

A Simple Stand Growth Model Based on Canopy Dynamics and Biomechanics

Thomas J. Dean, Mauricio Jerez, and Quang V. Cao

Abstract: A new approach to simulating net forest growth is presented. The model is based on density effects on mean crown dimensions and the stem geometry required to counteract the bending moment generated from wind action on the crown. Stem geometry is based on the constant-stress principle of stem formation. Various structural and growth properties of hypothetical loblolly pine stands growing on a range of site indexes and with a range of initial tree densities are calculated with the model and compared with published values and well-known patterns. Size-density relations calculated with the model are consistent with converging, curvilinear lines reported for slash pine and loblolly pine plotted on log-transformed axes. Linear relationships between mean crown length and mean spacing agree with observations from various coniferous species, and culmination of current annual increment corresponds with the rapid changes in canopy structure reported with Sitka spruce. Overestimations of mean annual increment appear to result from differences in canopy dynamics in the loblolly pine plots used to fit the model's regression equations and the canopy dynamics in the loblolly pine plantations used for comparisons. The model has the potential to create an alternative approach for accessing environmental changes on forest growth and yield to complement extant carbon-balance models. *FOR. SCI.* 59(3):335–344.

Keywords: loblolly pine, constant-stress model, simulation, leaf area, crown dynamics, net growth

THE SIZE OF TREE STEMS HAS BEEN LONG KNOWN to be a function of crown size (Larson 1963). Physiologically based growth models incorporate this concept by expressing crown size in terms of the amount of carbohydrate produced by the foliage and partitioning the carbohydrate to the physical structures servicing the crown. Since the introduction of the BIOMASS model by McMurtree and Wolf (1983), this approach has produced sophisticated and useful models for linking the environment to forest production (e.g., Valentine 1988, Aber and Federer 1992, Cropper and Gholz 1993, Landsberg and Waring 1997). Crown size can also be expressed in terms of wind drag. From this point of view, biomechanical principles determine the stem cross-sectional area required to counteract the drag. When combined with population and crown dynamics in a developing stand, biomechanics create a conceptual framework for predicting aboveground stem production without contradicting the principles of carbon balance in biomass accumulation.

Metzger (1893) is credited for adapting the principles of beam mechanics to describe stem size and shape as a function of crown size. He reasoned that efficient allocation of carbohydrate would result in a stem that tapered to equalize wind-induced bending stress along the stem. According to the theory, bending stress is constant when the diameter of a circular beam varies with the cube root of bending moment at a cross section. Bending moment (the turning force) is the product of the force applied to the beam

and the distance between the cross section and where the force is applied. The lateral force on the tree is created by frictional drag of wind through the crown, which Metzger equated to the sail area of the crown and lateral wind pressure. The equivalent location where a distributed force such as wind acts on a beam stem is the centroid of the force. Metzger equated the vertical distance between a stem's cross section and the centroid of the crown to the lever arm.

Dean and Long (1986) transformed the flexure formula that Metzger (1893) had redefined for trees into a general equation for stem diameter based on the two morphological variables that determine bending moment at a particular height h on the stem, leaf area above h (A_{Lh}) and the leverage at h , which is the distance between h and the median of A_{Lh} . The equation is called the constant-stress model of stem formation and predicts stem diameter at any height h (D_h) with the equation

$$D_h = a(A_{Lh} S_h)^x, \quad (1)$$

where a is the proportionality constant and $x = 1/3$ for a circular stem with uniform physical properties that is rigidly anchored and subject to only small deflections from horizontal forces applied to the crown. By transforming Equation 1 into circular area, Dean (2004) demonstrated that the constant-stress model could account for the basal area growth of even-aged stands with discrete changes in crown

Manuscript received August 29, 2011; accepted May 31, 2012; published online June 28, 2012; <http://dx.doi.org/10.5849/forsci.11-108>.

Thomas J. Dean (fwdean@lsu.edu), Louisiana State University Agricultural Center, School of Renewable Natural Resources, Baton Rouge, LA. Mauricio Jerez (mjerezr@cantv.net), Universidad de Los Andes. Quang V. Cao (qcao@lsu.edu), Louisiana State University Agricultural Center, Center of Renewable Natural Resources, Baton Rouge, LA.

Acknowledgments: We thank Scott D. Roberts for allowing us to use some of the data he destructively collected in a 10-year-old loblolly pine stand. This study was supported in part by McIntire-Stennis Project LAB94096. This article is published with the approval of the Director of the Louisiana Agricultural Experiment Station as publication number 2012-241-7023.

Copyright © 2013 by the Society of American Foresters.

dimensions. In this way, Dean (2004) was able to quantify stem growth on the basis of not only leaf area but also changes in the vertical structure of foliage, the first time stem growth was related to leaf area and crown structure simultaneously.

The constant-stress model has been confirmed for a range of coniferous species (Jokela et al. 1989, Dean et al. 2002, Lundqvist and Elfving 2010) but only by comparing actual stem geometry to the geometry of an ideal, circular, cantilever beam. Direct tests of the principle are nearly impossible because of the difficulty in directly measuring drag in trees and in calculating the propagation stress throughout the stem. Detailed modeling efforts conflict because of the simplifying assumptions necessary to produce tractable solutions (e.g., West et al. 1989, Morgan and Cannell 1994, Mattheck 2000, Niklas and Spatz 2000). Bending experiments, however, repeatedly confirm that trees respond to experimental manipulations of sway (Jacobs 1954, Dean 1991, Valinger 1992, Meng et al. 2006). Regardless of the status of the principle as a verified mechanism of stem formation, the concept as expressed by Equation 1 has proven useful in relating stem diameter to crown morphology (Dean and Baldwin 1996, Meng et al. 2007). This situation is analogous to Valentine and Mäkelä's (2005) use of the pipe model of Shinozaki et al. (1964) as a means of calculating stem respiration in a carbon-balance model; i.e., the model may not be correct in every detail, but it adequately quantifies the sapwood in the stem and, thus, carbon lost from stem respiration.

Most silvicultural treatments affect the accumulation and distribution of leaf area (Long et al. 2004). A growth model based on Equation 1 can provide simple analyses of the response of stand production to changes in canopy dynamics and possible novel explanations for observed trends. For example, Dean (2004) found that for growth efficiency in terms of basal area increment per unit leaf area to remain constant in developing loblolly pine plantations, the product of leaf area and leverage must constantly increase above a specific rate; otherwise, efficiency drops. At any point during stand development, the volume of the average tree can be determined by the current combination of average leaf area per tree and the average vertical distribution of leaf area. Growth would be the simple difference between volumes at two points in time. The objective of this article is to present such a model and evaluate the model with respect to known patterns of stand growth.

The Model

The model proceeds by rotating through two modules on an annual basis. The first module calculates the amount and vertical distribution of leaf area of the average tree in the stand. The second module calculates mean stem volume from the leaf area characteristics. The first module represents the effects of population density, age, and site quality on the size and shape of the live crown. This module is largely empirical in this model version, but it could be replaced with process-oriented algorithms that simulate the amount and vertical distribution of leaf area. The second

module represents the effect of the constant-stress principle of stem formation on stem size and taper.

