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# Biomathematical Growth Equations for Natural Longleaf Pine Stands

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**ABSTRACT.** Simultaneous stand level basal area projection and survival prediction equations with useful extrapolative properties are derived from assumptions that reflect many of the currently accepted concepts about stand development. Both equations are modifications of the Chapman-Richard's growth curve which has parameters for the asymptote and the annual rate of growth towards the asymptote. The original form is modified by defining the asymptote and annual growth rate as functions of changing stand conditions. For basal area projection the asymptote is a function of number of trees which approaches zero as density declines. The rate of approach to the asymptote is a function of growth in average dominant and codominant trees and change in average stand age. The survival equation is a reverse Chapman-Richard's curve that approaches zero over time. The asymptotic value is a decreasing function of basal area in accordance with the self-thinning rule. Additional terms controlling the rate of movement away from the asymptote are a minimum mortality rate for low density stands and ingrowth of new trees into the smallest diameter class for young stands with vigorous basal area growth. Nonlinear three-stage least squares procedures are used to simultaneously fit both equations to a natural longleaf pine (*Pinus palustris* Mill.) permanent plot data set. Predictions are verified using cross-validation procedures, and long-range extrapolations are demonstrated and discussed. FOR. SCI. 37(1):227-244.

**ADDITIONAL KEY WORDS.** Chapman-Richards, survival, basal area prediction.

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**M**ATHEMATICAL MODELS OF FOREST STAND DEVELOPMENT provide information for resource management decision making. Growth and yield predictions are used to construct long range strategic plans, update standing inventories, develop harvest schedules, and speculate about impacts of new silvicultural practices and genetically improved seedlings. In most cases these models are used by professional foresters with a biological background who can be expected to judge the accuracy and logic of the predictions and to know when extrapolations of a model are within reasonable bounds. With the proliferation of microcomputers and of computer-based growth models there is an increased potential for misuse by users who are not qualified to judge the accuracy of a prediction. It is the responsibility of the modeler to design models that not only provide accurate predictions within the range of observable data, but also produce reasonable and logical extrapolations. To be successful, models must be based on our best current understanding of the relationships that determine tree and stand development, in addition to the relationships inherent in a data set. By necessity these models will somewhat reflect the beliefs of the modeler, but as our understanding improves, future models will need to be developed to incorporate these changes.

The objective of this manuscript is to develop stand level basal area and survival prediction equations that explicitly incorporates some commonly held beliefs about long-term stand development. In most cases these beliefs are used to build constraints on predictions that lead to models with known extrapolative properties. First, the biological rationale which leads to each equation is presented. Next, the extrapolative properties of each equation individually and as a system of equations are discussed. Finally, the equations are fit to a natural longleaf pine data set to demonstrate these properties.

## MODEL DEVELOPMENT

### BASAL AREA

Pienaar and Turnbull (1973) stated that the distinction between an empirical and biologically based model is "mainly in the fact that certain features are incorporated in the model on logical grounds based on past experience and not necessarily because these features are observed in the sample data being analyzed." For basal area, this means the model should be nondecreasing in the absence of mortality, have a single inflection point, and approach a relatively stable maximum over time. These properties imply a sigmoid shaped model. The widely used Chapman-Richard's growth model (Chapman 1961, Richards 1959) is a general sigmoid-shaped function that can be derived by considering the growth rate of any population as the difference between the anabolic rate (constructive metabolism) and catabolic rate (destructive metabolism):

$$\frac{dB}{dA} = nB^m - kB \quad (1)$$

where  $B$  is basal area and  $A$  is stand age. Murphy (1983) gave the integration between an initial age,  $A_1$ , and future age,  $A_2$ , to be:

$$B_2 = \left( \frac{n}{k} - \left( \frac{n}{k} - B_1^{(1-m)} \right) e^{-k(1-m)(A_2-A_1)} \right)^{\frac{1}{1-m}} \quad (2)$$

which can be reparameterized to the following basal area projection equation:

$$B_2 = [B_{asm}^\gamma - (B_{asm}^\gamma - B_1^\gamma) e^{\beta(A_2-A_1)}]^\frac{1}{\gamma} \quad (3)$$

where

$B_i$  = basal area per unit area at time  $i$ ,  $i = 1, 2$

$B_{asm}$  = maximum basal area, often considered a parameter to be estimated

$A_i$  = stand age at time  $i$

$\gamma, \beta$  = parameters to be estimated.

By setting  $B_1 = 0$  for  $A_1 = 0$  the projection equation is equivalent to the yield equation used by Pienaar and Turnbull (1973) to test numerous hypotheses about basal area yields per acre. Harrison and Daniels (1988) substituted average height of the dominant and codominant trees for stand age to combine effects of site with

age in a single variable. Murphy (1983) generalized the age term to any function of age,  $f(A_1, A_2)$ :

$$B_2 = [B_{asm}^\gamma - (B_{asm}^\gamma - B)^\gamma e^{f(A_1, A_2)}]^{1/\gamma} \quad (4)$$

Murphy (1983) chose the function,  $f$ , to be  $\beta(\ln(A_2) - \ln(A_1))$  to best describe growth in natural even-aged loblolly pine stands. The resulting basal area yield equation has also been used by Farrar (1985) for natural even-aged longleaf pine stands.

