An Individual Stand Growth Model for Mean Plant Size Based on the Rule of Self-thinning

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ABSTRACT

A growth model for pure, even-aged stands of plants is asymptotically bounded above by the self-thinning rule that relates maximum plant size to stand density. The model characterizes accretion in mean size as a deviation from the limiting size. It consists of a function relating mean size to time and density and a companion survival model. The growth model is obtained by substituting the survival model for density in the mean size relationship. Model flexibility is demonstrated by fitting it to annual remeasurements of mean size and number of plants per unit area in a stand of *Pinus taeda* L.

Key words: 3/2-power rule, mortality, survival, stand dynamics, plant growth model, loblolly pine.

INTRODUCTION

As plants grow in even-aged, pure stands, competition for some site-specific limiting growth factor intensifies with time (t), resulting in decelerating individual plant growth rates. The more plants per unit area (ρ), the sooner this competition begins. As a result, average plant size (δ) increases in relation to both ρ and t. Yoda *et al.* (1963) reported a plant growth relationship involving a density-dependent, maximum mean value of δ, called δ_m, for monocultures of these even-aged plants. The model for the limiting size is

$$\delta_m = \gamma\rho^{-\beta}, \tag{1}$$

where the value of the parameter γ depends on the species and the productivity of the site on which the stand is growing, and the value of the rate parameter β is dependent upon what measure of plant size is of interest, as well as upon other aspects of the space occupancy of the plants. A value for β can either be derived theoretically from assumed geometric relationships or estimated empirically by model fitting.

The universality of this limiting size relationship has generated widespread interest in developing models of δ that are bounded by eqn (1). It has become standard practice to illustrate the operation of this rule empirically by plotting $\ln(\delta)$ versus $\ln(\rho)$, obtained from repeated measurements over time. The path formed by the $\ln(\rho)$,$\ln(\delta)$-points (routinely called a ρ,δ-trajectory) approaches the linear relationship

$$ln(\delta_m) = \ln(\gamma) - \beta(\ln(\rho)). \tag{2}$$

Smith and Hann (1984) described the ρ,δ-trajectory directly by expressing $\ln(\delta)$ as a function of $\ln(\rho)$, such that it is bounded above by eqn (2). Hozumi (1977) followed a different modelling approach based on a system of relationships consisting of a survival function, $\rho = \Delta_1(t)$, and a δ-response surface, $\delta = \Delta_2(t, \rho)$. The system is constrained by having β take a limiting value as a function of $\ln(\delta)$ and $\ln(\rho)$ as $t \to \infty$. Naito (1983) generalized this solution using Richards' (1959) growth function. Both Hozumi and

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Naito then obtained a ρ,δ-trajectory from the (Δ_1, Δ_2) system of relationships by eliminating t from Δ_2 via the inverse of Δ_1.

Our system, like Hozumi's, involves a survival function and a δ-response surface, but differs in the way these are derived and how the limiting size constraint is imposed. Our solution links change in δ to the limiting size surface given by eqn (1); that is, we describe the difference $\delta_m - \delta$ as a function of t. The path of δ for a given stand is identified in Fig. 1 as the mean size locus. The mean size locus is asymptotically bounded above by the limiting size surface, is guided by the survival function (Δ_1) in the (t, ρ) plane, and resides on the δ-response surface (Δ_2).

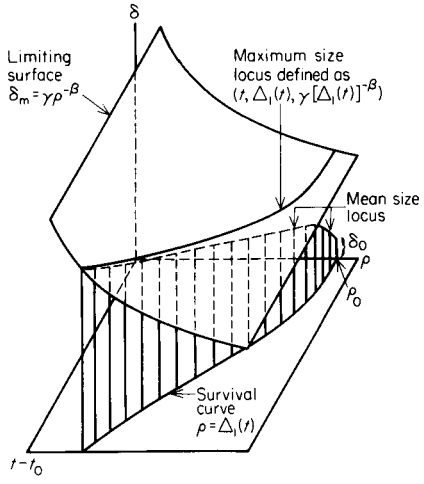

FIG. 1. A generalization of how the variables t (a measure of time), ρ (the number of plants per unit area), and δ (a measure of mean size) are related, where the mean size locus of δ is formed from the intersection of two surfaces $\rho = \Delta_1(t)$ and $\delta = \Delta_2(t, \rho)$.

