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An evaluation of the uniform stress hypothesis based on stem geometry in selected North American conifers

Received: 1 October 2001 / Accepted: 17 June 2002 / Published online: 13 August 2002
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Abstract The uniform stress hypothesis of stem formation was evaluated by comparing stem taper of *Abies balsamea*, *Abies lasiocarpa*, *Picea rubens*, *Pinus contorta*, *Pinus elliotii*, *Pinus palustris*, *Pinus ponderosa*, *Pinus taeda*, and *Pseudotsuga menziesii* to the taper expected if stems develop to uniformly distribute bending stress. The comparison was conducted by regressing stem diameter at height h (D_h) against bending moment at h (M_h) using the model $D_h = \phi (M_h)^\delta$ where ϕ and δ are fitted coefficients, and testing for $\delta=0.333$, the hypothesized value. Twelve curves were fitted with the model. Seven of the fitted values of δ were significantly different from 0.333,

but eight of the values were within $\pm 10\%$ of 0.333 and eleven values were within $\pm 15\%$ of 0.333. Where the fitted value of δ was $>15\%$ of 0.333, residuals were biased with height. Fit by relative height, values of δ were within $\pm 10\%$ of 0.333 for large portions of these stems. While most of the fitted values of δ support the uniform-stress hypothesis, the values of δ for *Pseudotsuga menziesii* trees clearly did not. Many of the fitted values of ϕ were inversely related to the modulus of elasticity (E) of green wood reported for these species. With the exception of *Pseudotsuga menziesii*, growing conditions appeared to account for extraordinary values of ϕ . Increases in ϕ with stem height corresponded with reported decreases in E with height. The covariance between ϕ and E suggests some regulation of bending curvature by adjustments in cross-sectional area. These results suggest that stems taper to maintain a uniform bending curvature and that when E is relatively constant within and among stems, diameter along the stem or across stems can be predicted from bending moment using a simple power function.

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Keywords Crown structure · Bending moment · Wind · Leaf area · Stem mechanics

Introduction

The principles governing stem formation remain controversial, despite more than a century of study. While consensus exists on the two primary functions of the stem, physical support and water conductance, no single, acceptable explanation exists on how the stem accomplishes either of these functions individually, let alone simultaneously. Many studies have demonstrated that changes in the lateral forces on stems cause corresponding changes in stem diameter, and other studies have shown that changes in resource availability affect the relationship between stem sapwood cross-sectional area and leaf area (Jacobs 1954; Keane and Weetman 1985; Dean 1991; Jaffe and Forbes 1993; Valinger et al. 1994; White et al.

1998). Studies have also demonstrated that mechanical forces and environmental conditions have significant, simultaneous interactions on both the physical and physiological properties of the stem (Dean 1991; Fredericksen et al. 1994).

Physical support appears to be the most frequent avenue pursued in identifying a principle of stem formation. Early attempts compared stem geometry to reference shapes that represented hypothesized mechanical principles such as uniform bending stress, but such simple shapes could account for only a portion of the stem (e.g., Metzger 1893; Larson 1963; Newnham 1965; Long et al. 1981). Advances in computational capacity allow a more direct evaluation of physical stresses and strains within the stem (West et al. 1989; Morgan and Cannell 1994; Niklas and Spatz 2000); however, the difficulty in measuring wind profiles in stands with tall trees and collecting detailed field data on a large number of trees and species has also limited the generality of these tests.

The hydraulic relationship between foliage and the main stem has been examined on many species over the last two decades, and the data required to study the hydraulic architecture of the stem are nearly identical to the data required to investigate the mechanical behavior of the stem using the analysis technique of Dean and Long (1986). Dean and Long (1986) derived a regression model from the flexure formula for cantilever beams that predicts stem diameter at height h on the stem (D_h) as a simple power function of the bending moment acting at that height (M_h):

$$D_h = \phi (M_h)^\delta, \quad (1)$$

where ϕ and δ are fitted coefficients. This derivation applies to vertically oriented, tapered beams that are rigidly fixed at the base and withstanding forces that cause only small deflections so that gravity effects on bending moment are negligible. The bending moment M_h in Eq. 1 is the product of wind pressure acting on the leaf area above height h (A_h) and the leverage exerted on the stem cross-section at h (l_h). Dean and Long (1986) originally applied this equation to monocultures of even-aged *Pinus contorta* var. *latifolia* Engelm. and assumed that average wind pressure is constant across trees within the stand. This allowed the simplifying assumption that $M_h = A_h \cdot l_h$, but it also created the assumption of constant wind speed within the canopy. Dean and Long (1986) also assumed that the leverage exerted at height h is the distance from h to the center of leaf area, which they defined as the height that bisects the vertical distribution of leaf area into equal quantities. Within the crown-free portion of the stem, leaf area and the height of the center of leaf area remain constant. Within the crown, the height of the center of leaf area increases with h depending on the remaining leaf area above h . Under conditions of constant vertical wind velocity and small deflections in the stem, uniform bending stress along the stem and across trees is indicated by a fitted value of δ of 0.333. With data from mature *P. contorta*, collected from mature trees, Dean and Long (1986) found a fitted value for

δ of 0.313 when Eq. 1 was fit with multiple diameter measurements per stem and a value of 0.321 when the equation was fit with single diameter measurements at 1.37 m above the ground (breast height). West et al. (1989) found that tree morphology predicted with Eq. 1 and $\delta=0.333$ resulted in uniform bending stress within the stems of *Eucalyptus regans* F. when wind velocity is mild and constant with height.

