Mean stem size and total volume development of various loblolly pine seed sources planted at one location

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Data from one location of the loblolly phase of the Southwide Pine Seed Source Study were analyzed to determine the effect of seed source on the self-thinning trajectory for loblolly pine (*Pinus taeda* L.). Stand trajectories for mean stem size and total volume were examined. Seed source affected the level of both the mean stem size and total volume per unit area trajectories. The rate of change of mean stem size and of total volume per unit decrease in number of stems did not appear to be affected by seed source. The levels of the stand trajectories for total volume per unit area were positively correlated with the site indexes of the seed sources at this location. These results indicate that site productivity of loblolly pine, measured by total volume production per unit area and mean stem volume, varies by seed source.

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Des données provenant d'un endroit particulier parmi les diverses provenances d'une étude portant sur les sources de semences dans l'aire du Pin à encens (*Pinus taeda* L.) ont été analysées afin de déterminer l'effet de la source de semences sur le degré d'éclaircie naturelle du Pin à encens. Les variations entre peuplements quant à la dimension moyenne des tiges et au volume total ont été examinées. La source de semences a affecté à la fois la dimension moyenne des tiges et le volume total par unité de surface. Le taux de changement de la dimension moyenne des tiges et du volume total par unité de diminution du nombre de tiges n'a pas semblé affecté par la source de semences. Les niveaux de trajectoires des peuplements quant au volume total par unité de surface étaient positivement corrélés avec les indices de qualité de station des sources de semences à cet endroit particulier. Ces résultats montrent que la productivité stationnelle de Pin à encens, telle que mesurée par la production en volume total par unité de surface et par le volume moyen des tiges, varie suivant la source de semences.

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Introduction

Yoda *et al.* (1963) put forward their representation of the relationship between the number of individual plants and their average mass in a stand with complete crown closure as

$$[1] \quad \log(V) = k + b \log(N)$$

where V is the average stem volume, N is the number of surviving stems, k is a constant, b is $-3/2$, and log indicates the natural logarithm. This has been called the self-thinning line and is often called the $-3/2$ power rule. Plots of the relationship between the logarithm of average volume and the logarithm of the number of surviving stems for a given stand through time are called stand trajectories. There has been a plethora of reports giving evidence in support of a constant slope (b) of $-3/2$ (White and Harper 1970; Hozumi 1977; White 1980), and Westoby (1984) provides numerous references. The rule has been used as the basis for stand growth models (Smith and Hann 1984, 1986; Lloyd and Harms 1986) and as a basis for forest management decisions (Drew and Flewelling 1977, 1979; Long 1985).

Recently, the formulation of the $-3/2$ power rule as a law of forest stand behavior has been the subject of criticism in the literature. Weller (1987) and Zeide (1985, 1987) question the universality of the rule on statistical and theoretical grounds. In particular, they question the universality of the slope, $-3/2$, for the relationship in eq. 1. Using published yield tables for southern pines, Zeide (1985) states that the relationship of log(average volume) to log(number of stems) is curvilinear rather than linear. This curvilinearity was also reported using long-term (50 years) data from natural stands (Peet and Christensen 1987). Long-term (44 years) data from loblolly pine (*Pinus taeda* L.) spacing studies on the North Carolina Coastal Plain (Hafley *et al.* 1982) and the South Carolina Piedmont (30 years)[1] (Harms and Lloyd 1981) show a curvilinear stand trajectory for plantations.

Zeide (1985) and Weller (1987) showed that the stand trajectories vary with species, site quality, and shade tolerance. Nance *et al.* (1987) suggest the stand trajectories may vary intraspecifically as well. Using only age 25 and 30 data from thinned plots, Schmidtling (1988) concluded that there was some evidence for genetic variation in final yield. This paper reports the results of a study to determine whether differences in the stand trajectories of loblolly pine exist at the seed source (provenance) level.

