
Basal Area Increment and Growth Efficiency as Functions of Canopy Dynamics and Stem Mechanics

Thomas J. Dean

ABSTRACT. Crown and canopy structure correlate with growth efficiency and also determine stem size and taper as described by the uniform stress principle of stem formation. A regression model was derived from this principle that expresses basal area increment in terms of the amount and vertical distribution of leaf area and change in these variables during a growth period. This model was fit to data collected from five studies analyzing various effects of cultural practices, atmospheric deposition, and stand density on the growth of loblolly pine (*Pinus taeda*), slash pine (*P. elliottii*), or lodgepole pine (*P. contorta*). For both southern pines, the model was fit to individual-tree data and plot totals measured on 1- to 4-yr-old trees and from 12- to 20-yr-old trees. The model was also fit to data measured on approximately 90-yr-old lodgepole pine trees in northern Utah. The model explained an average of 85% of the variation in individual-tree basal area increment and an average of 86% of variation in gross basal area increment per hectare. By comparison, leaf area alone explained an average of 54% of the variation in the increment of individual-tree stem volume and an average of 50% of the gross increment in stem volume per hectare. The value of the exponent in the model implicates stem mechanics in stem growth, and fitted exponents were all within 7% of the exponent derived from the uniform stress model. Isolines of basal area increment and basal area growth efficiency based on fitted equations indicate that increments in the product of leaf area and height to center of leaf area must increase yearly for either basal area increment or growth efficiency to be constant with age. *FOR. SCI.* 50(1):106–116.

Key Words: Leaf area, growth, wood properties, stem mechanics, uniform stress principle.

THE EQUATION $I = A \cdot E$, where I = stem increment, A = leaf area, and E = leaf area efficiency is a perfect description of growth, because E is calculated as I/A . But while the equation is a simple identity, analyzing the relationships between leaf area, stem increment, and stem increment per unit leaf area has produced many

useful insights into the ecology and management of forests, especially regarding efficient canopy structures (Assmann 1970, p. 121, Waring 1983, Dean et al. 1988, Long and Smith 1990, Colbert et al. 1990, Jack and Long 1991, Kuuluvainen and Kanninen 1992, Roberts et al. 1993, McCrady and Jokela 1998,).

Thomas J. Dean, Associate Professor, School of Renewable Natural Resources, LSU AgCenter, Baton Rouge, LA 70803—Phone: 225-578-4216; Fax: 225-578-4227; E-mail: fwdean@lsu.edu.

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In addition to affecting growth efficiency, crown and canopy structure appear to determine the size and geometry of stems in a manner generally consistent with shapes that uniformly distribute bending stress along their length (Dean et al. 2002). The equation describing this relationship was originally termed the constant stress model (Dean and Long 1986a) but is more appropriately named the uniform stress model (Morgan and Cannell 1994). It is based on the flexure formula, which calculates bending stress due to a force applied to a simple cylindrical beam, the leverage exerted by the force, and the diameter of the beam. The resulting equation relates stem geometry to leaf area and the vertical distribution of leaf area:

$$D_h = a(A_h S_h)^{1/3} \quad (1)$$

where D_h is stem diameter at height h , a is a constant, A_h is leaf area above height h , and S_h is the distance between height h and the center of leaf area above height h (Dean and Long 1986a). Because the cambium exhibits localized responses to such factors as wounding and growth stresses (Kuroda and Shimaji 1984, Kubler 1998), Equation (1) is a tree-level, summary description of stem diameter subject to the following constraints from a theoretical basis: (1) it represents an equilibrium condition and does not apply when A_h is reduced by disease, herbivory, drought, or pruning; (2) deflections produced by wind drag on the foliage must be small so that gravitational effects on bending stress are negligible; (3) vertical wind profiles must be uniform; and (4) the stem is rigidly anchored in the ground. Despite these constraints, Dean et al. (2002), in a survey of nine, commercially important, coniferous species in North America, found that with the exception of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), stem taper as defined by the exponent in Equation (1) was generally within 15% of the theoretical exponent, 0.33—most of the fitted exponents were within 10% of the theoretical exponent. Dean et al. (2002) found that a 10% deviation in a fitted exponent from the theoretical value translated into less than a 10% difference between measured stem diameter and the expected diameter under the uniform stress principle for most of the stem.

Since leaf area and the vertical distribution of leaf area adequately define stem diameter, changes in leaf area and height to the center of leaf area should also define diameter increment, and thus, the change in cross-sectional area at any stem height h . By setting h to either 1.37 or 0 m for breast height or groundline, Equation (1) describes the combined effect of whole-tree leaf area and the height to the center of that leaf area on diameter at breast height or groundline diameter, respectively. An equation describing the effects of leaf area and its distribution on basal area at either of these stem heights is produced by substituting Equation (1) for diameter in the equation for the area of a circle:

$$B = (a\pi/4) \cdot (AS)^{0.67}, \quad (2)$$

where B is basal area at $h = 1.37$ or 0 m, π is 3.14, A is total leaf area per tree, and S is the distance between h and the height to the center of leaf area. Discrete increments in the

product of leaf area and the distance between h and height to the center of leaf area will result in discrete increments in basal area according to the equation

$$\Delta B = (a\pi/4) \left(\left((A_0 \cdot S_0) + \Delta(A \cdot S) \right)^{0.67} - (A_0 \cdot S_0)^{0.67} \right), \quad (3)$$

where ΔB is basal area increment at $h = 1.37$ or 0 m during the growth interval, A_0 and S_0 = total leaf area and distance between h and height to the center of leaf area, respectively, at the beginning of the growth interval, and $\Delta(A \cdot S)$ is the increment in the product of total leaf area and distance between h and height to center of leaf area during the growth interval. Since the vertical distribution of leaf area is strongly related to crown structure, Equation (3) is a single equation that expresses stem growth in terms of leaf area and the predominant factor known to affect growth efficiency.

