77*	2.25	2.60	2.67	0.0476

1/ Error = average deviation from predicted plot height, in feet.

2/ MSE = mean square error from the analysis of variance.

3/ An asterisk denotes significance at the 0.05 probability level.

The analyses of variance for plot-to-plot variation in both site index and model coefficients also appear in table 1. Of the 15 plantations, 7 showed significant (at the .05 level) effects of seed source on site index without showing significant seed source effects on B_1 coefficients. Three plantations showed significant seed source effects in both site index and B_1 coefficients, while two showed significant seed source effects only in B_1 coefficients. The remaining three plantations did not show significant seed source effects in either site index or B_1 coefficients.

The B_1 coefficients and site index values for each seed source in each plantation are given in tables 2 and 3. Except for the series 1 plantation in south Mississippi, the variation in B_1 coefficients was not large. Conversely, differences in site index values were consistently greater than 5 feet and occasionally greater than 10 feet.

Table 2.--Site index (S_I) and model coefficients (B1) for series one seed sources in each planting

Plantation		Seed Source								
		E MD	SE NC	E NC	SW GA	N AL	N AL	SE LA	E TX	SW AR
E NC	B1	-2.27	-2.78	-2.55	-2.72		-2.42	-2.38	-2.50	-2.65
	S_I	64.50	69.50	68.00	65.00		60.00	66.00	62.00	58.00
SW GA	B1	-3.24	-2.98	-3.11	-3.03	-3.18	-3.19	-2.74	-2.86	-3.02
	S_I	55.95	56.50	56.50	55.25	51.00	52.00	56.50	53.25	50.25
E NC	B1	-2.60	-2.69	-2.54	-2.54		-2.58	-2.66	-2.45	-2.57
	S_I	63.25	71.50	66.25	65.75		63.75	66.00	63.25	63.00
N AL	B1	-2.87	-2.79	-2.86	-2.88	-2.93	-3.03	-2.76	-2.77	-3.02
	SI	68.50	73.00	75.50	72.00	67.50	69.00	72.50	66.50	64.50
SW AR	B1	-2.90	-2.78	-2.66	-2.71	-2.83	-2.82	-2.60	-2.37	-2.39
	S_I	68.25	68.75	70.23	67.75	67.00	66.50	65.50	60.50	57.75
S MS	B1	-3.32	-3.00	-3.17	-3.57		-3.14	-2.41	-2.63	-2.95
	S_I	56.50	49.50	53.50	54.50		52.00	57.00	45.50	42.50
E MD	B1	-2.82	-3.07	-3.00	-3.21	-3.03	-3.02	-3.42	-3.31	-2.99
	S_I	56.00	52.75	52.50	48.00	49.50	48.00	46.00	49.25	48.00
SE LA	B1	-2.41	-2.12	-2.69	-2.29		-2.70	-2.27	-2.56	-2.42
	S_I	65.75	67.25	76.00	70.25		71.75	73.50	71.75	67.50

Table 3.--Site index (S_T) and model coefficients (B_1) for series two seed sources in each planting

Plantation number		Seed Source								
		SE NC	W SC	NE GA	NE AL	NE MS	SE LA	SW AR	W TN	NW GA
W SC	B_1	-2.13	-2.46	-2.44	-2.39	-2.47	-2.02	-2.26	-2.50	-2.61
	S_I	52.75	57.25	59.50	52.00	56.25	50.25	51.75	56.00	59.75
N MS	B_1	-3.69	-3.70	-3.79	-3.94	-3.85	-3.73	-3.78	-3.93	-3.64
	S_I	70.75	63.25	66.25	64.50	64.76	70.50	67.75	64.75	66.25
E NC	B_1	-2.66	-2.77	-2.52	-2.77	-2.62	-2.68	-2.81	-2.52	-2.60
	S_I	71.75	70.00	64.25	68.25	67.50	68.50	62.75	60.50	65.00
C AL	B_1	-2.76	-3.04	-3.25	-3.03	-3.05	-2.78	-2.62	-3.18	-3.07
	S_I	57.00	56.75	60.00	59.75	59.25	64.25	53.50	57.75	59.75
S MS	B_1	-3.11	-3.18	-3.09	-3.39	-3.38	-2.69	-3.28	-3.48	-2.90
	S_I	53.50	52.00	52.00	52.00	49.50	56.50	50.00	46.50	46.00
SW AR	B_1	-2.81	-2.95	-3.10	-3.16	-2.94	-2.70	-2.86	-3.18	-3.08
	S_I	70.75	70.00	70.50	69.75	69.50	68.00	61.75	67.00	70.75
SE LA	B_1	-2.47	-2.46	-2.52	-2.42	-2.63	-2.56	-2.52	-2.60	-2.54
	S_I	73.75	68.50	69.00	66.25	67.25	75.75	67.50	65.50	70.00

