

Predicting branch diameters on second-growth Douglas-fir from tree-level descriptors

Douglas A. Maguire, Stuart R. Johnston, and James Cahill

Abstract: The quality of lumber and veneer recovered from logs of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is directly influenced by the maximum limb size attained on the crop tree. Because limb sizes are influenced by stand-density regimes, a need has arisen for quantitative tools that link a wide array of silvicultural regimes to wood-product quality by accounting for silvicultural effects on crown development. An equation for estimating maximum branch size at a given level within the live crown was developed from data collected on 96 felled sample trees in the Coast Ranges and Cascade foothills of Oregon and Washington. Height and basal diameter of the largest branch within each live whorl were measured on each felled tree, and a predictive equation was developed by various regression techniques. The final mixed-effects nonlinear model estimates maximum branch size as a function of depth into crown and tree diameter at breast height, height, and live crown length.

Résumé : La qualité du bois scié et du contreplaqué tirés des billes de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) est directement liée à la dimension maximale des branches sur les arbres récoltés. Étant donné que la dimension des branches est influencée par les régimes de densité des peuplements, il est devenu nécessaire d'avoir un outil quantitatif qui relie une vaste gamme de régimes sylvicoles à la qualité des produits du bois en tenant compte des effets de la sylviculture sur le développement de la cime. Une équation servant à estimer la dimension maximale des branches à un niveau donné dans la cime vivante a été développée à partir des données recueillies sur 96 arbres échantillons abattus dans la chaîne côtière et au pied de la chaîne des Cascades dans les États de l'Oregon et de Washington. La hauteur et le diamètre à la base de la plus grosse branche dans chaque verticille vivant ont été mesurés sur chaque arbre abattu et une équation de prédiction a été développée en utilisant diverses techniques de régression. Le modèle final, un modèle non linéaire à effets mixtes, permet d'estimer la dimension maximale des branches en fonction de la profondeur dans la cime, de la hauteur et du diamètre à hauteur de poitrine de l'arbre, et de la longueur de cime vivante.

[Traduit par la Rédaction]

Introduction

Branch diameters on individual logs have a strong influence on lumber and veneer grade recovery in young-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Fahey et al. 1991). One index of branch size for individual logs is the average of the largest diameter in each radial quadrant of the log, hereafter referred to as LLAD. In logs with an LLAD of 2.5 cm (1 in.), for example, the volume of No. 1 and Select Structural lumber averaged 35% of the total recovered volume but dropped to less than 10% when LLAD increased to 4.4 cm (1.75 in.) (Fahey et al. 1991). It is important to recognize that, despite current log grading criteria that entail discrete grade breaks in the Pacific Northwest and elsewhere, lumber grade recovery is a continuous function of LLAD, regardless of whether lumber is graded visually or machine-stress rated. Hence, even a small increase in average branch size has a deleterious effect on the quality of

lumber recovered from trees and logs. Furthermore, this relationship suggests that log grades defined in part by relatively coarse breaks in branch size do not reflect more subtle differences in tree attributes and log quality resulting from alternative management regimes under intensive silviculture. In fact, it is common practice in the Pacific Northwest to sort and market logs by finer quality distinctions than those delineating conventional grades.

Although branch diameter is highly correlated with product grade recovery, managers have had few quantitative tools available for linking silvicultural practices (e.g., initial spacing, thinning regime, harvest age) to branch development. Because it is impractical to measure branch diameters on standing or even felled trees, it would be helpful to have a technique for estimating branch diameters by exploiting their correlation with more easily measured tree-level dimensions such as diameter at breast height (DBH), height, and crown length. Silvicultural treatments have been shown to profoundly impact crown development (Curtis and Reukema 1970), and many stand simulators include crown length (or height to crown base) as an integral part of the prediction system (e.g., Hann et al. 1994). Numerous equations have been developed for estimating maximum branch diameter from standard tree dimensions, both for branch whorls near the crown base (Maguire et al. 1988, 1991) and for whorls throughout the crown (Colin and Houllier 1991; Maguire et al. 1994; Roeh and Maguire 1997). The latter models have typically been derived as segmented polynomials, and the

Received January 15, 1999. Accepted June 13, 1999.

D.A. Maguire.¹ Department of Forest Resources, Oregon State University, Corvallis, OR 97331, U.S.A.

S.R. Johnston. USDA Forest Service, Siuslaw National Forest, P.O. Box 67, Mapleton, OR 97453, U.S.A.

J. Cahill. Ross Complex, Bonneville Power Administration, TNF-Ampu 1, P.O. Box 491, Vancouver, WA 98666, U.S.A.

¹Corresponding author. e-mail: doug.maguire@orst.edu

Table 1. Distribution of the 96 sample trees by DBH and plot relative density (Curtis 1982).

Relative density (m ² ·ha ⁻¹ ·cm ^{-0.5})	Number of trees by DBH class (cm)			
	15–40	40–60	60–86	Total
<5	7	9	5	21
5–8	20	18	10	48
>8	14	10	3	27
Total	41	37	18	96

models developed to date for Douglas-fir in western North America have been applicable either to only relatively young trees (Maguire et al. 1994; Roeh and Maguire 1997) or to only whorls at crown base (Maguire et al. 1988, 1991). The primary objective of the research reported here was to develop a more comprehensive model for predicting maximum branch diameters across the size range of Douglas-fir typically encountered in managed second-growth stands of the Coast Range and Cascade Mountains in Oregon and Washington. The secondary objective was to investigate the relative performance of some alternative model forms, including models that explicitly recognize multiple observations from individual subject trees.

Methods

Study area and data collection

All plots were located within the Western Hemlock Zone of western Oregon and Washington (Franklin and Dyrness 1973), ranging from Olympia, Wash., in the north (47°00'N) to Oakridge, Oreg., in the south (43°45'N). Plots were equally distributed between the Coast Range and lower elevations of the Cascade Mountains. Sample stands were selected to represent a wide array of stocking levels and different stages of development for managed, even-aged stands of Douglas-fir, including both naturally regenerated and planted stands. The 48 sample plots were randomly located in those portions of the stands with relatively uniform stocking, and stands with evidence of any disease or recent density management were avoided. If a candidate stand had been thinned it was required to have resumed crown recession, thereby providing evidence that crown length and stand density were in dynamic equilibrium (that is, crown lengths represented the maxima possible for the current stand density). All trees were measured for DBH (nearest 0.1 cm) on variable radius plots of basal area factor (BAF) 4.6 m²·ha⁻¹ (20 ft²·acre⁻¹). Sample plots ranged in relative density (Curtis 1982) from 3.0 to 13.0 m²·ha⁻¹·cm⁻² (6.8–90.0 ft²·acre⁻¹·in.⁻²) and in quadratic mean diameter from 22 to 72 cm (Tables 1 and 2). A subsample of heights was measured to meet standards for estimating King's (1966) site index, which ranged from 34 to 48 m at 50 years (Table 2).

The first Douglas-fir tree on each plot encountered in moving clockwise from true north and the first tree encountered in moving clockwise from true south were sampled. Three attributes were recorded for each tree: (i) height to crown base, HCB (nearest 0.1 m), defined as the lowest whorl that both contains at least one live branch and is contiguous with other live whorls forming the main crown;

Table 2. Means and ranges for various branch, tree, and stand attributes.