The primary objective of this study is evaluate the uniform stress principle of stem formation as a basis for describing basal area increment by fitting a regression model based on Equation (3) to permanent-plot data collected for three important species of pine: loblolly pine (*Pinus taeda* L.), slash pine (*Pinus elliottii* var. *elliottii* Engelm.), and lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.). The studies for which these data were collected were designed to detect various treatment effects on growth providing the additional opportunity to determine how treatments or growing conditions might affect the ability of the uniform stress principle to account for basal area increment. To contribute to the understanding of stem growth, a growth equation based on stem mechanics should be able to explain a greater proportion of growth than the more common approaches based on the equation $I = A \cdot E$. Therefore, the secondary objective of this study was to compare the explanatory power of the uniform stress principle in accounting for basal area increment to the power of leaf area alone in accounting for stem volume increment. The implications of Equation (3) in regards to canopy dynamics, stem growth, and growth efficiency are explored based on the results of this analysis.

Methods and Materials

Data

Data from five studies with loblolly pine, slash pine, or lodgepole pine are used in this analysis (Table 1). These studies were established for a variety of objectives, but each had recorded measurements for calculating basal area, stem volume, leaf area, and height to the center of leaf area from two to six times on the same trees at various intervals. The objectives and site descriptions of these studies have been published previously. In the studies from the Cooperative Research in Sustainable Silviculture and Soil Productivity (CRiSSSP) and the Forest Response Program (FRP) described by Carter et al. (2002) and Dean and Johnson (1992), respectively, seedlings were planted at a fixed spacing in plots and subjected to various cultural or air quality treatments. Loblolly pine was planted in the CRiSSSP studies, and slash pine was planted in the FRP study. In the studies from Lee Forest described by Dicus and Dean (1999), loblolly

Table 1. Sources and summary descriptions of the data sets used in this study.

Species	Name of study	Descriptive citation	Location	Ages measured (yr)	Typical measurement interval
Loblolly pine	Cooperative Research in Sustainable Silviculture and Soil Productivity (CRiSSSP) Lee Forest	Carter et al. (2002)	Fred, Texas & Pine Grove, Louisiana	1–4	Annually
		Dicus and Dean (1999)	Pine, Louisiana	12–17	Annually
Slash pine	Forest Response Program (FRP) Woodworth	Dean and Johnson (1992)	Gainesville, Florida	2–3	Monthly
		Baldwin et al. (1995)	Woodworth, Louisiana	17–22	Annually
Lodgepole pine	Utah study	Dean et al. (1988)	Logan, Utah	~80–95	16 yr

pine seedlings were planted at two spacings. In the study from Woodworth, Louisiana, described by Baldwin et al. (1995), slash pine seedlings were planted at a range of spacings then thinned to a common level of growing stock when the trees were 17 yr old. The site for the Utah study was described by Dean et al. (1988), and data for this study were collected within an area of even-aged monocultures of lodgepole pine that had naturally regenerated, probably following a stand replacing fire.

The data from the CRiSSSP studies were collected at the sites located at Fred, Texas, and Pine Grove, Louisiana. At both locations, plots were assigned to blocks according to topography and surface drainage, and factorial combinations of treatments were randomly assigned to the plots. A harvesting-impact treatment and a bedding treatment were common at both sites. The two levels of harvesting-impact consisted of high and minimum disturbance methods. The high-disturbance method involved cutting trees with a mechanical feller-buncher and dragging them to the landing with a rubber-tired, grapple skidder. The minimal-disturbance method consisted of felling trees with chainsaws, limbing and topping them in place, and lifting the commercially valuable portion of the bole from the plot before taking the log to the landing. The high-disturbance method removed large amounts of organic matter from the site and in many cases, compacted the soil as a result of machine traffic on the site. Minimum-disturbance harvesting removed the least amount of organic matter possible and avoided soil compaction associated with machine traffic. The two levels of bedding were bedding and no bedding. Two levels of fertilization were included in the study at Fred, Texas: no fertilization and broadcast application of diammonium phosphate at a rate of 250 kg/ha. Two levels of weed control were included in the study at Pine Grove, Louisiana: no control and application of a mixture of imazapyr and sulfometuron (0.25 kg/ha active ingredient of each) sprayed over the top of the seedlings three months after planting. Prior to planting at both locations, mixtures of imazapyr and either glyphosate or tricopyr were applied at site preparation rates.

The data from the FRP study were collected between 1988 and 1990 from an open-top chamber study near Gainesville, Florida, investigating the effects of factorial combinations of acidic precipitation and ozone concentration on select families of slash pine. Data from only one family are used in this study. Three levels of acidic pre-

cipitation were produced by adding a mixture of sulfuric and nitric acid at a respective 70:30 ratio to purified water to produce pH values of 3.3, 4.3, and 5.3. Rain water was simulated with the addition of various background ions. The pH level of 4.3 was considered ambient for the area at the time of the study. Ambient rain was excluded from the seedlings, and the simulated rain applied at periodic, controlled rates. The four levels of ozone exposure in the study were carbon-filtered air (to minimize ozone exposure), ambient concentration, and two-times and three-times ambient concentrations produced with real-time control procedures (Dean and Johnson 1991).

The study at Lee Memorial forest, located approximately 20 km west of Bogalusa, Louisiana, was part of a species-spacing trial established in 1981. The data used in this study were collected from plots planted with loblolly pine at initial spacings of 1.2 and 2.4 m. Competing vegetation was not controlled in the four plots used in this study until 1992. The study at Woodworth, Louisiana, was planted at range of initial spacings in 1977 with slash pine, and competing vegetation controlled with fire. When the trees were 17 yr old, the original objective of this study to follow the growth and yield of slash pine was expanded when the plots were thinned to investigate the effects of initial spacing on thinning response.

The lodgepole pine data collected in Utah were originally part of an analysis of stem volume increment, growth efficiency, leaf area, and canopy structure (Dean et al. 1988). Trees were initially measured in 1984—trees in four of the plots were remeasured in 2000.

Stem diameter (either breast height or at ground line), total tree height, and height to the base of the live crown were measured in each study monthly or annually, with the exception of lodgepole pine (Table 1). If the live crown extended below breast height, groundline diameter was measured. Basal area increment was calculated for each tree in the plot. Leaf area per tree was calculated with locally developed equations for the CRiSSSP, FRP, Lee Forest, and Utah studies (Table 2). For the Woodworth study, foliage mass per tree was calculated with published equations for slash pine and converted to projected leaf area with a specific leaf area of 3.57 m²/kg. Height to the center of leaf area for each tree was assumed to be the vertical midpoint of the live crown and was calculated as the midpoint between the base of the live crown and total tree height. Stem volume was calculated for

Table 2. Equations for calculating projected leaf area (A , m^2) and total stem volume (V , m^3) for the studies used in this analysis.