In this study, we use data for a number of commercially important coniferous species within North America to evaluate the hypothesis that stem form serves to equalize bending stress within stems. We do this by comparing fitted values of δ to the theoretical value of 0.333. We also examine the commonality of fitted coefficients among species to identify generalities in bending mechanics and to investigate factors that may influence bending mechanics within and among species. By fitting the regression equation of Dean and Long (1986) to data from a relatively large number of trees across a range of species, we attempt to overcome the problems of accounting for only a portion of stem geometry and the narrow scope of inference from calculating bending stress on a small number of trees of a single species.

Materials and methods

Data

Fourteen data sets representing nine species were used in this analysis. Ten data sets were constructed during previous studies (Table 1). Four data sets were collected with the specific intent of evaluating the uniform stress hypothesis in *Pinus taeda* L. (Table 2). In eight of the ten data sets used for other studies, leaf area was determined directly by stripping and weighing foliage or indirectly with the use of regression equations relating foliage mass to individual branch diameters. In one study, Baldwin et al. (1997), using the methods of Valentine et al. (1994) determined foliage within a section of the crown by expanding the foliage on a randomly selected branch by its probability of being selected, which was proportional to the squared diameter of all branches within the section. Leaf area in the study by Albaugh et al. (1998) was determined using locally developed regression equations based on stem dimensions measurable at ground level. Leaf area was measured as either projected or total surface area of the needles. Most of the studies characterized the vertical distribution of leaf area by recording leaf area for each whorl of branches, each individual branch, or for specified intervals within the crown. In three studies, only total leaf area per tree was available. Most of the studies characterized leaf area at its growing season peak, although two of the *Pinus taeda* studies and the *Pseudotsuga menziesii* (Mirb.) Franco study determined leaf area at the winter season minima. Ages of the trees measured in these studies ranged from 10 to 166 years old. Diameter at breast height ranged from 25 to 513 mm, and height ranged from 2.6 to 27.9 m.

Trees destructively sampled in studies specifically intending to evaluate the uniform stress hypothesis were harvested from *Pinus taeda* plantations located in eastern Texas, southeastern Louisiana, and east central Mississippi (Table 2). The data from Fred, Tex. and Pine Grove, La. is from a study investigating the impacts of harvest intensity and early cultural treatments on growth of *P. taeda* (Carter et al. 2002). Only data from the control treatments are used in this analysis. Near Starkville, Miss., trees were sampled from a small plantation consisting of different *P. taeda* families planted in row plots (Roberts et al. 2002). Only data from trees in the "woods run" family are included in this analysis. Near Pine, La., *P. taeda* trees

Table 1 Sources of data used in this study

Principal citation	Species	n	Leaf area determination				Range in tree characteristics			
			Interval	Method	Projected or all-sided	Month measured	Age (years)	DBH (mm)	Height (m)	A ₁ (m ²)
Gilmore et al. (1996)	<i>Abies balsamea</i>	39	By whorl	Branch eqns	Projected	July	17–84	25–297	4.0–19.6	0.8–167.4
Maguire and Bennett (1996)	<i>Pseudotsuga menziesii</i>	27	By branch	Branch eqns	Projected	October–April	10–28	50–384	7.3–26.3	25.1–256.7
Maguire et al. (1998)	<i>Picea rubens</i>	16	By branch	Branch eqns	Projected	July	Uneven	110–483	9.5–23.7	23.8–401.7
O'Hara and Valappil (1995)	<i>Pinus ponderosa</i>	114	Crown total	Direct	All-sided	June–July	12–70	43–292	3.5–19.1	5.7–194.1
Roberts and Long (1992)	<i>Abies lasiocarpa</i>	49	0.5 m	Direct	Projected	August	66–131	62–316	5.4–20.1	1.1–76.3
Dean and Long (1986)	<i>Pinus contorta</i>	39	1.0 m	Direct	projected	September	~70	58–316	8.4–23.6	0.6–84.5
Mitchell et al. (1999)	<i>Pinus palustris</i>	23	By branch	Direct	projected	July–August	19–166	33–513	2.8–25.5	0.6–287.0
Jack (unpublished data)	<i>Pinus elliotii</i>	19	By branch	Direct	projected	August	60–61	118–480	13.9–27.9	5.1–174.5
Baldwin et al. (1997)	<i>Pinus taeda</i>	30	Crown total	pps	all-sided	August–September	13–41	102–363	11.0–26.2	27.5–341.9
Albaugh et al. (1998)	<i>Pinus taeda</i>	818	Crown total	Whole-tree eqns	projected	December	10–11	26–212	2.6–10.0	0.4–31.7

Table 2 Sample statistics for stem diameter, total tree height, and projected leaf area (A₁) for destructively harvested *Pinus taeda* L. trees in Texas, Louisiana, and Mississippi. Stem diameter is root

collar diameter for trees four-years old or less and is diameter at breast height (1.37 m) for trees 12 years old and older

Location	n	Month measured	Section length (m)	Age (years)	Range		
					Diameter (mm)	Height (m)	A ₁ (m ²)
Pine Grove, La.	12	September	0.15	2	6–20	0.56–1.02	0.03–0.44
Fred, TX	12	August	0.50	4	8–118	0.93–5.19	0.19–24.6
Starkville, Miss.	7	August	1.00	14	89–259	8.9–25.9	4.98–54.69
Pine, La.	28	December	1.00	12	20–167	3.7–13.4	0.20–16.01

were sampled from a spacing trial in the Lee Memorial Forest. Trees were selected from plots with original spacing of 1.2×1.2 m and 3.4×3.4 m.