Attribute	Min.	Mean	Max.
Branch (n = 2056)			
Branch diameter (cm)	0.3	3.2	8.2
Branch height (m)	2.37	24.74	51.60
Depth into crown (m)	0.34	10.05	33.10
Relative depth into crown	0.02	0.51	1.00
Tree (n = 96)			
Breast height age (years)	20	42	74
DBH (cm)	19.6	44.8	89.9
Total height (m)	18.22	34.20	55.10
Crown length (m)	10.20	19.22	33.10
Height to crown base (m)	1.10	14.97	31.30
Crown ratio	0.36	0.58	0.95
Stand (n = 48)			
Quadratic mean diameter (cm)	21.8	39.6	72.4
Trees/ha	88	438	1106
Relative density (m ² ·ha ⁻¹ ·cm ^{-0.5})	3.00	6.96	12.96
Site index (m at 50 years; King 1966)	33.8	40.7	47.9

(ii) breast height age; and (iii) total height, THT (nearest 0.1 m). Height of attachment (nearest 0.1 m) and basal diameter (nearest mm) of the largest live branch were measured on every whorl between full crown base and the tip of the tree. Branch basal diameter was measured by caliper on both the vertical and horizontal axes (relative to the standing tree) at distance from the bole equal to approximately one branch diameter. All analyses were based on the geometric mean diameter (BD) of the horizontal and vertical measurements.

Data analysis

Numerous regression models were explored for predicting maximum branch diameter at a given depth into live crown (DINC; see Table 3 for variable definitions). Other tree, stand, and site variables were added to improve prediction accuracy for individual trees (Table 3). The models screened included log–log models, weighted and unweighted linear models, and weighted and unweighted nonlinear models with various combinations of predictor variables. Models were compared by a modified likelihood criterion (Furnival 1961), which is equivalent to the root mean squared error (RMSE) for untransformed BD and a rescaled RMSE for weighted or transformed BD. Residuals were also plotted against relative depth into crown to assess the efficacy of each model in depicting trends in maximum branch diameter through the crown.

For comparison to earlier analyses, the model presented by Maguire et al. (1991) was refitted to the new data:

$$[1a] \quad \ln(\text{BD}) = \alpha_0 + \alpha_1 \times \ln(\text{DINC}) + \alpha_2 \times \ln(\text{DBH}) \\ + \alpha_3 \times \ln(\text{RD}) + \alpha_4 \times \text{SITE} + \varepsilon$$

where α_0 – α_4 are parameters to be estimated from the data and ε is a random error or disturbance. This model was monotonic increasing with depth into crown (DINC). In contrast, Colin and Houllier (1991) demonstrated a peaking behavior of maximum branch diameter over DINC in

Table 3. Variables used or tested in developing regression models for predicting maximum branch diameter at different positions in the crown.

Variable	Definition
BD	Diameter of largest whorl branch (cm)
SITE	Site index (m at 50 years; King 1966)
RD	Curtis' (1982) relative density (plot basal area/(quadratic mean diameter) ^{0.5})
THT	Total tree height (m)
DINC	Depth into crown, or distance from tree tip to branch base (m)
DBH	Diameter at 1.37 m from ground (cm)
HCB	Height to crown base (m)
CL	Crown length (m) = THT – HCB
CR	Crown ratio (CL/THT)
<i>h</i>	Height of whorl branch above crown base (m)
RDINC	Relative depth into crown, DINC/CL

Norway spruce (*Picea abies* (L.) Karst.) and modeled this behavior with a segmented-polynomial model. Because a similar behavior has been observed in Douglas-fir (Maguire et al. 1994; Roeh and Maguire 1997), various segmented-polynomial models were fitted to the data as one set of alternative model forms. The basic model was a quadratic-quadratic model (Max and Burkhart 1976) over DINC with a join point at β_4 , interpretable as a specific relative depth into the crown. The basic model form was

$$[2a] \quad BD = \beta_1 \times DINC + \beta_2 \times DINC^2 + \beta_3 \times I \\ \times (\beta_4 - DINC/CL)^2 + \epsilon$$

where

$$I = \begin{cases} 0, & \text{if } [DINC/CL - \beta_4] < 0 \\ 1, & \text{if } [DINC/CL - \beta_4] \geq 0 \end{cases}$$

where β_1 – β_4 are parameters to be estimated from the data, CL is crown length, and ϵ is as defined above. Additional models were explored in which the parameters β_1 , β_2 , and β_3 were considered as functions of other tree attributes, including DBH, THT, crown ratio (CR), THT/DBH, and CL. Because the join point was estimated from the data, all segmented models were fitted by weighted nonlinear least squares.

A function developed by Kozak (1988, 1997) for describing stem taper was also modified for application to the trend in branch diameter over height within the crown. In this approach, branch diameters for a specific tree were expressed as a proportion of the predicted maximum branch diameter attainable for a tree of given DBH, height, and CL. The model form was developed by assuming that the maximum branch diameter for a whorl was a nonlinear function of predicted maximum crown width or, in a sense, that branch diameter and branch length were functionally related:

$$[3] \quad MBD = g_1 CW^{g_2}$$

where MBD is the estimated maximum branch diameter for the tree (cm), CW is the stand-grown maximum crown width (m) ($CW = MCW \times CR^{0.014 \ 315 \ 09 \ CL + 0.072 \ 240 \ 24 \ DBH/THT}$; Hann 1997), MCW is the open-grown maximum crown width (m) ($MCW = 1.4081 + 0.5616DBH - 0.003 \ 448 \ DBH^2$; Paine

and Hann 1982), and g_1 and g_2 are parameter estimates. The general form of the model for estimating largest crown width of a stand-grown tree has been applied previously (Ritchie and Hann 1985; Maguire 1994; Dubrasich et al. 1997), but parameter estimates in this analysis were taken from an equation developed for Douglas-fir in western Oregon (Hann 1997).

Given MBD, the equation for describing the trend in branch diameter over depth into crown could be expressed as

$$[4] \quad \frac{BD}{MBD} = X^C + \epsilon$$

where $X = (1 - Z^{0.5})/(1 - p^{0.5})$, $Z = h/CL$, $p = f(DBH, THT, CR)$, h is height of branch from crown base (m), ϵ is random error or disturbance, and C was a function of various transformations of branch position (Z) and tree descriptors such as DBH, THT, CL, CR, HCB, DBH/THT, and THT/DBH. This model was initially introduced into the forestry literature as a variable-exponent stem taper model in which the ratio X is formulated to range between zero at the tip of the tree and one at relative height p (Kozak 1988). In the present application, branch diameter is constrained to equal zero at tree tip and predicted maximum branch diameter (MBD) at relative height p . Because p was designed to represent the relative height of the largest branch, it was expected to vary by CR and (or) other tree dimensions; hence, an equation was developed from the data to express p as a function of subject tree dimensions. Finally, substitution of eq. 3 into eq. 4 and rearranging provided a potentially more flexible model form:

$$[5a] \quad BD = \gamma_1 CW^{\gamma_2} X^C + \epsilon$$

where BD, CW, X , and C are defined as above and γ_1 and γ_2 are parameters to be estimated from the data. Relative performance of different predictor variable combinations was assessed by an all-subsets regression on a logarithmically transformed model, followed by selection and fitting of corresponding nonlinear models that exhibited biologically reasonable behavior. All alternative models were compared by Furnival's (1961) index of fit.

The models developed from these static data offer unbiased estimates of maximum branch sizes by crown position; however, allowance for a decrease in branch diameter near crown base could potentially cause successive estimates of

maximum branch diameter in a given whorl to decline over time under some conditions. In fact, preliminary tests of some segmented-polynomial equations in the growth model ORGANON (Hann et al. 1994) indicated that this decline over time may occur as an artifact of the model form. Although this behavior is clearly not realistic, too little is known at present about the growth dynamics of individual branches to guide development of a sufficiently detailed prediction equation to apply in a dynamic context. In the interim, an alternative prediction equation was developed by constraining estimated branch diameter to be monotonic increasing over depth into crown. This constraint was achieved by holding p in eq. 4 equal to zero and by requiring the function, C , in eq. 4 to be a nonlinear function of Z :

$$[6a] \quad \text{BD} = \lambda_1 \text{CW}^{\lambda_2} \text{W}^C + \varepsilon$$

where $W = (1 - Z^{0.5})/(1 - p^{0.5})$; $Z = h/\text{CL}$; $p = 0$; λ_1 and λ_2 are parameters to be estimated from the data; and BD , CW , and C are defined as above. Predictions from this equation are potentially biased near the crown base for any given year but are expected to yield accurate trends in maximum branch diameter as the crown recedes up the bole in a simulation context (see Maguire et al. 1991).

