A system of nonlinear simultaneous equations for crown length and crown radius for the forest dynamics model SORTIE-ND

Derek F. Sattler and Valerie LeMay

Abstract: A system of equations was developed to predict crown length (CL) and crown radius (CRAD) for trees in structurally complex stands. The equations address two problems that often arise in crown allometry. First, relationships between the main stem and the crown are likely to change with intertree competition. Therefore, explicit measures of density were used along with main stem measurements as explanatory variables. Second, the physiological relationship between CL and CRAD is often overlooked when modeling crowns. This relationship is incorporated through the use of a simultaneous system of equations. Parameters were estimated using nonlinear three-stage least squares (N3SLS) in which first-stage equation estimates of CRAD are used to estimate CL and vice versa in the second and third stages of N3SLS. The equations were fitted and validated for four species: lodgepole pine (*Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson), hybrid spruce (*Picea engelmannii* Parry ex Engelm. × *P. glauca* (Moench) Voss), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), and trembling aspen (*Populus tremuloides* Michx.). The intent is to use the equations as alternatives to the crown equations in the spatially explicit forest growth model SORTIE-ND that use only main stem variables in estimating crowns over time.

Résumé : Un système d'équations a été développé pour prédire la longueur (LC) et le rayon (RC) de la cime des arbres dans des peuplements structurellement complexes. Les équations abordent deux problèmes d'allométrie de la cime qui se posent souvent. Premièrement, il est probable que les relations entre la tige principale et la cime changent en fonction de la compétition entre les arbres. Par conséquent, des mesures explicites de densité ont été utilisées avec des mesures de la tige principale comme variables explicatives. Deuxièmement, la relation physiologique entre LC et RC est souvent négligée lorsqu'on modélise la cime. Cette relation est incorporée via l'utilisation d'un système simultané d'équations. Les paramètres ont été estimés à l'aide de la méthode des moindres carrés non linéaire qui comporte trois étapes; les estimations de RC générées par les équations de la première étape sont utilisées pour estimer LC et vice versa lors des deuxième et troisième étapes. Les équations ont été ajustées et validées pour quatre espèces : le pin tordu latifolié (*Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson), l'épinette hybride (*Picea engelmannii* Parry ex Engelm. × *P. glauca* (Moench) Voss), le douglas de Menzies bleu (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) et le peuplier faux-tremble (*Populus tremuloides* Michx.). L'intention est d'utiliser ces équations au lieu des équations de cime du modèle de croissance forestière spatialement explicite SORTIE-ND qui utilise seulement les variables de la tige principale pour estimer la cime à différents moments.

[Traduit par la Rédaction]

Introduction

Estimates of crown size are often used to infer tree vigor (Assmann 1970; Valentine et al. 1994), basal area increment (Hasenauer and Monserud 1996; Monserud and Sterba 1996), and wood quality (Kellomäki et al. 1999; Valentine and Mäkelä 2005). Crown size is also used in light interception models to estimate the amount of shade cast by trees and, therefore, the amount of light available to neighbouring trees (Canham et al. 1999). Predictions of crown size are usually based on allometric relationships with easily measured dimensions of the main tree stem such as total tree height (HEIGHT) and diameter at breast height (DBH) (Hasenauer and Monserud 1996; Baldwin and Peterson 1997; Gilmore 2001). When applied to stands that remain within a narrow stocking range, the use of only main stem dimensions may adequately describe variations in crown size for some tree species as the response of both the crown and main stem dimensions are limited. However, when applying allometric crown equations across a wider range of densities, using only main stem dimensions as explanatory variables may not accurately estimate crown dimensions (Hynynen 1995; Hase-

Received 3 November 2010. Accepted 7 April 2011. Published at www.nrcresearchpress.com/cjfr on 28 July 2011.

D.F. Sattler* and V. LeMay. Department of Forest Resources Management, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

Corresponding author: Derek F. Sattler (e-mail: dsattler@ualberta.ca).

*Present address: Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada.

nauer and Monserud 1996). In these cases, the addition of competition-related variables has proven useful (Rouvinen and Kuuluvainen 1997; Rudnicki et al. 2004; Meng et al. 2007).

Another challenge when developing allometric crown equations is to ensure that the dimensional relationships built into the equations have a well-established biological basis (Vanclay 1994). One relationship that has seen little use in crown modelling is the effect of crown length (CL) on crown radius (CRAD) and vice versa. The basis of this physiological relationship is the hierarchy of branch control that extends from the main stem to first order, second order, and all subsequent branch orders, a process known as epinastic control. For trees with strong epinastic control such as hybrid spruce (*Picea engelmannii* Parry ex Engelm. × *P. glauca* (Moench) Voss) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), the amount and direction of lateral branch growth is closely maintained by the terminal leader (Oliver and Larson 1996). Although lodgepole pine (*Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson) and aspen (*Populus tremuloides* Michx.) have relatively weaker epinastic control, the correlation between terminal growth and lateral shoot growth remains high under most conditions (Remphrey and Pearn 2003; Lindgren et al. 2007). A feedback effect ensues as changes in crown radius lead to changes in light capture, resulting in either an increase in CL through height growth or a decrease in CL due to an increased rate of crown recession relative to height growth. Where estimates of both crown dimensions (CL and CRAD) are needed, it may be possible to incorporate this feedback relationship by using a simultaneous system of equations in which CL is used to estimate CRAD and vice versa.

Of particular interest to this study is the prediction of tree crown size within the spatially explicit forest growth and dynamics model SORTIE-ND (Coates et al. 2003; Astrup 2006). A key component of SORTIE-ND is a light behaviour that predicts incident radiation at any given point within a stand based on the sky brightness distribution at a referenced latitude. Within a simulated treed plot, light attenuation occurs as rays pass through individual tree crowns. The amount of shade cast by each tree is a function of its crown size and species-specific light transmission coefficients (Pacala et al. 1993, 1996). The growth of mature and newly regenerated trees in SORTIE-ND is largely a function of how much light a tree receives, measured as the percentage of full sun received at a point and reported in the model as a global light index (GLI) value.

