

AN EMPIRICAL FUNCTION FOR PREDICTING
SURVIVAL OVER A WIDE RANGE OF DENSITIES^{1/}

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Abstract.--A flexible sigmoid function of the form $S = 1/[1 + (H/H_c)^\theta]$, where S is survival expressed as the ratio of number of living trees (N) to the number of trees at stand establishment (N_i), H is mean stand height, H_c is mean height at $S = 0.5$, and θ is an exponent defining the shape of the curve, was fit to a set of loblolly pine survival data covering a range of densities from 1000 to 16,000 trees per acre. The equation provided an adequate fit to the data with r^2 values from 0.76 to 0.98. The estimated parameters H_c and θ were found to be correlated to initial density. Both can be predicted satisfactorily with regressions of the form $H_c = b_0 N_i^{b_1}$, and $\theta = b_0 + b_1/N_i$.

INTRODUCTION

Reliable prediction of survival is essential to accurate prediction of growth and yield. A number of mathematical models have been used with varying degrees of success to describe the relationship between survival or mortality and selected characteristics of the stand, but a completely adequate model has yet to be developed (Burkhart et al. 1981, Somers et al. 1980). The difficulty in obtaining a satisfactory model stems from the fact that mortality is extremely variable, depending as it does on competitive ability and inherent growth rate of the species, and such external factors of site as soil moisture and nutrients. Further difficulties in modelling are encountered when attempts are made to include catastrophic mortality caused by such isolated occurrences as insects, disease, fire, and wind and ice storms.

Survival curves have a characteristic sigmoid shape over the course of stand development. The form of survival curve for a particular stand depends primarily on the number of trees established, inherent growth rate, and the site quality. Logically, the curve should be describable in terms of one or more of these variables, and in

fact the published models show that initial number of trees and stand height as well as age are predictors of survival.

An empirical model is presented in this paper that closely fits survival data obtained from experimental plots of loblolly pine (*Pinus taeda* L.) grown over a wide range of densities. Preliminary results suggest that the model may be useful as a general survival function for cases where mortality is more or less regular.

THE MODEL

Sigmoid response curves are common in biological systems, and many different forms of equations have been suggested to describe various growth and development phenomena. The particular form chosen to model survival was

$$S = 1/[1 + (H/H_c)^\theta] \quad (1)$$

where S is survival expressed as the ratio of number of surviving trees (N) to number of trees at stand establishment (N_i), H is mean stand height, H_c is mean stand height at $S = 0.5$, and θ is an exponent defining the shape of the curve. Expressions of this form are described by Thornley (1976) as threshold response curves of the switch-off type. The function varies between 1 and 0, approaches 1 for $H \ll H_c$ and falls monotonically, tending to zero for $H \gg H_c$, and passing through the value 0.5 for $H = H_c$. The higher the value of θ , the higher the value of S for $H < H_c$, the steeper the fall of the curve in the region $H = H_c$, and the smaller the value of S for $H > H_c$. There is a point of inflection at

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$$\frac{H}{H_c} = \left[\frac{\theta - 1}{\theta + 1} \right]^{1/\theta} \quad (2)$$

As θ increases, the point of inflection moves closer to $H/H_c = 1$.

This equation was selected because of its simple algebraic form and because its properties appeared to fit a wide range of survival curves.

Mean stand height was selected as the predictor variable because it is an indicator of both the stage of biological development of the trees making up the stand, and the quality of the site. Height is also a measure of the age of the trees, and is somewhat sensitive to stand density.