Multiple observations of branch diameter were collected from each of the 96 sample trees (average of 21 observations per tree); hence, the data violated the assumption of independence and zero autocorrelation. Therefore, final models were fitted as nonlinear mixed-effects models (Goldstein 1995; Davidian and Giltinan 1995; Pinheiro and Bates 1995), using PROC NLMIXED in Release 7 of SAS (Wolfinger 1999). One way that these models can accommodate the potential autocorrelation in the data and, thereby, provide valid tests on model parameters, is to take a random parameters approach to random tree-level effects. Gregoire et al. (1995) and Tasissa and Burkhart (1998) have demonstrated the application of mixed-effects models to repeated-measure and hierarchical (multilevel) data in forestry. The structure of the branch diameter data described above was simpler than the data structure characterizing these previous applications since trees were not measured repeatedly over time. Plots of residuals on a tree-by-tree basis and trials with alternative random effect formulations suggested that equations 1a, 2a, 5a, and 6a could be generally written as

$$[1b] \quad \ln(\text{BD})_i = \mathbf{S}_i \boldsymbol{\alpha} + \mathbf{A}_i \boldsymbol{\delta}_i + \boldsymbol{\varepsilon}_i$$

$$[2b] \quad \text{BD}_i = f(\mathbf{T}_i, \boldsymbol{\beta}, \mathbf{B}_i, \boldsymbol{\delta}_i) + \boldsymbol{\varepsilon}_i$$

$$[5b] \quad \text{BD}_i = g(\mathbf{U}_i, \boldsymbol{\gamma}, \mathbf{C}_i, \boldsymbol{\delta}_i) + \boldsymbol{\varepsilon}_i$$

$$[6b] \quad \text{BD}_i = h(\mathbf{V}_i, \boldsymbol{\lambda}, \mathbf{D}_i, \boldsymbol{\delta}_i) + \boldsymbol{\varepsilon}_i$$

where BD_i is a $j \times 1$ vector of branch diameters observed on tree i ; \mathbf{S}_i is a $j \times p$ matrix of fixed-effect covariates; $\boldsymbol{\alpha}$ is a $p \times 1$ vector of fixed parameters; f , g , and h are nonlinear functions; \mathbf{T}_i , \mathbf{U}_i , and \mathbf{V}_i are $j \times k$ matrices of fixed-effect covariates, where k is variable from equation to equation; $\boldsymbol{\beta}$, $\boldsymbol{\gamma}$, and $\boldsymbol{\lambda}$ are $m \times 1$ vectors of fixed parameters, where m varies from equation to equation; \mathbf{A}_i , \mathbf{B}_i , \mathbf{C}_i , and \mathbf{D}_i are $j \times q$ matrices of random-effect covariates, where q varies from equation to equation; $\boldsymbol{\delta}_i$ is an $r \times 1$ vector of random parameters with $\boldsymbol{\delta}_i \sim N(\mathbf{0}, \mathbf{M}_i)$; and $\boldsymbol{\varepsilon}_i$ is a $j \times 1$ vector of random errors with $\boldsymbol{\varepsilon}_i \sim N(\mathbf{0}, \mathbf{R}_i)$. In this particular application, $r = 1$ so

$\boldsymbol{\delta}_i$ is a scalar and it is assumed that $\boldsymbol{\delta}_i \sim N(0, \sigma_u^2)$. After accounting for this random tree effect, subjective evaluation of residuals suggested it was reasonable to assume that $\boldsymbol{\varepsilon}_i \sim N(\mathbf{0}, \sigma_e^2 \mathbf{I})$. Models with alternative sets of fixed covariates and with alternative formulations of random tree effects were compared by Akaike's information criterion (AIC), and nested models were compared by likelihood ratio tests (LRT). Equations 1b, 2b, 5b, and 6b were also evaluated on the basis of residual plots, with emphasis on residuals plotted against relative depth into crown to assess the efficacy of each model in depicting trends in maximum branch diameter through the crown.

Validation

Relative performance of the segmented-polynomial (eq. 2b) and variable-exponent models (eqs. 5b and 6b) was evaluated on three independent data sets. The first data set (SMC) was assembled by the Pacific Northwest Stand Management Cooperative for relatively young Douglas-fir trees (see Maguire et al. 1994), the second data set (ODF) was generated as part of a wood-quality study conducted by the Oregon Department of Forestry (B. Voelker, personal communication), and the third (SWOR) served as the database for a branch prediction model for southwestern Oregon Douglas-fir (Maguire et al. 1991). The SMC data set consisted of maximum whorl branch diameters and corresponding heights on individual Douglas-fir trees sampled from the Coast Range and Cascade foothills. The ODF data set contained the diameter and height of the largest branch in each quadrant of individual trees sampled from the Elliott State Forest, located in the Coast Range of Oregon. The SWOR data set was constructed by measuring the diameter and height of the branch corresponding to the maximum crown radius in each of the four cardinal directions. Validations were conducted visually by plotting the differences between observed and predicted branch diameters on relative depth into crown.

Results

Parameter estimates for the model reported by Maguire et al. (1991) and refitted to the new data were similar to those previously estimated, but neither relative density nor site index had a significant additional effect on branch diameter (Table 4).

The following four-variable model was selected as the best segmented-polynomial equation for predicting maximum branch diameters within the crowns of second-growth Douglas-fir trees:

$$[2c] \quad \text{BD}_{ij} = \beta_{21} \times \text{DINC} + \beta_{22} \times \text{DBH} \times \text{DINC} \\ + \beta_{23} \times \text{DINC}^2 + \beta_{24} \times \text{CL} \times I((\beta_{25} \times \text{CL}) \\ - \text{DINC}/\text{CL})^2 + \delta_i \times \text{RDINC} + \boldsymbol{\varepsilon}_{ij}$$

This model was weighted by DINC^{-1} to ensure conformity to the regression assumption of constant variance. Total height and DBH were inserted into the basic model (eq. 2b) to account for systematic variation in maximum branch diameter trends among trees of differing size (Table 5). As measured by a generalized coefficient of multiple determina-

Table 4. Parameter estimates and standard errors for eq. 1b (model form applied by Maguire et al. (1991)).

Parameter	Estimated value	SE
α_0	-1.229 324	0.209 020
α_1	0.568 053	0.005 038
α_2	0.311 746	0.039 956
α_3	-0.011 452 9 ^{ns*}	0.035 481 7
α_4	-0.000 529 98 ^{ns}	0.003 914 73
σ_u^2	0.014 642 1	0.002 383
σ_e^2	0.035 549 7	0.001 135

*ns, not significantly different from zero ($\alpha = 0.05$).

Table 5. Parameter estimates and standard errors for the best segmented-polynomial model (eq. 2c).

Parameter	Estimated value	SE
β_{21}	0.557 3	0.013 74
β_{22}	0.002 923	0.000 252
β_{23}	-0.039 33	0.000 73
β_{24}	0.001 074	0.000 031
β_{25}	0.194 2	0.008 7
σ_u^2	0.542 6	0.084 6
σ_e^2	0.168 3	0.005 4

tion (R_g^2 ; Kvålseth 1985), approximately 97% of the variation in branch diameter was accounted for by the model ($R_g^2 = 0.97$).