Study	Leaf area		Stem volume	
	Equation	Reference	Equation	Reference
CRiSSSP				
Fred	$A = 0.000738 D^{1.8091} Ht^{0.9916} + 0.7321 H - 0.1996 F + 1.0813 B^*$	Local equation	$V = 8.3192 (D/1000)^{1.1849} Ht^{1.9342} \dagger$	Local equation
Pine Grove	$A = 0.0043 D^{1.581} Ht^{0.2068} - 0.0054 H - 0.0200 W - 0.00234 B^{\dagger\dagger}$	Local equation	$V = 1.8235 (D/1000)^{0.7449} Ht^{1.0763}$	Local equation
Lee Forest	$A = 0.0289 dbh^{2.6514} / Ht^{0.4201} \S$	Local equation	$V = 0.3091 (dbh/100)^{1.8672} Ht^{0.9686}$	Local equation
FRP	$A = (A_s/g)^f (1/S)^{\parallel}$	Dean and Johnson (1992)	$V = a D^b Ht^c \#$	Dean and Johnson (1992)
Utah	$A = 0.028 (A_s)^{1.56} / S^{0.74}$	Dean and Long (1986b)	$V = 0.0029 + 0.103 (dbh/100)^{1.773} Ht^{1.305}$	Dean et al. (1988)
Woodworth**	$A = 3.57 (0.454) (3.055 dbh^{3.321} Ht^{1.251})$	Lohrey (1984)	$V = (0.0283) (0.00445 dbh^{2.072} Ht^{1.136})$	Lohrey (1985)

* D = groundline diameter (mm); Ht = total height (m); H , F , and B = indicator variables for harvesting impact, fertilization, and bedding, respectively.
 † V for the CRiSSSP and FRP studies expressed in terms of liters; otherwise V is in m^3 .
 †† W = indicator variable for bedding.
 § dbh = diameter at breast height (cm).
 ‖ A_s = sapwood cross-sectional area (cm^2); g and f = treatment and age-specific constants.
 # a , b , and c = treatment and age-specific constants.
 ** dbh and Ht in inches and feet, respectively.

each tree in a plot from stem diameter and tree height using either locally derived or published equations (Table 2).

In addition to the wide range of ages included in this study, a wide range of tree and plot characteristics were included in this study (Table 3). The mean diameter of individual tree stems from the various studies ranged from 30 to 183 mm, and mean heights ranged from 2.1 to 17.8 m. For the plot-based studies, quadratic mean diameter ranged from 134 to 216 mm, and mean tree density ranged from 422 to 2031 trees/ha.

Analysis

The ability of the uniform stress principle to account for basal area increment was determined by analyzing the fit of the following regression model to the various datasets:

$$\Delta B = \left(\beta_0 + \sum_{j=1}^k (\beta_{j+2} \cdot I_j) \right) \times \left(((A_0 \cdot S_0) + \Delta(A \cdot S))^{\beta_1} - (A_0 \cdot S_0)^{\beta_2} \right) \quad (4)$$

where, $\beta_0 - \beta_{k+2}$ are regression coefficients, $I_j - I_k$ are indicator variables representing the simple effects for the various treatments or initial spacings included in the different studies (Table 4), and k is the number of indicator variables needed to represent the effects analyzed for the various studies. To simplify the analysis, indicator variables are only added to the constant of the uniform stress model. This seems justified because according to the analysis of Dean et al.

Table 3. Summary statistics for basic tree and stand characteristics of the data used in this study.

Study	h	D_h^*				H_t^\dagger				$H_{lc}^{\dagger\dagger}$				Leaf area			Tree density			ΔB_h^\S		
		\bar{x}	Quantile			\bar{x}	Quantile			\bar{x}	Quantile			\bar{x}	Quantile		\bar{x}	Quantile		\bar{x}	Quantile	
			10	90		10	90		10	90		10	90		10	90		10	90		10	90
Tree-level	(m)	(mm)				(m)				(m)				(m ²)			(n/a)			(mm ²)		
CRiSSSP	0	30	6	60	2.5	0.4	5.6	0.5	0.0	1.2	2.2	0.0	5.8				1,069	85	2670			
Lee Forest	1.37	116	67	172	12.3	9.5	14.9	7.9	6.0	9.6	8.1	1.7	17.8				782	0	1996			
FRP	0	47	27	76	2.1	1	3.7	0.2	0.0	0.3	1.7	0.3	4.2				263	75	566			
Utah	1.37	183	98	272	17.8	13	22.3	13.4	10.9	15.6	18.7	1.4	44.6				591	81	1236			
Stand-level	(m)	(mm)				(m)				(m ² /m ²)				(trees/ha)			(m ² /ha)					
Lee Forest	1.37	134	101	173	12.9	11.3	14.5	7.8	6.4	9.1	1.6	1.2	1.9	2031	837	3662	1.60	0.16	3.07			
Woodworth	1.37	216	170	267	18.2	16.5	20.1	10.8	9.2	11.9	1.5	0.3	2.4	422	140	630	1.16	0.70	1.75			

* Stem diameter at height h on the stem. With the exception of the CRiSSSP and FRP, studies where h = ground line, h = 1.37.
 † Total tree height.
 †† Height to the base of the live crown.
 § Annual periodic basal area increment.

Table 4. Description of indicator variables (I_j) used in the regression models for this analysis. The implied control when all $I_j = 0$ is indicated.