[1]Unpublished 25- and 30-year data for the South Carolina spacing study are on file at the USDA Forest Service Southeastern Forest Experiment Station, Charleston, SC.

Methods

Hypothesis

The question that formed the basis of the investigation can be stated as follows: Does the self-thinning trajectory vary among seed sources planted at the same initial density on the same site? An additional question of interest concerns whether variation in these self-thinning trajectories is associated with height growth or site index.

Data

Data appropriate for this analysis should be derived from stands with the following attributes: (*i*) they include different genetic sources of loblolly pine planted in source blocks at the same initial density on the same site, (*ii*) crown closure has occurred and competition-induced mortality has begun, (*iii*) they have suffered no major catastrophic losses, and (*iv*) they have never been thinned. All four conditions are met by the stands used in this analysis.

The data used in this analysis are part of the Southwide Pine Seed Source Study (SWPSSS), which was established in 1952–1953 to determine the degree to which genetic variation in four southern pine species is associated with geographic variation in climate and physiography. Detailed descriptions of the design and installation of the SWPSSS are given by Wells and Wakeley (1966) and Wells (1983). Buford and Burkhart (1987) showed that the shapes of the height–age curves did not vary by seed source but that the level of the height–age curves (site index) did vary by seed source in these data.

The Washington Parish, Louisiana, series 2 planting of the loblolly phase of the SWPSSS was used in this study. All other locations of the SWPSSS had been thinned or had suffered major catastrophic mortality and were therefore unsuitable for the analysis. Seeds from nine geographic areas were planted in source plots. The plots were arranged in a randomized complete block design with the four blocks as replications. Each source plot contained 121 trees on a 1.8 × 1.8 m (6 × 6 ft) spacing. The inner 49 trees (7 × 7 rows) were measured at 1, 3, 5, 10, 16, 20, 25, 27, and 30 years. Borders are 3-5 m (12-15 ft) wide and measurement plots are 0.016 ha (0.04 acres) in size. Examination of survival data indicated that the period of rapid mortality had begun at this location by age 16. Data at ages 10, 16, 20, 25, 27, and 30 years were used because diameter at breast height had not been measured before age 10. All 36 of the plots (seed source × block combinations) at this location were used in this analysis.