Equation 3 was weighted by CW^{-1} to correct for nonconstant variance. The regression relationship between maximum branch diameter and predicted crown width was highly significant ($P < 0.001$) and apparently nonlinear, since g_2 was marginally different from one ($p \approx 0.057$, $F_{[1,94]} = 3.69$ for $g_2 = 1$ vs. g_2 free; also see Table 6). Equation 5 invariably performed better than eq. 4 as judged by Furnival's (1961) index, so models resulting from scaling BD to predicted MBD as depicted in the latter model were not explored further. The two final Kozak models were fitted by weighted nonlinear least squares, applying a weight of $DINC^{-1}$. Resulting parameter estimates were applied as initial estimates in nonlinear mixed-effects models. All parameters for each model (γ_1 - γ_6 and λ_1 - λ_4) were estimated simultaneously by minimizing the negative log likelihood function in the final mixed-effects models (Wolfinger 1999). In the first model, C was a nonlinear function of Z :

$$[5c] \quad BD_{ij} = (\gamma_{11}CW^{\gamma_{12}} + \delta_i)X^C + \epsilon_{ij}$$

where $C = \gamma_{13}Z^{\gamma_{14}}$, $p = \gamma_{15}CR^{\gamma_{16}}$, and X and Z are defined as above. In the second model, C was a linear function of Z and exponentiated DBH/THT ratio:

$$[5d] \quad BD_{ij} = (\gamma_{21}CW^{\gamma_{22}} + \delta_i)X^C + \epsilon_{ij}$$

where $C = \gamma_{23}Z + \gamma_{24}e^{-DBH/THT}$, $p = \gamma_{25}CR^{\gamma_{26}}$, and X and Z are defined as above. Parameters γ_{11} - γ_{16} and λ_{21} - λ_{26} were all

Table 6. Parameter estimates and standard errors for the maximum branch diameter model (eq. 3).

Parameter estimate	Estimated value	SE
g_1	0.405 987	0.060 879
g_2	1.158 207	0.071 340

Table 7. Parameter estimates and standard errors for the unconstrained and constrained Kozak models (eqs. 5c, 5d, and 6c).

Parameter	Estimated value	SE
Equation 5c		
γ_{11}	0.3520	0.0427
γ_{12}	1.1580	0.0556
γ_{13}	0.6869	0.0147
γ_{14}	1.3290	0.1023
γ_{15}	0.5126	0.0286
γ_{16}	0.5587	0.1063
σ_u^2	0.1810	0.0280
σ_e^2	0.1620	0.0052
Equation 5d		
γ_{21}	0.3513	0.0431
γ_{22}	1.1635	0.0562
γ_{23}	0.6912	0.0157
γ_{24}	-0.1715	0.0811
γ_{25}	0.5225	0.0281
γ_{26}	0.6567	0.1452
σ_u^2	0.1883	0.0295
σ_e^2	0.1629	0.0052
Equation 6c		
λ_1	0.3676	0.0439
λ_2	1.1501	0.0548
λ_3	0.5569	0.0109
λ_4	2.7096	0.0826
σ_u^2	0.1839	0.0285
σ_e^2	0.1669	0.0053

significantly different from zero ($\alpha = 0.05$; Table 7), and both variable-exponent models were superior to the segmented-polynomial model as judged by AIC (Table 8). Likelihood ratio tests indicated that (i) both γ_{16} and γ_{26} were significantly different from one ($P < 0.005$ and $P = 0.042$, respectively) and (ii) both eqs. 5c and 5d were significantly improved by allowing p to vary by CR rather than holding it constant ($P < 0.005$ in both cases).

Maximum BD peaked only slightly higher in the segmented-polynomial model, at approximately 80 versus 90% of DINC for variable-exponent eqs. 5c and 5d (Fig. 1). On

Fig. 1. Trend in maximum whorl branch diameter (BD) over depth into crown (DINC) for (a) a small tree, (b) a medium-sized tree, and (c) a large tree. Curves represent predictions from five different models: (i) swor, original equation form reported by Maguire et al. (1991) for southwestern Oregon (eq. 1b); (ii) seg, best segmented-polynomial model (eq. 2c); (iii) varexpZ, unconstrained variable-exponent model (eq. 5c); (iv) varexpDH, unconstrained variable-exponent model (eq. 5d); and (v) cvarexp, constrained variable-exponent model (eq. 6c).

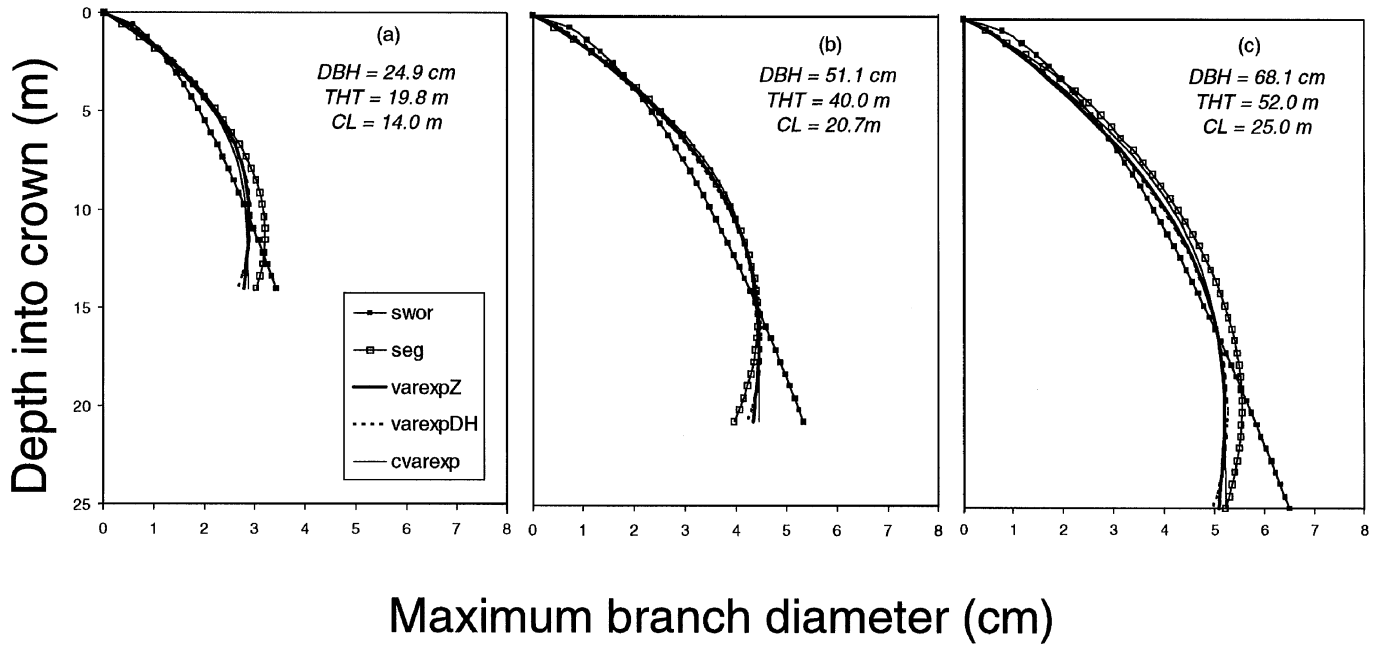


Table 8. Akaike’s information criterion (bigger is better) and $-2 \log$ likelihood for final model forms (eqs. 2c, 5c, 5d and 6c).

Equation No.	AIC	$-2 \log$ likelihood
2c	-1243	2472.1
5c	-1190	2363.3
5d	-1196	2375.8
6c	-1215	2417.7

the 96 sample trees, maximum BDs were observed at RDINCs between approximately 0.45 and 1.0 (Fig. 2). Residuals from eqs. 5c and 5d behaved slightly more favorably over RDINC (Fig. 3).