The model is coded as a data step in SAS (version 9.1; SAS Institute, Inc., Cary, NC) and requires site index (mean height of the tallest half of the trees at age 25 years) as a measure of site quality and number of surviving trees per ha at a starting age as a measure of stand density to start. Growth is simulated each year, at which point new values for stand density and average tree height are predicted. Together with site index, these variables determine crown length, total leaf area, and leaf area distribution. These values are used by the constant-stress model to compute diameters along the stem at fixed heights, including quadratic mean dbh. Total volume of the average tree is obtained by summing all sections. The above steps allow the computation of leaf area index, stand basal area, stand volume, mean annual increment (MAI), and current annual increment. The process is repeated until the end of the desired growing period is reached.

Stand Survival

Changes in tree density are predicted with a modified version of the stand survival system from Cao et al. (2000). Current stand survival (N_i) at time i is predicted from stand size and density of the previous year as follows:

$$N_i = N_{i-1} - (N_{i-1} - N_{m,i}) \exp[b_1 (Q_{m,i-1} - Q_{i-1})] + \varepsilon, \quad (2)$$

where Q_{i-1} is quadratic mean diameter (cm) at time $i - 1$, $Q_{m,i-1}$ is maximum attainable stand diameter (cm) for a given stand density at time $i - 1$, N_{i-1} is number of trees per ha at time $i - 1$, $N_{m,i}$ is lower limit of stand survival at time i subject to maximum mortality, b_1 is a regression coefficient, and ε is random error. The time course of maximum quadratic mean diameter ($Q_{m,i}$) follows the self-thinning curve

$$Q_{m,i} = b_2 N_i^{-0.623} [1 - \exp(b_3 N_i^{b_4})] + \varepsilon, \quad (3)$$

where b_j 's are coefficients estimated with nonlinear regression. The lower limit of stand survival for the next year ($N_{m,i+1}$) is given by

$$N_{m,i+1} = N_i \left(\frac{t_{i+1}}{t_i} \right)^{b_5-1} \exp[b_5 (t_{i+1}^{b_6} - t_i^{b_6})] + \varepsilon, \quad (4)$$

where t_i and t_{i+1} are stand ages in years at times i and $i + 1$, respectively.

Heights

Mean tree height (H_T , in m) and mean height to the crown midpoint (H_{MC} , in m) are calculated with empirical functions of stand age (t), site index (SI), and stand survival (N , in number of trees per ha) at age t :

$$H_T = b_7 (t^{b_8}) (SI^{b_9}) (N^{b_{10}}) + \varepsilon \quad (5)$$

and

$$H_{MC} = b_{11} (t^{b_{12}}) (SI^{b_{13}}) (N^{b_{14}}) + \varepsilon. \quad (6)$$

Mean crown length (CL), mean live crown ratio (CR), and mean height to the base of the live crown (H_B) are calculated from H_T and H_{MC} : $CL = 2(H_T - H_{MC})$; $CR = CL/H_T$; and $H_B = H_T - CL$.

Leaf Area

Mean leaf area per tree (A_L , in m^2) is predicted from a best-fit equation:

$$A_L = b_{15}H_T^{b_{16}} + b_{17}CL^{b_{18}} + \varepsilon. \quad (7)$$

Roberts et al. (2003) developed similar equations for calculating tree leaf area with various height measurements.

Leaf area distribution on an average tree is assumed to follow an S_B function (Jerez et al. 2005). The cumulative fraction of leaf area, $F(x)$, from the crown tip to any point x within the crown is

$$F(x) = \Phi \left[\gamma + \delta \ln \left(\frac{x}{1-x} \right) \right], 0 \leq x \leq 1, \quad (8)$$

where $x = (H_T - h)/CL$, h is height from the ground to that point, $\Phi(\cdot)$ is the standard normal cumulative distribution function, and γ and δ are S_B shape parameters. The parameters γ and δ are computed from the predicted 15th (x_{15}) and 50th (x_{50}) percentiles of leaf area by use of the following system developed by Jerez et al. (2005)

$$\delta = \frac{z_{15}}{\ln \left(\frac{x_{15}}{1-x_{15}} \right) - \ln \left(\frac{x_{50}}{1-x_{50}} \right)}; \quad (9)$$

$$\gamma = -\delta \ln \left(\frac{x_{50}}{1-x_{50}} \right); \quad (10)$$

$$x_{15} = \exp(b_{19} + b_{20}CR + b_{21}H_T + b_{22}H_{MC} + b_{23}t) + \varepsilon; \text{ and} \quad (11)$$

$$x_{50} = \exp(b_{24} + b_{25}CR + b_{26}H_T + b_{27}H_{MC} + b_{28}t) + \varepsilon, \quad (12)$$

where z_{15} is z of the normal distribution at the 15th percentile of leaf area.

Diameters

The constant-stress model (Equation 1) cast as a regression model is

$$D_h = b_{29}(A_{Lh} S_h)^{b_{30}} + \varepsilon. \quad (13)$$

If the value of h is inside the crown, the cumulative fraction of leaf area (p) from the crown tip to h is computed by use of Equation 8, i.e.,

$$p = F(x), \text{ where } x = (H_T - h)/CL. \quad (14)$$

Stem diameter at that point is computed from Equation 13 with

$$A_{Lh} = p(A_L), \text{ and} \quad (15)$$

$$S_h = CL(x - x_{p/2}), \quad (16)$$

where $x_{p/2} = y/(1 + y)$, $y = \exp\{[\Phi^{-1}(p/2) - \gamma]/\delta\}$ and $\Phi^{-1}(\cdot)$ is the inverse cumulative density function of the standard normal distribution. If the diameter point is below the crown, A_{Lh} from Equation 13 is leaf area of the entire crown or A_L , and S_h is given by

$$S_h = H_{LM} - h, \quad (17)$$

where $H_{LM} = H_T - CR(x_{50})$ is height to the median of leaf area. The predicted diameter at $h = 1.37$ m is assumed to represent quadratic mean diameter (Q , in cm) of the stand (Dean and Long 1992).

Volume

Stem taper is generated by calculating values of d_h at 0.1-m intervals. Outside bark volume of the j th section (V_j , in m^3) is computed by use of Smalian's formula as follows:

$$V_j = K l_j (d_{1j}^2 + d_{2j}^2), \quad (18)$$

where $K = \pi/40,000$ is a constant to convert diameter from centimeters into area in square meters, $l_j = 0.1$ m is section length, and d_{1j} and d_{2j} are diameters in centimeters at both ends of the section. Finally, total volume of the average tree is obtained by summing all sections. Smalian's formula, which assumes that the section is a paraboloid, should be adequate for computing volumes of 0.1-m sections (Figueiredo Filho et al. 2000).

