ESTIMATING VOLUME POTENTIAL IN GENETIC TESTS USING GROWTH AND YIELD MODELS

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Abstract.--Genetic field tests are subjected to many disturbances such as damage from diseases, insects, fire, wind, and ice. The differences in standing volume among plots in many older genetic field tests largely reflect differences in density due to uncontrolled disturbances rather than inherent differences in growth rate. Hence, standing volume is often subject to large experimental errors which makes it unsatisfactory for measuring genetic differences in growth rate.

Height of dominant-codominant trees is much less dependent on density and therefore is a better measure of inherent growth rate differences. Growth and yield models can be used to translate differences in dominant-codominant height into volume differences expected in the absence of uncontrolled disturbances. This approach is illustrated with loblolly pine data from the Southwide Pine Seed Source Study.

Additional keywords: Plot size, provenance testing, loblolly, *Pinus taeda.*

Genetic field tests of forest trees, like operational plantations, are subject to fire, insects, disease, high winds, and other disturbances. These disturbances kill trees and hence lower the density (number of surviving trees per acre) of affected plots, thus altering plot volume, diameter growth, basal area, and most other common measures of productivity. Thinning has similar effects. Plot-to-plot variations in density often induce large experimental errors and destroy the utility of volume and other density-dependent traits as measures of genetic potential.

Fortunately, not all growth traits are density-dependent. In fact, the height growth of dominant-codominant trees in even-aged stands is relatively free of density effects over a wide range of densities (Smith 1962). This is one reason foresters have long used site index, which is the mean height of dominant-codominant trees at a specified index age, as a universal measure of the potential productivity of forest land.

In large-plot field tests of genetic material (in contrast to individual tree or row plots), the mean height of the dominant-codominant trees within a plot should be relatively free of density effects. If one genetic group produces taller dominant-codominant trees than another group of the same age on

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the same site, then the taller group is expected to have higher volume production. Whether the taller group consistently produces more volume than the shorter one will depend largely on the density variation among plots in the field test, a nongenetic effect.

The Southwide Pine Seed Source Study is **an** example of a large-plot genetic field test in which large differences in dominant-codominant heights between seed sources are easily detected; yet volume differences are generally neither large nor strongly related to dominant-codominant height growth after nearly 30 years in the field. Typically, the field plots have been affected by fusiform rust, bark beetles, high winds, thinnings, and other disturbances. Therefore actual volume production of a seed source probably does not reflect its potential volume for the cases where density is controlled.

In this paper, we develop a method for obtaining expected plot volumes for large-plot genetic field tests. The method is based on the application of a growth and yield model (Feduccia et al. 1979) which uses the site index and initial density of a plot as variables to produce the expected volume of that plot--assuming it develops in the absence of disturbances. We applied the method to the loblolly pine phase of the Southwide Pine Seed Source Study. Extensions of the method to other problems in assessing genetic potential in field tests are discussed.

MATERIALS AND METHODS

Complete details of the loblolly phase of the Southwide Pine Seed Source Study are given by Wells and Wakeley (1966) and Wells (1969). Fifteen seed sources are represented, and 16 plantings survive after 25 years in the field. The seed sources and plantings are divided into two series. Series 1 sources represent the major part of the range. Series 2, with the exception of the southeastern Louisiana seed source, is restricted to an east-west transect from North Carolina to Arkansas. Seed was collected in 1951 from at least 20 trees in each area, and seed from all trees within a source was composited. A randomized complete-block design with four replications was used for each planting. Plots consist of 121 trees at 6- by 6-foot spacing; the inner 49 trees were periodically measured, and the outer two rows served as buffers against competition from other trees.

Measurements were made at 1, 3, 5, 10, 15, 20, and 25 years after planting in most plantations, but occasionally they were made at 16, 22, or 27 years in some plantations. Total height of all trees was recorded at each measurement age along with survival and damage from insects or disease. Diameter at breast height (d.b.h.) was recorded for each tree starting with the 10th-year measurement.

Light thinnings were done in most plantings to equalize the number of trees in each plot, but despite efforts to avoid it, wide variations in density from plot to plot still occurred because of mortality due to disease, insects, and other uncontrollable factors.