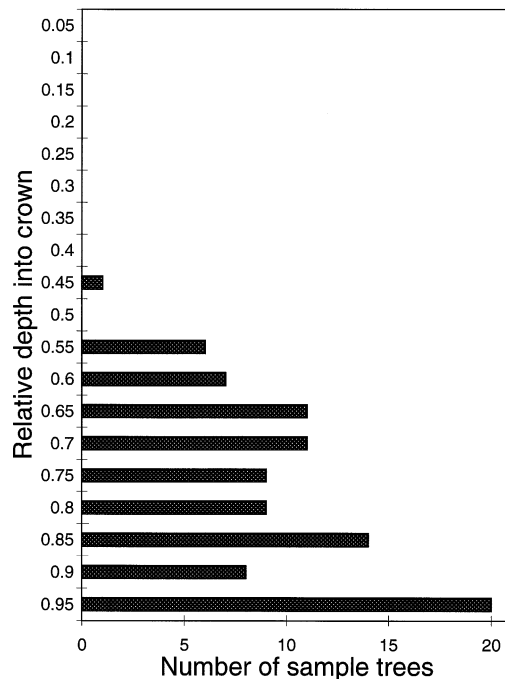
As would be expected, the constrained variable-exponent model (eq. 6b) produced a slightly smaller AIC than its unconstrained counterpart (eq. 5c; Table 8). The final constrained model was

$$[6c] \quad BD_{ij} = (\lambda_1 CW^{\lambda_2} + \delta_i) W^C + \epsilon_{ij}$$

where $C = \lambda_3 Z^{\lambda_4}$, $p = 0$, and W and Z are defined as above. Parameter estimates λ_1 – λ_4 were significantly different from zero, and a likelihood ratio test indicated that λ_4 was significantly different from one ($P < 0.005$). Although the behavior of eq. 6c was quite similar to eqs. 5c and 5d (Fig. 1), a likelihood ratio test indicated the significance of allowing for a peak in maximum branch diameter above crown base ($P < 0.005$ for testing significant difference between eqs. 5c and 6c).

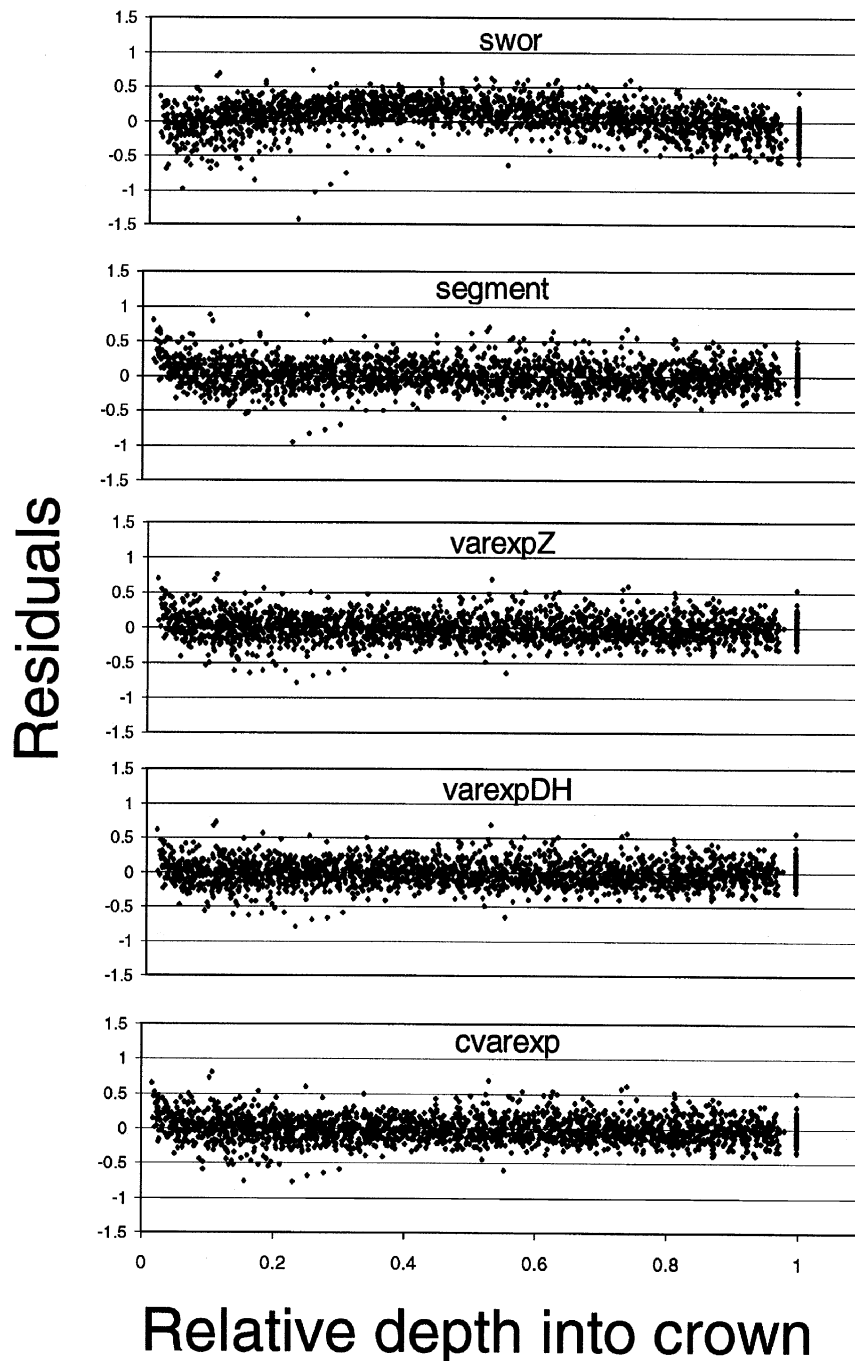
Each of the five primary models displayed some small biases in predicted branch diameter for the validation data

Fig. 2. Histogram showing the relative depth into crown at which maximum branch diameter occurred for individual sample trees (mean relative depth = 0.79).



sets, depending on the depth into crown (Figs. 4–6). In the SMC data set, the segmented-polynomial model tended to underpredict branch diameter above midcrown and overpredict below midcrown; in contrast, the variable-exponent models tended to underpredict at all crown levels, although

Fig. 3. Residual plots for each branch diameter prediction model: (a) swor, southwestern Oregon model (eq. 1b); (b) segment, segmented-polynomial model (eq. 2c); (c) varexpZ, unconstrained variable-exponent model (eq. 5c); (d) varexpDH, unconstrained variable-exponent model (eq. 5d); and (e) cvarexp, constrained variable-exponent model (eq. 6c).



the magnitude of differences was generally smaller (Fig. 4). This difference between observed and predicted values may be attributable, at least in part, to the low relative densities of many SMC plots.