Pienaar and Turnbull (1973) concluded that the same asymptotic basal area is attainable over a wide range of initial densities. The lowest initial densities, however, tended to have the lowest estimates of the asymptotic value. A declining asymptotic basal area for decreasing densities is biologically reasonable since stands that do not completely occupy a site will be restricted by the maximum diameter growth of each individual tree, and in the limit, zero trees should imply zero basal area. Combining these relationships led to the following model for basal area:

$$B_2 = [B_{asm_2}^\gamma - (B_{asm_1}^\gamma - B)^\gamma e^{f(A_1, A_2)}]^{1/\gamma} \quad (5)$$

where  $B_{asm_i}$  = a function,  $g(T)$ , of the trees per unit area,  $T$ , at time  $i$ .

The function,  $g(T)$ , must approach zero as the number of trees approach zero and increase to the relatively stable maximum identified by Pienaar and Turnbull (1973) as trees per unit area increases. The function should not restrict basal area increment except for densities approaching an open grown condition. The following function fits these requirements:

$$B_{asm} = \alpha_0(1 - e^{\alpha_1 T}) \quad (6)$$

where  $\alpha_0 > 0$  and  $\alpha_1 < 0$ .

It could also be hypothesized that  $B_{asm}$  should include a function of the site potential to account for the differences in carrying capacity for different environmental conditions. This hypothesis would imply that some resource in the environment has a fixed total amount, and basal area growth must slow down as this resource is used up. While this may be true for some extreme conditions, such as phosphorus deficient sites, the total amount of any resource is rarely fixed but rather the rate at which the resource is made available limits the growth of the trees. Over time these higher growth rates for better sites will yield larger basal areas that can never be attained by lower sites if mortality eventually restricts the asymptotic value [Equation (6)]. If survival is not included in the relationship then it would be necessary to include site in the asymptotic function to achieve the same effect (Pienaar 1979). As will be seen, inclusion of mortality in the basal area prediction produces higher basal area carrying capacities for better sites when the stand is fully stocked.

The function  $f(A_1, A_2)$  represents the rate at which basal area approaches the asymptote,  $B_{asm}$ . The function must be restricted to be negative for all values (so  $0 < e^{f(A_1, A_2)} < 1$ ) implying a nondecreasing function of basal area towards the asymptote. To combine the effects of site and stand age, the growth of average height of dominant and codominant trees was used as the main predictor variable (Harrison and Daniels 1988). An additional function, time, was included to predict

a minimum level of basal area growth for mature stands when height growth virtually stops. The function chosen was:

$$f(A_1, A_2) = \beta_1(H_2 - H_1) + \beta_2(A_2 - A_1) \quad (7)$$

where

$H_i$  = average height of dominant and codominants at time  $i$

$A_i$  = average stand age at time  $i$

$$\beta_1, \beta_2 < 0$$

The final form of the basal area yield equation is:

$$B_2 = [B_{asm_2}^\gamma - (B_{asm_1}^\gamma - B)^\gamma] e^{\beta_1(H_2 - H_1) + \beta_2(A_2 - A_1)} \frac{1}{\gamma}$$

$$B_{asm_i} = \alpha_0(1 - e^{\alpha_i T_i}); \quad i = 1, 2$$

$$\alpha_0, \gamma > 0$$

$$\alpha_1, \beta_1, \beta_2 < 0 \quad (8)$$

#### TREE SURVIVAL

Many of the mortality functions in use for even-aged stands describe a reverse sigmoid shape beginning at a maximum value equal to planting density and decreasing through a single inflection point towards zero. The generalized Chapman-Richard's growth model can produce such a shape if the parameter,  $\gamma$ , is negative and the function,  $f$ , is always positive:

$$T_2 = [T_{asm_2}^\gamma - (T_{asm_1}^\gamma - T)^\gamma] e^{f(A_1, A_2)} \frac{1}{\gamma} \quad (9)$$

where  $T_{asm_i}$  = asymptotic trees per unit area at time  $i$ ,

$$F(A_1, A_2) > 0$$

$$\gamma < 0$$

How this survival function operates can be more clearly explained if rewritten as:

$$T_{asm_2}^\gamma - T_2^\gamma = (T_{asm_1}^\gamma - T)^\gamma e^{f(A_1, A_2)} \quad (10)$$

The differences on both sides of the equation represent scaled distances of the density from the asymptotic value. A negative value for the scaling parameter,  $\gamma$ , drives the asymptotic value to zero as the asymptote goes to infinity which in effect removes it from the equation. If the asymptote is constructed to be very large initially and to decrease over time, then survival in young stands is controlled by the exponential function, a function of age, and older stands by the asymptote which is a function of the competitive status of the stand. Since the scaling parameter,  $\gamma$ , is negative, the difference in both cases will also be negative, and an increasing absolute difference implies an increasing distance from the asymptote. So long as the asymptote is constant, mortality is controlled by the value of the exponential. Positive values of the function,  $f(A_1, A_2)$ , will produce values of the exponential greater than one and thereby mortality by increasing the distance

from the asymptote. Conversely, negative values of  $f(A_1, A_2)$  will decrease the distance from the asymptote predicting ingrowth of new trees in the stand.

