Leaf area prediction models for *Tsuga canadensis* in Maine[1]

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Abstract: *Tsuga canadensis* (L.) Carr. (eastern hemlock) is a common species throughout the Acadian forest. Studies of leaf area and growth efficiency in this forest type have been limited by the lack of equations to predict leaf area of this species. We found that sapwood area was an effective leaf area surrogate in *T. canadensis*, though adding crown length to the sapwood equations improved model performance. Prediction bias was observed at the upper end of our data for the best sapwood equation. Sapwood area at crown base did not predict leaf area as well as sapwood area at breast height. Equations using crown length or crown volume alone were the least effective of all models tested. Models using stem cross-sectional area inside the bark or tree basal area with a modified live crown ratio produced results comparable with those of the best sapwood-based model and were unbiased across the range of our data. There findings verify the value of nonsapwood-based approaches to *T. canadensis* leaf area prediction.

Résumé : La pruche du Canada (*Tsuga canadensis* (L.) Carr.) est une espèce fréquente partout dans la forêt acadienne. Il y a eu peu d'études qui portent sur la surface foliaire et l'efficacité de croissance dans ce type de forêt à cause de l'absence d'équations permettant de prédire la surface foliaire de cette espèce. Nous avons découvert que la surface de bois d'aubier est un substitut efficace pour prédire la surface foliaire chez la pruche du Canada quoique l'ajout de la longueur de la cime aux équations qui utilisent le bois d'aubier améliore la performance du modèle. Un biais dans la prédiction a été observé à la limite supérieure des données avec la meilleure équation utilisant le bois d'aubier. La surface de bois d'aubier à la base de la cime ne prédisait pas la surface foliaire aussi bien que la surface de bois d'aubier à hauteur de poitrine. Les équations qui utilisent seulement la longueur ou le volume de la cime sont les moins efficaces de tous les modèles testés. Les modèles qui utilisent la surface radiale de la tige sans écorce ou la surface terrière de l'arbre, avec ou sans un rapport modifié de cime vivante, ont produit des résultats comparables à ceux du meilleur modèle basé sur le bois d'aubier et étaient non biaisés pour toute l'étendue des données. Ces résultats permettent de vérifier la valeur des approches qui ne sont pas basées sur le bois d'aubier pour la prédiction de la surface foliaire de la pruche du Canada.

[Traduit par la Rédaction]

Introduction

The ecophysiological basis of production silviculture is greatly enhanced when stand density and structure are described directly in terms of leaf area (LA) rather than traditional empirical measures based on numbers and sizes of stems (O'Hara 1996, 1998). The use of LA in structural control requires accurate and efficient means of estimating the amount of foliage on standing trees. Equations that predict LA from diameter or basal area have a long history but are often inaccurate (Marshall and Waring 1986; Bormann 1990). Sapwood area has become the preferred predictor based on the close biological relationship between the conducting xylem and the foliage it supports.

Tsuga canadensis (L.) Carr. (eastern hemlock) is a common species in the Lake States and New England, including the southern part of the Acadian forest. Although LA equations have been developed for other conifers in this forest type (Marchand 1984; Coyea and Margolis 1992; Gilmore et al. 1996; Maguire et al. 1998), no equations exist for *T. canadensis*. This deficiency has been an impediment to research on LA and growth efficiency (stem volume growth per unit LA) in northeastern forests. The research reported here explores allometric leaf area equations for *T. canadensis* and compares these models to equations published for other species in this and other regions.

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Study area

The stand sampled in this study is part of a long-term silvicultural experiment on the 1540-ha Penobscot Experimental Forest (PEF) in east-central Maine, located at approximately 44°52′N, 68°38′W. The PEF was purchased in 1950 by a number of industrial landholders and leased to the USDA Forest Service to allow that agency to begin experiments to study uneven- and even-aged silvicultural systems. Ongoing treatments and remeasurements follow a long-term study plan that ensures consistency in management over time. The 6.6-ha study stand is one of two replicates of

Table 1. Characteristics of twenty trees sampled in 1996 to develop *Tsuga canadensis* leaf area prediction models.

	Minimum	Mean ± SE	Maximum
Diameter at 1.3 m (cm)	6.8	28.2±2.8	48.4
Height (m)	5.61	14.71±1.11	20.95
Crown length (m)	3.63	11.36±0.85	16.94
Live crown ratio	0.62	0.78±0.02	0.95
Crown projection area (m^2)[a]	7.41	33.80±4.39	73.55
Sapwood area at 1.3 m (cm^2)	24.72	303.4±45.4	663.69
Sapwood area at crown base (cm^2)	17.94	245.1±35.2	547.45
Projected leaf area (m^2)	10.54	118.58±17.21	267.58

[a]Crown projection area = $\sum(\pi r_i^2)/4$, where the r_i are the four individual radius measurements (Gregoire and Valentine 1995).