Measurement techniques for all four studies generally followed those of Dean and Long (1986). Trees were sectioned into fixed intervals based on size: the smallest interval was 0.15 m and the largest interval was 1.0 m. Sectional leaf area was determined by measuring fresh foliage mass in the section, correcting for moisture content in the foliage, and converting mass to area with specific leaf area. Moisture content and specific leaf area were determined from subsamples of foliage collected from each section. For the trees sampled at Lee Forest, one branch was selected from each meter section with probability proportional to the product of the square of individual branch diameter and branch length. Foliage was stripped from the branch and converted to section values by dividing the branch leaf area by the selection probability of that branch. Outside bark stem diameter was measured at the bottom of each section for trees in all four studies. Bark thickness was measured at the bottom of each section for the trees sampled near Starkville, Miss. and Pine, La.. Bark thickness was measured at every other section for the trees sampled near Fred, Tex. and was not measured at all on the trees sampled near Pine Grove, La.. Only outside bark diameters are used in this analysis.

The 14 data sets were reduced to 12 by combining the three *P. taeda* data sets with projected leaf area measured during the summer (Pine Grove, La.; Fred, Tex.; Starkville, Miss.). The *P. taeda* data set from Baldwin et al. (1997) was evaluated separately because they measured all-sided needle area. The data collected near Pine, La. and the data collected by Albaugh et al. (1998) both reflect seasonal minimum projected leaf area in *P. taeda*, but were evaluated separately because analysis revealed substantial differences in the trees at these two locations.

Analysis

Fitted coefficients were determined with a derivative-free, nonlinear-regression algorithm (Ralston and Jennrich 1978) as implemented in the Statistical Analysis System (SAS, version 8.03). For data sets with multiple stem diameter measurements, the experimental values of ϕ and δ are the respective mean values averaged over the individual trees unless stated otherwise. Goodness of fit was evaluated with residuals plotted against bending moment. They were also evaluated against relative stem height to determine how well the model described stem taper. A value of α of 0.10 was used for statistical comparisons of fitted values of δ with the theoretical value of δ .

Table 3 Summary statistics for ϕ and δ from fitting $Y=\phi X^\delta$, where Y = stem diameter (ob, mm) and X = bending moment (m^3 , the product of leaf area and leverage above the cross-section where stem diameter was measured), to individual trees from a range of coniferous species. Leaf areas are seasonal maximums (with one exception) and were measured as projected areas

Species	ϕ		δ		$H_0: \bar{\delta}=0.333$ P-value
	Mean	SE ^a	Mean	SE	
<i>Abies balsamea</i>	29.26	1.66	0.334	0.017	0.950
<i>Abies lasiocarpa</i>	37.50	1.04	0.288	0.008	<0.001
<i>Picea rubens</i>	30.96	3.75	0.309	0.022	0.330
<i>Pinus contorta</i> ^b	39.17	1.89	0.283	0.016	0.008
<i>Pinus taeda</i> (summer)	25.47	4.87	0.285	0.051	0.390
<i>Pinus taeda</i> (winter)	28.12	1.85	0.349	0.025	0.540
<i>Pseudotsuga menziesii</i>	37.23	2.14	0.254	0.017	<0.001

^a SE = mean value of standard errors for the individual-tree values of either ϕ and δ

^b Data of Dean and Long (1986) refit for mature and sapling trees combined

Results and discussion

Multiple stem diameters

The values of $\bar{\delta}$ for *Abies balsamea* (L.) Mill., *Picea rubens* Sarg., and *Pinus taeda* measured during the winter are all within 10% of the theoretical value of δ while values of $\bar{\delta}$ for *Abies lasiocarpa* (Hook) Nutt., *Pinus contorta*, and *P. taeda* measured during the summer are within 15% of the theoretical value of δ . The value of $\bar{\delta}$ for *Pseudotsuga menziesii* is 24% less than the theoretical value of δ (Table 3). The null hypothesis $\bar{\delta} = 0.333$ cannot be rejected for those data sets with values of $\bar{\delta}$ within 10% of 0.333, and it cannot be rejected for the *Pinus taeda* data collected during the summer with a value of $\bar{\delta}$ that deviates 14% from 0.333. The null hypothesis is rejected for the other data sets.

Stem geometry integrates the mechanical properties of the xylem as affected by the recent history of the physical forces acting on the stem; consequently, while the long-term average value of δ should be 0.333, the mean value of δ at any time for an individual tree may deviate from the expected value. Therefore, a more appropriate criterion than testing the null hypothesis of $\bar{\delta} = 0.333$ might be whether an experimental value of δ is within an acceptable tolerance limit of the theoretical value.

Deviation in fitted values of δ from the theoretical value occur when stem taper is either greater or less than the taper expected under the uniform stress hypothesis: fitted values less than 0.333 correspond to more cylindrical stems, and fitted values greater than 0.333 correspond to more rapidly tapering stems (Fig. 1a). A 10% tolerance limit around the theoretical value of δ translates into differences between measured and expected diameters that are quite small. For example, given a hypothetical tree that just above butt swell has a maximum stem diameter of 270 mm and a bending moment of