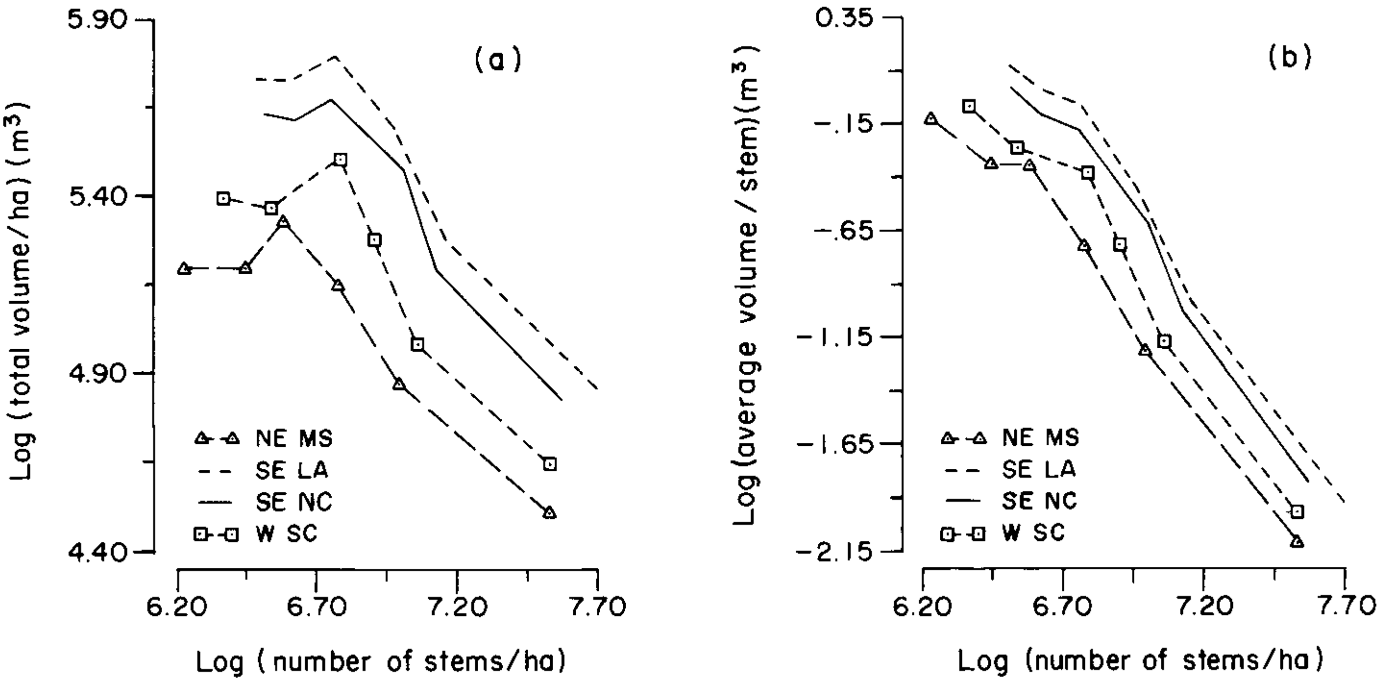

FIG. 1. Logarithm of total volume per hectare (a) and logarithm of mean stem volume (b) versus logarithm of number of surviving stems per hectare at ages 10, 16, 20, 25, 27, and 30 years for selected seed sources planted in Washington Parish, Louisiana.

Analysis

Total cubic-foot volume inside bark was calculated for each tree at each age, using the equation

$$[2] \quad V_{ib} = 0.00296 + 0.00193881(D^2H)$$

where V_{ib} is volume inside bark, D is diameter at breast height, and H is total height (Van Deusen *et al.* 1981). An assumption made here is that stem form does not vary appreciably among the seed sources. Van Deusen *et al.* (1981) showed that eq. 2 is widely applicable for loblolly pine. At each age, average stem volume, total volume per area, their respective logarithms, and the logarithm of the number of stems per area were calculated for each source in each block. An example of the behavior of the plot trajectories, using data from selected seed sources at this location, is shown in Fig. 1.

Regression as a means of fitting eq. 1 has been criticized by Weller (1987) and Mohler *et al.* (1978), based in part on the resulting bias in the estimate of b. Leduc (1987) states that the reduced major axis technique is more appropriate than linear regression when specifically testing whether the slope of eq. 1 is equal to any constant, say $-3/2$. The objective of this analysis, however, is not to compare fitted slopes with a given constant, but to compare the stand trajectories of the seed sources at this location. For this reason, and because portions of the following work use a nonlinear model, regression techniques were used for this analysis. The least squares analysis described in the following section does not yield maximum levels of the stand line. However, the resulting fitted curves do allow differentiation among seed sources to be examined and interpreted.

Mean stem size

Plots of the logarithm of average stem volume versus the logarithm of number of stems surviving for each source are curvilinear (e.g., Fig. 1b). Zeide (1987) suggested the power function for modeling the stand trajectory. A function that fits the behavior of the trajectories well in the range of the data is

$$[3] \quad Y = b_1 + b_2 e^{b_3 X}$$

where

Y = log(average volume per stem)
X = log(number stems surviving per acre, N)
b_i = parameters to be estimated, i = 1, 2, 3
log = natural logarithm