Study	Treatment type	Indicator variable						Implied control
		I_1	I_2	I_3	I_4	I_5	I_6	
CRiSSSP	Cultural treatment	Harvest	Fertilization	Herbaceous weed control	Bedding			n/a
Lee Forest	Initial spacing	2.4 × 2.4 m						1.2 × 1.2 m
FRP	Ozone exposure and rain pH	Carbon filtered	2 × ambient [O ₃]	3 × ambient [O ₃]	3.3 pH rain	5.3 pH rain		Ambient -3.3 pH rain
Utah	n/a							n/a
Woodworth	Initial spacing	1.2 × 1.8 m	1.8 × 1.8 m	1.8 × 2.4 m	2.4 × 2.4 m	3.1 × 3.1 m	4.3 × 4.3 m	1.2 × 1.2 m

(2002), the exponent in the uniform stress model [Equation (1)] is only minimally affected by species and growing conditions. Treatment interactions were not included in Equation (4). The explanatory power of Equation (4) to account for variation in basal area increment was compared to the percentage of variation in stem volume increment explained by leaf area alone by fitting the following regression model to the various datasets:

$$\Delta V = \left(\gamma_0 + \sum_{j=1}^k (\gamma_{j+1} \cdot I_j) \right) \cdot A_0^{\gamma_1}, \quad (5)$$

where ΔV = stem volume increment, A_0 = initial leaf area, $\gamma_0 - \gamma_{k+1}$ = regression coefficients, and I_j = indicator variables for the k number of treatments included the studies.

Equations (4) and (5) were fit to individual-tree data from all of the studies used in this analysis. For the Lee Forest and Woodworth studies, the equations were fit to plot-level summations of individual-tree values expressed as per hectare equivalents (*c.f.*, Dean 2001). Plot values are gross values of ΔB , ΔV , and $\Delta(A \cdot S)$.

Table 5. Fit index, fitted coefficients, and significant coefficients for indicator variables for the various data sets used to fit the nonlinear regression model

$$\Delta B = \left(\beta_0 + \sum_{j=1}^k (\beta_{j+2} \cdot I_j) \right) \cdot \left((A_0 \cdot S_0) + \Delta(A \cdot S) \right)^{\beta_1} - (A_0 \cdot S_0)^{\beta_2},$$

where ΔB = basal area increment, A_0 and S_0 = initial leaf area and distance between h and height to the center of leaf area at the beginning of the growth period, $\Delta(A \cdot S)$ = change in the product of leaf area and the height to the center of leaf area during the growth period, $\beta_0 - \beta_{k+2}$ = regression coefficients, I_j = indicator variables for the k number of treatments included in the study. h is stem height where basal area is measured (0 m for the CRiSSSP and FRP studies; 1.37 m otherwise). For plot-level studies, the values of ΔB and $\Delta(A \cdot S)$ are gross values.

Study	Coefficients			Indicator variables*						n	FI^\dagger
	β_0	β_1	β_2^\ddagger	I_1	I_2	I_3	I_4	I_5	I_6		
Tree level ^{††}											
CRiSSSP	728.50	0.546		76.93	24.28	ns	42.97			1336	92.9
FRP	1386.60	0.568		ns	ns	ns	-99.08	-117.70		934	97.6
Lee Forest	550.10	0.679		ns						1207	79.8
Utah	200.80	0.642	0.630							111	79.0
Woodworth	722.00	0.624		32.39	36.86	ns	32.9	ns	ns	3021	75.2
Plot level ^{‡‡}											
Lee Forest	0.005	0.689		ns						20	85.4
Woodworth	0.003	0.699		ns	ns	-0.0002	-0.0004	-0.0007	ns	175	86.7

* Indicator variables defined in Table 4.

† Fit index = $\sum (y - \hat{y})^2 / \sum (y - \bar{y})^2$; \hat{y} = predicted value of y and \bar{y} = mean value of y .

†† Basal area increment in tree-level analyses expressed in terms of mm²/mo for the FRP; mm²/yr otherwise.

‡ $\beta_2 = \beta_1$ unless stated otherwise.

‡‡ For plot-level studies, gross basal area increment expressed in terms of m² ha⁻¹ yr⁻¹.

The equations were fit to the various datasets using a derivative-free, nonlinear regression algorithm (Ralston and Jennrich 1978). Fits of Equation (4) to individual-tree data from the Lee Forest and Woodworth studies were weighted with the reciprocal of the error variance of the regression model determined with a procedure described by Neter et al. (1996, p. 406-409). Quality of fit was determined with the fit index and with analyses of residuals plotted against leaf area, height to the center of leaf area, and other relevant variables. The fit index is the proportion of the total variation in the dependent variable explained by the fitted model. It is analogous but not equal to the coefficient of determination of linear regression since the residuals from nonlinear regression do not necessarily sum to zero.

Results

Basal Area Increment

Acceptable fits of Equation (4) to the data were obtained with $\beta_1 = \beta_2$ with the exception of the lodgepole pine data collected in northern Utah (Table 5). Equation (4) explained from approximately 75 to nearly 98% of the variation in basal

area increment for the various datasets regardless of whether basal area was measured at ground level or breast height or whether the model was fit to individual-tree data or plot totals. The residuals of the fitted equations were unbiased with respect to either individual-tree products of leaf area and distance from h to the center of leaf area (Figure 1) or plot totals of the products (Figure 2). The precision of the fitted equations to predict basal area increment appeared related to the developmental stage of the trees. Fits of the equation to data from the individual seedlings and saplings in the CRiSSSP and FRP studies resulted in fit indices that were approximately 10–15 percentage points higher than the fit indices resulting from regressing Equation (4) on the data from the pole- and sawtimber-sized trees in the other studies.

For all studies with $h = 1.37$ m, the average value of β_1 was 0.67, identical to the theoretical value of the exponent shown in Equation (3). The average value of β_1 for the studies with $h = 0$ m was 0.557. The base of the stem is commonly excluded from analyses of the uniform stress hypothesis because of butt swell (Dean and Long 1986a, Dean et al. 2002); consequently, the fitted value of β_1 at $h = 0$ m would not be expected to be 0.67. With exception of the fit to the individual-tree data collected at Woodworth, the approximate 95% confidence intervals for the fitted values of β_1 include the value 0.67 for all studies where $h = 1.37$ m, regardless of whether Equation (4) is fit to individual-tree data or plot-level data. The failure to reject the hypothesis that $\beta_1 = 0.67$ depends on the standard error of the coefficient; consequently, the failure to reject the hypothesis due to imprecise fits can be incorrectly taken as support for the hypothesis. Conversely, coefficients that are within an acceptable tolerance limit of an expected value but are statistically distinguishable from it due to a precise fit to data can also be incorrectly taken as evidence against a hypothesis. Dean et al. (2002) argued that an acceptable tolerance limit for the exponent in the uniform stress model is $\pm 10\%$. Such a tolerance in the exponent results in less than a 10% difference in measured stem diameters and ideal stem diameters according to the uniform stress model except for the top portion of the stem and excluding butt swell. Morgan and Cannell (1994) allowed for a 10% difference between the diameters calculated with their simulation of bending stress within the stem and measured diameters. For the studies where $h = 1.37$ m, the highest and lowest fitted values of β_1 are only 3.3% greater and 6.5% less than the theoretical value of 0.67, respectively, suggesting that the measured values of basal area increment in these studies are extremely close to the basal area increment that would be expected under the uniform stress hypothesis for given combinations of $A_0 \cdot S_0$ and $\Delta(A \cdot S)$.