Coefficients

Coefficients for the model's equations were estimated from fits of the equations to data or were taken from the literature (Table 1). When coefficients were determined from data, models were fit with a derivative-free, curvilinear regression algorithm. Coefficients in Equations 2, 3, 4, 5, and 6 were determined with loblolly pine data collected from repeatedly measured plots originally established by the USDA Forest Service, Southern Research Station for developing growth-and-yield equations. The data are described in detail by Baldwin and Feduccia (1987). Trees ranged in age from 11 to 45 years and were measured either once or two to four times at 5-year intervals. Plots were located in Louisiana, eastern Texas, and western Mississippi. Coefficients in Equations 7 and 13 were estimated with loblolly pine data collected from 158 destructively measured trees ranging in age from 4 to 36 years. The 4-year-old trees were measured in eastern Texas, and the 36-year-old trees were measured in southeastern Louisiana. The sites and procedures for measuring these trees are described by Dean et al. (2002). The 14-year-old trees were located in central Mississippi. The site and procedures for measuring these trees are described by Roberts et al. (2004). The 10-year-old trees were measured in southeastern Mississippi. The sites and procedures for measuring these trees are described by Roberts et al. (2003).

The estimated values of the coefficients agree with previous observations. Toward the upper end of stand density, mean tree height is negatively affected by density (Jack and Long 1991), which accounts for the negative exponent for N in Equation 5 (b_{11}). The positive exponent for N in Equation

Table 1. Model coefficients and statistics for regression models listed by equation number in the text.

Component	Equation	<i>n</i>	Fit index ^a	Sy.x ^b	Parameter	Estimate	SE ^c	Reference
Survival	2	1097	0.76	186.5	<i>b</i> ₁	−0.1624	0.0087	
					<i>b</i> ₂	2150.0000	38.2100	
					<i>b</i> ₃	−0.0536	0.0061	
	3	174	0.98	0.9	<i>b</i> ₄	0.5239	0.0265	
					<i>b</i> ₅	−0.0438	0.0015	
					<i>b</i> ₆	1.0712	0.0781	
Heights	4	878	0.82	159.5	<i>b</i> ₇	0.6608	0.0629	
					<i>b</i> ₈	0.5400	0.0115	
					<i>b</i> ₉	0.6429	0.0188	
					<i>b</i> ₁₀	−0.0484	0.0044	
	5	415	0.96	0.066	<i>b</i> ₁₁	0.1536	0.0152	
					<i>b</i> ₁₂	0.6808	0.0126	
					<i>b</i> ₁₃	0.7740	0.0193	
					<i>b</i> ₁₄	0.0142	0.0046	
					<i>b</i> ₁₅	0.0002	0.0002	
					<i>b</i> ₁₆	4.0378	0.4091	
Leaf area	7	161	0.82	13.9	<i>b</i> ₁₇	1.1491	0.6258	
					<i>b</i> ₁₈	1.4287	0.2257	
					<i>b</i> ₁₉	−2.8155		
					<i>b</i> ₂₀	2.4191		
					<i>b</i> ₂₁	−0.2006		
					<i>b</i> ₂₂	0.3360		
<i>x</i> ₁₅	11				<i>b</i> ₂₃	−0.0313		Jerez et al. (2005)
					<i>b</i> ₂₄	−1.3859		
					<i>b</i> ₂₅	1.2516		
					<i>b</i> ₂₆	−0.1362		
					<i>b</i> ₂₇	0.2124		
					<i>b</i> ₂₈	−0.0185		
					<i>b</i> ₂₉	2.4617	0.0405	
					<i>b</i> ₃₀	0.3467	0.0025	
<i>x</i> ₅₀	12							Jerez et al. (2005)
Stem diameter	13	1188	0.95	1.9				

Published values were incorporated for Equations 12 and 13.
^a Fit index = $100 \cdot \sum(y - \hat{y})^2 / \sum(y - \bar{y})^2$; \hat{y} = predicted value of y and \bar{y} = mean value of y .
^b SE of \hat{y} .
^c SE of b_i , where i = coefficient number.

6 for calculating height to the middle of the crown (b_{15}) is consistent with the inverse relationship between mean live crown ratio and stand density demonstrated for a number of coniferous species by Long (1985). This relationship results in increasing height to the middle of the crown with increasing density with age and site quality held constant. The exponent for mean tree height in Equation 7 (b_{17}), 4.0378, is similar to the exponent estimated by Roberts et al. (2003) when fitting leaf area per tree to a power function of mean height. The fitted exponent for the constant-stress model (Equation 13, b_{30}) is only 4% larger than the theoretical value of $1/3$.

Results and Discussion

To demonstrate stand development patterns produced by the model, the model was run with nine combinations of site index and initial trees/ha (SI = 12, 18, and 24 m at 25 years and N_0 = 1,200, 1,800, and 2,400 trees/ha) for 35 years (t = 10 through 45 years) in yearly increments. The time courses of size and density calculated with the model are consistent with the converging curvilinear patterns for a range of initial tree densities such as those shown by previous investigators (Smith and Hann 1986, Tang et al. 1995, Cao and Dean 2008) (Figure 1). The length of the size-density trajectories is correlated to site index, corresponding to the slower rate of stand development on poorer

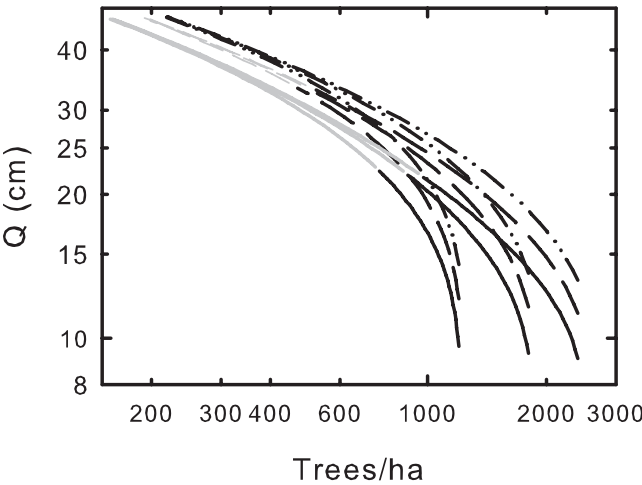


Figure 1. Plotted trajectories of average stand diameter (Q) and trees/ha calculated with the model. Black lines represent a time interval from $t = 10$ to $t = 45$. Gray lines represent the trajectory for the additional time required to attain a specified value of Q . Line patterns vary by site index (at base age 25 years): —, 12 m; ---, 18 m; - · -, 24 m.

sites. Stand development is so much slower with SI = 12 m that a stand on such a low-quality site would need an additional 45 years for its trajectory to reach the same value of Q attained at age 45 years by a stand on a site with a

index of 24 m. In contrast, a stand growing on a site with a site index of 18 m would need an additional 15 years.