For all trees, the assumed crown shape in SORTIE-ND is a vertical cylinder that is defined by an estimate of CL and CRAD. Generally, CL is defined as the length of the live crown along the main stem, and CRAD is defined as the average radius of the crown calculated from several points around the main stem. There is, however, no set definition of CL or CRAD in SORTIE-ND, and different measurement methods have been used (Canham et al. 1999). All freely available versions of the SORTIE model estimate CL as a function of total tree height and CRAD as a function of DBH (Pacala et al. 1993, 1996). The relationships are expressed through exponential or Chapman–Richards equations in which users must provide their own set of species-specific parameters. An advantage of this simple approach to estimating crown size is that the equations avoid overspecification and thus are suitable for a wide range of species (Catovsky et al. 2002; Astrup and Larson 2006). The crown equations, however, do not explicitly account for the potential effects of crowding on crown dimensions. Therefore, there can be a tendency for the equations to overestimate crown axes in dense stands and underestimate axes in open stands (Astrup 2006). This, in turn, has been shown to result in under- or over-estimates of growth for canopy trees, as well as understory regeneration (Astrup and Larson 2006). For stands in which the effects of crowding on crown dimensions are not well reflected through changes in HEIGHT and DBH, SORTIE-ND model predictions could be improved by including explicit measures of density in the crown allometry equations. Furthermore, we speculated that further improvements to the predictive abilities of the crown equations could be made by accounting for the strong relationship that is often seen between CL and CRAD.

The main objective of this study was to develop equations for CL and CRAD that would serve as alternatives to the current crown allometry equations in the SORTIE-ND growth model, particularly when applying the model to a diverse range of stand densities. The following main criteria were used to guide model development: (*i*) the models should be able to account for the effects of crowding on crown size; (*ii*) the equations should take advantage of the concomitant relationship between the crown axes by using CRAD as one of the predictor variables for CL and vice versa, resulting in a simultaneous system of equations; and (*iii*) the predictor variables included in the chosen system of equations should be able to provide accurate and reliable predictions for the most common tree species within the central interior of British Columbia (BC).

Once the simultaneous system of crown models was developed, parameters were estimated for lodgepole pine, hybrid spruce, Douglas-fir, and trembling aspen using data collected from stands of central interior BC.

Methods

Study area

Data for this study included stands located within 250 km of Williams Lake, BC (52°08′18.59″N, 122°08′31.07″W). Many of the sampled stands were located on the Chilcotin Plateau, situated within the former Cariboo Forest Region. This area has a long history of disturbance events caused by mountain pine beetle (*Dendroctonus ponderosae* Hopkins (MPB)) (Stockdale et al. 2004; Aukema et al. 2006), although evidence suggests that stand replacing and low intensity ground fires have also played a major role in influencing stand structure (Hawkes et al. 2004). The combination of disturbance events has resulted in the creation of uneven-aged, mixed-species stands throughout much of the Chilcotin Plateau (Heath and Alfaro 1990).

Sampling approach and data description

Sampling was carried out in the summer of 2006. Circular plots of 11.28 m radius were systematically located in 53 natural, unmanaged stands, beginning with a random starting point. In each plot, the DBH (cm) and HEIGHT (m) were

Table 1. Summary statistics for trees in the model data set.

		DBH (cm)		HEIGHT (m)		CL (m)		CRAD (m)	
Species	No. of trees	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Aspen (*Populus tremuloides* Michx.)	58	15.51	5.53	15.39	4.98	5.62	2.31	1.84	0.46
Lodgepole pine (*Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson)	451	14.37	5.27	12.76	4.26	5.35	2.30	1.14	0.41
Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco)	55	18.79	11.64	15.61	7.38	8.58	4.28	1.82	0.65
Hybrid spruce (*Picea engelmannii* Parry ex Engelm. × *glauca* (Moench) Voss)	78	15.84	7.32	13.39	5.90	9.91	4.04	1.52	0.51

Note: DBH, diameter at breast height; HEIGHT, total tree height; CL, crown length; CRAD, crown radius; SD, standard deviation.

measured on live trees greater than 7.5 cm DBH. Measurements for CL (m) and CRAD (m) were collected from two randomly selected live, healthy trees of every species in the plot. CL was defined as the length of the live crown from the top the tree to the last live branch at the base of the crown, not allowing for more than 1 m between the live branch defining the base of the crown and the continuous live crown above. Measurements were collected using a Haglöf Vertex III hypsometer (Haglöf Sweden AB, Långsele, Sweden). CRAD was defined as the average of four measurements of lateral branch extension. The first of the four radii was measured by standing beneath the outer edge of the branch with the longest lateral extension and measuring to the main stem. Subsequent measurements were collected at 90° angles.

The model data set included 650 trees with crown measures, 140 from the Interior Douglas-fir (IDF) zone and 302 from the Sub-Boreal Spruce (SBS) and Sub-Boreal Pine Spruce (SBPS) zones (Meidinger and Pojar 1991). Data from the all three zones were pooled for the analyses as sample sizes for aspen, Douglas-fir, and hybrid spruce were small. Although the data were from different Biogeoclimatic Ecosystem Classification (BEC) zones, the sampling locations were quite close and climatic differences are assumed to be minimal. The mean number of stems per hectare (TPH) for trees > 7.5 cm DBH was 740 (standard deviation (SD) = 256, given in parentheses), and the mean basal area per hectare (BA; $m^2 \cdot ha^{-1}$) was 18.31 (7.00). Measurements of average DBH, HEIGHT, CL, and CRAD are summarized in Table 1.

Development of crown equations

As noted, three criteria were used to guide development of the system of crown allometry equations. The first criterion required that the crown equations be suitable for use within natural, unmanaged stands displaying a wide range of densities, as past disturbances have created a landscape composed of stands of varying degrees of maturity and density. The response of crowns to changes in density that are the result of silvicultural treatments such as thinning was not a criterion on which to evaluate the crown equations as the data available to test the models were collected from unmanaged stands. To render the equations suitable for use over a wide range of stand densities, distance-independent measures of competition were included as possible explanatory variables in the system of equations. Although the intention was to use the simultaneous system of crown equations within the spatially explicit model SORTIE-ND, the models could also be used in the absence of stem-mapped data. Further, the availability of spatially referenced data is limited; therefore, using distance-independent measures of competition allows the system of crown equations to be applied more widely. Measures of stand density that were tested included BA, TPH, relative density (RD; the ratio of BA to the square root of the quadratic mean diameter), and the basal area of trees taller than the target tree (BALHT) ($m^2 \cdot ha^{-1}$).