With the exception of the herbaceous-weed-control treatment at the Pine Grove, Louisiana, site, each treatment included in the analysis of the CRiSSSP dataset had significant and positive effects on the constant in Equation (4) (Table 5). Harvesting method had the largest effect on the constant and indicated that seedlings planted in plots harvested with high disturbance methods increased basal area more rapidly than

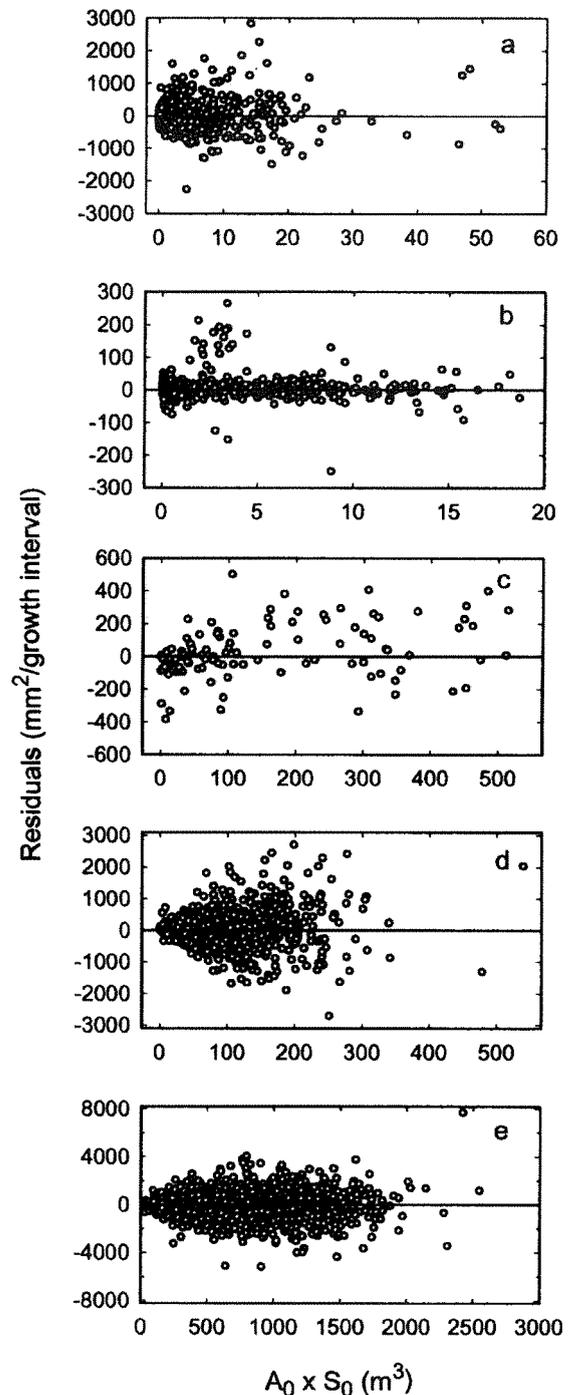


Figure 1. Residuals from fitting the following nonlinear regression model to the various datasets for individual trees:

$$\Delta B = \left(\beta_0 + \sum_{j=1}^k (\beta_{j+2} \cdot I_j) \right) \cdot \left(\left((A_0 \cdot S_0) + \Delta(A \cdot S) \right)^{\beta_1} - (A_0 \cdot S_0)^{\beta_2} \right),$$

where ΔB = basal area increment, A_0 and S_0 = initial leaf area and distance between h and height to the center of leaf area at the beginning of the growth period, h = stem height diameter measured (0 or 1.37 m), $\Delta(A \cdot S)$ = change in the product of leaf area and distance between h and height to the center of leaf area during the growth period, $\beta_0 - \beta_{k+2}$ = regression coefficients, and I_j = indicator variables for the k number of treatments included in the study. When fit to all but the Utah dataset, $\beta_2 = \beta_1$. Growth intervals are yearly for the CRiSSSP (a), Utah (c), Lee Forest (d), and Woodworth (e) studies and monthly for the FRP study (b).

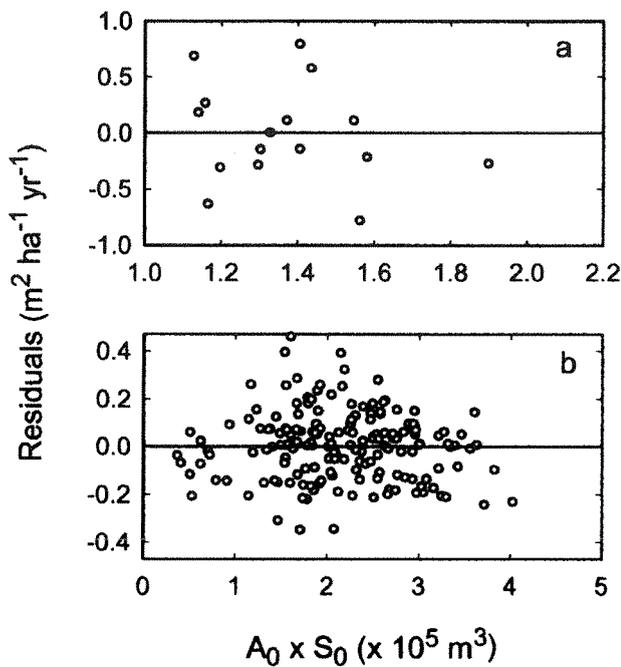


Figure 2. Residuals from fitting the following nonlinear regression model to the Lee Forest (a) and Woodworth (b) datasets summarized at the plot level:

$$\Delta B = \left(\beta_0 + \sum_{j=1}^k (\beta_{j+2} \cdot I_j) \right) \cdot \left(\left((A_0 \cdot S_0) + \Delta(A \cdot S) \right)^{\beta_1} - (A_0 \cdot S_0)^{\beta_1} \right),$$

where ΔB = gross basal area increment, A_0 and S_0 = initial leaf area and distance between breast height (1.37 m) and height to the center of leaf area at the beginning of the growth period, $\Delta(A \cdot S)$ = gross change in the product of leaf area and the distance between breast height and height to the center of leaf area during the growth period, $\beta_0 - \beta_{k+1}$ = regression coefficients, and I_j = indicator variables for the k number of treatments included in the study.

seedlings planted in plots harvested with minimum disturbance methods for given values of $A_0 \cdot S_0$ and $\Delta(A \cdot S)$. Fertilization had the next largest effect followed by bedding.

Table 6. Fit index, fitted coefficients, and significant coefficients for indicator variables for the various data sets used to fit the nonlinear regression model

$$\Delta V = \left(\gamma_0 + \sum_{j=1}^k (\gamma_{j+1} \cdot I_j) \right) \cdot A_0^{\gamma_1},$$

where ΔV = stem volume increment, A_0 = initial leaf area at the beginning of the growth period, $\gamma_0 - \gamma_{k+1}$ = regression coefficients, I_j = indicator variables for the k number of treatments included in the study.

Study	Coefficients		Indicator variables*						n	FI^\dagger	
	γ_0	γ_1	I_1	I_2	I_3	I_4	I_5	I_6			
Tree level											
CRiSSSP ^{††}	1.306	1.031	-0.294	0.188	-0.602	-0.241				1336	87.9
FRP ^{††}	0.303	0.462	ns	ns	ns	ns	ns			934	30.0
Lee Forest [§]	0.003	0.689	-0.003							1207	45.7
Utah [§]	0.004	0.407								111	29.0
Woodworth [§]	0.005	0.654	ns	ns	ns	ns	ns	-0.0005		3021	75.2
Plot level											
Lee Forest	9.59	1.732	ns							20	66.2
Woodworth	17.34	0.538	ns	ns	ns	ns	ns	-3.5400		175	33.1

* Indicator variables defined in Table 4.

† Fit index = $\sum (y - \hat{y})^2 / \sum (y - \bar{y})^2$; \hat{y} = predicted value of y and \bar{y} = mean value of y .

†† Volume increment in terms of liters/yr for the CRiSSSP study and liters/mo for the FRP study.

§ Volume increment in terms of m³/yr.

|| For all plot-level studies, gross volume increment in terms of m³ ha⁻¹ yr⁻¹.

The only significant indicator variables in the fit of Equation (4) to the Forest Response Program data stood for acidic precipitation and each of these coefficients were negative. This indicates that when subjected to simulated rain with a pH that deviates from the long-term average around Gainesville, Florida, basal area increment for given values of $A_0 \cdot S_0$ and $\Delta(A \cdot S)$ decreases relative to the basal area increment observed with simulated ambient rainfall. None of the ozone concentrations resulted in significant coefficients for associated indicator variables.

Spacing effects on the constant in Equation (4) were inconsistent. At Lee Forest, spacing had no significant effect on the fit of Equation (4) to either the individual-tree data or the plot totals. For the Woodworth study, initial spacing significantly affected the value of the constant, but the spacings that affected the fitted constant varied depending on whether the equation was fit to the individual-tree data or the plot totals. When Equation (4) was fit with the individual-tree data, coefficients representing the initial spacings 1.2×1.8 , 1.8×1.8 , and 2.4×2.4 m were significant, and when the equation was fit to the plot-summarized data, the coefficients representing the initial spacings 1.8×2.4 , 2.4×2.4 , and 3.1×3.1 m were significant. In addition to different spacings affecting the fits of Equation (4), the sign of the significant coefficients were all positive when fit to the individual-tree data and were all negative when fit to the plot-summarized data.

Stem Volume Increment

With one exception, fits of Equation (5) to the various datasets explained substantially less variation in stem volume increment than the variation in basal area increment explained by Equation (4). In three of the studies, Equation (5) explained less than 34% of the variation in stem volume increment where Equation (4) explained an average of 88% of the variation in basal area increment (Table 6). In three other studies, Equation (5) explained less than 67% of the variation in stem volume increment where Equation (4)

explained an average of 80% of the variation in basal area increment. Only for the CRiSSSP study did the precision of fit of Equation (5) to the data come close to the precision of the fit of Equation (4) to same dataset; however, the fit index of Equation (5) for this dataset was still inferior to the fit index for Equation (4) by five percentage points.

Discussion

Curve Fits

Equation (4), based on the uniform stress principle, provides a means for including the effects of crown or canopy structure in the relation between leaf area and stem growth that results in a superior accounting of basal area increment in these five studies than the accounting of stem volume increment provided by a leaf area alone [Equation (5)]. In addition, while the relationship between volume increment and leaf area may be age specific (e.g., Jokela and Martin 2000), Equation (4) accounts for variation in basal area increment in these studies across age classes and even within a single growing season. While the improvement could be due to the added variables in the equation and a two-dimensional dependent variable in contrast to the three-dimensional variable of stem volume, that the fitted values of β_1 , the primary exponent in Equation (4), are all within 7% of the exponent derived from the uniform stress principle supports the basic hypothesis that the uniform stress principle can be used to predict basal area increment from the increment in bending stress implicated from annual accumulations of leaf area and changes in the vertical distribution of leaf area. The potential stem growth represented by foliage is not always realized because of suboptimal environmental conditions during the growing season and competitive pressure from neighboring vegetation. The predictive value of Equation (3) may lie in its ability to account for suboptimal conditions and competition through changes in crown and canopy structure that occur during a growth period.