The functional form of the asymptotic number of trees,  $T_{asm}$ , for a given basal area comes from the relationship known as the self-thinning rule or  $-3/2$  power law that relates maximum number of trees to average tree size. This empirical rule has been used as a forest management tool to index the competitive stress in a stand (Reineke 1933, Drew and Flewelling 1977, 1979, Flewelling 1981). The self-thinning rule has also been explicitly added to growth models (Smith and Hann 1986, Lloyd and Harms 1986) and implicitly implied by other models (Harrison and Daniels 1988). Expressions of the self-thinning rule using quadratic mean diameter as the measure of average tree size can be solved in terms of the asymptotic density for a given basal area in the following manner:

$$\ln(T_{asm}) = \delta_0 + \delta_1 \ln(Q) \quad (11)$$

where

$Q$  = quadratic mean diameter

$$= \left( \sum_{i=1}^n \frac{D_i^2}{n} \right)^{\frac{1}{2}}$$

$$= \left( \frac{B}{kT_{asm}} \right)^{\frac{1}{2}}$$

$D_i$  = dbh for tree  $i$

$n$  = number of trees in stand

$B$  = basal area per acre

$T_{asm}$  = trees per acre along self-thinning line

$k$  = 0.005454

Combining terms and solving for  $T_{asm}$  gives:

$$T_{asm} = e^{\delta_0} \left( \frac{B}{kT_{asm}} \right)^{\frac{\delta_1}{2}}$$

$$T_{asm}^{\frac{2+\delta_1}{2}} = e^{\delta_0} \left( \frac{B}{k} \right)^{\frac{\delta_1}{2}}$$

$$T_{asm} = e^{\frac{2\delta_0}{2+\delta_1}} \left( \frac{B}{k} \right)^{\frac{\delta_1}{2+\delta_1}}$$

which can be reparameterized to:

$$T_{asm} = \left( \frac{B}{\alpha_0} \right)^{\alpha_1} \quad (12)$$

The function  $f(A_1, A_2)$  in Equation (9), must be positive to produce a nonin-

creasing function of density over time. The simplest function to meet this requirement would be:  $f(A_1, A_2) = \beta_1(A_2 - A_1)$ . However, density is not always a nonincreasing function over time especially in young natural stands with ingrowth of trees into the smallest diameter class. The basal area in stands under going ingrowth can be characterized by low basal areas initially along with significant increases in basal area due to the infusion of additional trees. To account for this the following term was added to  $f(A_1, A_2)$ :

$$\beta_2(B_2^{\beta_3} - B_1^{\beta_3})$$

A negative value for the parameter,  $\beta_3$ , scales the difference between initial and future basal area so that the largest difference occurs when the initial basal area is small for the same actual growth in basal area. Also, the negative value for  $\beta_3$  makes the difference between the basal areas negative, for positive basal area growth. This along with a positive value for the parameter,  $\beta_2$ , predicts a smaller value for  $f(A_1, A_2)$ , which causes an increase in survival or ingrowth as the value of  $f(A_1, A_2)$  becomes negative.

The final function was:

$$T_2 = [T_{asm_2}^\gamma - (T_{asm_1}^\gamma - T_1^\gamma)e^{\beta_1(A_2 - A_1) + \beta_2(B_2^{\beta_3} - B_1^{\beta_3})}]^{\frac{1}{\gamma}}$$

$$T_{asm_i} = \left(\frac{B_i}{\alpha_0}\right)^{\alpha_i}; i = 1, 2$$

$$\alpha_0, \beta_1, \beta_2 > 0$$

$$\alpha_1, \gamma, \beta_3 < 0 \tag{13}$$

#### LOGICAL PROPERTIES OF THE BASAL AREA EQUATION

1. *Step Invariant.* This is a useful mathematical property first put forth by Clutter (1963), that two successive predictions from  $A_1$  to  $A_2$  and then from  $A_2$  to  $A_3$  should mathematically give the same predictions as a single step from  $A_1$  to  $A_3$ . This property can be easily shown by substituting the expression for  $A_2$  into the prediction at  $A_3$  and simplifying.
2. *Increasing Average Diameter Along Asymptotic Basal Area Line.* Decreasing trees creates a declining asymptotic basal area but in such a way that the quadratic mean diameter increases:

$$Q = \left[\frac{B_{asm}}{kT}\right]^{\frac{1}{2}} = \left[\frac{\alpha_0(1 - e^{\alpha_1 T})}{kT}\right]^{\frac{1}{2}}$$

$$\frac{dQ}{dT} = \frac{\alpha_0}{2kQT^2} [e^{\alpha_1 T}(1 - \alpha_1 T) - 1] \tag{14}$$

which is negative (implying increasing  $Q$  for decreasing  $T$ ) for all values of  $T$  since  $\alpha_1 < 0$  and  $e^{-x}(1 + x) < 1$  for all  $x > 0$ . This property is necessary for the simultaneous equations because movement along this function over time is through mortality of trees which predicts a decline in basal area, but in such a manner that the average size of the trees continues to increase.

3. *Decreasing Basal Area Through Heavy Mortality.* The basal area projection equation approaches an asymptotic value in a nondecreasing manner. However, the asymptotic value is a function of trees per unit area which also changes over time. Heavy mortality

can cause a large enough decline in the asymptotic value that a decrease in basal area is predicted, as would be biologically reasonable.

### LOGICAL PROPERTIES OF THE SURVIVAL EQUATION

1. *Step Invariant.* In the same way as the basal area equation.
2. *Minimum Mortality Rate.* An explicit minimum mortality rate can be derived for stands that have no ingrowth and a low enough basal area so that the asymptotic trees per acre becomes very large and  $T_{asm}^\gamma$  approaches zero (since  $\gamma < 0$ ). Under these circumstances Equation 13 simplifies to:

$$\begin{aligned} T_2 &= (T_1^\gamma e^{\beta_1(A_2 - A_1)})^{\frac{1}{\gamma}} \\ &= T_1 e^{\frac{\beta_1}{\gamma}(A_2 - A_1)} \end{aligned}$$

which can be equated to a compound interest rate formula for mortality:

$$T_2 = \frac{T_1}{(1 + i)^{(A_2 - A_1)}}$$

which equates to:

$$\begin{aligned} \frac{T_1}{(1 + i)^{(A_2 - A_1)}} &= T_1 e^{\frac{\beta_1}{\gamma}(A_2 - A_1)} \\ i &= e^{-\frac{\beta_1}{\gamma}} - 1 \end{aligned} \tag{15}$$

