A COMPETITION FUNCTION FOR TREE AND STAND GROWTH MODELS[1/]

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Abstract.--A two term function is described that is significantly correlated with annual diameter growth of individual loblolly pine (*Pinus taeda* L.) trees. One term expresses competition in the whole stand; the other is a measure of the competitive advantage of individual trees. The function operates by reducing the effective growing space of a tree, defined as the space available per tree in stands that are actively self-thinning.

INTRODUCTION

Computer simulation is a relatively new technique for studying tree growth and stand development. Mathematical models are the heart of simulation, and, of the types that have been proposed, the more interesting and useful project growth of individual trees rather than the entire stand. There are two types of these single-tree models: one requires information about the physical location of each stem in the plot or stand and is called a distance-dependent model; the other requires only a list of tree diameters and is called a distance-independent model (Munro 1974).

Both single-tree models project growth of individual trees according to some function of their size and competitive status in the stand. One approach is to adjust an assumed or estimated potential growth rate for a tree of given age or size by a component that gauges the intensity of competition. Another approach is to predict actual growth with a regression equation that contains a competition component.

In the distance-dependent model this component may be a competition index that relates d.b.h. or crown size to distance between the subject tree and its competitors. The competitors are chosen by a rule based on size and distance from the subject tree. In the distance-independent model the competition component usually expresses the relative position of a tree in the stand based on its d.b.h. in relation to some reference d.b.h.

The component that estimates competition is an essential part of single-tree models. It controls diameter and height growth and helps determine mortality. Various forms have been proposed, but none have yet proved to be entirely satisfactory (Alder 1979, Alemdag 1978, and Daniels 1976). All have failed to predict diameter growth with the desired precision and accuracy.

In this paper, I describe a new measure of competition. It is a mathematical function for the distance-independent model, but it also can be adapted to distance-dependent models. Development of this function is in a preliminary stage but, as the correlation data given below show, it has promise of becoming a useful addition to growth modeling.

THE COMPETITION FUNCTION

Underlying assumptions for the function are: (1) rate of growth depends on growing space, S_i, and (2) competition from its neighbors reduces the effective growing space of a tree to a fraction of the space available to it. The function, $f(S_i)$, estimates this fraction; for the ith tree, diameter growth, DG, can be estimated by a regression equation of the form:

$$DG_i = b_0 + b_1 (S_i)(f(S_i)) \qquad (1)$$

where S_i is growing space area of a tree defined as a function of d.b.h. The rationale and derivation of S_i and $f(S_i)$ are as follows.

Figure 1 shows typical development of pure, even-aged stands of loblolly pine. These data are from a study of the effects of extreme density on stand growth (Harms and Langdon 1976). The figure shows quadratic mean stand diameters for ages 6 through 20 years plotted over surviving numbers of trees in stands having initial densities

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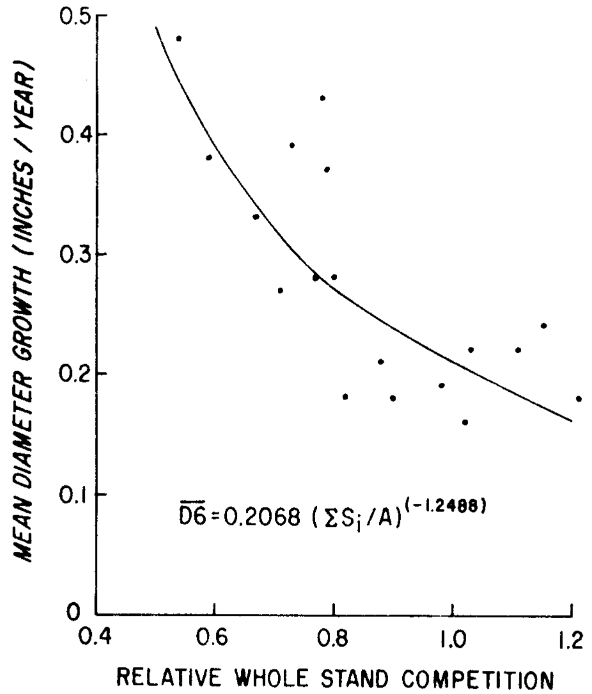

Figure 2.--Mean annual stand diameter growth of loblolly pine at age 14 in relation to stand level competition expressed in terms of the critical growing space, $\Sigma S_i/A$.