DERIVATION

The single stand model

The basic structural component of any plant growth model is a mathematical description of change over time of a single plant or a group of plants on some unit area. The rule of self-thinning operates for an individual stand so a model based on its principles logically starts with a single stand. By single stand we mean a group of plants of the same species and age and containing a sufficient density of individual plants for the self-thinning processes to operate, but limited in size to an area of uniform site productivity. This means that assumptions for model development treat initial density and site productivity as constants. Relaxation of this constraint will require future research.

The δ-response model

An examination of Fig. 1 shows that the maximum difference between δ_m on the limiting surface and δ occurs when $t = t_0$ where t_0 is the beginning age of the time span being covered by t. This maximum difference is defined as

$$A_\delta = \gamma\rho_0^{-\beta} - \delta_0, \tag{3}$$

Where δ_0 is the initial mean size of the ρ_0 plants per unit area in the stand at age t_0. The difference $\delta_m - \delta$ decreases from A_δ toward 0 as t increases. The key step in model development is describing the relationship between $\delta_m - \delta$ and t as

$$\delta_m - \delta = A_\delta - F(t:A_\delta,\phi), \tag{4}$$

where F comes from a class of growth functions having the property

$$F(t:A_\delta,\phi) = A_\delta f(t:\phi), \tag{5}$$

such that $F(t:A_\delta, \phi) \to A_\delta$ as $t \to \infty$. So function f must have the properties

$$f(t:\phi) \to 1, \text{ as } t \to \infty, \tag{6}$$

and

$$f(t_0:\phi) = 0. \tag{7}$$

The vector ϕ contains dimensionless parameters to be estimated in a model fitting process described later. The δ-response surface model Δ_2 is obtained by substituting eqn (3) and eqn (5) into eqn (4) and solving for δ, yielding

$$\delta = \gamma\rho^{-\beta} - (\gamma\rho_0^{-\beta} - \delta_0)(1 - f(t:\phi)). \tag{8}$$

Equation (8) has the properties that $\delta = \delta_0$ at $t = t_0$ and $\delta \to \delta_m$ as $t \to \infty$.

The survival model

For fully-stocked stands of perennial plants such as trees, competition-based periodic mortality converges to 0 at some advanced, but imprecisely defined age. Beyond that age, mortality agents like disease, insects, and drought begin to open the stand beyond the ability of the surviving plants to use the growth potential of the site fully. Beyond this point the self-thinning rule does not apply because the mortality is not the direct result of competition for space or limiting growth factors. We will define the point at which the self-thinning rule would indicate no further mortality as the number of plants surviving at that time (ρ_1), and hereafter refer to it as the limiting density. Hence, ρ_1 also is the point beyond which the self-thinning rule and the limiting size relationship are not expected to serve as models, and stands of this type will have a mean size less than the maximum given by eqn (1).

Since ρ is the number of surviving plants per unit area at time t, the cumulative mortality occurring after time t_0 equals $\rho_0 - \rho$. For time spans during which the stand is undisturbed by natural catastrophies or human activities, the change over time in mortality, $\rho_0 - \rho$, follows a sigmoidal path. This suggests a model of the form

$$\rho_0 - \rho = G(t:A_\rho,\eta), \tag{9}$$

where G has properties analogous to those of F as given in eqn (5), eqn (6), and eqn (7) and where η is a vector of dimensionless parameters. In terms of the limiting density, the asymptote of G is

$$A_\rho = \rho_0 - \rho_1. \tag{10}$$

Invoking the property described in eqn (5) for G and substituting eqn (10) into eqn (9) produces the survival model

$$\rho = \rho_0(1 - g(t:\eta)) + \rho_1 g(t:\eta). \tag{11}$$

This has the properties that $\rho = \rho_0$ at $t = t_0$ and $\rho \to \rho_1$ as $t \to \infty$.