3. *Increasing Quadratic Mean Diameter Along Self-Thinning Line:* Increasing basal area along the self-thinning line causes a decrease in survival, but in such a way that the quadratic mean diameter continues to increase:

$$Q = \left[ \frac{B}{kT_{asm}} \right]^{\frac{1}{2}} = \left[ \frac{B^{1 - \alpha_1}}{k\alpha_0^{\alpha_1}} \right]^{\frac{1}{2}} \tag{16}$$

which increases as  $B$  increases since  $\alpha_1 < 0$  so  $1 - \alpha_1 > 1$ . This property is different than movement along the asymptotic basal area function given above because it relates to well-stocked stands undergoing competition-induced mortality. It is a necessary property of the survival equation because even as stands experience mortality, the average size of the surviving trees should continue to increase.

### LOGICAL PROPERTIES OF COMBINED EQUATIONS

Since the basal area projection equation and the survival equation are mutually dependent, a simultaneous solution to both equations is required. Appendix A describes an algorithm that can be used to solve the future basal area and survival equations. Each of the following properties are consequences of the simultaneous solution, in that they are not explicitly included in either equation. These properties could and have been included explicitly in models using independent basal area and survival equations.

1. *Declining Basal Area.* Effects of catastrophic mortality from sources such as hurricanes, fire, insects, and disease can be simulated by adding functions to increase mortality. The effects on basal area prediction will be automatically adjusted by reducing predicted basal areas through declines in asymptotic basal area.
2. *Effect of Site on Survival.* It has been hypothesized that mortality is higher on better sites because of the increased competition from the dominant and codominant trees. For combinations of basal area and density far from the self-thinning line, mortality is

controlled by the minimum mortality rate which is not affected by site. As stands approach, the self-thinning line and competition-induced mortality becomes the major source of mortality, then the equations will indirectly predict an increase in mortality. This relationship can be deduced because a better site implies more basal area growth, and increased basal area will lower the asymptotic trees per acre which in turn predicts fewer trees in the future.

3. *Effect of Site on Basal Area Carrying Capacity.* It has been hypothesized that the basal area carrying capacity is higher on better sites. Although the asymptotic basal area is not explicitly a function of site, the predicted attainable basal area for fully stocked stands with the same initial density supports this hypothesis. Due to differing growth rates, the maximum attainable basal area on better sites will take longer to attain on lower sites, but only if no mortality occurs. The additional mortality on the lower sites due to the longer time period will restrict the attainable basal area through the asymptotic basal area function. Therefore, the actual attainable basal area on lower sites in fully stocked stands will be less than on better sites.
4. *Inclusion of Ingrowth.* The survival equation predicts an increase in the number of trees per acre if the basal area growth is sufficiently high. For plantations this ingrowth may be reset to zero, in which case the predicted basal area increment is reduced accordingly.

## DATA

The data set as described by Kush et al. (1968) consists of 203 permanent plots with at least one remeasurement in naturally regenerated, even-aged longleaf pine stands located in central and southern Alabama, southern Mississippi, southwest Georgia, and northern Florida. The original study was established from 1964 to 1967 by the USDA Forest Service to cover a wide range of ages, densities, and sites (Farrar 1978). Additional plots were added at each remeasurement period to fill in an approximate rectangular distribution of age, site index (base age 50), and residual basal area classes. For this purpose most of the plots have been thinned to specified basal area classes. A description of plots by age, site, and residual basal area is given in Table 1, and the means and ranges of basic stand variables is given in Table 2. Growth models were developed using the first 5-year growth period (Farrar 1979) and subsequently updated by the second growth period (Farrar 1985).

The initial set of plots has now been measured for the fourth growth period and, accounting for new plots added and plots lost to catastrophic mortality and harvesting, gives a grand total of 756 growth measurements. Some of the plots that sustained insect and hurricane damage were remeasured following the damage before dropping them from the study. Because of the unique ability of these equations to account for catastrophic mortality in basal area if survival is known and vice versa, all of these plots were included in the analysis.

## RESULTS

The basal area projection and survival equations were fit using three-stage nonlinear least squares methodology (Borders 1989) for simultaneous systems of equations. Initial values for the parameters were generated by fitting each equation independently using standard nonlinear procedures. The parameters  $\alpha_0$  and  $\alpha_1$  in the asymptotic equation,  $T_{asm}$ , [Equation (13)] were poorly estimated be-

TABLE 1.

Number of observations by site, initial age, and residual basal area in the natural longleaf pine data set.

Site index (ft)	Stand age (yr)	Residual basal area							Total
		<25	25-50	50-75	75-100	100-125	125-150	>150	
		..... ( $ft^2/ac$ ) .....							
45-55	9-20	—	—	—	—	—	—	—	0
	21-40	—	—	1	1	—	—	—	2
	41-60	—	5	8	10	5	—	—	28
	61-80	—	5	5	4	2	—	—	16
	81-100	—	2	2	2	2	—	—	8
55-65	9-20	1	—	—	4	—	—	—	5
	21-40	1	10	3	7	7	2	1	31
	41-60	—	8	1	4	9	11	—	33
	61-80	—	9	7	2	2	5	5	30
	81-100	—	1	6	6	3	—	—	16
65-75	9-20	17	9	4	3	—	—	—	33
	21-40	2	21	15	11	3	1	—	53
	41-60	—	8	17	5	6	4	—	40
	61-80	4	11	18	11	15	6	2	67
	81-100	—	9	10	9	6	6	—	40
75-85	9-20	12	10	7	2	—	—	—	31
	21-40	1	19	38	35	30	11	—	106
	41-60	—	24	22	19	18	11	2	96
	61-80	—	9	3	10	14	5	2	43
	81-100	—	—	—	—	—	—	—	0
85-95	9-20	—	—	—	—	—	—	—	0
	21-40	—	—	—	2	1	4	—	7
	41-60	—	—	3	15	5	3	—	26
	61-80	—	—	6	7	2	1	1	17
	81-100	—	—	—	—	—	—	—	0
	Total	38	160	176	169	130	70	13	756