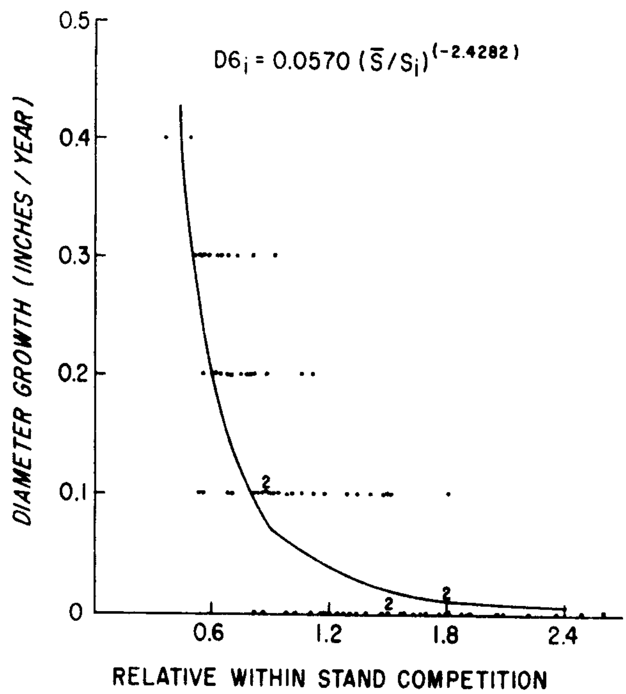

Figure 3.--Annual tree diameter growth of loblolly pine at age 18 in relation to within stand competition, $\overline{S}/S_i$.

The relationship of individual tree growth rate to the second component, $\overline{S}/S_i$, is shown in figure 3 for data from the 16,000-tree plots at age 18. A regression of the form

$$\mathrm{Log}_{10} DG_i = b_0 + b_1 \mathrm{Log}_{10}(\overline{S}/S_i) \qquad (5)$$

where the variables are as defined above, was fit to the data. The regression was also significant at the 1% level and had an r^2 value of 0.57. The curve with its equation is shown in figure 3. There is a rapid decrease in diameter growth rate as the ratio, $\overline{S}/S_i$, increases to 1, which identifies the average critical growing space of the stand. At values greater than 1 growth becomes negligible as growing space decreases.

The form of the competition function is

$$f(S_i) = \left[1 + (\Sigma S_i/A)^{\phi_1}(\overline{S}/S_i)^{\phi_2}\right]^{-1} \qquad (6)$$

This particular form was suggested by Aikman and Watkinson (1980) and corresponds to the threshold response curves described by Thornley (1976). These are sigmoidal curves which describe plant growth responses to a critical growth factor. In the competition function, this growth factor is growing space, and the critical level is assumed to be the apparent critical growing space, S_i, per tree as defined by the self-thinning line.

The function approaches 1 as either of the competition terms approaches zero, indicating that there is little competition. It appraoches zero when $\Sigma S_i/A$ becomes 1 and $\overline{S}/S_i$ becomes large, indicating maximum competition for a tree in the lowest diameter class. The exponents ϕ_1 and ϕ_2 govern the severity of the effects of the two components on growth rate.

TEST RESULTS

The competition function was tested by fitting equation (1) to annual growth data taken from the stands in figure 1. The product of the apparent critical growing space, S_i, and the competition function, $f(S_i)$, is the independent variable and defines the effective or useable growing space of the individual tree. Separate regressions were fit to data from sets of plots having initial densities of 1000 and 16,000 trees per acre for stand ages 10, 12, 14, 16, and 18 years. The exponents of $f(S_i)$ were given the arbitrary values of 2 for ϕ_1 and 4 for ϕ_2. All regressions were statistically significant at the 1% level. Table 1 presents values of the regression and correlation coefficients.

Most of the intercepts had values near zero, and over half the slopes had values between 0.006 and 0.007. Differences among regressions, however, were significant. The correlation coefficients increased with age for both densities because the large variation in growth of young stands tended to decrease as the stands got older of 1000, 2000, 4000, 8000, and 16,000 trees per acre. The resulting curves show that as mean stand diameter increases with age, mortality induced by the intensifying competition for growing space gradually reduces the numbers of stems. At some point, depending on initial density, the relationship between mean d.b.h. and number of stems becomes linear on a log-log scale. The linear portion corresponds to the -3/2 power law proposed by Yoda and others (1963) to describe self-thinning populations of plants. The line is also equivalent to the stand density index relationship published by Reineke in 1933.