When the projection length is set to reach a specified average stand diameter instead of a specified age, the converged lines stack according to site index (Figure 1). Mathematically, for a given value of N , smaller diameters are calculated for stands on the poorer sites due to smaller values of mean leaf area per tree, which is a direct result of shorter trees and crown lengths (Equations 5 and 6). The lower leaf areas translate into smaller values of Q and V . Mathematical analysis of the origins of the self-thinning equation, either in terms of mean tree volume or average stand diameter, typically shows a dependence of the intercept of the log-transformed equation on site quality (e.g., Tang et al. 1994, Hamilton et al. 1995, Bi 2001). Verifying such an effect with field data is difficult (Tang et al. 1995, Jack and Long 1996), but it has been shown for loblolly pine grown in South Africa (Strub and Bredenkamp 1985). Various studies indirectly support the idea that site index affects the height of the self-thinning curve through its positive relationship with leaf area index. Hamilton et al. (1995) showed analytically that the intercept of the log-transformed self-thinning equation is a function of leaf area index, and Long and Smith (1990) showed that site index for lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) is correlated with leaf area index. Dean and Long (1985), working with data published by Cannell (1982), found that trees per ha and foliage mass per hectare explained more than 75% of the variation in mean stem weight for five tree genera. If that holds true for other species, by fixing foliage mass at different levels, the regression equation for *Pinus* published by Dean and Long (1985) could reproduce the correlation between the relative height of the size-density trajectories and site index produced by this model.

According to the model, the time course of mean crown length is linearly related to mean distance between surviving trees (Figure 2). Like the size-density trajectories, the lines representing the various initial tree densities converge to common lines stacked according to site quality. The shorter crowns at the wider spacings with decreasing site quality occur due to shorter trees and smaller heights to the middle of the crown (Equations 5 and 6). Literature values of mean crown length and mean intertree distance for loblolly pine lie above and below the line formed with the simulated values (Figure 2). Ordinary least-squares regression through these points produces the equation $CL = 2.7 + 1.0 S_T$, where S_T is the mean intertree distance, which is similar to the equations fit to the simulated data. Linear relationships between mean crown length and intertree distance have also been reported for radiata pine (*Pinus radiata* D. Don) in New Zealand (Beekhuis 1965), Sitka spruce in Wales, UK (*Picea sitchensis* [Bong.] Carr.), and loblolly pine in the western extent of its range in the southern United States (Valentine et al. 1994).

The curved tails at the left end of the lines relating mean crown length to mean intertree distance represent the period of development before stem exclusion as the crown length extends with tree height until canopy closure initiates self-pruning (Figure 2). During this period, the rate change in height exceeds the rate of change in live crown length,

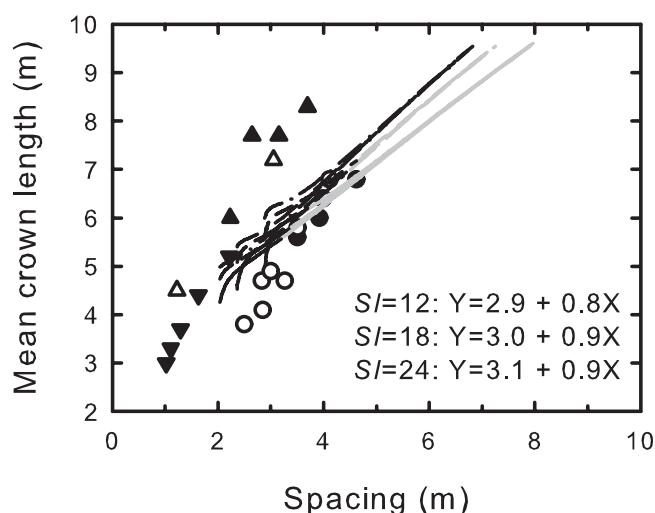


Figure 2. Time course of mean live crown length as a function of mean, intertree distance between surviving trees as calculated with the model. Black lines represent a time interval from $t = 10$ to $t = 45$. Gray lines represent the additional time required to attain a specified value of mean crown length. Line patterns vary by site index: —, 12 m; ---, 18 m; - · -, 24 m. Equations are least-square fits to calculated data by site index. Symbols represent data from previous studies with loblolly pine: ●, Baldwin et al. (2000); ○, Buford (1991); ▲, Harms et al. (1994); △, Will et al. (2010); ▼, Harms and Langdon (1976).

resulting in a rapid decline in the mean live crown ratio, according to the model (Figure 3a). After mean live crown ratio reaches a minimum, it begins to increase slowly with increasing mean live crown length. The minimum live crown ratio probably corresponds to the onset of the stem exclusion phase of stand development as defined by Oliver (1981). As the hypothetical stands develop toward self-thinning, the relationship between live crown ratio and crown length converges for all initial densities within a site index. During this segment of the curves, mean tree height is shorter on the poorer sites and tallest on the best sites for a given value of CL, resulting in the stacking of the converged lines according to site quality (Figure 3a). From the onset of stem exclusion through self-thinning, mean crown length increases nearly 4 m, but different rates of self-pruning and height growth result in only a small increase in mean live crown ratio, from a low of approximately 0.25 to a high of approximately 0.30.

Ford (1982) hypothesized that the culmination of current annual increment in pole-sized Sitka spruce stands occurred during rapid redistribution of foliage in the crowns. The crown relationships calculated with the model appear to support this hypothesis. Whereas Ford (1982) suspected that the production peak was due to positioning of a greater proportion of new, more efficient foliage at the top of the tree during this period, the model suggests that for loblolly pine the culmination of current annual increment is due to a rapid increase in the amount of leverage exerted on the stem (Figure 3b and c). More precisely, the rising edge of the peak in the current annual increment corresponds with the sharp increase in leverage, and the peak value of current annual increment corresponds with the inflection point of the curve between leverage and mean live crown length.