Significant coefficients for indicator variables indicate that the relationship between basal area increment, initial crown size, and crown dynamics during the growth period is affected by cultural treatments, acidic precipitation, and differences in initial spacing (Table 5). In this analysis, indicator variables modify the proportionality constant in the uniform stress model, which according to analyses by Dean et al. (2002), seems to vary with inherent, species-specific differences or environmentally induced changes in mechanical properties of the stem. Plants have evolved a wide range of mechanisms for avoiding, resisting, or tolerating physiological strains (Levitt 1980, p. 10–18). Plants must also develop means for coping with the physical strain of bending (Niklas and Speck 2001). Bending strain can be measured as the radius of stem curvature caused by lateral loading on the crown. If this strain is maintained within some biological limit, changes in the mechanical properties of the stem will be compensated by opposing changes in stem cross-sectional area—such changes would be reflected in the fitted value of the constant in Equation (4).

In loblolly pine, fertilization generally decreases specific gravity in approximate proportion to the amount of nitrogen

added to the site (Zobel and van Buijtenen 1989, p. 226). Since stem flexibility is a function of specific gravity, lower specific gravity should result in larger cross-sectional area of the stem to regulate bending curvature. Fertilization and bedding in the CRiSSSP study directly or indirectly affected soil nitrogen availability as evidenced by elevated nitrogen-mineralization rates (Carter et al. 2002); indicator variables representing these two treatments had significantly positive coefficients in Equation (4) (Table 5). While Vitousek and Matson (1985) reported significant increases in mineral-nitrogen availability the first 2 yr after herbicide application, soil samples collected from the Pine Grove, Louisiana, site revealed no significant effect of herbicide application on mineral-nitrogen availability (Yildez 1997); the herbaceous-weed-control treatment had no significant effect on the fit of Equation (4) to the CRiSSSP dataset.

The treatment that had the largest effect on the constant in the fit of Equation (4) to the CRiSSSP dataset was degree of disturbance associated with harvesting the previous stand (Table 5). For given values of $A_0 \cdot S_0$ and $\Delta(A \cdot S)$, the severe disturbance associated with harvesting the stand with conventional machinery caused the trees planted on those sites to increase stem basal area more rapidly than trees planted on sites where the previous stand that had been harvested without machine traffic on the site. The proximate cause for this effect is not clear. While no significant differences in mineral-nitrogen availability existed between the two harvesting intensities at the Fred, Texas, site (Carter et al. 2002), seedlings planted on the conventionally harvested plots probably experienced greater wind exposure than seedlings planted on the hand-felled plots because conventional, whole-tree harvesting generally left the sites bare of any standing vegetation, alive or dead. Dean et al. (2002) found that open-grown slash pine and loblolly pine with high exposure to wind had relatively higher values of the constant in Equation (1) than stand-grown trees; a higher, treatment-induced constant in the uniform stress model would translate into a positive coefficient for an indicator variable representing that treatment.

According to Zobel and van Buijtenen (1989, p. 232), the effects of initial spacing and thinning on wood properties can vary widely. From their review, they conclude that normal spacings used in commercial forestry have little if any effect on the mechanical properties of the xylem in loblolly pine, unless soil moisture is limiting. In that case, wider spacings produce wood with higher specific gravity. This would account for the lack of a significant effect of initial spacing on the fit of Equation (4) to the Lee Forest data. In contrast to loblolly pine, Clark and Saucier (1989) found a gradual reduction in wood specific gravity with initial spacing of slash pine growing in the Piedmont of South Carolina. Thinning, however, can increase wood specific gravity by lengthening the availability of soil moisture during the growing season and prolonging the production of latewood (Zobel and van Buijtenen 1989, p. 236). The fit of Equation (4) to the Woodworth data may reflect such complicated relationships between initial spacing and thinning on the mechanical properties of slash pine stems. Different initial spacings were

significant when Equation (4) was fit to individual-tree data than when it was fit to the plot-level data. Furthermore, the sign of the coefficients that were significant for the individual-tree data were all positive, whereas the sign of the coefficients that were significant for the plot-level summaries were all negative.

The fit of the Equation (4) to the FRP data suggests that environmental conditions that directly affect needle longevity do not necessarily alter the relationship between stem size and the quantity and distribution of leaf area. After 18 months of treatment, increasing ozone exposure decreased the number of needles produced by the primary meristems and reduced the longevity of the needles that were produced, resulting in lower leaf areas per tree (Dean and Johnson 1992, Byres et al. 1992). None of the indicator variables for ozone exposure in Equation (4) were significantly different than zero, however. Rain acidity had no effect on mean leaf area per tree or needle demography, but the indicator variables for rain acidity were all significantly less than zero. Extremely little work has been conducted on the effects of rain acidity on the mechanical properties of wood (Weber and Grulke 1995). The main constituent of the rain mixture applied to these slash pine trees was sulfur, and the negative coefficients indicate that the acidity and the sulfur added with the 3.3 pH rain or subtracted with the 5.3 pH rain decreased increments in stem cross-sectional area relative to $A_0 \cdot S_0$ and $\Delta(A \cdot S)$, which could result from increased wood specific gravity.

Implications of Curve Fits

Basal Area Increment

Since Equation (3) defines basal area increment with two composite variables, constant increments in basal area can be mapped within a Cartesian coordinate system defined by $A_0 \cdot S_0$ and $\Delta(A \cdot S)$. A typical set of isolines reveal that constant values of basal area increment require larger values of $\Delta(A \cdot S)$ as the value of $A_0 \cdot S_0$ increases (Figure 3). In other words, the tree or stand must either continue to accumulate leaf area, increase the height to the center of leaf area, or both to maintain a constant basal area increment. While this may be possible for individual trees in a stand, stand-level values of leaf area in pine typically decline after peaking during canopy closure (Long and Smith 1992, Vose et al. 1994). While Equation (3) predicts declining basal area increment with declining leaf areas at the stand level, it also predicts declining basal area increments for any value of $\Delta(A \cdot S)$ that is less than the minimum indicated by the isoline. Stem volume increment is nearly linearly related to basal area increment in these studies for both individual trees and plot sums. Therefore, declining volume increment may also occur when values of $\Delta(A \cdot S)$ drop below a critical values.