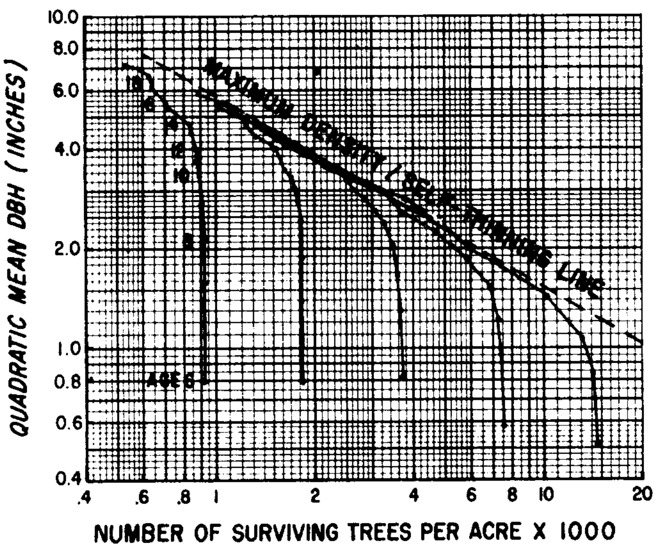

Figure 1.--Stand density-size relationships of self-thinning loblolly pine stands of initial densities of 1000, 2000, 4000, 8000, and 16,000 trees per acre for ages 6 through 21 years.

The self-thinning law implies that a plant of given weight or size requires a certain minimum growing space for its continued survival and development. As growing space falls below the minimum required, growth falls off and death eventually follows for some trees. The self-thinning line defines the apparent critical growing space S_i. The competition function is based on certain relationships that can be deduced from the self-thinning law.

For the loblolly pine data in figure 1, the self-thinning line can be described by the regression equation:

$$\mathrm{Log}_{10}\overline{D} = 2.5277 - 0.5896\ \mathrm{Log}_{10}(\rho) \qquad (2)$$

where $\overline{D}$ = quadratic mean d.b.h. and ρ = number of surviving trees per acre. The regression was fitted to data from plots having an initial density of 16,000 trees per acre and ages 10 thru 20 years. The mean apparent critical growing space, $\overline{S}$, is the reciprocal of the number of trees per unit area, ρ, and can be obtained by rearranging (2) so that

$$\mathrm{Log}_{10}\overline{S} = (-4.2871 + 1.6960\ \mathrm{Log}_{10}(\overline{D})) + \mathrm{Log}_{10}43560 \qquad (3)$$

where $\overline{S}$ is in units of square feet. The apparent critical growing space, S_i, of any tree, i, can be calculated by substituting D_i for $\overline{D}$ in (3).

Summing the estimated S_i over all the trees in a stand of area, A, yields the minimum growing space needed by the stand, ΣS_i. Dividing ΣS_i by stand area gives a measure of occupancy (relative stand density), $\Sigma S_i/A$. This ratio is one component of the competition function and expresses competitive status or stress for the stand. The ratio will take values from near zero at low site occupancy to 1 or slightly above at full occupancy. As the ratio approaches 1, competition becomes increasingly severe until at a value of 1 the stand reaches the self-thinning condition of a fully occupied site as represented by the self-thinning line.

Even under conditions of maximum competition, not all trees in an even-aged stand are competing equally. Larger trees are known to have a competitive advantage over their smaller neighbors, especially those in the lower crown classes. Consequently, a second component is necessary to account for differences in competitive advantage for individual trees. A simple way to express the position of a tree in the stand is as a ratio, $\overline{S}/S_i$, of the average critical growing space of the stand to the critical growing space of an individual tree. The value of the ratio increases from less than 1 for larger than average growing space to greater than 1 as growing space falls below average.