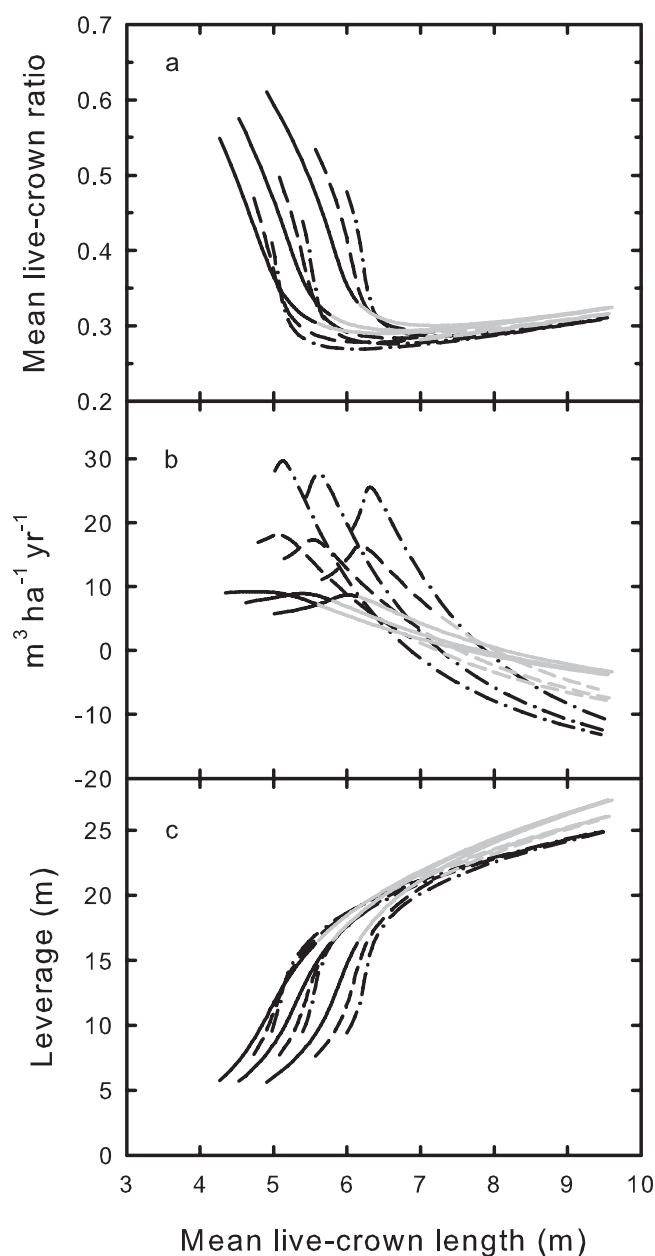


Figure 3. Model calculations of mean live crown ratio (a), current annual increment (b), and height to the median leaf area (leverage) (c) are plotted as a function of mean live crown length through time. Black lines represent a time interval from $t = 10$ to $t = 45$. Gray lines represent the additional time required to attain a specified value of mean live crown length. Line patterns vary by site index: —, 12 m; ---, 18 m; - · -, 24 m.

After this inflection point, current annual increment starts a steady decline although leverage continues to increase. Part of this decline is explained by mortality, but part is also due to the slower basal area increment. According to the analysis conducted by Dean (2004), constant basal area increment requires some minimum rate of increase in the product of leverage and leaf area; below that rate, basal area increment and, presumably, current annual increment will fall.

Values of Q projected with the model increase with age and with increasing site quality (Figure 4a). The resulting curves, however, are concave, indicating that the diameter growth is increasing with age. Although convex curves are

more typical, the projected accumulation of diameter matches the overall pattern in diameter growth observed in the loblolly stands whose data were used to fit Equations 5 and 6 (Figure 4b). According to the model, initial tree density has only a small effect on the value of Q in contrast to the observed density effect on diameter. Equation 13 has no parameter to account explicitly for density: density effects originate from the equations to predict mean tree height and mean height to the middle of the crown (Equations 5 and 6, respectively) that are subsequently used to calculate leverage and leaf area. Apparently, the effects of tree density in the model are insufficient to create the spread of average stand diameter seen in the field data. Whereas Dean et al. (2002) noted that open-grown slash pine trees had higher values of the proportionality constant in the constant-stress model (Equation 1) than slash pine trees grown at higher stand densities in plantations, the bulk of evidence suggests that the source of this error lies in calculating the effect of density on mean crown properties. Both Dean and Long (1986) and Meng et al. (2007) fit Equation 13 to lodgepole trees (512 and 3,480 trees, respectively) and found no bias in the fit due to stand density. Densities in those studies ranged from 530 to 5,600 trees/ha in the first study and from 3 to 93% relative density in the second study. Lundqvist and Elfving (2010) fit the constant-stress model to data from Scots pine (*Pinus sylvestris* L.) that was planted to produce localized ranges of growing space from 0.7 to 1.4 m² and found no density effect on the fit after 14 or 16 years of growth.

MAI calculated with the model follows the classic pattern of culminating at a higher value and an earlier age as site index increases (Figure 5a). The model also indicates that MAI culminates at higher values and earlier ages as initial tree density increases for a given site index. The values calculated with the model fall within the range of the values for the plots whose crown data were fit to Equations 5 and 6, although the shape of the curves differs (Figure 5b). Compared with published values of MAI for loblolly pine, however, the values calculated with this model are high. For example, Hennessey et al. (2004) reported an average MAI for unthinned, 24-year-old loblolly pine stands of 7.5 Mg ha⁻¹ year⁻¹ compared with a calculated value of 14.6 Mg ha⁻¹ year⁻¹. One obvious source for differences between measured and calculated value of MAI is different survival rates. Another source is differences in stem form.

Comparison of model calculations with the published chronology of stand development for a spacing study at Calhoun Experimental Forest in South Carolina suggests that the overestimation of MAI is again due to differences in crown dynamics. Balmer and Jorgensen (1975), Harms and Lloyd (1981), DeBell et al. (1989), and Buford (1991) published plot means of stem and crown metrics for this study at 5-year increments from 15 to 30 years. These data are compared with the values calculated with the model with N_0 set to the surviving trees/ha at age 15 years. The model projects much higher values of MAI through time than the actual values (Figure 6a), nearly twice the value at age 30 years for the plots with the highest tree density. Model projections of survival do not account for the difference because the model predicts lower survival for all plots

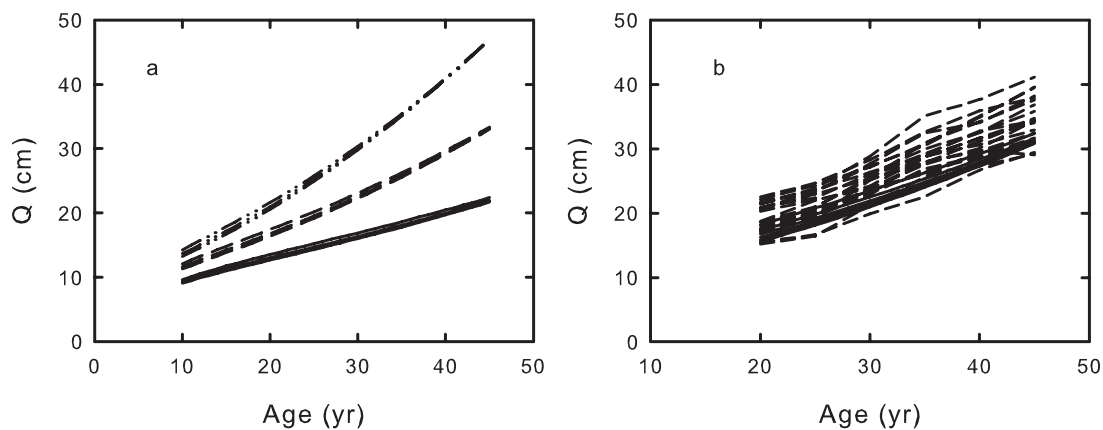


Figure 4. Plots of average stand diameter (Q) with age. (a) Model calculations for initial tree densities of 1,200, 1,800, and 2,400 trees/ha for three site indexes. Line patterns vary by site index: —, 12 m; ---, 18 m; - · -, 24 m. (b) Values from data collected in Louisiana for a growth-and-yield study. Data were selected from plots growing on site indexes between 16 and 18 m. Solid lines are the model calculations of Q with site index = 17 and initial tree densities ranging from 500 to 2,000 trees/ha in increments of 300 trees/ha, spanning the range of tree densities in the growth and yield data at age 20 years.