Growth Efficiency

Dividing both sides of the fit of Equation (4) to the various datasets used in this analysis by leaf area per tree or per hectare produces an expression that describes growth efficiency in the same two composite variables that describe basal area increment. Consequently, isolines for growth efficiency can also be drawn within a Cartesian coordinate plane defined by $A_0 \cdot S_0$ and $\Delta(A \cdot S)$. Typical isolines of growth

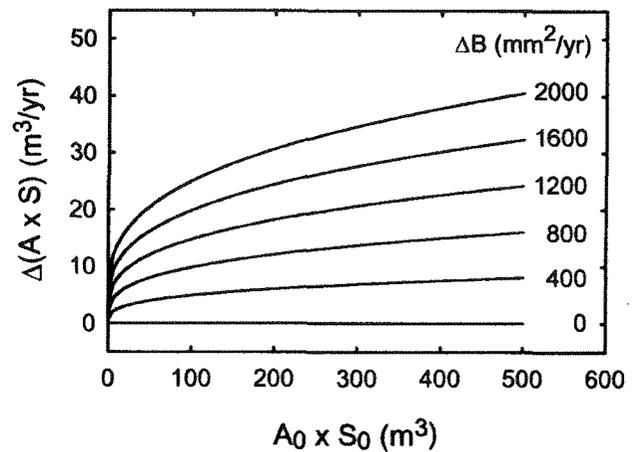


Figure 3. Isolines for annual basal area increment (ΔB) as a function of the product of leaf area and the distance between breast height (1.37 m) and height to the center of leaf area at the beginning of the year ($A_0 \cdot S_0$), and change in the product during the growing season $\Delta(A \cdot S)$ calculated from the fit of the following nonlinear regression model to the individual-tree data collected at Lee Forest:

$$\Delta B = \beta_0 \cdot \left(\left((A_0 \cdot S_0) + \Delta(A \cdot S) \right)^{\beta_1} - (A_0 \cdot S_0)^{\beta_1} \right),$$

where $\beta_0 - \beta_1$ = regression coefficients.

efficiency shown for the Woodworth study curve slightly upwards from the origin (Figure 4). The shape of the isolines indicates that to maintain constant growth efficiency, the value of $\Delta(A \cdot S)$ must increase at an accelerating rate as $A_0 \cdot S_0$ increases. Slower rates result in decreasing growth efficiency with tree or stand development.

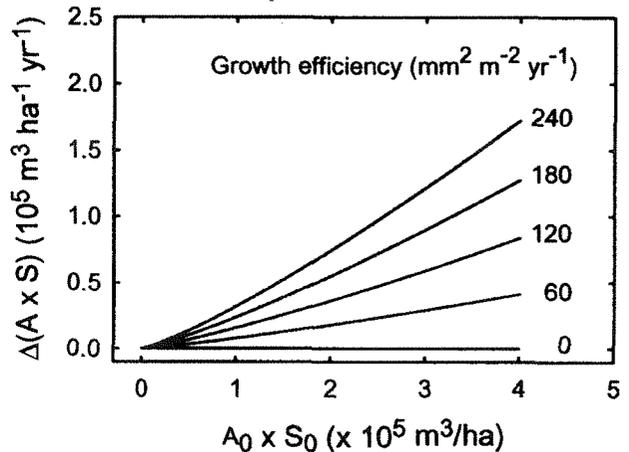


Figure 4. Isolines for growth efficiency as a function of the per hectare totals of the product of individual-tree leaf area and the distance between breast height (1.37 m) and height to the center of leaf area at the beginning of the year ($A_0 \cdot S_0$), and the individual-tree changes in the product during the growing season $\Delta(A \cdot S)$. Growth efficiency calculations based on the fit of per hectare values of basal area increment to the stand-level data collected for the Woodworth study with the nonlinear regression equation

$$\Delta B = \beta_0 \cdot \left(\left((A_0 \cdot S_0) + \Delta(A \cdot S) \right)^{\beta_1} - (A_0 \cdot S_0)^{\beta_1} \right),$$

where ΔB annual basal area increment, and $\beta_0 - \beta_1$ = regression coefficients. Growth efficiency calculated by dividing the fitted equation by corresponding predicted values of peak leaf area per hectare prior to the current growing season.

The isolines for basal area growth efficiency indicate that for a cultural treatment or environmental change to increase growth efficiency, it must produce a substantial change in the product of leaf area and height to center of leaf area. The need for not only significant but large changes in the product of leaf area and height to center of leaf area in order for significant increases in growth efficiency to occur can be demonstrated with data from the CRiSSSP study. For the first 3 yr after fertilization, the mean value of $\Delta(A \cdot S)$ of the fertilized trees was significantly higher than that of the unfertilized trees resulting in significant differences in the mean value of $A_0 \cdot S_0$ at the beginning of the two subsequent growing seasons (all values of $P < 0.06$). Despite significant differences in crown properties and dynamics, however, fertilization had no significant effect on growth efficiency ($P > 0.10$). Fertilizer effects are typically a function of the application rate. In the CRiSSSP study, 45 kg/ha of elemental nitrogen was applied at the time of planting. Other studies that observed significant increases in volume growth efficiency applied either a large dose of elemental N in a single application or supplied optimum nutrition on an annual basis (Brix 1983, Albaugh et al. 1998). While change in height to center of leaf area could not be calculated from these reports, substantial increases in foliage increment occurred in studies reporting significant increases in growth efficiency.

Conclusions

The fits of Equation (4) to these data support the hypothesis that discrete changes in basal area increment for the species and conditions included in this study can be explained with the geometry necessary to maintain uniform bending stress along the surface of tree stems. The apparent link between stem geometry and crown dynamics provides an additional avenue for analyzing the response of stem growth and physiology to factors such as site quality, age, silvics, and stand density. Dividing both sides of Equation (4) by leaf area produces an equation that expresses basal area growth efficiency also in terms of crown and canopy dynamics. Both equations indicate that for basal area increment and basal area growth efficiency to remain constant through time, the value of $\Delta(A \cdot S)$ must increase for each successive growth period; constant values of $\Delta(A \cdot S)$ will cause basal area increment and basal area growth efficiency to decline with tree or stand age.

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