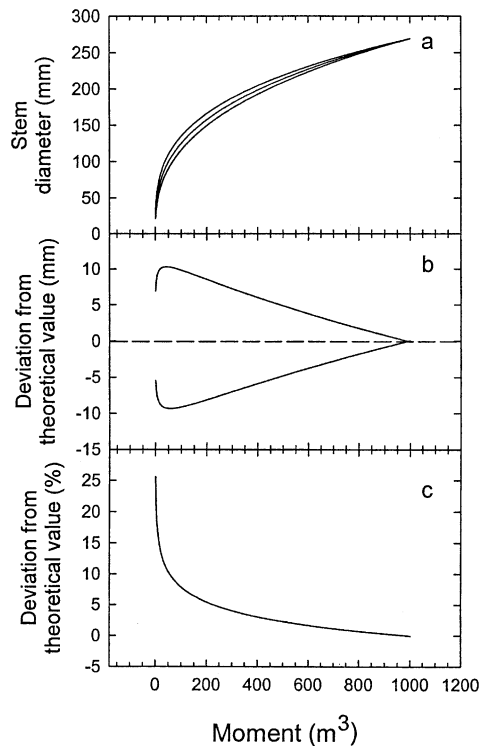


Fig. 1a–c Comparison of stem diameter calculated as a function of bending moment raised to a range of exponents for a hypothetical tree with a base diameter of 270 mm. Constants in the power functions adjusted such that all three exponents result in predicted stem diameter of 270 mm at a bending moment of 1,000 m^3 . **a** Curves produced with the theoretical exponent 0.333 (middle line), the theoretical exponent -10% (top line), and $+10\%$ (bottom line). **b** Absolute differences between stem diameter calculated with the theoretical exponent and the theoretical exponent $+10\%$ (top line) and with the theoretical exponent -10% (bottom line). **c** Absolute value of the relative differences (in percent) between stem diameter calculated with the theoretical exponent and $\pm 10\%$ of the theoretical exponent. Increasing bending moment corresponds with decreasing tree height

1,000 m^3 , the absolute difference between measured and ideal stem diameters is less than 10 mm across the range of bending moment (Fig. 1b). In this example, the maximum difference between measured and expected stem diameters is 25% at the lowest value of bending moment at the top of the stem and drops quickly below 10% of the expected diameter at one-tenth of the maximum bending moment (Fig. 1c). The 10% difference that was tolerated by Morgan and Cannell (1994) between the diameters calculated with a simulation model of bending stress dynamics and measured stem diameters is actually larger than the difference between measured and ideal stem diameters for 90% of the range in bending moment in this example with a $\pm 10\%$ tolerance in $\bar{\delta}$. According to this sensitivity analysis, the diameters measured on these trees and the diameters expected with the uniform stress hypothesis must be nearly identical to result in values of $\bar{\delta}$ that are within $\pm 10\%$ of 0.333.

For *A. balsamea*, *Picea rubens*, and *Pinus taeda* measured during the winter, where the value of $\bar{\delta}$ is within

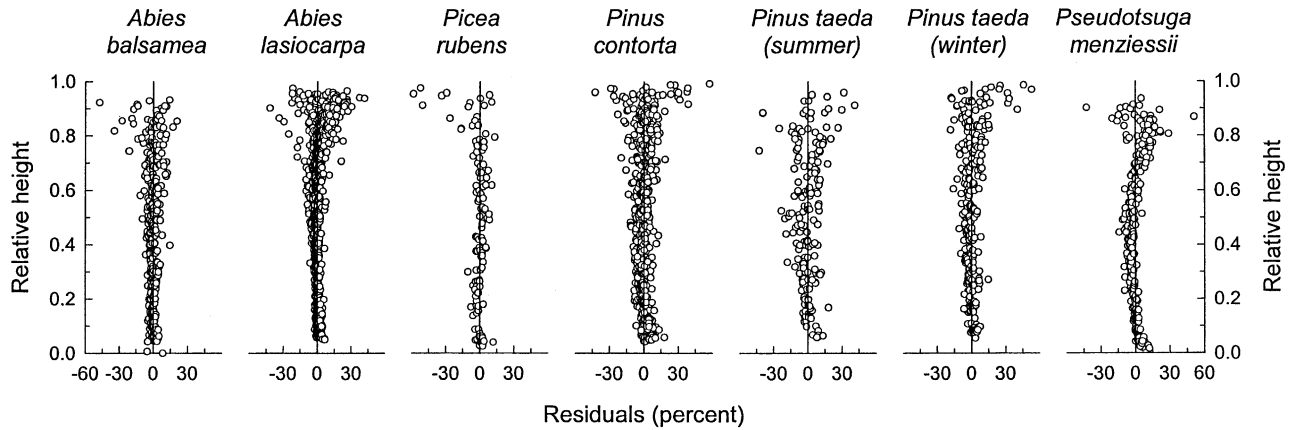


Fig. 2 Residuals (in percent) of the fit of Eq. 1 to data sets with multiple stem diameter measurements as a function of relative height. Residuals calculated as predicted stem diameter minus observed stem diameter

10% of the theoretical value of δ , the residuals between the predicted and measured stem diameters are closely and uniformly distributed around zero when plotted as a function of relative tree height (Fig. 2). Furthermore, with one exception, individual-tree values of δ for these three species were generally unrelated to a tree's environment or competitive status within the stand. The exception was the suppressed crown class of the *A. balsamea* trees where the value of δ was significantly greater than mean values for trees in other crown classes; otherwise, no differences in the mean values of δ existed between open-grown, co-dominant, and intermediate crown classes. This indicates that suppressed *A. balsamea* trees have more taper than *A. balsamea* trees in superior canopy positions (cf. Fig. 1a). This agrees in part with King (1986) who found that understory saplings of *A. saccharum* Marsh. had higher values of a somewhat analogous exponent than overstory trees. However, among the various ages of *Picea rubens* trees sampled from uneven-aged stands, regression analysis indicated that fitted values of δ were independent of tree height ($P=0.861$) and thus, canopy position. The different spacing of *Pinus taeda* trees measured in the winter had no significant effect on the fitted value of δ for these trees ($P=0.302$). West et al. (1989) also found that similar estimates of δ were unrelated to crown class or thinning history in *E. regens*.