The growth model

Growth in δ is characterized by movement along the mean size locus depicted in Fig. 1. This movement is a function of only one variable, t, since for a particular stand the quantities t_0, ρ_0, δ_0 and ρ_1 are constants and the variable ρ is a function of t. A growth model expressing δ as a function of t is obtained by substituting the survival expression from eqn (11) in the place of ρ in the δ-response surface model of eqn (8), yielding

$$\delta = \gamma(\rho_0(1-g(t:\eta))+\rho_1 g(t:\eta))^{-\beta}-(\gamma\rho_0{}^{-\beta}-\delta_0)(1-f(t:\phi)). \quad (12)$$

As is the case with the δ-response model in eqn (8), the growth model in eqn (12) yields $\delta = \delta_0$ at $t = t_0$. However, the growth function differs in that it approaches a maximum value of $\gamma\rho_1{}^{-\beta}$ as $t \to \infty$.

EXAMPLE

The data base

We have fitted the above relationships to forest tree data. The data consist of tree counts (ha^{-1}) and diameter at breast height (DBH in cm, at 1·37 m height) of loblolly pine (*Pinus taeda*, L.) growing on four 0·04 ha plots for each of five initial density treatments. Harms and Langdon (1976) described the study design and summarized the results until 14 years. The data used to test the performance of our model come from the four plots that were thinned to 4942 trees ha^{-1} (2000 $acre^{-1}$) at 3 years. There was some disturbance mortality following the thinning treatment, but survival on the four plots had stabilized by 6 years at an average of 4556 trees ha^{-1}. This particular treatment was selected because the stand had developed in both the premortality stage and in the self-thinning stage and had also been in the self-thinning stage long enough to have approached the limiting mean size surface. To reduce variation in survival estimates due to the small plot size, the four plots were averaged, producing 17 t,ρ,δ-points (6 to 22 years). The measure of mean size for this example is

$$\delta = (\Sigma D_i^2/n)^{0.5}, \quad (13)$$

which is the quadratic mean DBH of the n surviving trees on each plot when D_i is the DBH of the ith tree. We used eqn (13) because of the ease and accuracy with which DBH can be measured, because of the importance of DBH in characterizing tree size, and because the quadratic mean is related to an important forest stand density measure called basal area (B), defined as the sum of cross-sectional areas at breast height. If B is expressed in m^2 ha^{-1}, then

$$B = 0{\cdot}000078539\,8\,\Sigma D_i^2. \quad (14)$$

These measures also have application in estimating growth and yield of wood volumes of forest stands. Because of the relationships among dimensions, volumes, weights, and area occupied, there may be particular relevance for other kinds of plant communities.

Choosing f *for the* δ*-response surface*

Our method of investigating the form of $f(t:\phi)$ was to solve the δ-response model in eqn (8) for $f(t:\phi)$ and then to evaluate the resulting quantity

$$f(t:\phi) = 1-(\gamma\rho^{-\beta}-\delta)/(\gamma\rho_0{}^{-\beta}-\delta_0) \quad (15)$$

for each of our 17 ρ,δ-points and plot these over t. It is necessary to have values of γ and β to complete the computation in eqn (15). We chose to use a geometrically derived

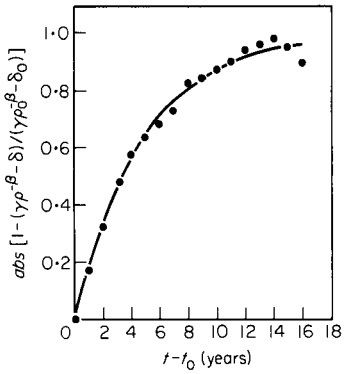

FIG. 2. The relationship of a dimensionless ratio obtained from solving eqn (8) for $f(t:\phi)$.

value for β of 1/2 because estimating it from data produced fitted models that yielded anomulous predictions when extrapolated. The empirical value of β also seemed too sensitive to variation in the data near the limiting surface. The value of 1/2 worked well. Further, 1/2 is the value β must take for basal area to remain constant, which is the expected response of stands after they have reached the carrying capacity of the site. An approximate value of γ was obtained using the functional relationship between the quadratic mean DBH in eqn (13) and basal area in eqn (14). This relationship produces

$$\gamma = (B_{\max}/0{\cdot}000\,078\,539\,8)^{0{\cdot}5}, \tag{16}$$

where $B_{\max}$ is an experience-based value for the maximum attainable basal area for the particular species of trees. In this case, we used $B_{\max} = 43{\cdot}6$ m^2 ha^{-1} (190 ft^2 acre^{-1}), which produced $\gamma = 745$. Using $\gamma = 745$ and $\beta = 1/2$, we evaluated the expression in eqn (15) for the 17 ρ,δ-points and plotted these over t in Fig. 2.