cause only one plot was within 90% of the asymptotic line given by Reineke (1933) for longleaf pine (Table 2). Therefore, these parameters were fixed to the asymptotic line given by Reineke (1933). Transforming his equation to asymptotic trees for a given basal area gave the following equation:

$$T_{asm} = \left( \frac{B}{993.4} \right)^{-4} \quad (17)$$

The remaining parameters were estimated from the fit data set, the results given in Table 3. All of the parameters for both basal area and survival met theoretical limitations, and the adjusted ratio between regression and corrected total sum of squares were 97.5% and 95.6%, respectively. The minimum mortality rate as a function of the parameters in the survival equation [equation (6)] was 0.98% per year.

Verification of the basal area projection and survival equation was done using a

TABLE 2.

Basic statistics for the initial variables in the natural longleaf pine data set.

	Mean	Range
Average stand age (yr)	48.1	9.0-98.3
Site index (ft at 50 yr)	72.6	49.2-91.0
Basal area (ft <sup>2</sup> /ac)	77.3	0.9-167.4
Trees (1/ac)	318.0	15-2080
Reineke's Stand Density Index	154.9	4.2-407.4

cross-validation technique (Efron and Gong 1983) which predicts each observation after removing it from the fitting procedure. For this data set, an observation was assumed to be a plot with all of its multiple remeasurements. Although the plots themselves cannot be assumed to be strictly independent of each other in a designed data set, this procedure gives the best indication of the predictive ability

TABLE 3.

Parameter estimates and fit statistics for predicting future basal area and survival in natural even-aged longleaf pine stands.

Parameter	Basal area		Survival	
	Estimate	Asymptotic std. err.	Estimate	Asymptotic std. err.
$\alpha_0$	188.8	12.3	993.4	—
$\alpha_1$	-0.01495	0.00146	-4	—
$\gamma$	0.1946	0.1501	-1.825	0.454
$\beta_1$	-0.02591	0.00472	0.01787	0.00843
$\beta_2$	-0.01271	0.00319	3.620	1.267
$\beta_3$			-0.7870	0.2499
$R_{ss}^*$	0.975		0.956	
$s_{y.x}$	5.80		68.8	

Model forms

$$B_2 = [B_{asm2}^\gamma - (B_{asm1}^\gamma - B)^\gamma] e^{\beta_1(H_2 - H_1) + \beta_2(A_2 - A_1)} \frac{1}{\gamma}$$

$$B_{asm_i} = \alpha_0(1 - e^{\alpha_1 T_i}); i = 1, 2$$

$$T_2 = [T_{asm2}^\gamma - (T_{asm1}^\gamma - T)^\gamma] e^{\beta_1(A_2 - A_1) + \beta_2(B_2^{\beta_3} - B_1^{\beta_3})} \frac{1}{\gamma}$$

$$T_{asm_i} = \left[ \frac{B_i}{\alpha_0} \right]^{\alpha_1}; i = 1, 2$$

$B_i$  = Basal area (ft<sup>2</sup>/ac) at time  $i$

$H_i$  = Average dominant and codominant tree height (ft) at time  $i$

$A_i$  = Average age of dominant and codominant trees (yrs) at time  $i$

$T_i$  = Total number of trees (1/ac) at time  $i$

\*  $R_{ss}$  is an estimate of the adjusted ratio between the regression and corrected total sum of squares. It is analogous to the adjusted  $R^2$  for linear equations.

of the system of equations short of a new data set from an independent source. Results of the cross-validation procedure are given in Table 4 for predictions of future basal area given the survival, future survival given basal area growth, and the simultaneous prediction of both basal area and survival. For all the predictions the average stand age and average dominant and codominant height are the observed values. The results indicate that on the average the simultaneous predictions are only slightly less accurate and precise for basal area and, in fact, slightly more accurate and precise for survival than the predictions when either future trees or basal area per acre is assumed to be known. The result for survival was not expected since predictions using the observed future basal area would normally be expected to do better on the average than predictions of survival using a predicted basal area. This unexpected result for survival is due to four observations near the self-thinning line where a small difference between predicted and observed future basal area produced a large change in predicted survival. These four plots accounted for a large part of the standard deviation and mean residual values. Dropping these observations made the mean and standard deviation of the residuals using the observed basal area (0.91 trees and 49.70 trees) smaller than the residuals using the predicted basal area (1.20 trees and 50.62 trees).

Figures 1 and 2 are examples of the basal area and survival predictions, respectively, over stand age. The examples were generated from simultaneous solution of the equations beginning with 200, 600, 1000, and 2000 trees per acre at age 15 on sites 50 and 90 ft (base age 50, site index equation from Farrar 1985). The initial basal area was predicted from the following equation fit to all plots less than 20 years of age:

$$Q = 0.5753 + 0.08522 H$$

$$(R^2 = 0.837 \quad s_{y.x} = 0.407) \quad (18)$$

where

$Q$  = quadratic mean diameter,

$H$  = average height of dominant and codominants.

Both sets of curves show classic sigmoid shapes very similar to other projection

TABLE 4.