In those species where the value of δ is outside of a $\pm 10\%$ tolerance limit around the theoretical value of δ , stem diameter is overpredicted near the base and the top of the stem and is underpredicted along the middle portion of the stem. This pattern is clearly evident for *Pseudotsuga menziesii*, mildly evident for *A. lasiocarpa* and *Pinus taeda* measured during the summer, and evident only near the base of the *Pinus contorta* stems. When a simple model such as Eq. 1 is fit to multiple measurements on a single stem, lack of fit indicates a high degree of autocorrelation (Neter et al. 1996, p. 497). The autocorrelation in the case of Eq. 1 derives from the inability of the regression model to account for other fac-

tors that apparently influence the fit of the equation to the stem taper data. An alternative approach for evaluating the uniform stress hypothesis is to fit Eq. 1 to stem diameters at specific intervals of relative stem height across trees in the data set, similar to fitting Eq. 1 to single measurements of stem diameter and bending moment at breast height across trees. This allows the estimates of ϕ and δ to vary along the stem as necessary and to be unconstrained by diameter at other locations on the stem. The basic statistical criterion for evaluating the uniform-stress hypothesis with stem geometry remains the same, but it extends to a set of fitted δ values instead of a single mean value.

With the exception of *Pseudotsuga menziesii*, the null hypothesis $\delta=0.33$ could not be rejected for a large portion of the stems of *A. lasiocarpa* and *Pinus contorta*, and for nearly every relative-height class for stems of *Pinus taeda* (Fig. 3). The fitted value of δ is statistically less than 0.333 along the lower and upper stem portions for *A. lasiocarpa* and *Pinus contorta* and, to some extent, *Pinus taeda* (Fig. 3). In the *Pseudotsuga menziesii* trees, the fitted value of δ is approximately 20% greater than the theoretical value of δ up to 60% of stem height. Bryant (1950) suggests that deviations in stem geometry from that consistent with uniform bending stress may be attributable to variations in wood mechanical properties as indicated by lower wood specific gravity in the upper part of the stem. Deviation in the value of δ from 0.333 has also been attributed to flexible anchoring in the soil (Newnham 1965).

One and two stem diameters per stem

The values of δ for *Pinus taeda* obtained from fitting Eq. 1 to the data sets with a single measurement of stem diameter at 1.37 m (breast height) are not significantly different than 0.333, regardless of how leaf area is expressed or what season it is measured (Table 4). The estimated value of δ for *Pinus ponderosa* Laws. stems with a single measurement of stem diameter at breast height is significantly different from 0.333, but the difference between the fitted and theoretical value is less than 10%. Residuals of the fits for both *P. taeda* and *P. ponderosa*

Table 4 Statistics of nonlinear curve fits of $Y=\phi X^\delta$, where Y = diameter at 1.37 m (ob, mm) and X = bending moment (m^3 , the product of leaf area and leverage at 1.37 m). Leverage calculated as the distance between midpoint of the live crown and stem height of 1.37 m

Species	ϕ		δ		SE _y (mm)	$H_0: \delta=0.333$ P value
	Est.	SE ^a	Est.	SE		
<i>Pinus taeda</i>						
Summer maximum, all-sided leaf area	29.51	3.80	0.314	0.019	19.37	0.326
Winter minimum, projected leaf area	40.51	0.51	0.330	0.004	6.99	0.445
<i>Pinus ponderosa</i>	31.11	1.69	0.303	0.008	19.86	<0.001

^a SE Standard error

Fig. 3 Fitted values of δ and ϕ for the data sets fit with Eq. 1 by relative height class. Open and filled circles for values of δ indicate significant and non-significant differences in δ from 0.333, respectively. Error bars represent $\delta \pm 1$ SE