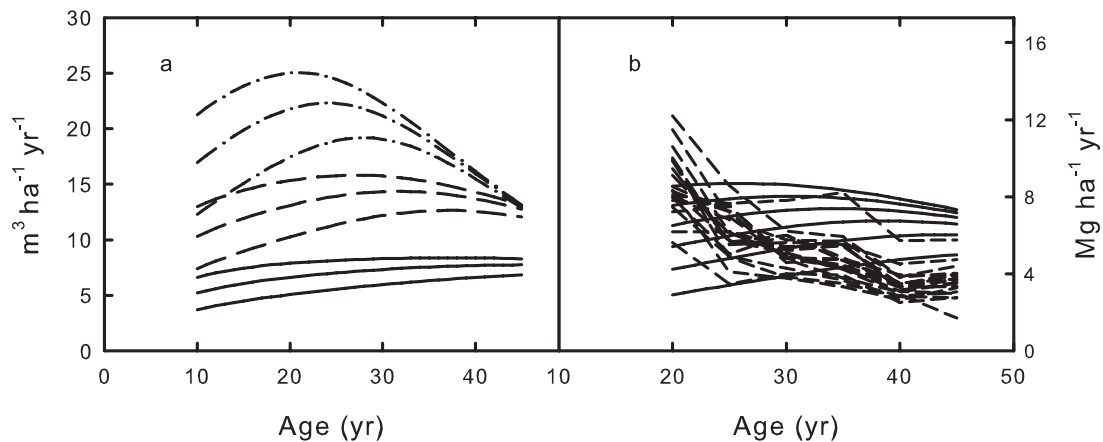


Figure 5. Plots of mean annual increment with age. (a) Model calculations for initial tree densities of 1,200, 1,800, and 2,400 trees/ha for three site indexes. Line patterns vary by site index: —, 12 m; ---, 18 m; - · -, 24 m. (b) Values from data collected in Louisiana for a growth-and-yield study. Data were selected from plots growing on site indexes between 16 and 18 m. Solid lines are the model calculations of Q with site index = 17 with initial tree densities ranging from 500 to 2,000 trees/ha in increments of 300 trees/ha, spanning the range of tree densities in the growth and yield data at age 20 years.

than was measured (Figure 6b). The discrepancy in calculated and measured values of Q would seem to account for the differences in the calculated and measured values of MAI because the model tends to underestimate average stand diameter at young ages and overestimate it at older ages (Figure 6c). This results in increasing overestimates of mean stem volume with average stand diameter (Figure 6d). Because the calculated values of mean tree height agree well with measured values of mean tree height with the exception of one spacing (Figure 6e), the overestimation would seem to arise from the constant-stress model overestimating D_h . This theory seems unlikely, however. When comparing the predicted and actual stem diameter, Dean et al. (2002) found that the constant-stress model produced unbiased estimates of D_h for 70% of the stem length for 30 loblolly trees ranging in height from 11 to 26 m. The model overestimated stem diameters in the upper 20% of the stem and 10% of the lower stem by approximately 20%: not enough, however, to account for the large discrepancy be-

tween calculated and measured values of MAI. Furthermore, with the published crown information for the last two measurement periods, calculated values of Q were on average only 5% larger than the corresponding field values (Figure 6f). Regional differences in the effect of tree density on vertical crown dimensions could cause the model to overestimate stem diameter and stem growth. Data on crown length collected over a wider region may produce a more general characterization of the effect of stand density on crown length and improve the accuracy in predicting average stand diameter and volume with this model.

Silviculturists work under the assumption that density and site quality effects on stand growth can be traced to canopy dynamics (Larson 1963, Long et al. 2004). The model presented here uses simple beam theory to connect canopy dynamics with stand growth by calculating the cross-sectional area needed to counteract the bending stress caused by wind sway. Overall, the model recreates developmental patterns of loblolly pine stands quite well.