The second criterion was that the physiological relationship that exists between CL growth and CRAD growth be factored into the crown equations. Because this would involve using CL as a predictor variable in the equation for CRAD and, similarly, CRAD as a predictor variable for the equation for CL, simultaneous regression techniques were required. In addition, individual tree size variables including HEIGHT, DBH, and slenderness (HEIGHT/DBH (H/D)) were tested in the equations. Lastly, the chosen system of equations should be capable of providing accurate estimates of crown size for a range of tree species, including fast-growing shade-intolerant species, as well as slower-growing shade-tolerant species. Lodgepole pine and trembling aspen are fast-growing, shade-intolerant species, whereas hybrid spruce and Douglas-fir have slower growth and are more tolerant of shade (Harlow et al. 1979). Furthermore, crowns of lodgepole pine and aspen tend to be smaller and sparser than those of hybrid spruce and Douglas-fir (Barclay 1998; Astrup and Larson 2006). Thus, these species represent two distinct growth patterns and crown forms. Given these two distinct growth patterns and crown forms, it seemed unlikely that a single set of predictor variables could be found such that each is statistically significant within the chosen system of equations for all four species tested. Thus, we evaluated possible predictor variables by considering their statistical significance across all four species.

Given these criteria, the following nonlinear equation was selected to estimate CL:

$$[1] \qquad \widehat{\mathrm{CL}} = \frac{\mathrm{HEIGHT}}{(1 + \mathrm{e}^{(-\beta \times X)})} + \varepsilon$$

where $\widehat{\mathrm{CL}}$ is the estimated length of the live crown, $\beta \times X$ is a linear combination of tree- and stand-level variables, and ε is the random error. Using eq. 1, the height of the tree whose crown is being estimated operates as the upper asymptote. Following Monserud and Marshall (1999), a power response function was selected to model CRAD, which took the following form:

$$\widehat{\mathrm{CRAD}} = b_0 \times X_1^{b_1} \times X_2^{b_2} \times \ldots \times X_i^{b_i} + \varepsilon \qquad [2]$$

where $\widehat{\mathrm{CRAD}}$ is the estimated average radius of the crown, X_i are a series of tree- and stand-level variables, b_i are parameters to be estimated, and ε is the random error.

Parameter estimation for simultaneous systems of equations

Because of the strong concomitant relationship that exists between CRAD and CL, using CRAD as a predictor variable in eq. 1 and CL as a predictor variable in eq. 2 is likely to improve prediction accuracy and ensure logical consistency. Treated in this manner, eqs. 1 and 2 become fitted as a simultaneous system of nonlinear equations. Fitting this simultaneous system using ordinary nonlinear least squares (OLS) would result in biased estimates of the coefficients, termed simultaneity bias (Zellner and Theil 1962; Gallant 1975; Judge et al. 1985). To remove simultaneity bias, a simultaneous system of nonlinear equations was fitted using nonlinear three-stage least squares (N3SLS) regression, with the following three stages:

1. In the first stage of N3SLS, a first-stage estimate of CRAD ($\mathrm{CRAD}_{\mathrm{first}}$) was estimated through a linear model using tree- and stand-level variables (termed "instrumental variables"), but excluding CL. The same basic procedure was used to obtain a first-stage estimate of CL ($\mathrm{CL}_{\mathrm{first}}$).
2. In the second stage, $\mathrm{CRAD}_{\mathrm{first}}$ was used as a predictor variable in eq. 1. Similarly, $\mathrm{CL}_{\mathrm{first}}$ was used on the right-hand side of eq. 2. This removes simultaneity bias that arises in simultaneous systems of equations. Each revised equation was then fitted using nonlinear least squares. The error terms of these second-stage equations were then used to estimate simultaneous correlation, the correlation of errors across the two equations of the system.
3. The estimated simultaneous correlation was finally used for the third stage in which the two equations were fitted as a system using a seemingly unrelated regressions approach.

Parameter estimates for each of the four species were obtained using the MODEL procedure in SAS (SAS Institute Inc. 2003). To aid convergence, a set of starting parameters for the N3SLS regression was obtained by first fitting eqs. 1 and 2 individually using nonlinear OLS regression. To test whether the first stage of the N3SLS regression removed simultaneity biases, a Hausman specification test was used (Wu 1973). It should be noted that the error terms of each equation were not subdivided into the error components (equivalent to a random intercept; Judge et al. 1985, pp. 521–522) of stand, plot, and tree levels. Although this is desirable because the data have a hierarchical structure, we did not alter the N3SLS fit for the following reasons: (*i*) heteroscedastic or simple correlated error structures in a simultaneous system of nonlinear equations can be addressed using PROC MODEL and other software with some difficulty, whereas more complex error structures such as error components of hierarchical data are very difficult to estimate and incorporate; and (*ii*) we expected that separating the error components into stand-level and tree-level errors would have little impact on the inclusion of parameters and variables in the simultaneous system of nonlinear equations, particularly because only large sample (i.e., asymptotic) properties hold (Judge et al. 1985, pp. 622–631).

Accuracy of fitted crown models

The accuracy of the system of crown equations for each species was assessed by calculating fit statistics for eqs. 1 and 2. Estimated errors (residuals) for CL and CRAD crown were summarized separately to obtain mean bias and root mean squared error (RMSE):

$$\text{Mean bias} = \sum_{i=1}^{n} \left[\frac{(Y_i - \widehat{Y}_i)}{n} \right] \qquad [3]$$

and

$$\text{RMSE} = \sqrt{\sum_{i=1}^{n} \left[\frac{(Y_i - \widehat{Y}_i)^2}{n} \right]} \qquad [4]$$

where Y_i is the actual value (i.e., measured CL and CRAD) for measurements 1 to n, $\widehat{Y}_i$ is the predicted value from the fitted equation, and n is the number of trees. The mean bias and RMSE values were calculated for each species using all observations. Additionally, mean bias was calculated by BA class. A pseudo-R^2 statistic was calculated as

$$\text{Pseudo-}R^2 = 1 - \frac{\sum_{i=1}^{n} (Y_i - \widehat{Y}_i)^2}{\sum_{i=1}^{n} (Y_i - \overline{Y})^2} \qquad [5]$$

and used as an additional diagnostic (Schabenberger and Pierce 2002). The significance of individual predictor variables was assessed through a series of t tests. A coefficient of partial determination (partial R^2) was calculated to assess the amount of variance explained by introducing an explicit measure of density to the system of equations.