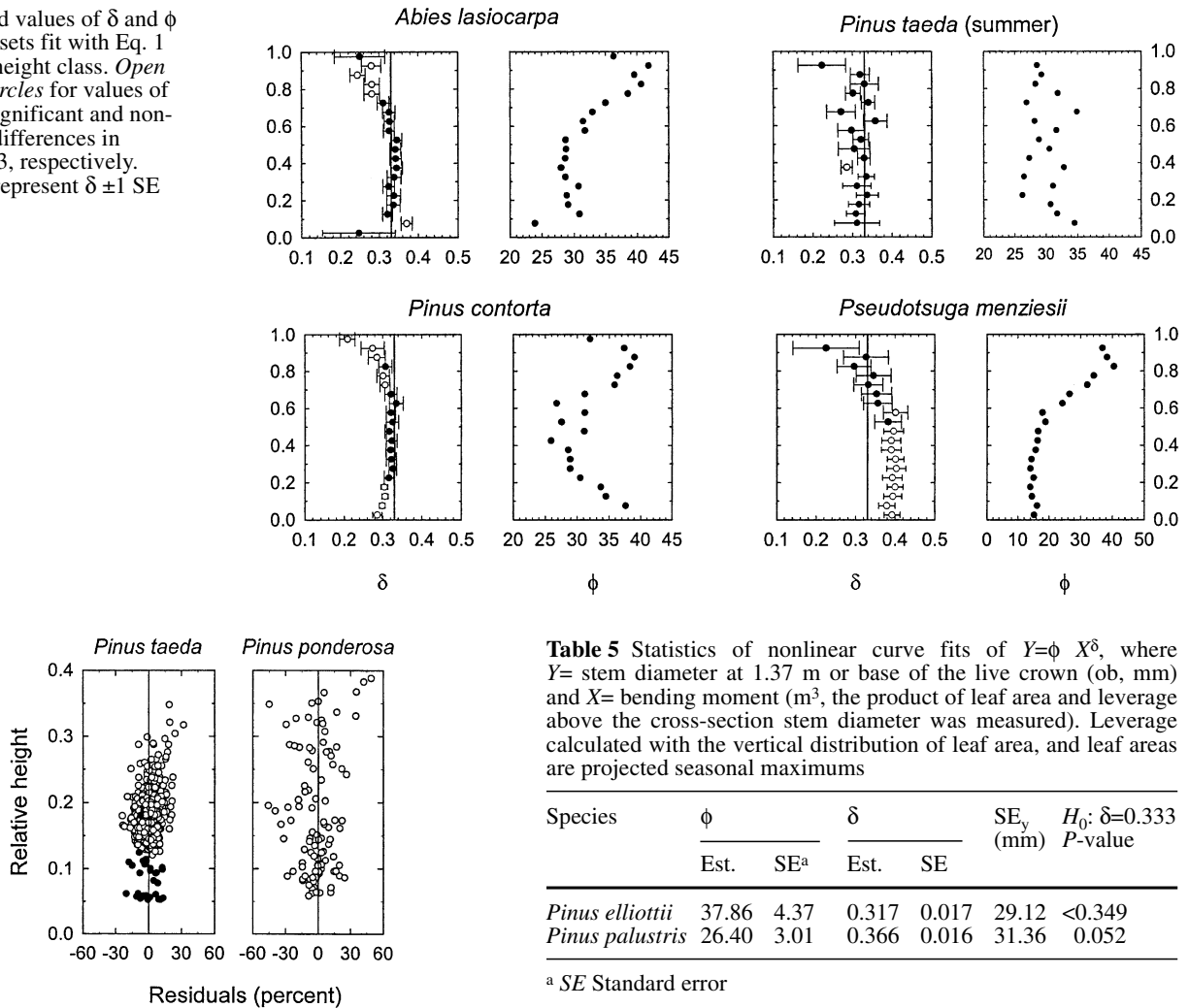


Table 5 Statistics of nonlinear curve fits of $Y=\phi X^\delta$, where Y = stem diameter at 1.37 m or base of the live crown (ob, mm) and X = bending moment (m^3 , the product of leaf area and leverage above the cross-section stem diameter was measured). Leverage calculated with the vertical distribution of leaf area, and leaf areas are projected seasonal maximums

Species	ϕ		δ		SE _y (mm)	$H_0: \delta=0.333$ P-value
	Est.	SE ^a	Est.	SE		
<i>Pinus elliotii</i>	37.86	4.37	0.317	0.017	29.12	<0.349
<i>Pinus palustris</i>	26.40	3.01	0.366	0.016	31.36	0.052

^a SE Standard error

Fig. 4 Residuals (in percent) of the fit of Eq. 1 to the data sets with one measurement of stem diameter at 1.37 m as a function of relative height. In the plot for *Pinus taeda*, open circles represent the data collected during the winter with projected leaf area and filled circles represent the data collected during the summer with all-sided leaf area. Data for *Pinus ponderosa* collected during the summer with all-sided leaf area. Residuals calculated as predicted minus observed

were unbiased with respect to relative tree height, with the exception of smaller *P. taeda* trees where breast height relative to total tree height is greater than about 0.3 (Fig. 4).

The estimated values of δ from fitting Eq. 1 to data with two stem diameter measurements (one at breast height and one at the base of the live crown) for *Pinus elliotii* var. *elliotii* Engelm. and *Pinus palustris* Mill. are both within 10% of the theoretical value of δ (Table 5), although the value for *P. palustris* is significantly greater than 0.333. With stem diameter measured at these two stem positions, residuals of the fits with respect to relative height are difficult to evaluate. Plotted against bending moment, the residuals are largely unbiased, but they reveal a small tendency to underpredict

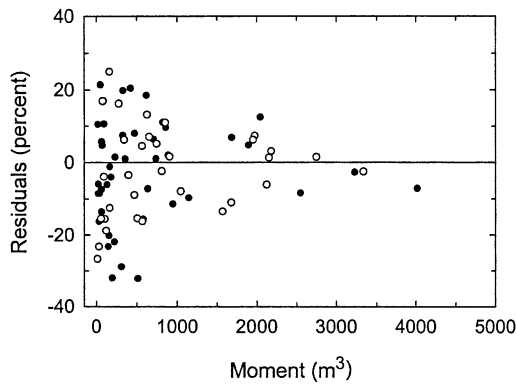


Fig. 5 Residuals (in percent) of the fit of Eq. 1 to the data sets with measurements of stem diameter at 1.37 m and at the base of the live crown. *Open circles* for *Pinus elliottii*, and *filled circles* for *Pinus palustris*. Residuals calculated as predicted minus observed

stem diameter at the higher bending moments for both species (Fig. 5).