Given the definition of X, eq. 3 simplifies to

$$[4] \quad Y = b_1 + b_2 N^{b_3}$$

where N and b_i are as defined above. The model in eq. 4 was fitted separately to the data from each seed source, with the blocks as replications. An approximate test of the hypothesis that b_3 = 1 in eq. 4 (Gallant 1987) is given by fitting eq. 4 and the following equation to the data for each seed source separately:

$$[5] \quad Y = b_1 + b_2 N$$

TABLE 1. Summary statistics for eqs. 4 and 5 for log(mean stem volume) for nine seed sources at one location

Seed source	Equation 4		Equation 5			
	SS	df	SS	df	L	$P > F$
303	0.3654	21	0.4175	22	2.99	0.098
307	1.3581	21	1.4792	22	1.87	0.186
311	1.2530	21	1.2568	22	0.06	0.803
317	1.3917	21	1.4138	22	0.32	0.570
321	1.7741	21	1.9013	22	1.51	0.233
323	1.3313	21	1.3356	22	0.07	0.796
327	1.3303	21	1.3606	22	0.48	0.496
329	0.7062	21	0.7981	22	2.73	0.113
331	1.5785	21	1.6073	22	0.38	0.542
Total	11.0085	189	11.5701	198		

NOTE: SS, sum of squares, or conditional error; L, likelihood-ratio statistic.

The results are summarized in Table 1. The reduction in sum of squares, or conditional error, technique (Swindel 1970; Gallant 1987) was used to calculate the F-tests in this analysis. Based on the likelihood-ratio test statistic, L, shown in Table 1, the hypothesis that $b_3 = 1$, or that the relationship between log(average stem volume) and number of surviving stems is linear in the range of the data, cannot be rejected for the seed sources at this location.

Comparing the stand trajectories for the seed sources further, we are interested in the slope of the line given in eq. 5. That is, do the rates of increase of average stem volume per unit loss in stems per unit area differ among the seed sources? Using the conditional error technique (Swindel 1970), an F-test for this hypothesis can be calculated using the results of fitting eq. 5 to the seed sources separately and fitting the following equation to the combined data:

$$[6] \quad Y = \sum_{k=1}^{9} b_{1k}X_k + b_2N$$

where

X_k = 1 if seed source is k
= 0 otherwise
b_{1k} = parameter to be estimated, $k = 1,\ldots,9$
b_2 = a common slope

The calculated F-statistic for testing the hypothesis of a common slope among the seed sources at this location is 0.912 with 8 and 198 degrees of freedom ($P > F = 0.307$). The estimated common slope (b_2) for eq. 6 is -0.003296 with a standard error of 0.0000846. An analysis of the residuals for eq. 8 showed no systematic variation or bias.

The next question of interest is whether the intercepts from eq. 6 are the same. That is, do the levels of the stand trajectories differ among the seed sources? Using the results of fitting a simple linear regression to give a common slope and common intercept for all sources combined, and fitting eq. 6 to the combined data, the calculated F-statistic for this test is 11.06 with 8 and 206 degrees of freedom ($P > F < 0.0001$). This test indicates that the hypothesis of equal intercepts, given the same slope, should be rejected.

If the hypothesis of equal slopes among the sources had been rejected, would the hypothesis of equal intercepts also have been rejected? Comparing the results of fitting eq. 5 to the seed sources separately with the results of fitting the following equation to the combined data:

$$[7] \quad Y = b_1 + \sum_{k=1}^{9} b_{2k}Z_k$$

where

Z_k = N if seed source is k
= 0 otherwise
b_{2k} = parameters to be estimated, $k = 1,\ldots,9$
b_1 = a common intercept

gives a calculated F-statistic of 2.77 with 8 and 198 degrees of freedom ($P > F = 0.006$). This indicates that the hypothesis of equal intercepts should be rejected in any case for these data.