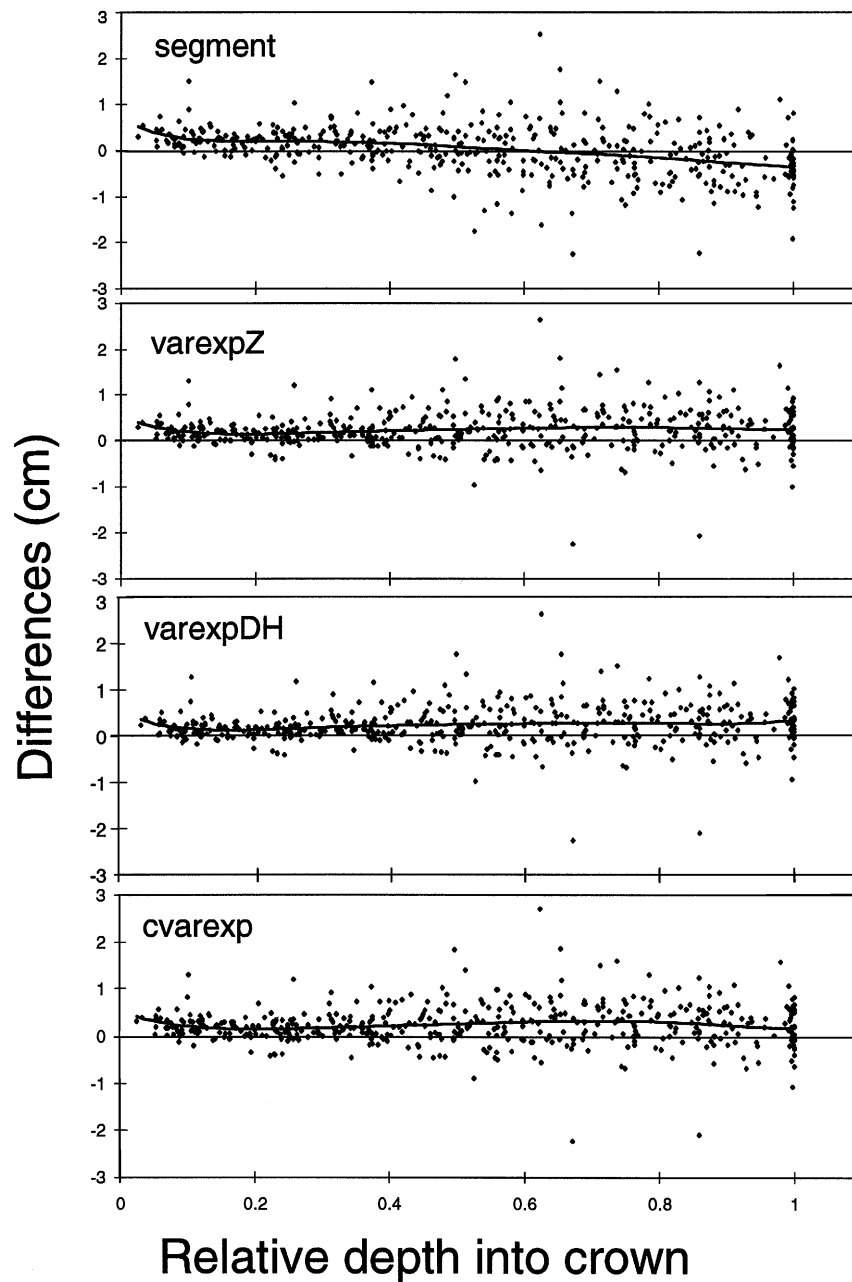
In the ODF data set, the segmented-polynomial model seems to demonstrate the least bias near the middle of the crown but overpredicts near crown base (Fig. 5). The vast majority of observations in this data set were made near crown base; hence, the range in relative crown depth runs only from about 0.55 to 1.00 (Fig. 5). The variable-exponent models appear to predict quite well for the lower 20% of the

crown. All models underpredicted slightly for the SWOR data (Fig. 6) but generally performed better than expected given the generally greater crown width, and probably branch diameter, for open-grown trees of a given diameter in southwestern Oregon (Paine and Hann 1982).

Discussion

The equation applied by Maguire et al. (1991) was insufficiently flexible to represent the true trend in BD over DINC (also see Maguire et al. (1994)). Even when this curve is re-

Fig. 4. Validation against Stand Management Cooperative data (Maguire et al. 1994). Differences between observed and predicted branch diameters representing the largest branch in whorls at various relative depths into crown: (a) segment, segmented-polynomial model (eq. 2c); (b) varexpZ, unconstrained variable-exponent model (eq. 5c); (c) varexpDH, unconstrained variable-exponent model (eq. 5d); and (d) cvarexp, constrained variable-exponent model (eq. 6c).

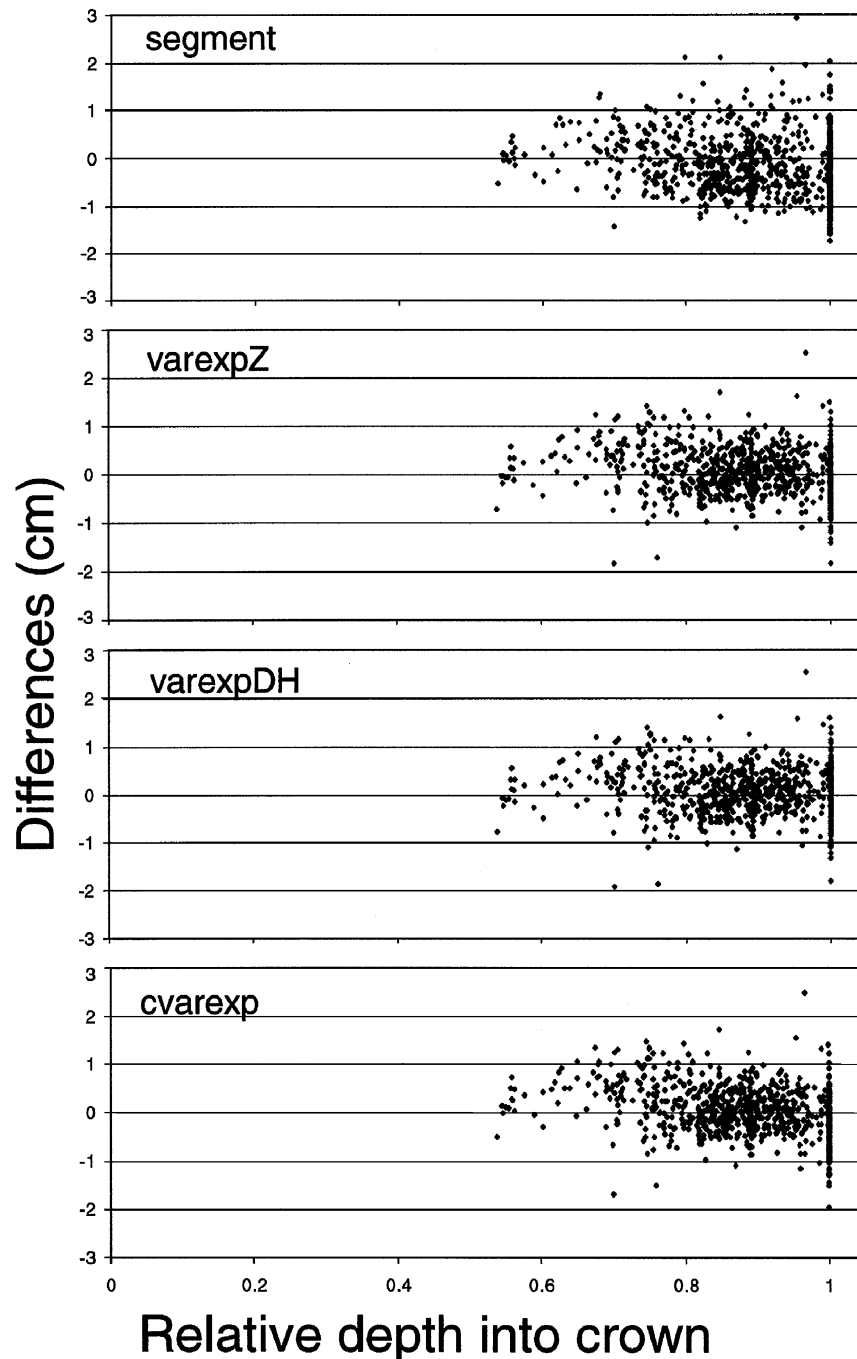


fitted to the new data covering the full range of heights within the crown and corrected for log bias (Flewelling and Pienaar 1981), the model form does not conform well to the trends in maximum branch size, in contrast to the segmented-polynomial and Kozak models. Likewise, it does not allow the consistently observed decreasing behavior in BD near the base of the live crown (Fig. 1). As a result, branch diameters at crown base are overestimated, and branch diameters in the middle third of the crown are underestimated.