The ability of Eq. 1 to predict diameter at breast height and at the base of the live crown indicates a consistent allometry between the vertical distribution of leaf area and stem diameter among the trees in these data sets. In other words, differences in leaf area among trees and resulting wind drag are compensated by stem diameter and the height to the center of leaf area so that internal bending stress generated by a given wind velocity will be uniform among trees. This consistency suggests that trees in superior canopy positions that are exposed to higher wind velocities withstand greater internal bending stresses than trees in inferior canopy positions. Such a consistent allometry among trees also suggests that factors influencing bending moment through effects on the vertical distribution of leaf will have predictable results on average stand diameter. Such a relationship between crown dimensions and average stand diameter has been demonstrated by Dean and Long (1992) for *P. contorta* and between crown dimensions and an index of stand density by Dean and Baldwin (1996) for *P. taeda*.

Fitted values of ϕ

While the uniformity of bending stress along the stem is reflected in the value of δ , the actual stress and curvature at a given stem height is determined by the relative size of the cross-section that is represented by ϕ . According to elementary mechanics, increasing values of ϕ will reduce the bending stress for a given bending moment, and if the stem is composed of a uniform material, the severity or radius of bending resulting from the applied force will be constant. Stems, however, are not composed of uniform material – the modulus of elasticity and a covariate of modulus of elasticity, specific gravity, generally decrease with stem height (Bryant 1950; Spatz and Bruechert 2000). Simply stated, the modulus of elas-

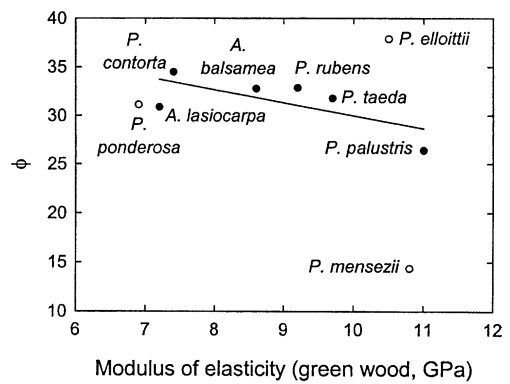


Fig. 6 Fitted values of ϕ as a function of the published value of the modulus of elasticity (E) for green wood. Equation for line fit with ordinary least squares is $\phi = 43.35 - 1.34 \cdot E$ ($r^2 = 0.48$) for data represented with *filled circles*. Values of ϕ for *Abies lasiocarpa*, *Pinus contorta*, *Pinus taeda*, and *Pseudotsuga menziesii* is the value determined at 12.5% of relative height (cf., Fig. 3).

ticity is a measure of flexibility, and if the modulus of elasticity in these trees decreases with height, maintenance of a constant bending curvature would require increasing values of ϕ with height as was observed for *A. lasiocarpa*, *Pinus contorta*, and *Pseudotsuga menziesii* (Fig. 4). Modulus of elasticity in juvenile stems may not vary sufficiently for the fitted value of ϕ to decline with height. The oldest *Pinus taeda* trees measured in the summer were 15-years old when measured, and in a plantation setting, a large portion of the xylem in these trees was probably immature (c.f. Clark and Saucier 1989). The fitted value of ϕ for this data set was effectively constant with height. This, however, does not seem to apply to the *Pseudotsuga menziesii* trees included in this study. These trees ranged in age from 10 to 28 years, which should have included trees with predominantly immature xylem, and yet, the fitted values of ϕ in these trees increase with relative height.

While upper stem measurements of modulus of elasticity were not included in these data sets, moduli of elasticity of boards cut from boles of these species have been measured by the United States Forest Products Laboratory (1974). If the value of ϕ is involved in maintaining bending curvature within certain biological limits, the fitted values of ϕ should be inversely related to the modulus of elasticity. The modulus of elasticity measured for green wood is linearly related to the fitted values of ϕ for *A. balsamea*, *A. lasiocarpa*, *Picea rubens*, *Pinus contorta*, *Pinus palustris*, and *Pinus taeda* (Fig. 6). This suggests that bending curvature may be uniform across species. The value of ϕ for *Pinus ponderosa* also appears related to the modulus of elasticity, but this value was not included in the regression since it was based on all-sided leaf area. The extraordinary values of ϕ for *Pseudotsuga menziesii* and *Pinus elliottii* are also not included in the regression. The high value of ϕ for the *Pinus elliottii* trees may be due to unusual wind exposure, and the low value of ϕ for *Pseudotsuga menziesii* appears to be associated with its extraordinarily high

Table 6 Statistics for multiple linear regression of the model $\phi = \beta_0 + \beta_1 \cdot \delta + \beta_2 \cdot H$, where ϕ and $\delta =$ respective values in Eq. 1 fit to data from individual trees with multiple measurements of stem diameter, $H =$ total tree height, and $\beta_0 - \beta_2$ are regression coefficients

Species	β_0	β_1	β_2	$H_0: \beta_2=0,$ P -value	R^2
<i>Abies balsamea</i>	56.980	-73.410	-0.285	0.157	0.460
<i>Abies lasiocarpa</i>	55.840	-74.450	0.222	0.223	0.400
<i>Picea rubens</i>	60.980	-131.830	0.591	0.009	0.810
<i>Pinus contorta</i>	46.490	-29.040	0.0940	0.437	0.010
<i>Pinus taeda</i> (summer)	10.970	52.470	-0.081	0.724	0.200
<i>Pinus taeda</i> (winter)	43.150	-46.170	0.1000	0.558	0.460
<i>Pseudotsuga menziesii</i>	70.660	0.802	0.802	0.002	0.680
Overall	48.170	0.308	-62.4000	<0.001	0.288