Model evaluation and validation

To assess the predictive capabilities of the chosen models, the predicted sum of squares statistic (PRESS) (Quan 1988) commonly used to validate single-equation models was extended to the system of equations used in this study. This method of model evaluation is suitable when sample sizes are too small for data-splitting methods (Stone 1974), which was a concern for Douglas-fir and aspen. To calculate the PRESS statistic for the system of equations, the *i*th observation from the model data set was deleted and then the remaining observations were used to refit the models using the N3SLS estimators. Refitting of the system of equations in this manner was repeated n times, where n is the sample size. Each time the coefficients for the system of equations were re-estimated, a predicted value, $\widehat{Y}_{j(j)}$, was obtained for the *j*th observation that was deleted, where $j(j)$ is used to denote that the predicted value is for the *j*th observation that was deleted. The PRESS statistic was calculated from the sum of squares prediction errors for each of the two models over all n observations:

Table 2. Estimated coefficients (Coeff.) and associated approximate standard errors (~SE) for first-stage equations of crown length ($\widehat{\mathrm{CL}}_{\mathrm{first}}$ (m)) and crown radius ($\widehat{\mathrm{CRAD}}_{\mathrm{first}}$ (m)) (eqs. 7 and 8, respectively).

		Aspen		Lodgepole pine		Douglas-fir		Hybrid spruce	
Equation	Coeff.	Estimate	~SE	Estimate	~SE	Estimate	~SE	Estimate	~SE
$\widehat{\mathrm{CL}}_{\mathrm{first}}$	a_1	–12.5190	8.6096	–4.4111	2.8202	10.1367	6.6075	–9.0538	7.4756
	b_1	0.1116	0.2232	0.2470*	0.0943	0.1010	0.0903	0.08282	0.2684
	c_1	1.4297	0. 9155	0.8283*	0.3904	0.2537	0.7236	2.4826*	1.2143
	d_1	67.9761	58.5727	40.2489	21.3063	–27.8023	51.4543	96.8422	62.2268
	e_1	–0.0286	0.0173	–0.0252*	0.0081	–0.0032	0.0132	–0.0503*	0.0223
	f_1	–0.4240	5.8307	–2.3591	2.5643	–3.2733	4.8140	–12.8396	8.5251
	g_1	–0.1387*	0.0404	–0.0478*	0.0181	–0.0741	0.0549	–0.0498	0.0457
$\widehat{\mathrm{CRAD}}_{\mathrm{first}}$	a_2	–2.8239	1.9125	1.3766*	0.3853	1.5847	1.1198	0.8761	0.9569
	b_2	0.0022	0.0496	0.0909*	0.0129	0.0408*	0.0153	0.0384	0.0344
	c_2	0.5048*	0.2034	–0.1533*	0.0533	–0.0257	0.1226	0.1398	0.1554
	d_2	27.1821*	13.0109	–6.5545*	2.9111	0.8538	8.7204	2.9593	7.9653
	e_2	–0.0105*	0.0038	0.0021*	0.0011	0.0012	0.0022	–0.0044	0.0028
	f_2	–2.4249	1.2952	0.7063*	0.3504	–0.1646	0.8159	–1.5425	1.0912
	g_2	0.0049	0.0090	–0.0061*	0.0024	–0.0153	0.0093	–0.0097	0.0058

Note: Variables associated with the coefficients are as follows: a_1 and a_2, intercept; b_1 and b_2, DBH (cm); c_1 and c_2, HEIGHT (m); d_1 and d_2, 1/DBH; e_1 and e_2, HEIGHT^2; f_1 and f_2, H/D (H/D is HEIGHT (m) over DBH (cm)); g_1 and g_2, basal area (BA, $\mathrm{m^2 \cdot ha^{-1}}$). An asterisk (*) indicates that the coefficient is significant ($p < 0.05$). DBH, diameter at breast height; HEIGHT, total tree height; CL, crown length; CRAD, crown radius.

[6] $$\mathrm{PRESS} = \sum_{i=1}^{n} (Y_j - \widehat{Y}_{j(j)})^2$$

where Y_j is the jth deleted observation. The PRESS statistic was compared with the error sum of squares (SSE) obtained in the original fit of the system of equations. PRESS values close to SSE support the internal validity of the model (Kutner et al. 2005).

Results

System of crown allometry equations

The instrumental variables used to obtain first stage estimates of CL were DBH, 1/DBH, HEIGHT, HEIGHT^2, H/D, and BA. The same set of instrumental variables was used to obtain first-stage estimates of CRAD. Thus, the first-stage equations for the N3SLS regression were

[7] $$\widehat{\mathrm{CL}}_{\mathrm{first}} = a_1 + b_1 \times \mathrm{DBH} + c_1 \times \mathrm{HEIGHT} + d_1 \times 1/\mathrm{DBH} + e_1 \times \mathrm{HEIGHT}^2 + f_1 \times H/D + g_1 \times \mathrm{BA}$$

[8] $$\widehat{\mathrm{CRAD}}_{\mathrm{first}} = a_2 + b_2 \times \mathrm{DBH} + c_2 \times \mathrm{HEIGHT} + d_2 \times 1/\mathrm{DBH} + e_2 \times \mathrm{HEIGHT}^2 + f_2 \times H/D + g_2 \times \mathrm{BA}$$

where $\widehat{\mathrm{CL}}_{\mathrm{first}}$ is the first-stage estimate of CL, $\widehat{\mathrm{CRAD}}_{\mathrm{first}}$ is the first-stage estimate of CRAD, and a_1 to g_1 and a_2 to g_2 are sets of species-specific parameters for the first-stage equations of $\mathrm{CL}_{\mathrm{first}}$ and $\mathrm{CRAD}_{\mathrm{first}}$, respectively (Table 2). Not all instrumental variables were significant in the equations for $\mathrm{CL}_{\mathrm{first}}$ and $\mathrm{CRAD}_{\mathrm{first}}$ for all four species tested. However, this combination of instrumental variables provided the best balance between precise estimates of $\mathrm{CL}_{\mathrm{first}}$ and $\mathrm{CRAD}_{\mathrm{first}}$ for the four species and the characteristics desired of instrumental variables within a system of equations (Bowden and Turkington 1984).

Using N3SLS regression to simultaneously estimate parameters in eqs. 1 and 2, the predictor variables that provided precise estimates of CL for all four species tested included HEIGHT, $\mathrm{CRAD}_{\mathrm{first}}$, and BA. Precise estimates of CRAD were obtained for all four species using DBH, $\mathrm{CL}_{\mathrm{first}}$, H/D, and BA. Thus, for the second and third stage of N3SLS regression, the equations were

[9] $$\widehat{\mathrm{CL}} = \frac{\mathrm{HEIGHT}}{(1 + \mathrm{e}^{(-\beta \times X)})}$$

where

$$\beta \times X = a_3 + b_3 \times \mathrm{HEIGHT} + c_3 \times \widehat{\mathrm{CRAD}}_{\mathrm{first}} + d_3 \times \mathrm{BA}$$

and

[10] $$\widehat{\mathrm{CRAD}} = a_4 \times \mathrm{DBH}^{b_4} \times \widehat{\mathrm{CL}}_{\mathrm{first}}^{c_4} \times H/D^{d_4} \times \mathrm{BA}^{e_4}$$

where a_3 to d_3 and a_4 to e_4 are sets of species-specific parameters for the third-stage estimates of CL and CRAD, respectively. The parameter estimates and associated standard error for eqs. 9 and 10 are given in Tables 3 and 4.