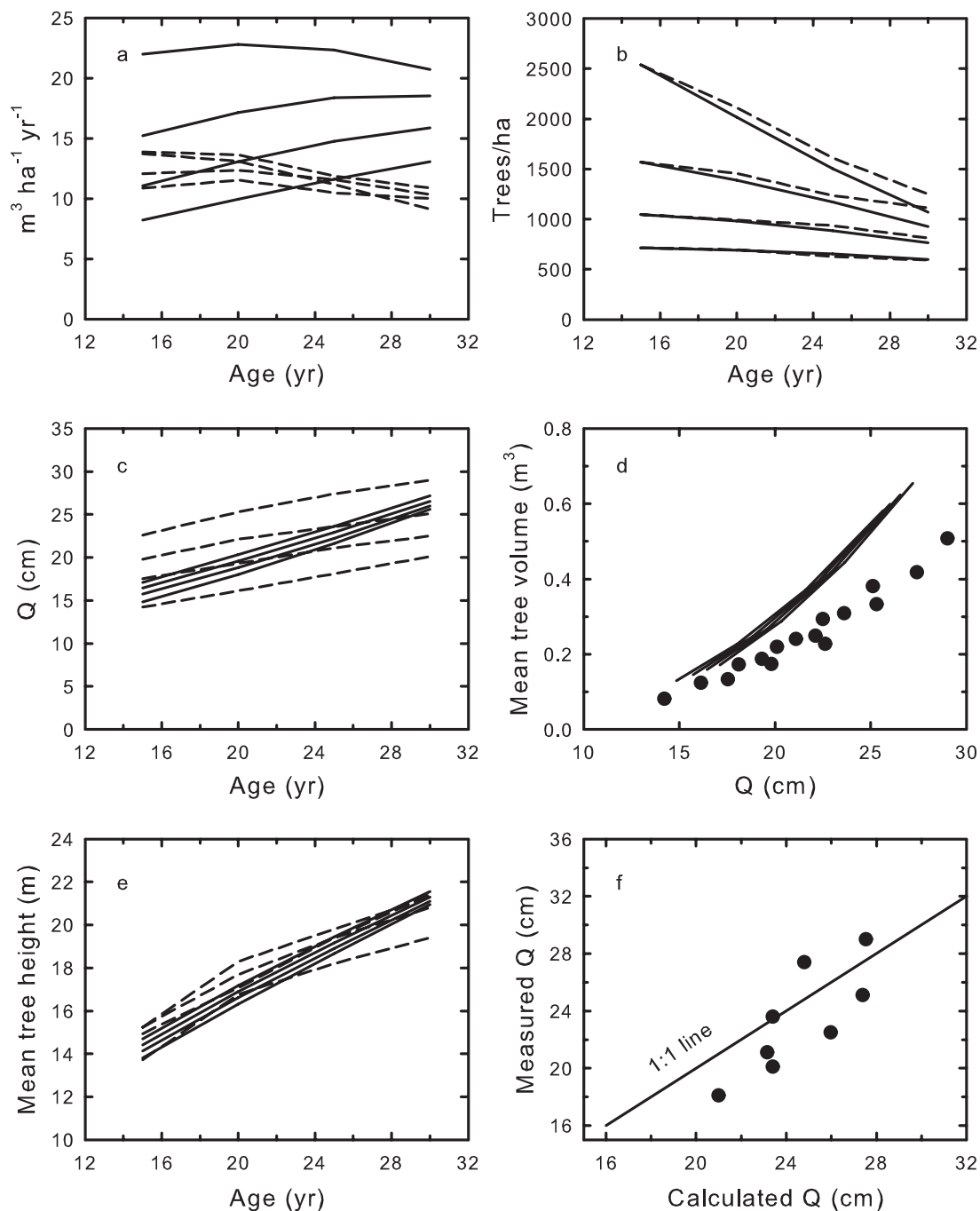


Figure 6. Model comparisons with data collection from a spacing study at the Calhoun Experimental Forest in South Carolina. Plots of mean annual increment (a), survival (b), average stand diameter (c), and mean tree height (e) with age are shown. —, model calculations; ---, field data. d. Calculated values of mean tree volume as a function of calculated values of average stand diameter. ●, field data. (f) Scattergram of field values of average stand diameter (Q) as a function of values of Q calculated with the constant-stress model (Equation 17) using field values of leverage and predicted leaf area. Predicted leaf area was calculated with Equation 11 using field values of mean tree height and mean live crown length.

Discrepancies between model simulations and field data were most severe where observed canopy dynamics did not match simulated dynamics. The most uncertain component of the model is simulating average crown length without stem diameter as a predictor variable. We analyzed several approaches including the tree-spacing approach of Valentine et al. (1994), but the best approach based on fit and model stability was to calculate crown length from mean

height to the middle of live crown predicted from age, site index, and trees/ha (Equation 6). This equation did not represent the full range of possible tree density effects on the crown dimensions of loblolly pine, however, because of the data available to fit the model. The overall accuracy of the model is likely to be improved with data from a geographic region larger than the western Gulf region of the United States. Other possible modifications to the model

include calculating merchantable volume because stem diameter is calculated every 0.1 m of stem height and incorporating thinning effects because thinning temporarily fixes the bottom of the crown.

Literature Cited

- ABER, J.D., AND C.A. FEDERER. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92(4):463–474.
- BALDWIN, V.C., AND D.P. FEDUCCIA. 1987. *Loblolly pine growth and yield prediction of managed West Gulf plantations*. USDA For. Serv., Res. Paper SO-236. 27 p.
- BALDWIN, V.C., K.D. PETERSON, A. CLARK, R.B. FERGUSON, M.R. STRUB, AND D.R. BOWER. 2000. The effects of spacing and thinning on stand and tree characteristics of 38-year-old loblolly pine. *For. Ecol. Manage.* 137(1–3):91–102.
- BALMER, W.E., AND J.R. JORGENSEN. 1975. *Effects of various spacings on loblolly pine growth 15 years after planting*. USDA For. Serv., Res. Note SE-211. 8 p.
- BEEKHUIS, J. 1965. Crown depth of radiata pine in relation to stand density and height. *N. Z. J. For.* 10:43–61.
- BI, H. 2001. The self-thinning surface. *For. Sci.* 47:361–370.
- BUFORD, M.A. 1991. Performance of 4 yield models for predicting stand dynamics of a 30-year-old loblolly pine (*Pinus taeda* L.) spacing study. *For. Ecol. Manage.* 46(1–2):23–38.
- CANNELL, M.G.R. 1982. *World forest biomass and primary production data*. Academic Press, San Francisco, CA. 391 p.
- CAO, Q.V., AND T.J. DEAN. 2008. Using segmented regression to model the density-size relationship in direct-seeded slash pine stands. *For. Ecol. Manage.* 255(3–4):948–952.
- CAO, Q.V., T.J. DEAN, AND V.C. BALDWIN JR. 2000. Modeling the size-density relationship in direct-seeded slash pine stands. *For. Sci.* 46(3):317–321.
- CROPPER, W.P., AND H.L. GHOLZ. 1993. Simulation of the carbon dynamics of a Florida slash pine plantation. *Ecol. Model.* 66(3–4):231–249.
- DEAN, T.J. 1991. Effect of growth rate and wind sway on the relation between mechanical and water-flow properties in slash pine seedlings. *Can. J. For. Res.* 21(10):1501–1506.
- DEAN, T.J. 2004. Basal area increment and growth efficiency as functions of canopy dynamics and stem mechanics. *For. Sci.* 50(1):106–116.
- DEAN, T.J., AND V.C. BALDWIN. 1996. The relationship between Reineke's stand-density index and physical stem mechanics. *For. Ecol. Manage.* 81(1/3):25–34.
- DEAN, T.J., AND J.N. LONG. 1985. Response of self-thinning to artificially reduced levels of leaf area in monocultures of *Trifolium pratense*. *Ann. Bot.* 55:361–366.
- DEAN, T.J., AND J.N. LONG. 1986. Validity of constant-stress and elastic instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. *Ann. Bot.* 54:833–840.
- DEAN, T.J., AND J.N. LONG. 1992. Influence of leaf area and canopy structure on size-density relations in even-aged lodgepole pine stands. *For. Ecol. Manage.* 49:109–117.
- DEAN, T.J., S.D. ROBERTS, D.W. GILMORE, D.A. MAGUIRE, J.N. LONG, K.L. O'HARA, AND R.S. SEYMOUR. 2002. An evaluation of the uniform stress hypothesis based on stem geometry in selected North American conifers. *Trees* 16(8):559–568.
- DEBELL, D.S., W.R. HARMS, AND D. WHITSELL. 1989. Stockability: A major factor in productivity differences between *Pinus taeda* in Hawaii and the southeastern United States. *For. Sci.* 35(3):708–719.
- FORD, E.D. 1982. High productivity in a pole stage Sitka spruce stand and its relation to canopy structure. *Forestry* 55(1):1–17.
- FIGUEIREDO FILHO, A., S.A. MACHADO, AND M.R.A. CARNEIRO. 2000. Testing accuracy of log volume calculation procedures against water displacement techniques (xylometer). *Can. J. For. Res.* 30(6):990–997.
- HAMILTON, N.R.S., C. MATTHEW, AND G. LEMAIRE. 1995. In defense of the $-3/2$ boundary rule: A re-evaluation of self-thinning concepts and status. *Ann. Bot.* 76(6):569–577.
- HARMS, W.R., D.S. DEBELL, AND C.D. WHITESSELL. 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. *Can. J. For. Res.* 24:511–521.
- HARMS, W.R., AND O.G. LANGDON. 1976. Development of loblolly pine in dense stands. *For. Sci.* 22(3):331–337.
- HARMS, W.R., AND F.T. LLOYD. 1981. Stand structure and yield relationships in a 20-year-old loblolly pine spacing study. *South. J. Appl. For.* 5(3):162–166.
- HENNESSEY, T.C., P.M. DOUGHERTY, T.B. LYNCH, R.F. WITTWER, AND E.M. LORENZI. 2004. Long-term growth and ecophysiological responses of a southeastern Oklahoma loblolly pine plantation to early rotation thinning: Long-term production dynamics of loblolly pine stands in the southern United States. *For. Ecol. Manage.* 192(1):97–116.
- JACK, S.B., AND J.N. LONG. 1991. Analysis of stand density effects on canopy structure—A conceptual approach. *Trees* 5(1):44–49.
- JACK, S.B., AND J.N. LONG. 1996. Linkages between silviculture and ecology: An analysis of density management diagrams. *For. Ecol. Manage.* 86(1–3):205–220.
- JACOBS, M.R. 1954. The effect of wind sway on the form and development of *Pinus radiata* D. Don. *Aust. J. Bot.* 2(1):35–51.
- JEREZ, M., T.J. DEAN, Q.V. CAO, AND S.D. ROBERTS. 2005. Describing leaf area distribution in loblolly pine trees with Johnson's SB function. *For. Sci.* 51:93–101.
- JOKELA, E.J., R.B. HARDING, AND C.A. NOWAK. 1989. Long-term effects of fertilization on stem form, growth relations, and yield estimates of slash pine. *For. Sci.* 35(3):832–842.
- LANDSBERG, J.J., AND R.H. WARING. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95(3):209–228.
- LARSON, P.R. 1963. *Stem form development of forest trees*. Forest Science Monograph 5. 42 p.
- LONG, J.N. 1985. A practical approach to density management. *For. Chron.* 61:23–27.
- LONG, J.N., T.J. DEAN, AND S.D. ROBERTS. 2004. Linkages between silviculture and ecology: Examination of several important conceptual models. *For. Ecol. Manage.* 200(1–3):249–261.
- LONG, J.N., AND F.W. SMITH. 1990. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: The influence of site quality and stand structure. *J. Appl. Ecol.* 27(3):847–856.
- LUNDQVIST, L., AND B. ELFVING. 2010. Influence of biomechanics and growing space on tree growth in young *Pinus sylvestris* stands. *For. Ecol. Manage.* 260(12):2143–2147.
- MATTHECK, C. 2000. Comments on "Wind-induced stresses in cherry trees: Evidence against the hypothesis of constant stress levels" by K.J. Niklas, H.-C. Spatz, *Trees* (2000) 14:230–237. *Trees* 15:63.
- MCMURTRIE, R., AND L. WOLF. 1983. Above- and below-ground growth of forest stands: A carbon budget model. *Ann. Bot.* 52:437–448.
- MENG, S.X., V.J. LIEFFERS, D.E.B. REID, M. RUDNICKI, U. SILINS, AND M. JIN. 2006. Reducing stem bending increases the height growth of tall pines. *J. Exp. Bot.* 57(12):3175–3182.