Table 4.--Gain or loss in time required for nonlocal seed sources to grow to same height as local seed source in series two plantations

Plantation number	Measurement age (Years)	Mean height of local source (Feet)	Gain (+) or loss (-) in years to indicated height for seed source								
			SE NC	W SC	NW GA	NE AL	NE MS	SE LA	SW AR	W TN	NW GA
W SC	15	41.92	-1.4	*0.0*[1]	+0.4	-2.5	-0.9	-2.4	-2.2	-1.0	+0.1
	20	49.03	-1.6	*0.0*	+1.7	-2.5	-0.1	-3.5	-2.4	-0.1	+1.6
	25	57.38	-4.9	*0.0*	+1.4	-5.1	-1.1	-8.7	-5.5	-1.2	+1.7
N MS	15	41.01	+0.6	-0.9	-0.4	-1.0	*0.0*	+0.6	-0.1	-0.9	-0.0
	20	55.64	+0.8	-1.6	-0.6	-1.4	*0.0*	+0.7	-0.2	-1.2	-0.3
	25	68.10	+1.0	-2.3	-0.8	-1.6	*0.0*	+1.0	-0.2	-1.3	-0.6
E NC	15	48.36	*0.0*	-0.0	-1.2	-0.5	-0.2	+0.3	-2.2	-2.6	-1.1
	20	60.44	*0.0*	-0.1	-2.6	-0.9	-0.8	+0.2	-3.5	-5.0	-2.2
	25	71.76	*0.0*	-1.0	-5.6	-2.2	-2.5	-0.8	-5.9	-9.4	-4.6
C AL	15	41.30	-0.9	-1.6	-1.0	*0.0*	-0.8	+1.2	-2.0	-1.6	-0.8
	20	52.82	-2.2	-2.6	-1.2	*0.0*	-1.4	+1.2	-4.5	-2.3	-1.2
	25	59.67	-1.9	-1.9	+0.2	*0.0*	-0.3	+2.7	-5.3	-1.3	-0.1
SW AR	15	45.10	+2.4	+1.9	+1.6	+1.4	+1.8	+2.1	*0.0*	+0.8	+1.7
	20	56.84	+3.7	+3.3	+3.0	+2.8	+3.1	+3.1	*0.0*	+2.0	+3.2
	25	68.74	+4.4	+4.0	+3.9	+3.7	+3.7	+3.3	*0.0*	+2.6	+4.1
SE LA	16	56.11	-1.3	-3.3	-3.2	-4.4	-4.3	*0.0*	-3.9	-5.1	-2.9
	20	65.84	-2.2	-5.1	-4.8	-6.9	-6.1	*0.0*	-5.9	-7.3	-4.3
	27	75.76	-0.0	-4.1	-3.4	-6.6	-4.9	*0.0*	-5.0	-6.7	-2.7
S MS	15	42.65	-4.9	-5.9	-5.8	-5.9	-7.2	*0.0*	-6.9	-9.2	-8.9
	22	51.93	-3.8	-5.2	-5.2	-4.7	-6.7	*0.0*	-6.5	-9.4	-10.7
	27	56.65	-2.3	-3.9	-4.0	-3.1	-5.4	*0.0*	-5.3	-8.5	-11.1

1/ Italicized values designate local seed source.