Verification results for basal area and survival predictions in natural even-aged longleaf pine stands.

Equation <sup>2</sup>	Basal area <sup>1</sup>			Survival <sup>1</sup>		
	$\bar{R}$	$ \bar{R} $	$S_R$	$\bar{R}$	$ \bar{R} $	$S_R$
Given survival	0.04	3.81	5.77	—	—	—
Given basal area	—	—	—	1.15	22.40	71.80
Simultaneous	0.27	4.86	8.72	0.04	20.62	61.36

<sup>1</sup>  $\bar{R}$  = Average Residual.

$|\bar{R}|$  = Average Absolute Residual.

$S_R$  = Standard Deviation of Residual.

<sup>2</sup> Results are for predicting basal area given survival, survival given basal area, and simultaneous predictions of basal area and survival.

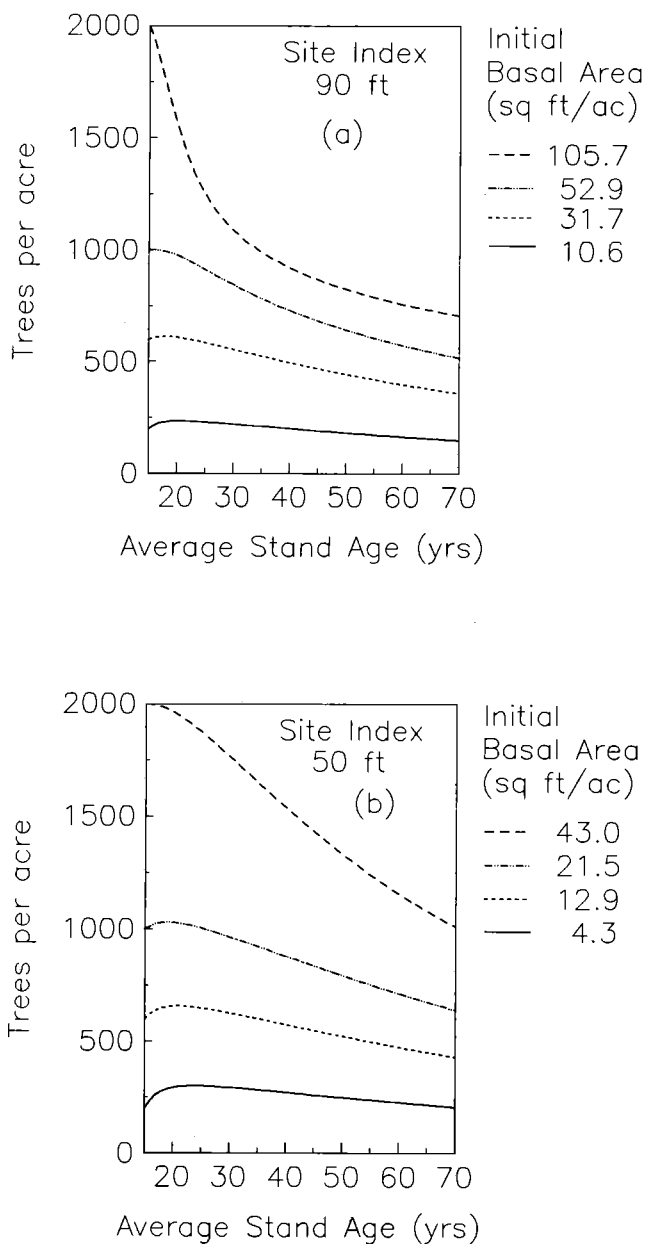


FIGURE 1. Basal area projections of eight hypothetical longleaf pine stands for four initial densities on two sites; (a) site index 90 ft and (b) site index 50 ft at 50 yr.

equations. Figure 3 combines the information in Figures 1 and 2 where each 5-year projection is shown by either a circle or square. The asymptotic basal area ( $B_{asm}$ ) and asymptotic survival curves ( $T_{asm}$ ) are included as reference lines to show movement over time towards and along these asymptotes.

Figure 3 demonstrates the combined effects of site and initial density on stand development. Stands of high densities on good sites quickly approach the self-thinning line where increases in basal area can only come about by overcoming the

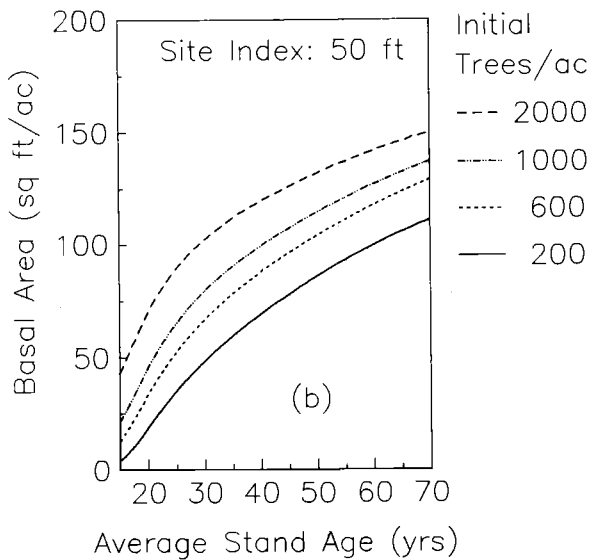
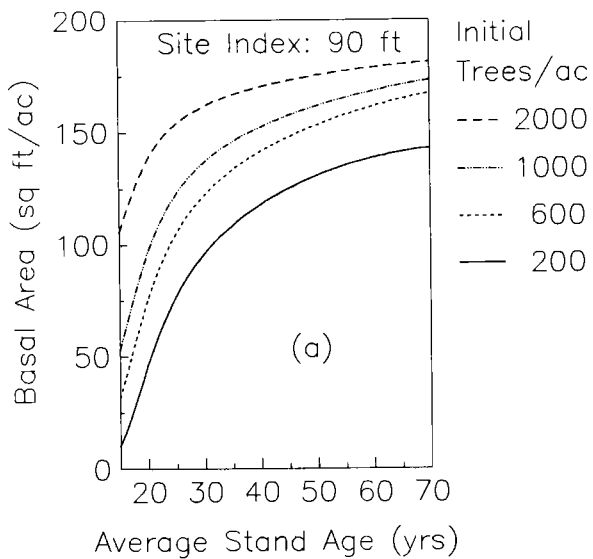