Total volume

The same series of analyses as described previously was carried out for the relationship between log(total volume per unit area) and log(number of stems). The relationship between these two variables is curvilinear (Fig. 1*a*), and eq. 3 with Y = log(total volume per unit area) and X = log(number of stems) fits the data well. For this portion of the analysis, Y is defined as log(total volume per unit area). The equation simplifies to the form of eq. 4, as in the previous case. An approximate test of the hypothesis that a linear model is adequate to describe the relationship, i.e., that $b_3 = 1$, is given by comparing the results of fitting eqs. 4 and 5 with the data for each source. The results are summarized in Table 2. Based on the approximate F-tests given in Table 2, the hypothesis $b_3 = 1$ cannot be rejected for eight of the nine seed sources at this location.

TABLE 2. Summary statistics for eqs. 4 and 5 for log(total volume per unit area) for nine seed sources at one location

Seed source	Equation 4 SS	Equation 4 df	Equation 5 SS	Equation 5 df	L	$P > F$
303	0.3798	21	0.3897	22	0.55	0.469
307	1.4400	21	1.4420	22	0.03	0.865
311	1.4475	21	1.5084	22	0.88	0.358
317	2.3513	21	2.6767	22	2.91	0.103
321	1.9512	21	1.9751	22	0.26	0.618
323	1.5916	21	1.7914	22	2.63	0.119
327	1.4989	21	1.6761	22	2.48	0.130
329	1.1621	21	1.6083	22	8.06	0.010
331	1.9238	21	2.0634	22	1.52	0.231
Total	13.7462	189	15.1311	198		

NOTE: SS, sum of squares, or conditional error; L, likelihood-ratio statistic.

Continuing the analysis, do the slopes, i.e., values of b_2 in eq. 5, differ among the sources? Equation 6 was fitted to the data. Comparing the results obtained with eq. 5 with those obtained with eq. 6, the calculated F-statistic for this test is 0.796 with 8 and 198 degrees of freedom ($P > F = 0.608$). The estimated common slope, b_2, for eq. 6 for log(total volume per unit area) is -0.001074 with a standard error of 0.0000959. Residual analysis of eq. 6 fitted to the data for total volume showed no systematic variation or bias.

Using the results of fitting eq. 6, and of fitting a simple linear regression to the combined data for log(total volume per unit area), the hypothesis of equal levels of the stand trajectories can be tested. The calculated F-statistic for this test is 10.54 with 8 and 206 degrees of freedom ($P > F < 0.0001$), indicating that the hypothesis of equal intercepts (levels), given the same slope, should be rejected.

If the hypothesis of equal slopes had been rejected, the calculated F-statistic comparing the results using eq. 5 with those using eq. 7 for total volume per unit area is 4.104 with 8 and 198 degrees of freedom ($P > F = 0.00015$). This also indicates that the hypothesis of equal intercepts should be rejected for these data.

Site index

The dominant height of each plot was calculated as the average height of the four tallest trees on that plot. This represents the tallest 250 trees per hectare (approximately 100 trees per acre). The correlation between the dominant heights of the seed sources at age 25 (site indexes) at this location and the levels of the total volume/area versus number of stems/area trajectories (intercept volume of eq. 6 fitted to the total volume data) is +0.865. This correlation is statistically significant at the 0.001 level, indicating a strong positive relationship between the level of the trajectory of total volume per unit area and the site indexes of the individual seed sources planted at this location.

Conclusions

The results of this study show that for the seed sources planted at this location, the slopes of the self-thinning trajectories do not differ by seed source, but the levels of the self-thinning lines do differ by seed source. In addition, there is a strong positive correlation between the level of the total volume trajectories and the site indexes of the seed sources at this location. In practical terms, for the same number of surviving stems per hectare, say 800 (325 stems/acre), which was reached between ages 20 and 27 years by the seed sources at this location, the differences in the levels of the stand trajectories for total volume per unit area development result in a range of 157–275 m^3/ha (2250–3930 ft^3/acre) for the seed sources at this location. These results indicate that site productivity of loblolly pine, measured by both mean stem volume and total volume produced per unit area, varies by seed source.

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