The two ratios $\Sigma S_i/A$ and $\overline{S}/S_i$ comprise the competition function. Their relationship to diameter growth is shown in figures 2 and 3. In figure 2, mean stand diameter growth at 14 years taken from the data in figure 1, is plotted over the corresponding value of $\Sigma S_i/A$. A regression of the form

$$\mathrm{Log}_{10}\overline{DG} = b_0 + b_1\ \mathrm{Log}_{10}(\Sigma S_i/A) \qquad (4)$$

where $\overline{DG}$ and $\Sigma S_i/A$ are defined as above, was fit to the data. The regression was significant at the 1% level and had an r^2 value of 0.60. Figure 2 shows the curve and its equation in exponential form. It is apparent that $\Sigma S_i/A$ is associated with a curvilinear decrease in mean stand diameter growth rate as the ratio increases to 1, the condition of maximum competition.

Table 1.--Regression coefficients for the competition function as fitted to selected diameter growth data.

Initial stand density	Coefficients	Age				
		10	12	14	16	18
no./acre		- - - - - - - - - - - - - - years - - - - - - - - - - - - - -				
	b_0	0.1811	0.0932	0.2184	0.0607	0.0327
1,000	b_1	0.0070	0.0064	0.0070	0.0041	0.0057
	r^2	0.33	0.28	0.34	0.51	0.47
	b_0	0.0324	0.0264	0.0821	0.0222	0.0069
16,000	b_1	0.0076	0.0119	0.0099	0.0077	0.0071
	r^2	0.18	0.39	0.38	0.55	0.65

and within-stand competition became more uniform. An example of the relationship is shown in figure 4 for age 18 and an initial density of 16,000 trees per acre.

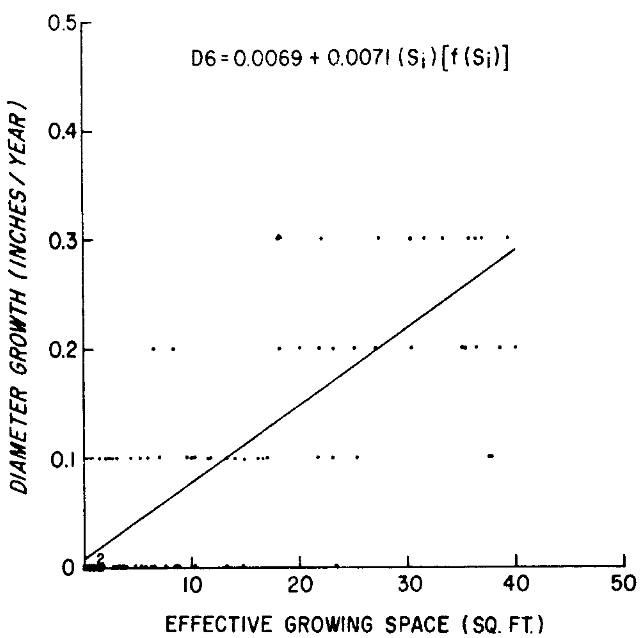

Figure 4.--Annual tree diameter growth of loblolly pine at age 18 in relation to effective growing space as estimated by the competition function, $f(S_i)$.

DISCUSSION

Only a few values for ϕ_1 and ϕ_2 have so far been tested. For ϕ_1, in addition to 2, 4 was used and the value for the exponent for the variable, $\Sigma S_i/A$, in the regression shown in figure 2 was tried. For ϕ_2, the values 4 and 8 were used. The value for the exponent for the variable $\bar{S}/S_i$, in the regression in figure 3 was also tried. The resulting regressions differed but little from those given in table 1.

In general, increasing the value of ϕ_1 will increase the severity of the restriction on growth caused by stand competition as ΣS_i approaches the area of the stand. Increasing the value of ϕ_2, on the other hand, increases the severity of competition from neighboring trees. As ϕ_2 becomes large, the competitive advantage of large trees over smaller ones increases rapidly. This feature of the function may permit adjustment or tuning of a growth model when its performance is being evaluated.

In its present form, the function operates at the stand level; it does not account for local competition experienced by a particular tree. Figures 3 and 4 show that there was considerable variation in the growth data used in the analysis. Trees of widely differing diameters often had the same growth rate. It is likely that local competition was responsible for some of this variation. Possibly, some form of competition index can be incorporated into the function, or perhaps the two terms can be modified to reflect more closely the growing space relationships of a subject tree and its competitors.

In conclusion, the preliminary tests of the function are encouraging. The two terms with their parameters may offer considerable flexibility in fitting it to different stages of stand growth and development. Further work is in progress.

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