A TEST CASE

The model was tested by fitting equation (1) to a set of survival data taken from a study of stand development in young even-aged loblolly pine (Harms and Langdon 1976). The data consisted of annual measurements of d.b.h., height, and survival from age 3 through 24 of a series of 0.1 acre density plots. Five density levels of 4 replications each were established at age 3 in a uniform stand of naturally regenerated seedlings by thinning plots back to 1000, 2000, 4000, 8000, or 16,000 trees per acre. These density levels will be referred to by number of trees present at age 3; thus 1M is an initial density of 1000 trees per acre. One plot of the 1M density was deleted from the data set because of unexplained, unnaturally high mortality in the 15th year. Mortality over all densities was quite high for the first 2 years following thinning after which it leveled off to a more expected pattern. This mortality was thought to be caused by the sudden release required to establish the treatment densities. To avoid inconsistencies in the data from this source, the number of trees present at age 6, when the plots appeared to have stabilized, was taken as the initial number (N_i) rather than the number at age 3.

Equation (1) was fitted to the data by estimating H_c and θ with a nonlinear least squares procedure. Initial values for H_c , the mean stand height at a survival of 50 percent, were estimated for each plot from scatter diagrams of the data. The starting value for θ was arbitrarily set at 2. The equation was fit separately to each plot, and then to each density with the plots pooled.

Scatter diagrams of the estimated parameters for the individual plot data show that both H_c and θ are correlated with initial density. The relation of H_c to density is very good (fig. 1). A regression of the form

$$\log_e H_c = b_0 + b_1 \log_e N_i \quad (3)$$

where H_c and N_i are defined as above, was fit to the data. Figure 1 shows the curve and its equation in exponential form. There is very little variation in H_c about the curve throughout the range of densities.

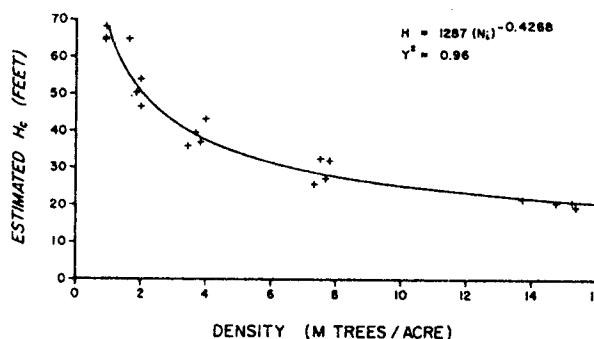


Figure 1.--Scatter diagram of estimated " H_c " in relation to initial density.

The relation between θ and initial density is much more variable, the greatest variation being at the 1M and 2M density levels (fig. 2). The variation is due to differences among these plots in the onset of mortality. High values of θ are associated with plots that were older and taller than average when mortality began. The values of θ for the denser plots in which mortality began at younger ages were much more closely grouped. A regression of the form

$$\theta = b_0 + b_1 \left[\frac{1}{N_i} \right] \quad (4)$$

was fit to the data, with θ and N_i as defined above. Figure 2 shows the curve and its equation. The regression is significant, but fit is rather poor because of the wide variation in the 1M and 2M plots. Additional data at lower densities will be needed to establish the best form of the regression.

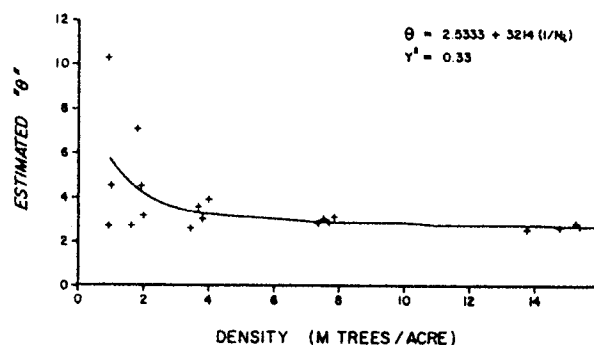


Figure 2.--Scatter diagram of estimated " θ " in relation to initial density.