FIGURE 2. Survival projections of eight hypothetical longleaf pine stands for four initial densities on two sites; (a) site index 90 ft and (b) site index 50 ft at 50 yr.

effect of heavy mortality. Although most dramatic for high initial densities the projections for the higher site index attains a higher maximum basal area than the lower site index even though the asymptotic basal area equation does not explicitly include a function of site. This result is primarily due to the early basal area growth on the better site which cannot be made up for by the lower site because of the loss of trees through mortality over time. Low densities and poorer sites

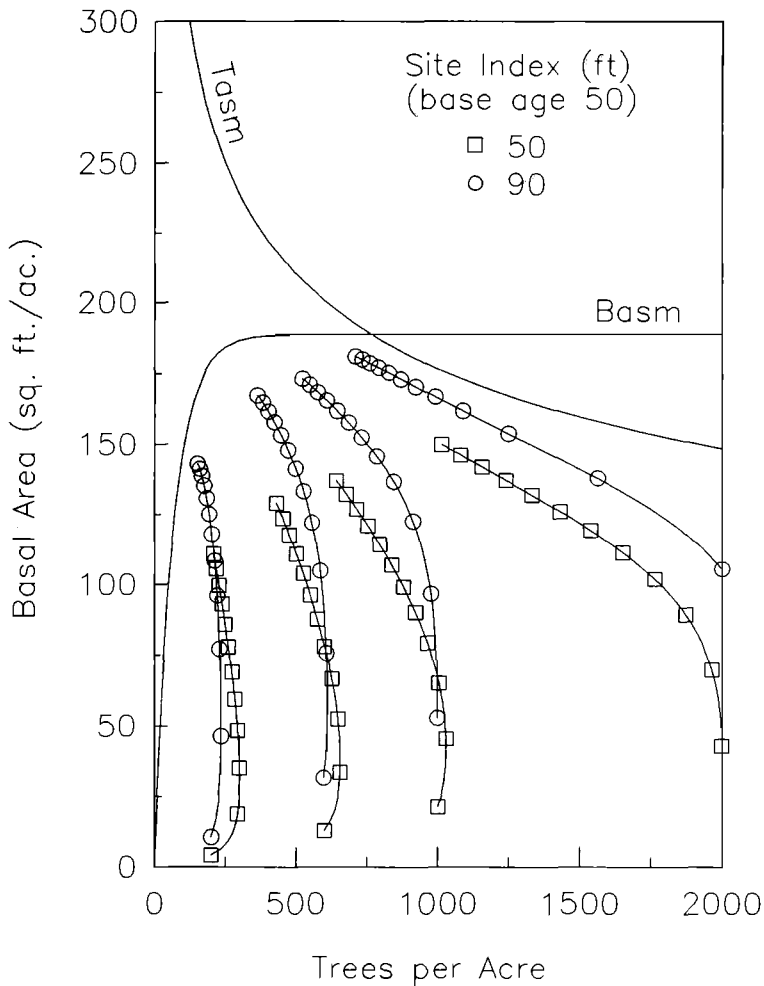


FIGURE 3. Basal area vs. survival projections of eight hypothetical longleaf pine stands on two sites and four initial densities.

are controlled by the minimum mortality rate and eventually by restrictions on the stand level growth of stands that do not fully capture the site.

## DISCUSSION

Simultaneous basal area projection and survival equations were derived from a set of assumptions of stand development. These assumptions, while empirical and controversial in some cases, provided valuable information that was used to constrain both the upper and lower end of growth and yield predictions. By explicitly including these relationships in the growth and yield system, it is hoped that extrapolations to new stand conditions will be improved. Included for survival are the self-thinning rule for high densities, minimum mortality rate for low densities, and ingrowth for young stands exhibiting relatively large increases in basal area. For basal area projection the assumptions about increased growth for better sites,

asymptotic basal area growth for low density stands, minimum growth for mature stands, and, most importantly, a decrease in basal area from heavy mortality were included. Although none of the predictions shown in Figure 3 demonstrate a decrease in basal area per acre, there was a plot in the data set that was nearly destroyed by hurricane Frederick. The plot showed a decline in basal area from 150 ft<sup>2</sup> to 10 ft<sup>2</sup> for a change in trees per acre from 140 trees to 5 trees, age from 65 years to 70 years, and height of dominants from 92 ft to 100 ft. Putting these values in the basal area projection equation predicts a future basal area of 12 ft<sup>2</sup> which only slightly over predicts the observed value of 10 ft<sup>2</sup>.