Table 2. Characteristics of sixty-nine branches sampled in 1996 and 1998 to develop *Tsuga canadensis* branch-level leaf area prediction models.

	Minimum	Mean ± SE	Maximum
Branch diameter (cm)	0.2	3.4±0.3	8.2
Height from ground (m)	1.89	9.11±0.54	19.79
Depth into crown (m)	0.31	6.06±0.48	15.76
Relative depth into crown	0.03	0.52±0.04	1.00
Leaf mass (g)	0.939	344.426±46.887	1632.015
Projected leaf area (m^2)	0.006	1.950±0.276	10.546
Specific leaf area (cm^2/g)	41.95	58.43±1.15	79.35

selection cutting on a 5-year cycle, with eight selection cuttings prior to our study. The structural goal was defined using the BD*q* (basal area, maximum diameter, *q*-factor) method with a *q* factor of 1.96 on 5-cm classes, a residual maximum diameter goal of 48 cm, and a target residual basal area (BA) of 26 m^2/ha (Seymour and Kenefic 1998).

Within-stand species composition is highly variable because of differences in soil drainage and stand structural condition. The dominant species are *T. canadensis*, *Picea rubens* Sarg. (red spruce), and *Abies balsamea* (L.) Mill. (balsam fir). Other species include *Thuja occidentalis* L. (northern white cedar), *Acer rubrum* L. (red maple), *Betula papyrifera* Marsh. (paper birch), *Picea glauca* (Moench.) Voss (white spruce), and other hardwoods (Kenefic and Seymour 1999). The species composition of this stand typifies much of the Acadian region, a transitional zone between the eastern hardwood and boreal forests.

Methods

A 25-m systematic grid was established in the study stand in 1995. A random sample of 50 *T. canadensis*, stratified by 5-cm diameter at breast height (DBH, 1.3 m) classes, was taken from 12.5-m radius plots centered on the grid points. The sample included trees at least 1.3 m in height, up to 50.0 cm DBH. Sampling was restricted to somewhat poorly, moderately well, and well-drained soils, and excluded areas encompassed by the USDA Forest Service continuous forest inventory plots. A subsample of 20 trees representing a range of heights and canopy positions was chosen for the leaf area study in May 1996 from the initial 50-tree sample (Table 1).

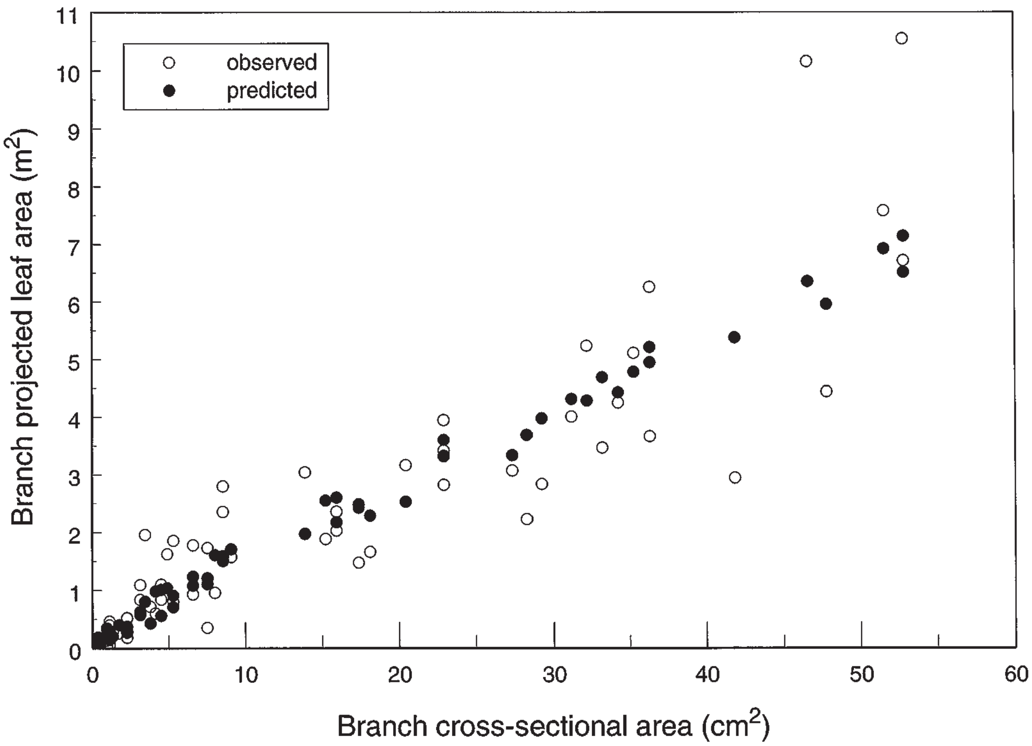
Tree height, DBH, bark thickness, crown class, crown radii in four cardinal directions, height to the lowest branch, and height to the lowest cluster of branches were measured on each sample tree prior to felling. The lowest cluster of branches (analogous to a true whorl) was defined as the first group of three or more closely spaced branches, unless a lower branch made up 40% or more of the crown projection area (CPA) at that height. Cross-sectional area inside the bark at breast height (ABH = π[(DBH/2) – bark thickness]^2) was calculated for each tree.