Among the different density-related variables tested in eqs. 1 and 2, BA proved to be the most consistent in terms of significance for the four species tested. Taking into account the relative contribution of BA to eqs. 9 and 10 across all species tested, BA was significant ($p < 0.05$) in the estimates of CL for aspen, lodgepole pine, and hybrid spruce but not for Douglas-fir. For estimates of CRAD, BA was only significant for aspen and hybrid spruce. For comparison, the next most consistent density-related variable, TPH, was only significant for estimates of CL and CRAD on lodgepole pine. For aspen, lodgepole pine, and hybrid spruce, the proportion of variability in CL explained through the use of BA in

Table 3. Estimated coefficients (Coeff.) and associated approximate standard errors (~SE) from N3SLS regression of $\widehat{CL}$ (eq. 9) in the system of equations.

	Aspen		Lodgepole pine		Douglas-fir		Hybrid spruce	
Coeff.	Estimate	~SE	Estimate	~SE	Estimate	~SE	Estimate	~SE
a_3	–0.7828	0.5991	–0.5740*	0.1592	–0.9731	0.5968	–1.4102*	0.5260
b_3	0.0193	0.0224	0.1193*	0.0117	0.0665*	0.0299	0.0735*	0.0227
c_3	0.1438	0.3222	–0.8384*	0.1174	–0.6138*	0.2804	–1.1201*	0.2503
d_3	0.0362*	0.0123	0.0128*	0.0059	–0.0296	0.0207	0.0368*	0.0173

Note: The variables associated with the coefficients are as follows: a_3, logistic function a parameter; b_3, HEIGHT (m); c_3, $CRAD_{first}$ (m); d_3, basal area (BA, $m^2 \cdot ha^{-1}$). An asterisk (*) indicates that the coefficient is significant (p < 0.05). N3SLS, nonlinear three-stage least squares; CL, crown length; HEIGHT, total tree height; CRAD, crown radius.

Table 4. Estimated coefficients (Coeff.) and associated approximate standard errors (~SE) from N3SLS regression of $\widehat{CRAD}$ (eq. 10) in the system of equations.

	Aspen		Lodgepole pine		Douglas-fir		Hybrid spruce	
Coeff.	Estimate	~SE	Estimate	~SE	Estimate	~SE	Estimate	~SE
a_4	0.4381*	0.1506	0.2916*	0.0325	1.3052	0.8620	0.2940*	0.0853
b_4	–0.3221	0.2123	0.5241*	0.0753	0.9812*	0.3147	–0.1425	0.3161
c_4	0.7211*	0.2534	0.0708	0.1127	–0.6055	0.3526	0.5355	0.3664
d_4	–0.9174*	0.3247	–0.4587*	0.0629	0.0297	0.2528	–1.1036*	0.2454
e_4	0.3772*	0.1313	–0.0707	0.0376	–0.3822	0.2578	0.2097*	0.0973

Note: The variables associated with the coefficients are as follows: a_4, power function a parameter; b_4, HEIGHT (m); c_4, $\widehat{CL}_{first}$ (m); d_4, basal area (BA, $m^2 \cdot ha^{-1}$). An asterisk (*) indicates that the coefficient is significant (p < 0.05). N3SLS, nonlinear three-stage least squares; CL, crown length; CRAD, crown radius; HEIGHT, total tree height.

eqs. 9 and 10 was 0.04, 0.02, and 0.22, respectively. For estimates of CRAD on aspen and hybrid spruce, the proportion of variability explained by BA was 0.13 and 0.03, respectively, whereas those for lodgepole pine and Douglas-fir were negligible.

$CRAD_{first}$ was a significant predictor variable for CL for lodgepole pine, hybrid spruce, and Douglas-fir. CL_{first} proved to be less useful when estimating CRAD and was significant only for aspen. The Hausman test indicated that simultaneity bias was removed from the simultaneous system of equations through the first stage of N3SLS; the predictor variables were not correlated with the residuals.

The overall performance of eqs. 9 and 10 as a system of equations was assessed through mean bias (m), RMSE (m), % RMSE, and pseudo-R^2 (Table 5). The mean bias (m) resulting from the fitted system of equations was low for all four species. Estimates of CL for hybrid spruce displayed the largest overall mean bias but even here showed only a slight tendency to underestimate CL. The relative predictive abilities between eqs. 9 and 10 assessed using RMSE showed that estimates of CRAD were more precise than estimates of CL for all four species (Table 5). Aspen and lodgepole pine, the two species with shorter crowns, had the largest % RMSE, indicating lower precision in the estimates of CL relative to those of Douglas-fir and hybrid spruce. In terms of the percentage of variation explained by eq. 9 within the system of equations, pseudo-R^2 values were higher for Douglas-fir and hybrid spruce, the two species with strong epinastic control (Table 5). The variability explained through eq. 10 was highest for lodgepole pine and hybrid spruce.

An examination of mean bias for different BA classes revealed that there were some over- and under-estimates of CL and CRAD. For CRAD, bias reported within each BA class was close to the overall mean bias values for CRAD presented in Table 5. Somewhat larger mean bias values associated with estimates of CL were noted for some BA classes. That both over- and under-estimates of CL and CRAD occurred at all density classes suggests that there were no systematic patterns of over- or under-estimation across the range of stand densities included in the model data set (Table 6).

Model evaluation and validation

An evaluation of the predictive capabilities of eqs. 9 and 10 within the system of equations using the PRESS statistic indicated that estimates of CRAD were more precise than estimates of CL for the range of data tested. For all four species, the PRESS values obtained for CRAD were close to those obtained using the original N3SLS estimates (Table 7). It was surprising to note the larger differences between PRESS values and the original SSE values obtained for estimates of CL on Douglas-fir and hybrid spruce given that these two species showed relatively high pseudo-R^2 values (Table 5). Conversely, PRESS values obtained for estimates of CL on aspen and lodgepole pine were in good agreement with the original SSE values despite these two species having higher % RMSE values.

Discussion

Estimates of crown dimensions have long been recognized as a critical component in both distance-independent and distance-dependent forest growth models (Mitchell 1975; Wykoff 1985). Many equations for crown size attempt to account for the effects of competition by (*i*) using measurements of the main stem that are sensitive to changes in density, or (*ii*) incorporating explicit measures of density.