As a further example assume that a stand is afflicted by some agent that causes an additional 5% mortality of those trees susceptible in addition to the mortality through competition. Figure 4 demonstrates the results predicted for stands with 0% to 100% susceptibility. The simulations are for a site index 90 ft, 600 trees/ac, and 31.7 ft<sup>2</sup> basal area per acre at age 15. For the stands having 75% and 100%

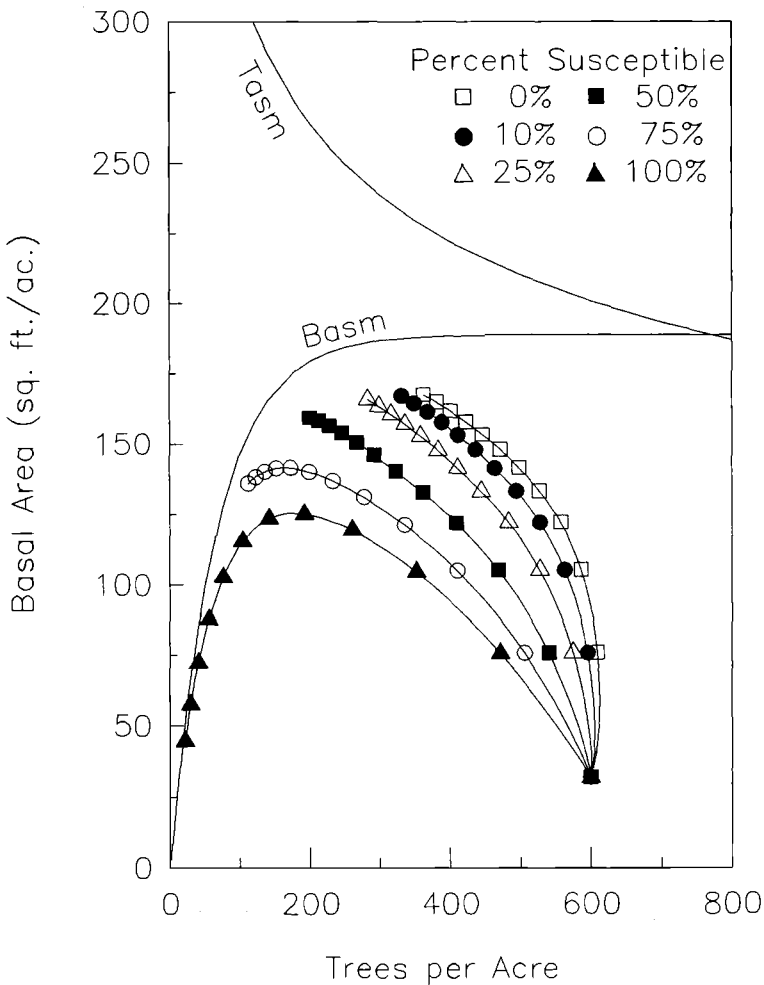


FIGURE 4. Effects of an additional 5% mortality on susceptible trees (from 0–100% susceptible) on basal area and survival of hypothetical longleaf pine stands.

susceptibility the mortality is severe enough to cause a predicted decline in basal area per acre after 50 years and 35 years of age, respectively.

In addition to the assumptions about stand development, each equation also incorporates some desirable mathematical properties. They are both sigmoid-shaped, which means they have a single inflection point and approach an asymptotic value over time. Both equations are step size invariant, implying the simultaneous system is also step size invariant. Finally and most importantly, all of the biological and mathematical properties were built into the system of equations from knowledge of stand development independent of any data set. It is believed that similar assumptions about stand development and desirable mathematical properties will prove useful in the modeling of other single species stands.

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## APPENDIX: SIMULTANEOUS SOLUTIONS

The simultaneous solution of the basal area projection and survival equation uses a modification of the secant method for finding the root of an equation. In general, the secant method finds the root of the following equation (Burden et al. 1981):

$$Y - f(Y) = 0$$

By assuming that the function can be approximated by a straight line through two starting points, one with a positive difference, and one a negative difference:

$$Y_a - f(Y_a) = D_a > 0$$

$$Y_b - f(Y_b) = D_b < 0$$

The equation for a line between the two points ( $Y_a, D_a$ ) and ( $Y_b, D_b$ ) is:

$$y = Y_a + (d - D_a) \left[ \frac{Y_b - Y_a}{D_b - D_a} \right]$$

The root of the equation is estimated when  $d = 0$  so:

$$y = Y_a - D_a \left[ \frac{Y_b - Y_a}{D_b - D_a} \right]$$

This gives a new difference:

$$D_c = y - f(y)$$

If the difference is positive then  $Y_a$  is replaced or if negative then  $Y_b$  is replaced. The procedure is repeated until the difference is as close to zero as desired.

Instead of a single equation the simultaneous solution of both equations requires a simple modification. The variable  $Y$  was chosen to represent survival. The function,  $f(Y)$ , is then the survival predicted from using  $Y$  to predict future basal area and then using this future basal area to obtain a new survival prediction. When these two estimates of survival agree, i.e., the difference is sufficiently close to zero, then the system of equations is solved. The first starting value,  $Y_a$  is set equal to  $T_1$  which assumes no mortality. Assuming no ingrowth is predicted, this must be the maximum number of trees in the future since the function is nonincreasing. No mortality means no change in maximum basal area which leads

to the maximum amount of future basal area. This maximum amount of basal area will then predict the maximum change in survival. This new estimate of survival is  $f(Y_a)$  and is also the second starting value,  $Y_b$ . Once again this new value is put into the basal area projection equation to get a new basal area which gives another estimate of trees surviving,  $f(Y_b)$ . This value is used to set the difference  $D_b$ .

If ingrowth is predicted then the value for  $Y_b$  will actually be greater than  $Y_a$  and the difference  $D_a$  will be negative, in which case  $y > Y_a > Y_b$ . Therefore replace  $Y_a$  with  $Y_c$  and repeat until the difference becomes positive.