The model presented by Maguire et al. (1991) also suffered from restricted distribution of sample branches within

sampled crowns. Although the branch diameter model represented by eq. 1b was logically constrained to pass through zero at the tip of the tree, virtually no data were included for the upper two thirds of the live crown; hence, DINC was confounded with CL (all branches with short DINC also occurred at or near crown base). The net result was that the equation was reasonable only for estimating BDs near crown base; that is, diameters in the upper half of the crown would be poorly estimated, a result that would be likely even if a more appropriate model form could have been identified. In contrast, the behavior of the models fitted to the western Or-

Fig. 5. Validation against Oregon Department of Forestry data (Elliott State Forest). Differences between observed and predicted branch diameters representing the largest branch in each quadrant around the tree: (a) segment, segmented-polynomial model (eq. 2c); (b) varexpZ, unconstrained variable-exponent model (eq. 5c); (c) varexpDH, unconstrained variable-exponent model (eq. 5d); and (d) cvarexp, constrained variable-exponent model (eq. 6c).

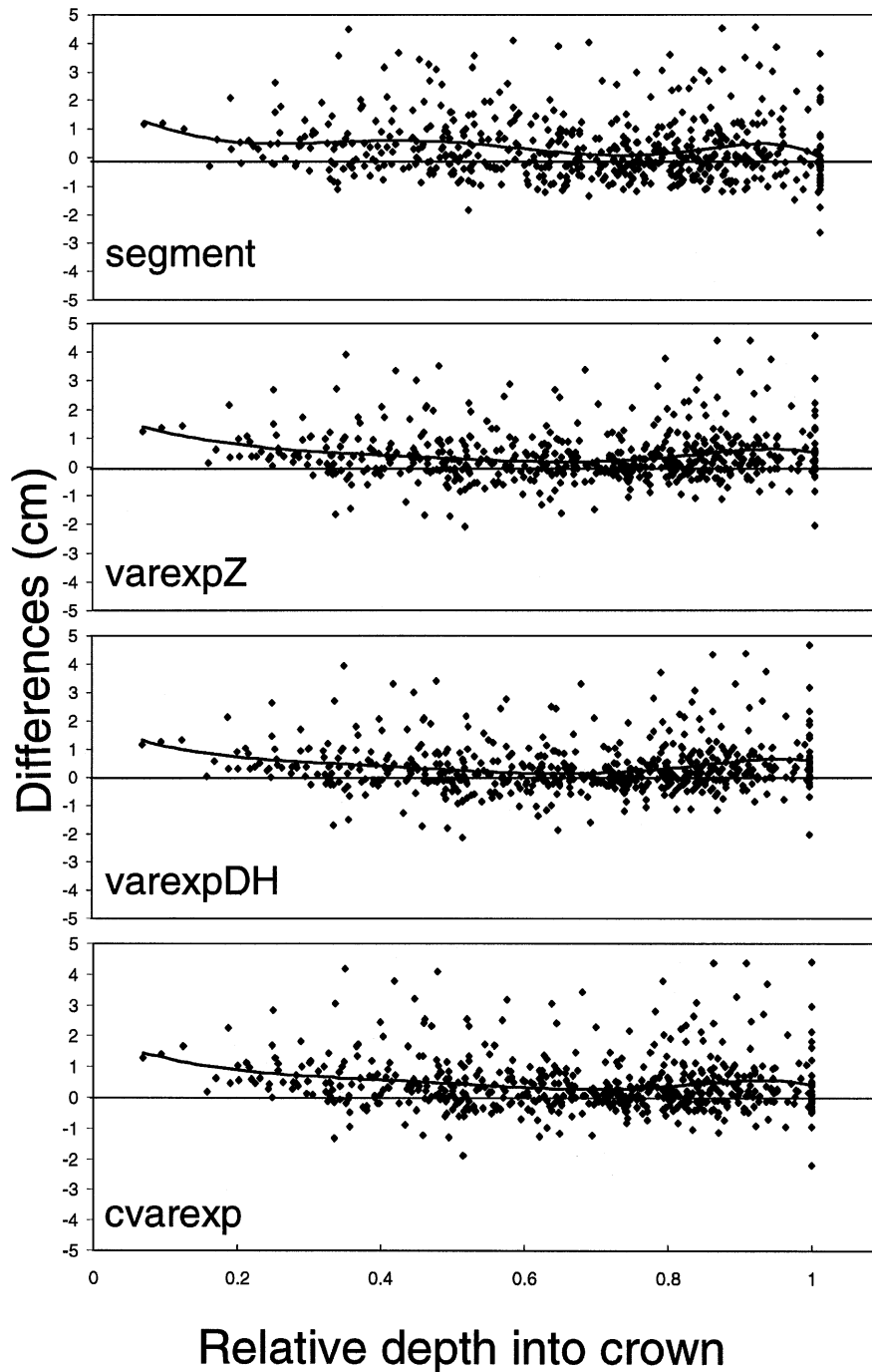


egon – Washington data behave more realistically between the tree tip and the lower third of the live crown. Furthermore, most of the sample trees have the branch of maximum diameter occurring above crown base, with these maxima occurring on average at 79% of DINC (Fig. 4). This peaking behavior has been previously documented in Douglas-fir (Maguire et al. 1994) and Norway spruce (Colin and Houllier 1991) and is consistent with patterns in Douglas-fir

crown profile described by Roeh and Maguire (1997) but differs somewhat from results presented by Hann (1999).

Branch diameter prediction equations can be incorporated into programs that consider wood quality in economic analyses of silvicultural treatments, for example, DFPRUNE (Fight et al. 1987) and TREEVAL (Briggs 1989). These programs require an estimate of knot size to help predict proportions of lumber and veneer grades that are recovered

Fig. 6. Validation against southwestern Oregon data (Maguire et al. 1991). Differences between observed and predicted branch diameters representing the longest branch in each cardinal direction around the tree: (a) segment, segmented-polynomial model (eq. 2c); (b) varexpZ, unconstrained variable-exponent model (eq. 5c); (c) varexpDH, unconstrained variable-exponent model (eq. 5d); and (d) cvarexp, constrained variable-exponent model (eq. 6c).



from trees grown under varying silvicultural regimes. Application of branch diameter prediction model eqs. 5c, 5d, or 6c requires input of only the DBH, total height, and crown length of the tree, yielding the expected maximum branch diameter for any arbitrary height between crown base and tip of the tree. Additional detail on number and size of branches can be added by combining predictions from other primary branching models and the models presented here; for example, the maximum branch diameter equation in the

system presented by Maguire et al. (1994) could be replaced with eq. 5c, 5d, or 6c.

Self-pruning or sloughing of dead branches below the live crown is extremely slow in second-growth Douglas-fir. Fahey et al. (1991) found that dead branches persisted on young trees long enough to affect wood quality in virtually all stands under 80 years of age, even under a wide range of growing conditions. Estimation of branch diameter at the base of the current live crown therefore allows rough esti-

Table 9. Range of crown ratios for tree diameters (DBH) and total heights represented in the modeling database.