Each sample tree was felled and a random branch removed from the lower, middle, and upper third of the crown (Table 2). Foliage samples were removed from all needle age-classes in approximate proportion to their occurrence and immediately frozen in a portable cooler for subsequent specific leaf area (SLA) determination. Remaining foliage and biomass components of each branch were stored in paper bags. Diameter above basal swelling and height of all live branches were measured for calculation of branch cross-sectional area and position within the crown. Diameter at crown base (DCB) was measured and cross-sectional disks approximately 1–2 cm thick were removed at stump height (0.1 m), breast height (1.3 m), lowest live branch, and at 2-m intervals from the lowest live branch to the tip. The sapwood–heartwood boundary was tentatively identified in the field by holding each disk to the sunlight, and tracing the apparent boundary between the translucent (water conducting) and nontranslucent zones with a fine-tipped permanent marker. Other translucent wetwood zones separated from the apparent sapwood by continuous opaque bands of growth rings were ignored.

Nine additional branches larger than 6 cm in diameter were sampled in June 1998 to supplement small sample size in this range. Trees larger than 29 cm DBH (the minimum DBH of trees in the 1996 sample with branches larger than 6 cm) were selected from the remaining trees in the initial 50-tree sample as potential sources of new branches. Updated height and crown measurements were taken. An arborist climbed to the top of each tree, measuring and numbering all branches above the threshold size. One branch was selected at random from each tree and lowered with cables to prevent breakage. Needle subsampling and drying procedures followed those described above.

Prior to drying, projected leaf area was determined for each branch based on two 100-needle subsamples taken from the bag of

Fig. 1. Observed and predicted branch projected leaf area (BLA) relative to branch cross-sectional area (XSECT), as a function of XSECT and relative depth into the crown (RDINC). BLA = $(-0.1589 + 0.4375\text{XSECT}^{0.33} + 0.4544\text{RDINC}^{0.33})^3$.



foliage frozen from that branch. Subsamples were limited to 100 needles because of the restricted field of vision associated with the Ag-Image optical analysis system (Decagon Devices, Inc.), which was used to obtain measurements in 1996. The 1996 projected leaf area values were consistently higher than those obtained in 1998 with the WinNEEDLE system (Régent Instruments, Inc.). Microscope analysis of needle cross sections using a calibrated stage micrometer revealed that the Ag-Image system overestimated needle width at the recommended grayscale threshold settings (M. Day, unpublished data). This was attributed to shadow effects, which are exacerbated by large pixel size. The WinNEEDLE system provides more accurate estimates of needle size because of its balanced-by-directional lighting system and higher resolution. Measurements from the two systems were compared, and a ratio correction factor of 0.81 was calculated from branches of similar size and crown position and applied to all branches measured in 1996 to obtain a corrected leaf area.

Each 100-needle subsample was dried in a convection oven at 65°C for 48 h and weighed to the nearest 0.0001 g. The area of each subsample was divided by its mass to determine SLA (cm^2/g). A single SLA was calculated for each branch by averaging the values obtained from the two subsamples. Whole-branch samples and the remaining frozen needles were dried in a drying room at 46°C for at least 72 h. Foliage and woody materials from each branch were hand separated and weighed to the nearest 0.0001 g. Branch-level projected leaf area (BLA) was calculated by multiplying dry foliage mass by a branch-specific SLA.