The total outside bark volume for all living trees at the last measurement age was computed by the standard conic formula:

$$= 0.02909 \cdot DBH2 \cdot H$$

where

V = outside bark volume in cubic feet
DBH = diameter at breast height in inches
H = total height in feet

The sum of these volumes for all trees on each plot was then computed and will be referred to herein as the "actual volume."

The growth and yield model (Feduccia et al. 1979) was developed for unthinned plantations of loblolly pine growing on cutover sites in the west gulf region of the United States. It is available in a computer program (named USLYCOWG) written in FORTRAN. Before describing the model further, it is necessary to introduce several terms and notations.

Notation	Meaning
Ap	Plantation age, the number of growing seasons since the seedlings were planted.
SI	Site index, the average height of dominant and codominant trees at a given index age (usually 25 years).
Tp	Number of trees planted per acre.
Ts	Number of trees per acre surviving at a given age Ap.

Basically, the model accepts three input values and from these predicts plot volume. The three input values are Ap, S_I, and either Ts, or Tp. Hence, there are two combinations, or survival options, allowed as input as defined below:

Survival Option	Input Values	Output
1	Ap, S_I, Ts	Predicted plot volume at age Ap for plot growing on land with site index S_I with Ts surviving trees per acre at age Ap. It is assumed that the plot developed to age Ap in the absence of artificial thinning, disease, or insect damage.
2	Ap, S_I, Tp	Predicted plot volume at age Ap for plot growing on land with site index S_I with Tp trees per acre initially planted. The model predicts survival at age Ap assuming the plot would experience about 30 percent mortality by age 3 and subsequently develop in the absence of artificial thinning, disease, or insect damage.

Since the number of surviving trees at age Ap (Ts) is given, option 1 does not require a survival model. Option 2 requires that a survival function predict Ts at age Ap, assuming the planting mortality to be around 30 percent (varying slightly with S_I). Hence, the program essentially reduces option 2 to option 1 by first predicting Ts and then generating volumes using that Ts, Ap, and SI.

Option 1 volume predictions apply to the case where one knows the number of trees surviving on a plot, the plot's age, and enough of the plot's history to determine that the plot has not been disturbed by artificial thinning, disease, or insect damage. Of course, the plots in this data set do not satisfy the last assumption, but it is interesting to compare the actual plot volume with that predicted by option 1. We used option 1 as a rough check on the model's ability to duplicate actual volume on our plots. On plots that were disturbed only slightly, option 1 volumes should be close to actual volumes.

Option 2 volume predictions apply to the case where one knows the number of trees planted (Tp) and the site index of the planting site (S_I) and wants to predict volume at age Ap, assuming that the plantation will not be disturbed by thinnings, disease, or insects. The model uses a survival function to first predict the number of surviving trees at age Ap and then predicts the volume of that stand using that Ts and the site index of the planting. In the present application, option 2 estimates seed source potential under conditions of average planting survival and stand development without disturbance by damaging agents or thinning.

We used both options of the model on data for each plot within each planting to predict total outside bark volume. For each plot, we input Ap equal to the last measurement age (either 25 or 27 years) and S_I equal to the mean dominant-codominant height at that age. The mean dominant-codominant height was computed as the average of the tallest two-thirds of the trees in the plot.

We analysed actual plot volumes and predicted plot volumes from option 2 for each planting using an analysis of variance of the following form:

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

Occasionally, a plot was missing in which case we used a missing plot substitution method. We also computed the coefficient of variation for each planting using the following formula:

$$CV = (\sqrt{MSE} / \bar{X}) \cdot 100$$

where

CV = coefficient of variation in percent
MSE = mean square error from analysis of variance
$\bar{X}$ = overall planting mean

RESULTS AND DISCUSSION

The correlations between actual and predicted seed source volumes using option 1 of the growth and yield model were quite high. In 14 of the 16 plantings the correlations were .80 or above and in 7 were .90 or above. It appears that the main effect of the disturbances was to simply reduce the number of surviving trees below that expected if suppression mortality had acted alone. The result is reassuring, since it tends to confirm that the model can provide realistic estimates of standing volume, given the number of surviving trees, the site index, and the age of the plot.