values of δ when fit by classes of relative height. The *Pinus elliottii* trees used in this study were sampled from a stand that had been thinned heavily and repeatedly throughout its existence; thus, they were essentially open grown without neighboring crowns to attenuate ambient wind velocities (S.B. Jack, personal communication). If wind exposure increases the inherent flexibility of the stem as suggested by the studies of Telewski and Jaffe (1986), increased stem diameter would be necessary to regulate bending curvature. Such an increase in diameter would be reflected in the value of ϕ . Greater wind exposure may also explain the difference in the two fitted values of ϕ for the *Pinus taeda* data collected during the winter (compare winter values for *P. taeda* in Tables 3, 4). The site where only a single stem diameter was measured was severely nutrient deficient, and the low leaf areas reported by Albaugh et al. (1998) may not have been high enough for the trees to mutually support each other. The site where multiple stem diameters were measured was of average quality, and the trees growing on this site were large enough to support each other against the wind. The fitted value of ϕ for the trees growing on the nutrient deficient site was 44% greater than the fitted value of ϕ for the trees growing on an average site for *P. taeda*.

Further evidence suggesting an effect of wind exposure on the value of ϕ is found in the differences in the fitted value of ϕ among various classes of exposure and crown position for *A. balsamea*. The mean value of ϕ for open-grown *A. balsamea* trees is significantly greater than mean values of ϕ for the other crown classes ($P < 0.001$), and the fitted value of ϕ for the largest of the open-grown *A. balsamea* trees was 23% greater than the mean of the other open-grown trees combined.

If the value of ϕ is influenced by wind exposure, the value of ϕ fitted for individual tree stems may be positively related to tree height. Multiple regression of individual trees values of ϕ regressed against tree height and the fitted value of δ does show a significantly positive relationship between ϕ and tree height (Table 6). (Values of δ are included in the regression model because of the high correlation between the exponent and the constant in simple power functions.) The relationship is weak, however, explaining only 29% of the variation in ϕ . By species, significant relationships between ϕ and tree height exist only for *Pseudotsuga menziesii* and *Picea rubens*. For the majority of the species and situations in-

cluded in this study, no relationship between the two variables is apparent. These results suggest that large differences in the wind exposure must exist to produce detectable differences in the value of ϕ .

Summary and conclusions

Seven of 12 estimates of δ in this study are statistically different than 0.333, the value consistent with the uniform stress hypothesis. However, 8 of the values of δ are within 10% of the theoretical value, and all but one of the fitted values of δ are within 15% of the theoretical value. Since a 10% deviation in the value of δ results in less than a 10% deviation in the stem diameter that would produce uniform bending stress within most of the stem, the uniform stress hypothesis closely describes stem taper for a majority of the species in this study and is a suitable approximation for three other species. The only species that clearly does not conform to the uniform stress hypothesis is *Pseudotsuga menziesii*.

The species used in this study were selected on the basis of available data. The variation and anomalies between the observed and ideal stem geometries found in this study is probably no different than the results that would be obtained with species selected at random. Regardless of how the species were selected, agreement with the hypothesis varied with species, indicating that additional species must be analyzed before the uniform stress hypothesis can be generally accepted.

The fit of Eq. 1 to the trees examined is unbiased across stem height when the difference between the theoretical and fitted values of δ is less than 10%. With greater deviations between the fitted and theoretical values of δ , the fit is biased over stem height. In three of the species, the bias appears to be due to increasing values of ϕ within the upper portions of the stem. Such increases in ϕ may be associated with greater stem flexibility within this portion of the stem and may indicate that stem diameter may serve to constrain wind-induced curvature within certain biological limits. Stem flexibility is indicated by the modulus of elasticity, and the fitted value of ϕ for various species in this study is inversely related to the reported values of modulus of elasticity of green wood for these species.

The results of this study lend support to the hypothesis of Wilson and Archer (1979) who suggested that

maintenance of bending strain may be a more general principle of stem formation than maintenance of uniform bending stress. Many plant processes function to minimize or regulate biological strain especially when a stress cannot be avoided; coarse adjustment of stem diameter to minimize or regulate the radius of curvature is a logical addition to the list of regulatory processes. When stem flexibility is fairly uniform along the stem, taper conforms to the uniform stress hypothesis. When stem flexibility increases substantially with stem height, maintenance of stem curvature may cause stem taper to deviate from what the uniform stress hypothesis predicts.

Individual tree leaf area and crown structure are determined by the proximity and relative size of the neighbors. These variables change with age and stand dynamics. The uniform stress hypothesis provides a means of translating these canopy dynamics into changes in stem size, especially when the hypothesis is applied to a given stem position where the modulus of elasticity is relatively constant among trees. With the additional understanding that stem diameter and flexibility may combine to produce a constant bending behavior, direct links between canopy dynamics, physiological processes, and stem growth may be possible, providing further quantitative insights into stand development from basic engineering principles apparent in stem form and size.

Acknowledgements We thank those that graciously allowed us to use their data: Drs. S.B. Jack and R.J. Mitchell of the Joseph E. Jones Ecology Center in Ichauway, Ga. for *Pinus elliotii* and *Pinus palustris* data; Dr. V.C. Baldwin Jr of the USDA Southern Research Station for *Pinus taeda* data; and Drs. Johnsen and H.L. Allen for the *P. taeda* data from the Southern Trees Research and Education Site (SETRES), a cooperative research effort between the USDA Southern Research Station and the North Carolina State University Forest Nutrition Cooperative. This work was supported with McIntire-Stennis funding to the Louisiana State University Agricultural Center.

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