Table 5. Mean bias (observed – predicted, m), root mean squared error (RMSE, m), percentage RMSE, and pseudo-R^2 results using N3SLS regression parameter estimates.

Species	Dependent variable	Bias (m)	RMSE (m)	% RMSE	Pseudo-R^2
Aspen	CL	–0.002	1.959	35	0.17
	CRAD	0.001	0.381	21	0.31
Lodgepole pine	CL	0.020	2.070	39	0.19
	CRAD	<0.001	0.285	25	0.52
Douglas-fir	CL	0.011	2.458	29	0.61
	CRAD	0.002	0.537	29	0.33
Hybrid spruce	CL	0.114	2.367	23	0.66
	CRAD	–0.015	0.321	21	0.60

Note: N3SLS, nonlinear three-stage least squares; CL, crown length; CRAD, crown radius.

Table 6. Mean bias (observed – predicted, m) by basal area (BA, $m^2 \cdot ha^{-1}$) class using N3SLS regression parameter estimates.

			Mean bias	
	BA ($m^2 \cdot ha^{-1}$)	No. of trees	CL	CRAD
Aspen	5	6	0.445	0.007
	15	27	–0.246	0.027
	25	17	–0.219	–0.025
	35	8	0.948	–0.037
Lodgepole pine	5	95	0.407	–0.008
	15	207	–0.280	0.020
	25	139	0.207	–0.030
	35	10	–0.018	0.092
Douglas-fir	5	0	—	—
	15	18	0.928	0. 014
	25	21	–1.056	0. 045
	35	16	0.379	–0. 068
Hybrid spruce	5	8	0.150	–0.099
	15	27	0.009	0.054
	25	26	0.513	–0.108
	35	17	–0.345	0.055

Note: N3SLS, nonlinear three-stage least squares; CL, crown length; CRAD, crown radius.

Table 7. PRESS statistic and SSE obtained using PRESS residuals.

Species	Dependent variable	PRESS	SSE
Aspen	CL	245.58	207.21
	CRAD	10.90	7.70
Lodgepole pine	CL	1981.58	1915.23
	CRAD	39.09	36.25
Douglas-fir	CL	458.13	308.12
	CRAD	19.17	14.39
Hybrid spruce	CL	593.04	414.53
	CRAD	9.41	7.53

Note: PRESS, predicted sum of squares statistic; SSE, error sum of squares; CL, crown length; CRAD, crown radius.

Often, the approach taken is dictated by the structural complexity within the stands of interest. For the present study, it was necessary to include dimensions of the main stem, explicit measures of stand density, and use the concomitant relationship between CL and CRAD to obtain good estimates of crown size for aspen, lodgepole pine, Douglas-fir, and hybrid spruce occurring in unmanaged stands.

Although the equations presented here may be more difficult to interpret than equations limited to one or two variables, they offer a good alternative to the current set of crown equations in SORTIE-ND. In terms of the accuracy and precision of the fitted crown models, the combination of variables chosen for eqs. 9 and 10 showed low mean bias for all species tested. Despite the fact that a limited amount of variability in CL and CRAD was explained by eqs. 9 and 10 for some species, the results are an improvement over the simpler crown equations currently used by SORTIE-ND given the wide range of densities present in the study area.

Crown equations that use only dimensions of the main stem such as HEIGHT and DBH have their advantages. By restricting the predictor variables to one or two measurements of tree size, the resulting equations may be applicable to a wider set of tree species, as the same basic structural relationship between the size of the crown and the dimensions of the main stem have been demonstrated on several trees species (Biging and Gill 1997; Soares and Tomé 2001; Gill and Biging 2002*a*, 2002*b*; Bechtold 2003). The main disadvantage is that changes in density that affect crown size are not always reflected by proportionate changes in stem size. For example, Hynynen (1995) reported changes in crown ratio in *Pinus sylvestris* 15 years after thinning but little change in the *H*/*D* ratio and had to add stand BA as a predictor variable for crown ratio. The disproportionate changes in crown size and stem size are most evident in data collected from a wide range of stand densities, which becomes problematic when fitting the equations. Our own evidence of this was seen in the over- and under-predictions of CL and CRAD in earlier tests of SORTIE-ND on stands from our study area (data not shown). Consequently, simple crown equations are most useful in situations in which the differences in densities from stand to stand are limited and stand structure is simple. For example, Gill et al. (2000) noted that their use of only DBH to estimate crown radius was likely helped by the fact that their data had been collected primarily from managed forests that had been treated to maintain a narrow stocking range.

Among the several density-related variables that were tested, BA best described the effect of density on CL and CRAD across all four species. In terms of its importance within the system of equations, BA was found to be significant more frequently for estimates of CL than for estimates of CRAD for the four species tested, reflecting the effect that stand density has on CL better than the effect of density on CRAD. No other density-related variable was significant for more than one of the four species tested for either CL or CRAD and, therefore, were not included in the final system of equations. Despite being significant in eq. 9 for aspen and lodgepole pine, BA explained only a small proportion of the variability in CL. On the other hand, BA explained a much larger proportion of the variability in CL for hybrid spruce. The proportion of variability in CRAD explained by BA was lower for hybrid spruce; nevertheless, the variable remained significant. This finding is likely related to the tendency of shade-tolerant species such as hybrid spruce to undergo a physiological shift in crown dimensions in response to changes in stand density, whereas the crowns of shade-intolerant species such as aspen and lodgepole pine tend to keep a relatively uniform crown form (Oliver and Larson 1996). The use of only BA as an explicit measure of density is consistent with several other studies of crown allometry (Holdaway 1986; Hynynen 1995; Monserud and Marshall 1999; Bechtold 2003).

The effects of CL on CRAD and vice versa were incorporated into eqs. 1 and 2 through the use of a simultaneous system of equations fitted using N3SLS. The use of CL_{first} and $CRAD_{first}$ within the system of equations was based on the hypothesis that a strong feedback mechanism existed between CL and CRAD within all four species included in the model data set. The feedback mechanism was assumed to exist as elongation of lateral branches is under at least partial control of the terminal leader (Pallardy 2008). Thus, increased terminal leader growth should result in increased lateral branch growth. In the absence of substantial crown rise, there should therefore be an effect of CL on CRAD. Conversely, as a result of increased radial branch growth, trees should experience an increase in photosynthate production resulting in increased elongation of the terminal leader, thus describing the effect of CRAD on CL.