Our first choice for $f(t:\phi)$ was

$$f(t:\phi) = (1-\exp(-\phi_1(t-t_0)))^{\phi_2}, \tag{17}$$

from Richards' (1959) growth model. This expression for $f(t:\phi)$ was substituted into the δ-response surface model, and the parameters γ, ϕ_1 and ϕ_2 were estimated using a derivative-free nonlinear least squares algorithm (SAS Institute, 1982). In this estimation process the rate parameter was fixed at $\beta = 1/2$. The resulting estimate of ϕ_2 was nearly equal to 1, so eqn (8) was reworked using $\phi_2 = 1$ in $f(t:\phi)$ from eqn (17), yielding the δ-response surface model

$$\delta = \gamma\rho^{-\beta} - (\gamma\rho_0{}^{\beta} - \delta_0)\exp(-\phi_1(t-t_0)). \tag{18}$$

Using $\gamma = 745$ from eqn (16) and $\phi_1 = 0{\cdot}25$ as starting values the nonlinear least squares estimation procedure required only eight iterations to produce the estimates $\gamma = 713$ and $\phi_1 = 0{\cdot}2079$. The model fit was examined by computing deviations for each of the 17 values of mean size as a percent of the observed mean size. The mean of the absolute values of these deviations was 1·8 per cent and the maximum deviation was 3·6 per cent.

Choosing g *for the survival curve*

Three forms of $g(t:\eta)$ were tested in the survival model. Again, the first we tried was Richards' function,

$$g(t:\eta_1,\eta_2) = (1-\exp(-\eta_1(t-t_0)))^{\eta_2}. \tag{19}$$

TABLE 1. *Nonlinear least squares estimates of the parameters for the Richards version of the survival model*

Limiting density (ha^{-1}) (ρ_l)	Parameter estimates		$\frac{\Sigma\lvert\rho-\hat{\rho}\rvert}{17}$ (ha^{-1})
	η_1	η_2	
247	0·1258	3·729	82
494	0·1357	3·967	81

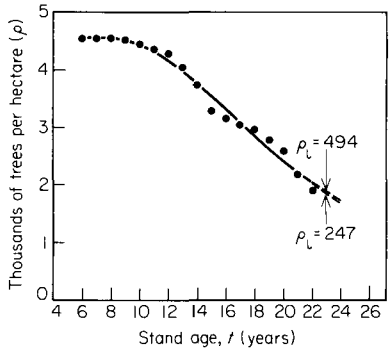

FIG. 3. The two empirical survival models (obtained by using eqn (19) for $g(t:\eta)$ in eqn (11)) almost coincide when $\rho_l(ha^{-1})$ is varied between 247 and 494 trees.

We also tried Weibull's (1951) function,

$$g(t:\eta_1,\eta_2) = 1-\exp(((t-t_0)/\eta_1)^{\eta_2}), \tag{20}$$

and another that Thornley (1976) named a threshold curve,

$$g(t:\eta_1) = ((t-t_0)/(t_c-t_0))^{\eta_1}/(1+((t-t_0)/(t_c-t_0))^{\eta_1}), \tag{21}$$

where t_c is the age at which half of the initial number (ρ_0) of plants are dead.

Experienced-based values of ρ_l were tested at 247 and 494 trees ha^{-1} (100 and 200 trees $acre^{-1}$, respectively). The η's in the survival model were estimated with nonlinear least squares for all six combinations of $g(t:\eta)$ and ρ_l. None of the models clearly outperformed the others, but the Richards form in eqn (19) did marginally better in terms of fit statistics. The estimates of η_1, η_2 and the fit statistics for the Richards model are presented in Table 1 for both of the ρ_l's. The two Richards-based survival curves plotted in Fig. 3 indicate little difference in the fits resulting from this range of ρ_l's.