Since option 1 volumes are not used again, we refer to option 2-derived volumes as "model-derived volumes," and concentrate on comparing these with actual volumes.

The coefficients of variation for model-derived volumes were smaller than those for actual volumes in all plantings (table 1). Each of the plantings has been damaged by destructive agents to some degree, and experimental error for actual volume is sensitive to this damage as shown by the high coefficients of variation. Only 1 planting had a coefficient of variation for actual volume under 10 percent, compared with 11 for model-derived volumes.

Significant F-ratios (at the 5 percent level) for seed source differences in actual volumes occurred in only five plantings, compared with nine for model-derived volumes. In 12 of 16 plantings F-ratios for model-derived volumes were greater than those for actual volumes. In four plantings however, the trend was reversed and inspection showed seed source variation in traits in addition to dominant-codominant height.

Fusiform rust resistance of certain sources strongly influenced volumes in one of the four plantings, for example, as did seed source-related variation in planting survival in another. When nonheight-related variation among seed sources was primarily responsible for survival at the last measurement age, the model-derived volume is not appropriate. These extreme cases are relatively uncommon but are not less important. Fortunately, an extension of the present method (Nance et al. 1981) has been developed for situations where disturbances such as fusiform rust or planting mortality must be considered in combination with growth traits in assessing genetic potential.

Table 1.--Comparison in 16 seed source plantings, of ANV of volume calcuated by 2 methods (sum of d^zh) and model-derived

Planting			Site index of local source	Computing method	Seed source F-ratio	Coefficient of variation
Location	Series	Age				
			Feet			***Percent***
03 1M	1	20	56	Actual	4.6*	15.9
				Model	11.0*	7.1
07 10	1	25	69	Actual	1.4	31.6
				Model	1.5	11.5
07 1P	1	25	66	Actual	0.6	40.2
				Model	2.6*	8.5
15 1M	1	25	55	Actual	4.4*	9.3
				Model	7.1*	5.7
26 1M	1	25	69	Actual	0.6	24.8
				Model	1.9	8.1
28 1M	1	27	57	Actual	1.1	37.3
				Model	1.7	18.3
32 1M	1	27	74	Actual	0.7	27.8
				Model	3.6*	7.7
36 1M	1	20	58	Actual	2.5	29.6
				Model	0.9	15.2
40 1M	1	25	59	Actual	0.6	19.5
				Model	3.6	6.7
07 2M	2	25	72	Actual	1.0	36.1
				Model	4.0*	8.6
13 2M	2	25	57	Actual	4.0*	21.0
				Model	2.4	14.0
25 2M	2	25	60	Actual	2.4	30.9
				Model	1.7	12.8
28 2M	2	27	56	Actual	4.7*	17.9
				Model	9.8*	5.1
29 2M	2	25	68	Actual	4.1*	30.4
				Model	3.0*	4.7
32 2M	2	27	76	Actual	2.7	23.8
				Model	4.9*	6.9
40 2M	2	25	62	Actual	0.6	27.0
				Model	4.1*	6.3