- MENG, S.X., V.J. LIEFFERS, AND S. HUANG. 2007. Modeling crown volume of lodgepole pine based upon the uniform stress theory. *For. Ecol. Manage.* 251(3):174–181.
- METZGER, K. 1893. Der Wind als massgebender Faktor für das Wachstum der Bäume. *Mündener Forstliche Hefte* 3:35–86.
- MORGAN, J., AND M.G.R. CANNELL. 1994. Shape of tree stems—A re-examination of the uniform stress hypothesis. *Tree Physiol.* 14(1):49–62.
- NIKLAS, K.J., AND H.C. SPATZ. 2000. Wind-induced stresses in cherry trees: Evidence against the hypothesis of constant stress levels. *Trees* 14(4):230–237.
- OLIVER, C.D. 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3:153–168.
- ROBERTS, S.D., T.J. DEAN, AND D.L. EVANS. 2003. Family influences on leaf area estimates derived from crown and tree dimensions in *Pinus taeda*. *For. Ecol. Manage.* 172:261–270.
- ROBERTS, S.D., A.L. FRIEND, AND P.D. GERARD. 2004. The effect of large applications of nutrients from organic waste on biomass allocation and allometric relations in loblolly pine. P. 398–402 in *12th Biennial southern silvicultural research conference*, Connor, K.F. (ed.). USDA For. Serv., Gen. Tech. Rep. SRS-71.
- SHINOZAKI, K., K. YODA, K. HOZUMI, AND T. KIRA. 1964. A quantitative analysis of plant form—The pipe model theory. I. Basic analysis. *Jpn. J. Ecol.* 14(3):97–105.
- SMITH, N.J., AND D.W. HANN. 1986. A growth model based on the self-thinning rule. *Can. J. For. Res.* 16(2):330–334.
- STRUB, M.R., AND B.V. BREDENKAMP. 1985. Carrying capacity and thinning response of *Pinus taeda* in the CTT experiments. *S. Afr. For. J.* 2:6–11.
- TANG, S., C.H. MENG, F.-R. MENG, AND Y.H. WANG. 1994. A growth and self-thinning model for pure even-age stands: Theory and applications. *For. Ecol. Manage.* 70(1–3):67–73.
- TANG, S., F.-R. MENG, AND C.H. MENG. 1995. The impact of initial stand density and site index on maximum stand density index and self-thinning index in a stand self-thinning model. *For. Ecol. Manage.* 75(1–3):61–68.
- VALENTINE, H.T. 1988. A carbon-balance model of stand growth: A derivation employing pipe-model theory and the self-thinning rule. *Ann. Bot.* 62(4):389–396.
- VALENTINE, H.T., A.R. LUDLOW, AND G.M. FURNIVAL. 1994. Modeling crown rise in even-aged stands of Sitka spruce or loblolly pine. *For. Ecol. Manage.* 69(1–3):189–197.
- VALENTINE, H.T., AND A. MÄKELÄ. 2005. Bridging process-based and empirical approaches to modeling tree growth. *Tree Physiol.* 25(7):769–779.
- VALINGER, E. 1992. Effects of wind sway on stem form and crown development of Scots pine (*Pinus sylvestris* L.). *Aust. For.* 55:15–21.
- WEST, P.W., D.R. JACKETT, AND S.J. SYKES. 1989. Stresses in, and the shape of, tree stems in forest monoculture. *J. Theor. Biol.* 140(3):327–343.
- WILL, R., T. HENNESSEY, T. LYNCH, R. HOLEMAN, AND R. HEINEMANN. 2010. Effects of planting density and seed source on loblolly pine stands in southeastern Oklahoma. *For. Sci.* 56(5):437–443.