The results indicated that the use of $CRAD_{first}$ as a predictor variable for CL proved more beneficial than using CL_{first} as a predictor variable for CRAD. $CRAD_{first}$ was significant for three of the four species tested, whereas CL_{first} was only significant for one of the four species. Based on these mixed results, it was unclear if differences in shade tolerance or crown form could be used to explain the tendency for CL_{first} to have less of an effect on CRAD than $CRAD_{first}$ on CL. Incorporating the feedback mechanism between CL and CRAD into crown allometry equations is not prevalent within the literature. This may be because the majority of forest growth models that simulate crowns are interested in only CL or its variant, crown ratio. Also, measuring both CL and CRAD on trees is less common due to added time and costs. However, because we had collected measurements of both CL and CRAD to simulate crowns in SORTIE-ND, we had the opportunity to further improve the crown equations by using the concomitant relationship in a system of equations. Problems of simultaneity bias and cross-equation correlation of errors were addressed through the use of N3SLS.

One of the main strengths of SORTIE-ND is its transportability, as is evident from the wide range of forest types to which it has been applied (Astrup 2006; Coates et al. 2003). However, because the allometric equations use a predefined set of predictor variables, the challenge is to find a single set of predictor variables that provides accurate and precise estimates for trees with different growth patterns. By doing so, the allometric equations contained within SORTIE-ND may be applied to a wide range of forest types. The four different species tested here represent two distinct growth patterns, as well as two distinct crown forms. Furthermore, the stands from which the trees in the model data set were sampled ranged from young fire-origin stands that had undergone severe natural thinning due to MPB to mature stands that had suffered only minor MPB attack. As a result of these differences, a single set of predictor variables for CL and CRAD could not be found that were significant for all four species. As an alternative, predictor variables were assessed based on their consistency across all four species, which is why predictor variables that were not significant for some species were kept in eqs. 9 and 10, as well as in eqs. 7 and 8. Although there was considerable variation in the density of stands included in the model data set, stands previously subjected to artificial thinning were not sampled. This must be considered when using the crown equations, as simulations of various forms of artificial basal area removal are possible within SORTIE-ND. Without the inclusion of a thinning response function in the crown equations, predicted crown sizes will likely show an unrealistic increase immediately following thinning (Hynynen 1995). This phenomenon would be most evident if output from SORTIE-ND was evaluated on a one-year time step but would appear more realistic following a longer time since thinning.

Results of the overall evaluation of the models through the PRESS statistic were generally positive as PRESS values were only marginally larger than SSE values, with two exceptions. Discrepancies between PRESS and SSE values for estimates of CL on Douglas-fir and hybrid spruce occur, despite the fact that the amount of variability explained in CL by eqs. 9 and 10 for these two species were the highest among the species tested. At least some of the discrepancy between PRESS and SSE values is likely to have arisen due to the combination of smaller sample size and the high amount of variability in CL for these two species.

Conclusions

Our findings that tree stem measurements alone could not account for density-related influences on crown size for Douglas-fir, aspen, lodgepole pine, and hybrid spruce fall in line with earlier studies on other commercially important tree species in the northern hemisphere. When developing crown models using data collected from stands with complex vertical structure and varying density, multiple measures of density should be considered to address the diverse set of interactions between intertree competition and growing space available for crown expansion. If multiple estimates of crown dimensions are needed, as is common in spatially explicit forest growth models such as SORTIE-ND, then it makes sense to use the one crown dimension to improve predictions of another as the different dimensions of the crown are often related through physiological processes. The results presented here at least partially support this and demonstrate how a set of consistent estimators of parameters can be estimated using N3SLS regression for resulting simultaneous system of equations.

Acknowledgements

This research was part of a Master of Science thesis by the lead author, Derek Sattler, completed at the University of British Columbia. We gratefully acknowledge the British Columbia Forest Science Program for providing financial support for this research project and for funding the collection of data as part of an affiliated research project. Furthermore, we thank Taehee Lee, Ruben Schulz, and Peter Marshall for collecting the field data used in this study.

References

Assmann, E. 1970. The principles of forest yield studies. Pergamon Press, Oxford, UK.

Astrup, R. 2006. Modelling growth of understory aspen and spruce in western boreal Canada. Ph.D. dissertation, University of British Columbia, Vancouver, British Columbia.

Astrup, R., and Larson, B.C. 2006. Regional variability of species-specific crown openness for aspen and spruce in western boreal Canada. For. Ecol. Manage. **228**(1–3): 241–250. doi:10.1016/j.foreco.2006.02.048.

Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A., and Taylor, S.W. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography, **29**(3): 427–441. doi:10.1111/j.2006.0906-7590.04445.x.

Baldwin, V.C., Jr., and Peterson, K.D. 1997. Predicting the crown shape of loblolly pine trees. Can. J. For. Res. **27**(1): 102–107. doi:10.1139/x96-100.

Barclay, H.J. 1998. Conversion of total leaf area to projected leaf area in lodgepole pine and Douglas-fir. Tree Physiol. **18**(3): 185–193. PMID:12651388.

Bechtold, W.A. 2003. Crown-diameter prediction models for 87 species of stand-grown trees in the eastern United States. South. J. Appl. For. **27**: 269–278.

Biging, G.S., and Gill, S.J. 1997. Stochastic models for conifer tree crown profiles. For. Sci. **43**: 25–34.

Bowden, R.J., and Turkington, D.A. 1984. Instrumental variables. Cambridge University Press, Cambridge, UK.

Canham, C.D., Coates, K.D., Bartemucci, P., and Quaglia, S. 1999. Measurement and modelling of spatially explicit variation in light transmission through interior cedar–hemlock forests of British Columbia. Can. J. For. Res. **29**(11): 1775–1783. doi:10.1139/x99-151.

Catovsky, S., Kobe, R.K., and Bazzaz, F.A. 2002. Nitrogen-induced changes in seedling regeneration and dynamics of mixed conifer – broad-leaved forests. Ecol. Appl. **12**(6): 1611–1625.

Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L., and Messier, C. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manage. **186**(1–3): 297–310. doi:10.1016/S0378-1127(03)00301-3.

Gallant, A.R. 1975. Seemingly unrelated nonlinear regressions. J. Econ. **3**: 35–50.

Gill, S.J., and Biging, G.S. 2002*a*. Autoregressive moving average (ARMA) models of crown profiles for two California hardwood species. Ecol. Model. **152**(2–3): 213–226. doi:10.1016/S0304-3800(02)00019-4.

Gill, S.J., and Biging, G.S. 2002*b*. Autoregressive moving average (ARMA) models of conifer crown profiles. J. Agric. Biol. Environ. Stat. **7**(4): 558–573. doi:10.1198/108571102762.