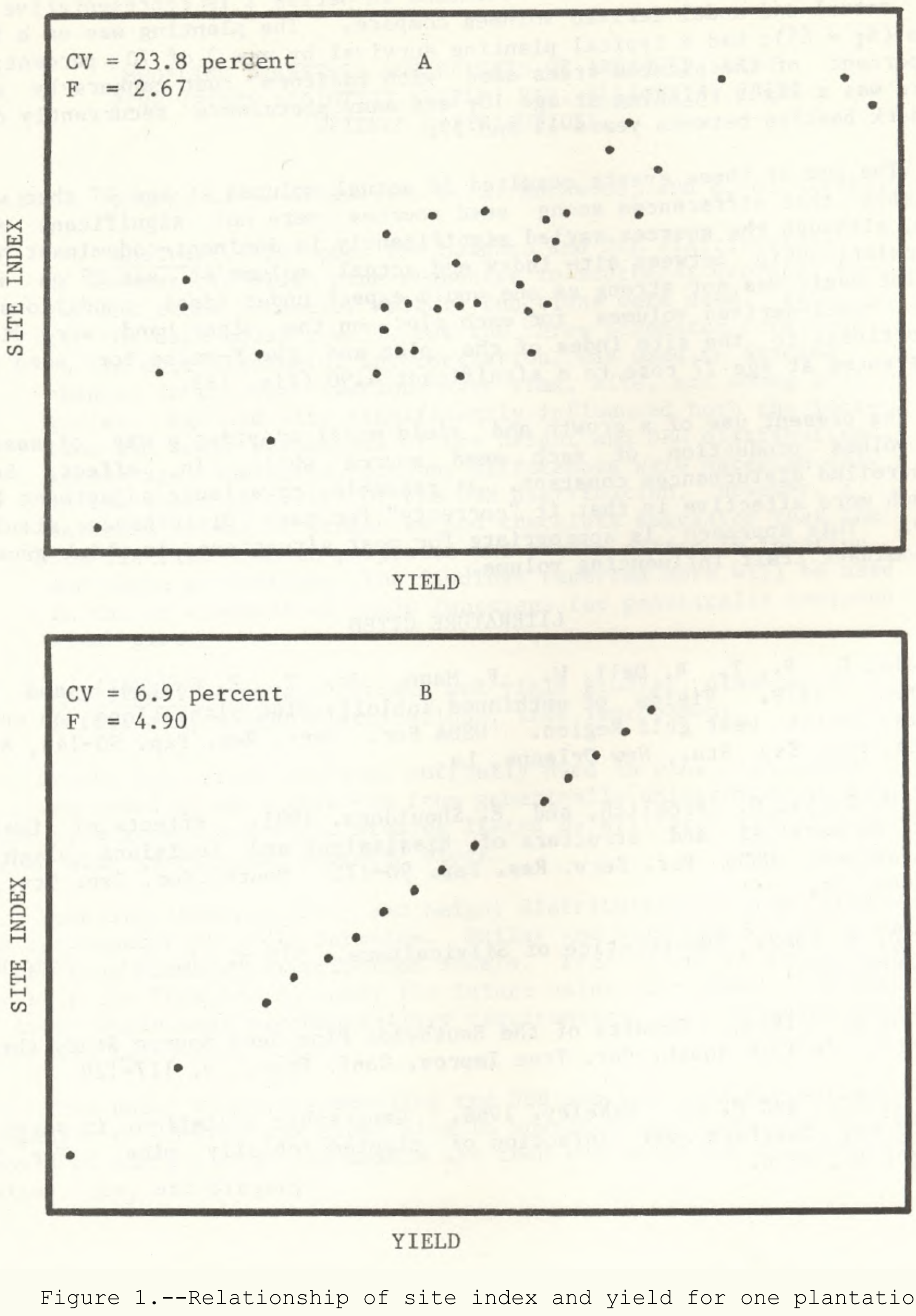

Figure 1.--Relationship of site index and yield for one plantation with actual volume (A) and model-derived volume (B).

A planting in southeastern Louisiana in Series 2 is representative of the way actual and model-derived volumes compare. The planting was on a fertile site (S_I = 65); had a typical planting survival by age 3 of 70 percent; about 10 percent of the planted trees died with fusiform rust cankers by age 10; there was a light thinning at age 10; and many plots were recurrently damaged by bark beetles between years 15 and 27.

The sum of these events resulted in actual volumes at age 27 that were so variable that differences among seed sources were not significant at that time, although the sources varied significantly in dominant-codominant height. The relationship between site index and actual volume at age 27 on a plot-by-plot basis was not strong as one would expect under ideal conditions (fig. 1A). Model-derived volumes for each plot, on the other hand, were directly proportional to the site index of the plot and the F-value for seed source differences at age 27 rose to a significant 4.90 (fig. 1B).

The present use of a growth and yield model provides a way of assessing the volume production of each seed source while, in effect, holding uncontrolled disturbances constant. It resembles covariance adjustment but it is much more effective in that it "corrects" for many disturbances simultaneously. This approach is appropriate for most situations in which growth is the dominant trait influencing volume.

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