Table 5.--Gain or loss in time required for nonlocal seed sources to grow to same height as local seed source in series one plantations

Plantation number	Measurement age (Years)	Mean height of local source (Feet)	Gain (+) or loss (-) in years to indicated height for seed source								
			E MD	SE NC	E NC	SW GA	N AL	N AL	NE AL	E TX	SW AR
E NC	15	48.06	-0.3	+0.0	*0.0* 1/	-1.2	----	-2.5	-0.1	-1.9	-3.5
	20	59.00	-1.3	+0.4	*0.0*	-1.4	----	-4.4	-0.6	-3.2	-5.3
	25	68.39	-3.2	+0.7	*0.0*	-2.0	----	-7.4	-1.8	-5.2	-7.8
SW GA	15	37.05	-0.4	+0.4	+0.1	*0.0*	-1.9	-1.5	+1.0	-0.3	-1.8
	20	47.07	-0.1	+0.5	+0.4	*0.0*	-2.5	-1.9	+1.0	-0.8	-2.7
	25	55.48	+0.3	+0.7	+0.7	*0.0*	-3.2	-2.3	+0.8	-1.5	-3.9
E NC	15	45.99	-0.7	+1.4	*0.0*	+0.3	----	-0.4	-0.5	-0.6	-0.6
	20	56.30	-0.9	+2.5	*0.0*	+0.5	----	-0.5	-0.5	-1.2	-0.9
	25	66.47	-2.4	+2.7	*0.0*	-0.5	----	-1.8	-1.6	-3.3	-2.5
N AL	15	46.98	-0.1	+1.2	+1.5	+0.8	-0.5	*0.0*	+1.1	-0.4	-1.5
	20	58.29	+0.1	+2.0	+2.5	+1.5	-0.2	*0.0*	+1.7	-0.6	-1.6
	25	69.23	-0.4	+2.1	+2.9	+1.5	-0.8	*0.0*	+1.7	-1.7	-2.6
SW AR	15	44.22	+1.5	+2.1	+1.8	+1.8	+1.2	+1.3	+1.1	+0.6	*0.0*
	20	53.88	+3.0	+3.7	+3.1	+3.1	+2.5	+2.7	+2.0	+0.7	*0.0*
	25	58.88	+5.9	+6.7	+5.9	+5.9	+5.3	+5.5	+4.5	+2.6	*0.0*
E MD	15	41.89	*0.0*	-0.3	+0.2	-0.8	-0.6	-1.1	-2.0	-1.0	-1.4
	20	56.15	*0.0*	-1.8	-1.2	-2.2	-2.5	-3.3	-3.8	-2.3	-4.0
	25	65.99	*0.0*	-0.4	+0.4	-0.6	-1.4	-2.5	-2.4	-0.6	-3.6
SE LA	16	54.02	-2.8	-1.8	-0.3	-1.0	----	-1.6	*0.0*	-1.3	-2.5
	20	64.00	-4.9	-4.4	-0.6	-2.6	----	-2.4	*0.0*	-2.4	-4.6
	27	73.55	-5.6	-6.1	+1.4	-2.6	----	-1.0	*0.0*	-1.3	-5.0
S MS	15	46.44	-6.1	-4.6	-7.4	-7.1	-7.9	-3.9	*0.0*	-6.1	-16.2
	22	50.78	-1.6	-0.1	-3.3	-2.5	-3.9	+0.2	*0.0*	-2.3	-14.4
	27	57.25	-0.7	+0.9	-3.0	-1.5	-3.9	+0.0	*0.0*	-2.8	-18.6

1/ Italicized values designate local source.

Summarizing the differences between seed sources in terms of time required to reach a given height is a convenient and practical way to express differences in site index curves. If the nearest seed source to each planting site is designated as "local," one might pose the following question: How much more (or less) time would be required for each "nonlocal" seed source to grow to the same height as the local source? The answer for selected ages beyond 10 appears in tables 4 and 5. For example, in the two southwestern Arkansas plantations, the nonlocal seed sources grew at a much faster rate than the local source, and this advantage translated into a gain of more than 5 years on a 25-year rotation. Wherever southwestern Arkansas or eastern Texas seed were planted, the slower growth amounted to a time lag of up to 5 or more years on a 25-year rotation.

The results presented here support the general conclusion that, at least for forest management applications, seed source differences in height growth could be incorporated into existing growth and yield models simply by adjusting site index potential without modifying the form of the guide curve. However, for applications of growth and yield models that require more precision, individual guide curves for different seed sources and different sites may be required. We emphasize that these results apply only to seed source differences in site index in plantations relatively undisturbed by destructive agents. The other components of growth and yield models (such as survival functions) might also be affected by seed source.

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