Gill, S.J., Biging, G.S., and Murphy, E.C. 2000. Modeling conifer tree crown radius and estimating canopy cover. For. Ecol. Manage. **126**(3): 405–416. doi:10.1016/S0378-1127(99)00113-9.

Gilmore, D.W. 2001. Equations to describe crown allometry of *Larix* require local validation. For. Ecol. Manage. **148**(1–3): 109–116. doi:10.1016/S0378-1127(00)00493-X.

Harlow, W.M., Harrar, F.S., and White, F.M. 1979. Textbook of dendrology. McGraw-Hill, Toronto, Ontario, Canada.

Hasenauer, H., and Monserud, R.A. 1996. A crown ratio model for Austrian forests. For. Ecol. Manage. **84**(1–3): 49–60. doi:10.1016/0378-1127(96)03768-1.

Hawkes, B., Taylor, S., Stockdale, C., Shore, T.L., Alfaro, R.I., Campbell, R., and Vera, P. 2004. Impacts of mountain pine beetle on stand dynamics in British Columbia. *In* Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia, 30–31 October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Information Report BC-X-399. pp. 175–195.

Heath, R., and Alfaro, R.I. 1990. Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle: a case study. J. Entomol. Soc. B.C. **87**: 16–21.

Holdaway, M.R. 1986. Modeling tree crown ratio. For. Chron. **62**: 451–455.

Hynynen, J. 1995. Predicting tree crown ratio for unthinned and thinned Scots pine stands. Can. J. For. Res. **25**(1): 57–62. doi:10.1139/x95-007.

Judge, G.G., Griffiths, R.C., Lutkepohl, H., and Lee, T.C. 1985. The theory and parctic of econometrics. 2nd ed. John Wiley and Sons, New York.

Kellomäki, S., Ikonen, V., and Kolstrom, T. 1999. Modelling the structural growth of Scots pine with implications for wood quality. Ecol. Model. **122**(1–2): 117–134. doi:10.1016/S0304-3800(99)00086-1.

Kutner, M.H., Nachtsheim, C.J., Neter, J., and Li, W. 2005. Applied linear statistical models. International Edition. McGraw-Hill, New York. pp. 214–232.

Lindgren, P.M., Sullivan, T.P., Sullivan, D.S., Brockley, R.P., and Winter, R. 2007. Growth response of young lodgepole pine to thinning and repeated fertilization treatments: 10-year results. Forestry, **80**(5): 587–611. doi:10.1093/forestry/cpm039.

Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. British Columbia Ministry of Forestry, Research Branch, Victoria, British Columbia, Spec. Rep. Ser. No. 6.

Meng, S.X., Lieffers, V.J., and Huang, S.M. 2007. Modelling crown volume of lodgepole pine based upon the uniform stress theory. For. Ecol. Manage. **251**(3): 174–181. doi:10.1016/j.foreco.2007.06.008.

Mitchell, K.J. 1975. Dynamics and simulated yield of Douglas-fir. Society of American Foresters, For. Sci. Monogr. 17.

Monserud, R.A., and Marshall, J.D. 1999. Allometric crown relations in three northern Idaho conifer species. Can. J. For. Res. **29**(5): 521–535. doi:10.1139/x99-015.

Monserud, R.A., and Sterba, H. 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. For. Ecol. Manage. **80**(1–3): 57–80. doi:10.1016/0378-1127(95)03638-5.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley and Sons, Inc., New York.

Pacala, S.W., Canham, C.D., and Silander, J.A., Jr. 1993. Forest models defined by field measurements. 1. The design of a northeastern forest simulator. Can. J. For. Res. **23**(10): 1980–1988. doi:10.1139/x93-249.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Jr., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. **66**(1): 1–43. doi:10.2307/2963479.

Pallardy, S.G. 2008. Physiology of woody plants. 3rd ed. Academic Press, San Diego (California), London (UK).

Quan, N.T. 1988. The prediction sum of squares as a general measure for regression diagnostics. J. Bus. Econ. Stat. **6**(4): 501–504. doi:10.2307/1391469.

Remphrey, W.R., and Pearn, L.P. 2003. Crown development of a clone of *Populus tremuloides* exhibiting "crooked" architecture and a comparison with wild-type trees. Can. J. Bot. **81**(4): 345–359. doi:10.1139/b03-028.

Rouvinen, S., and Kuuluvainen, T. 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. **27**(6): 890–902. doi:10.1139/x97-012.

Rudnicki, M., Silins, U., and Lieffers, V.J. 2004. Crown cover is correlated with relative density, tree slenderness, and tree height in lodgepole pine. For. Sci. **50**: 356–363.

SAS Institute Inc. 2003. SAS/ETS user's guide, version 9.1.3. SAS Institute Inc., Cary, North Carolina.

Schabenberger, O., and Pierce, F.J. 2002. Contemporary statistical models for the plant and soil sciences. CRC Press, Boca Raton, Florida.

Soares, P., and Tomé, M. 2001. A tree crown ratio prediction equation for eucalypt plantations. Ann. For. Sci. **58**(2): 193–202. doi:10.1051/forest:2001118.

Stockdale, C., Taylor, S., and Hawkes, B. 2004. Incorporating mountain pine beetle impacts on stand dynamics in stand and landscape models: a problem analysis. *In* Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia, 30–31 October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Information Report BC-X-399. pp. 200–209.

Stone, M. 1974. Cross-validation choice and assessment of statistical prediction. J. R. Stat. Soc. B, **36**: 111–147.

Valentine, H.T., and Mäkelä, A. 2005. Bridging process-based and empirical approaches to modelling tree growth. Tree Physiol. **25**(7): 769–779. PMID:15870047.

Valentine, H.T., Ludlow, A.R., and Furnival, G.M. 1994. Modelling crown rise in even-aged stands of Sitka spruce or loblolly pine. For. Ecol. Manage. **69**(1–3): 189–197. doi:10.1016/0378-1127(94)90228-3.

Vanclay, J. 1994. Modelling forest growth and yield: applications to mixed tropical forests. CAB International, Wallingford, UK.

Wu, D.M. 1973. Alternative tests of independence between stochastic regressors and disturbances. Econometrica, **41**: 733–750.

Wykoff, W.R. 1985. Supplement to the user's guide for the stand prognosis model, version 5.0. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, Gen. Tech. Rep. INT-193. pp. 44–52.

Zellner, A., and Theil, H. 1962. Three-stage least squares: simultaneous estimation of simultaneous equations. Econometrica, **30**: 54–78.