DBH (cm)	Total height (m)							
	15	20	25	30	35	40	45	50
20	0.72–0.77	0.47	0.60	—	—	—	—	—
30	0.70–0.80	0.45–0.95	0.43–0.60	0.44–0.56	—	—	—	—
40	—	0.72–0.95	0.51–0.71	0.42–0.68	0.45–0.64	0.46	—	—
50	—	—	—	0.46–0.83	0.36–0.86	0.37–0.58	0.39	—
60	—	—	—	—	0.72	0.40–0.74	0.39–0.54	0.63
70	—	—	—	—	—	—	0.47–0.56	0.43–0.53
80	—	—	—	—	—	0.67	—	0.38–0.58
90	—	—	—	—	—	—	—	0.48

mates of branch size indices for logs containing the lowest live whorl. In the absence of stand-density manipulations in particular, this maximum branch size changes relatively little for a reasonable distance above and below current crown base (Maguire et al. 1991).

As stated earlier, it is important to recognize that allowing the occurrence of maximum branch diameter above crown base in the model opens the possibility for inconsistent predictions of branch diameters at a given stem height over time. When applying the prediction equation to a tree measured or projected (for example, by a growth model) over time, certain combinations of DBH growth, height growth, and crown recession may lead to a decrease in maximum branch diameter predicted at a given whorl. Although the decrease in branch diameter near crown base in a static context is now well established, the dynamic behavior of crown dimensions and branch growth is incompletely understood at present. The past competitive environment experienced by the crown and the dynamics of branch growth are not fully depicted in the three basic tree dimensions applied here: tree DBH, total height, and crown length. The current prediction model maintains a biologically realistic allometric balance between branch diameters and these tree-level dimensions for the average tree. However, application to single trees over time should be done with caution, and eq. 6c is generally recommended until more information on branch growth is collected and interpreted to guide further model construction. As with any tree or stand growth model, inferring growth from cross-sectional rather than longitudinal data entails risks. Integration or summation of a well-formulated branch growth model should not only provide consistent cumulative growth but will also improve understanding of biological mechanisms producing certain allometries. Ultimately, the small differences in predicted values between eqs. 5c and 6c, and the very subtle peak in branch diameter afforded by eqs. 5c and 5d, suggest that the latter model may perform equally well in a dynamic context despite the fact that the peak is statistically significant. Of course, it is uncertain how the models will behave when extrapolated beyond the range of DBH, height, and crown length represented in the data set (Table 9).

Acknowledgments

This study was funded by the Timber Quality Research group of the USDA Forest Service Pacific Northwest Research Station. We gratefully acknowledge field work per-

formed by the late Tom Fahey and logistical support provided by Roger Fight and Sue Willits of the USDA Forest Service Pacific Northwest Research Station. Bill Voelker graciously provided validation data from a study conducted by the Oregon Department of Forestry in the Elliott State Forest. Numerous comments by Chris Keyes, John Moore, Duncan Wilson, and two anonymous reviewers led to significant improvements in the manuscript.

References

- Briggs, D.G. 1989. Tree value system: description and assumptions. USDA For. Serv. Gen. Tech. Rep. No. PNW-GTR-239.
- Colin, F., and Houllier, F. 1991. Branchiness of Norway spruce in north-eastern France: modelling vertical trends in maximum nodal branch size. *Ann. Sci. For.* **48**: 679–693.
- Curtis, R.O. 1982. A simple index of stand density for Douglas-fir. *For. Sci.* **28**: 92–94.
- Curtis, R.O., and Reukema, D.L. 1970. Crown development and site estimates in a Douglas-fir plantation spacing test. *For. Sci.* **16**: 287–301.
- Davidian, M., and Giltinan, D.M. 1995. Nonlinear models for repeated measurement data. Chapman & Hall, New York.
- Dubrasich, M.E., Hann, D.W., and Tappeiner, J.C., II. 1997. Methods for evaluating crown area profiles of forest stands. *Can. J. For. Res.* **27**: 385–392.
- Fahey, T.D., Cahill, J.M., Snellgrove, T.A., and Heath, L.S. 1991. Lumber and veneer recovery from intensively managed young-growth Douglas-fir. USDA For. Serv. Res. Pap. No. PNW-RP-437.
- Fight, R.D., Cahill, J.M., Snellgrove, T.A., and Fahey, T.D. 1987. PRUNE-SIM user's guide. USDA For. Serv. Gen. Tech. Rep. No. PNW-209.
- Flewelling, J.W., and Pienaar, L.V. 1981. Multiplicative regression with lognormal errors. *For. Sci.* **27**: 281–289.
- Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. No. PNW-8.
- Furnival, G.M. 1961. An index for comparing equations used in constructing volume tables. *For. Sci.* **7**: 337–341.
- Goldstein, H. 1995. Multilevel statistical models. Arnold, New York.
- Hann, D.W. 1997. Equations for predicting the largest crown width of stand-grown trees in western Oregon. Forest Research Laboratory, College of Forestry, Oregon State University, Corvallis. Res. Contrib. No. 17.
- Hann, D.W. 1999. An adjustable predictor of crown profile for stand-grown Douglas-fir trees. *For. Sci.* **45**: 217–225.

- Hann, D.W., Olsen, C.L., and Hester, A.S. 1994. ORGANON user's manual: edition 4.3 southwestern Oregon version and edition 1.3 western Willamette Valley version. Department of Forest Resources, Oregon State University, Corvallis.
- King, J.E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser Corp., Centralia, Wash. Weyerhaeuser For. Pap. No. 8
- Kozak, A. 1988. A variable-exponent taper equation. *Can. J. For. Res.* **18**: 1363–1368.
- Kozak, A. 1997. Effects of multicollinearity and autocorrelation on the variable-exponent taper functions. *Can. J. For. Res.* **27**: 619–629.
- Kvålseth, T.O. 1985. Cautionary note about R^2 . *Am. Stat.* **39**: 279–285.
- Maguire, D.A. 1994. Branch mortality and potential litterfall from Douglas-fir trees in stands of varying density. *For. Ecol. Manage.* **70**: 41–53.
- Maguire, D.A., Hann, D.W., and Kershaw, J.A. 1988. Prediction of branch diameter and branch distribution for Douglas-fir in southwestern Oregon. *In* Forest growth modelling and prediction. USDA For. Serv. Gen. Tech. Rep. No. NC-120. pp. 1029–1036.
- Maguire, D.A., Kershaw, J.A., and Hann, D.W. 1991. Predicting the effects of silvicultural regime on branch size and crown wood core in Douglas-fir. *For. Sci.* **37**: 1409–1428.
- Maguire, D.A., Moeur, M., and Bennett, W.S. 1994. Models for describing basal diameter and vertical distribution of primary branches in young Douglas-fir. *For. Ecol. Manage.* **63**: 23–55.
- Max, T.A., and Burkhart, H.E. 1976. Segmented polynomial regression applied to taper equations. *For. Sci.* **22**: 283–289.
- Paine, D.P., and Hann, D.W. 1982. Maximum crown-width equations for southwestern Oregon tree species. Forest Research Laboratory, Oregon State University, Corvallis. Res. Pap. No. 46.
- Pinheiro, J.C., and Bates, D.M. 1995. Approximations to the log-likelihood function in the nonlinear mixed-effects model. *J. Comput. Graphical Stat.* **4**: 12–35.
- Ritchie, M.W., and Hann, D.W. 1985. Equations for predicting basal area increment in Douglas-fir and grand fir. Forest Research Laboratory, College of Forestry, Oregon State University, Corvallis. Res. Bull. No. 51.
- Roeh, R., and Maguire, D.A. 1997. Crown profile models based on branch attributes in coastal Douglas-fir. *For. Ecol. Manage.* **96**: 77–100.
- Wolfinger, R.D. 1999. Fitting nonlinear mixed models with the new NLMIXED procedure. SAS Institute Inc., Cary, N.C. Pap. No. 287.