The primary objective of our work was to develop the self-thinning-constrained growth model given in eqn (12), but the most dramatic depiction of the self-thinning rule is seen in the ρ,δ-trajectory (Fig. 4). This trajectory is obtained by substituting $\Delta_1^{-1}(\rho)$ from the survival model for t in the δ-response model, that is, $\delta = \Delta_2(\Delta_1^{-1}(\rho), \rho)$. Figure 4 depicts the striking relationship among the limiting size curve (using $\hat{\gamma} = 713$ and $\beta = 1/2$), the observed ρ,δ-points, and the fitted ρ,δ-trajectory (using $t_0 = 6$, $\rho_0 = 4556$, $\delta_0 = 2{\cdot}0$, $\hat{\phi}_1 = 0{\cdot}2079$, $\hat{\eta}_1 = 0{\cdot}1258$, $\hat{\eta}_2 = 3{\cdot}729$, and $\rho_l = 247$). The ρ,δ-trajectory produced a mean for the absolute values of the percent deviations of 2·0 per cent and a maximum absolute percent deviation of 4·7 per cent.

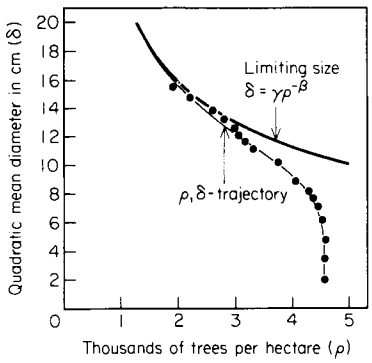

FIG. 4. The two curves consisting of the limiting size (obtained by using the nonlinear least squares estimate $\gamma = 713$ and the fixed value $\beta = 1/2$ in eqn (1)) and the empirical ρ,δ-trajectory (obtained from solving eqn (11) for t (yr) using eqn (19) for $g(t:\eta)$ and substituting this expression of ρ (ha^{-1}) into eqn (18)).

DISCUSSION

The model reported here is built on three concepts: (a) that there is a relatively stable limiting size–density relationship, (b) that change in size bears a strong relationship with time and density when expressed as a deviation from this limiting surface, and (c) that at some point in stand development self-thinning mortality is overtaken by non-competition-based mortality, so that (a) and (b) no longer hold. The δ-response surface that results from (a) and (b) is defined as a difference between the limiting surface of eqn (1) and a factor composed of the product of the maximum value of $\delta_m - \delta$, (A_δ in eqn (3)) times $1 - f(t:\phi)$. The formulation is a simple result that produces a flexible mathematical description of a relationship that is otherwise difficult to mimic.

The growth model given in eqn (12) is obtained by substituting the survival function into the δ-response model. The survival model is built on the third concept above, which says we can approximate the point where the self-thinning rule breaks down with an experience-based estimate of the number of surviving plants. An example using loblolly pine indicates that model accuracy is not significantly influenced by selecting ρ_1 from a range of values. Given the existence of ρ_1, the predictor of ρ is comprised of a simple weighted sum of ρ_0 and ρ_1. It is likely that the first action of most modellers would be to estimate ρ_1 from empirical data rather than to specify it subjectively from prior experience. However, from our experience it appears that noise in survival data, coupled with the fact that ρ_1 will almost always occur outside the range of the available data, makes estimates of ρ_1 from such data rather variable. For example, we obtained a very good fit when ρ_1 was estimated from the data, but its estimated value was so large that the resulting maximum mean size ($\gamma\rho_1^{\beta}$) was unrealistically small. In fact, an experience-based value of maximum mean size of a self-thinning stand can better be used to specify a reliable value of ρ_1.

In extending this single-stand model to populations of stands, we expect to encounter added complexities. For example, the parameters in ϕ and η may be related to ρ_0. It would also be desirable to eliminate δ_0 from any general model by replacing it with a function of t_0 and ρ_0. The effect(s) of productivity differences between sites on the parameters and on the model's structure must be taken into account when seeking more general applicability. It is obvious that extending this work to a population model will involve more recourse to empirical data than was the case in here. Since this model is built on the well-substantiated self-thinning rule, has structural simplicity, and can be

applied in a variety of ways, it is not only of value in representing the dynamics of particular stands, but also serves as a conceptual basis for extension to populations of even-aged stands.

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