Parameter estimates from the individual plots when pooled for each density are given in Table 1 together with the variation accounted for (r^2). The fit of the model was good, the r^2 increasing from 0.76 for the 1M density to 0.98 for the 16M density. The parameter values from the pooled analyses were used in the model to calculate estimated survival for each density level. The results are plotted in Figure 3 together with the actual mean survivals. The curves show that the model provides an adequate fit to the data over all densities with the possible exception of the 16M density for which early survival is underestimated. An explanation is being sought in further analyses of the data.

Table 1.--Parameter estimates for the survival function with the plots in each density pooled.

Density	H_c	θ	r^2
1M	65.81	4.7611	0.7618
2M	54.56	3.6826	0.8594
4M	39.46	3.2766	0.9580
8M	29.58	2.9687	0.9690
16M	20.62	2.7151	0.9851

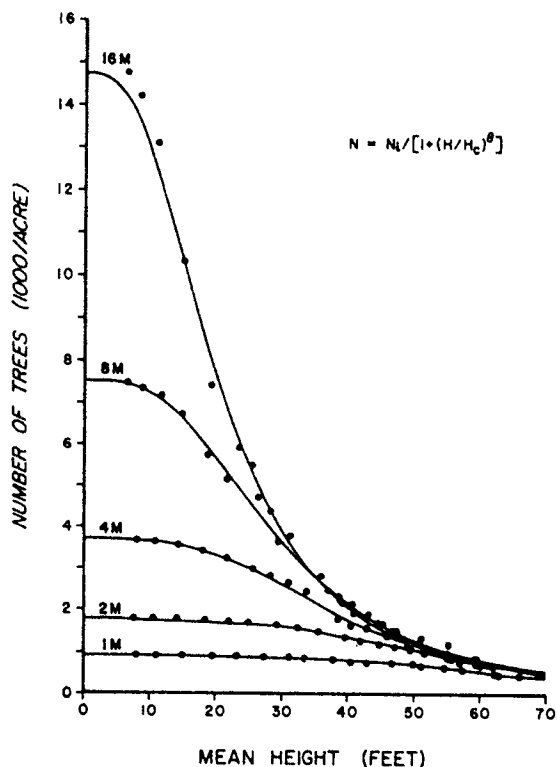


Figure 3.--Survival trends in relation to stand height for loblolly pine at five densities.

The entire data set with all 5 densities pooled also was fit, putting H_c values for each density equal to those given in Table 1. The value estimated for θ was 3.3319, the r^2 equalled 0.97. In spite of the high r^2 , predicted survival was greatly underestimated at the H/H_c values above about 1.4. This result shows, as do the values of θ in Table 1, and the regression in figure 2, that a constant value for θ probably cannot be used over the range of densities spanned by these data. However, a constant θ may be satisfactory over a more restricted range of densities.

DISCUSSION

The results presented here are preliminary but they show that the model has considerable promise. It gives an excellent fit to survival data of the kind used in the test. Work is in progress to test the model on data from different sites, from plantations, and from natural stands of lower initial densities extending to older ages.

The question of how well stand height alone can account for age and differences in site quality remains to be seen. It can be assumed that H_c for a constant N_1 will vary with site quality. For example, a given H_c will occur at a younger age on high sites than on low sites. What effect, if any, site has on the value of θ must be determined from actual data. If needed, a measure of site, or age, or other variable can be incorporated into the model indirectly as a variable in the regression predictors of H_c and θ , or directly by modifying the model term H/H_c so that

$$(x/x_c)^\theta = (x_1/x_{1c})^{\theta_1} (x_2/x_{2c})^{\theta_2} \dots (x_n/x_{nc})^{\theta_n} \quad (5)$$

where $x_1 \dots x_n$ are variables such as height and site index, and $\theta_1 \dots \theta_n$ are the corresponding exponents.

If mortality instead of survival must be predicted, equation (1) can be rewritten so that

$$M = \frac{(H/H_c)^\theta}{1 + (H/H_c)^\theta} \quad (6)$$

where M is mortality, the ratio of number of trees died (N_d) to initial number (N_1), and H , H_c , and θ are defined above.

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