It is difficult to consistently identify the *T. canadensis* sapwood–heartwood boundary, in part because of the potential for areas of translucent wetwood caused by bacterial infection in the heartwood. A 0.1 M solution of ferrous ammonium sulfate ($Fe(NH_4)_2(SO_4)_2{\cdot}6H_2O$) was applied to seasoned disks to identify the sapwood colorimetrically (Eades 1958). The field-marked sapwood boundary was either confirmed or adjusted in favor of the dye. The mechanism for this reaction is believed to be differences in the forms of tannins in the sapwood and heartwood (B. Goodell, personal communication). This was tested by applying a 0.01 M solution of anhydrous ferric chloride ($FeCl_3$) and a 0.25 mM solution of Ferrozine iron reagent, monohydrate ($C_{20}H_{13}N_4NaO_6S_2{\cdot}H_20$) (Hach Company) to a subsample of seasoned cross-sectional disks. Each disk was polished and width of the sapwood measured along the average stem radius with a Velmex measuring system (Velmex, Inc.). Sapwood area was determined for each disk as a function of stem diameter and sapwood radius at that location, and bark thickness at breast height.

Analysis

Branch-level equation

We compared linear and nonlinear equations of the form $y_i = f(\beta|x_i) + \epsilon_i$, where $\epsilon_i \overset{\text{iid}}{\sim} N(0, x_i^n\sigma^2)$, to identify an equation suitable for predicting BLA from branch cross-sectional area (XSECT) and branch position (iid, independently and identically distributed). Equations were weighted by x_i^n with n = 0, –1, –2, and –3 to identify the optimal weighting factor to correct for heteroskedasticity. Generalized R^2 (Kvålseth 1985) was calculated on the original scale using the corrected sum of squares $(1 - [\text{ssresid}/\sum(y_i - y_m)^2])$, where ssresid is the residual sum of squares, the y_i are the individual sample values, and y_m is the sample mean. Collinearity statistics were used to detect the presence and severity of multicollinearity between predictor variables. The condition index, or square root of the ratio of the largest to smallest eigenvalues in the correlation matrix for the independent variables, was calculated (Huang and Titus 1995). This value was compared with the proposed critical value for moderate multicollinearity (Belsley et al. 1980) to determine the degree of multicollinearity. Values less than 30 indicate that collinearity is not a serious problem. Furnival's (1961) index of fit (FI), a modified maximum likelihood criterion that allows concurrent evaluation of root mean square error, normality, and homoskedasticity, was used to identify optimal model forms. Index of fit has the advantage of simultaneously allowing comparison both across model forms and within models across weighting factors. The lower the FI value, the better the fit based on the criteria listed above.

Tree-level equation

Tree-level projected leaf area (PLA) was calculated for each sample tree by applying the branch-level model to each branch and summing the predicted BLA values. A number of linear and nonlinear, published and unpublished model forms were tested, and analysis was done as above to identify which was optimal. Both sapwood and nonsapwood-based models were explored.

Only equations with significant parameters ($\alpha = 0.05$) were considered, and plots of standardized residuals against predicted variables were used to verify homogeneous variance. Reasonable biologic behavior was taken into consideration, and evaluated using scatterplots of the sample data against the predictor equations.

Results

Branch-level projected leaf area

The average SLA was 58.43 cm^2/g but varied with branch position: SLA values were generally higher for branches lower in the crown. BLA was best expressed as a function of XSECT and relative depth into the crown (RDINC = (tree height – branch height)/(tree height – height to lowest live branch)). The significance of these predictor variables, but not the model form, is consistent with the findings of Maguire et al. (1998) for *P. rubens*. A comparison of a number of model forms and transformations showed that a linear model with a cube-root transformation was optimal (Fig. 1). This model behaved well over the range of data available in this study but was not tested outside this range. Bias correction was deemed unnecessary because the average predicted BLA transformed back to the original scale was only 3% less than the average observed BLA. The R^2 for this equation was 0.92. The intercept term was marginally nonsignificant (p = 0.057) but removing it from the model biased the residuals for small branches. The condition index was 12.3, indicating that multicollinearity is not a serious problem.

Tree-level projected leaf area

Thirteen models were tested for the tree-level equation (Tables 3 and 4). PLA was best estimated as a function of sapwood area at breast height (SA_{bh}) and crown length (CL = tree height – height to the lowest live branch). Model 4, weighted by SA_{bh}^{-2} to correct for increasing variance in the residual plots, had the lowest FI of those tested. The condition index was 12.9, indicating an acceptable level of multicollinearity between the predictor variables. Using the lowest cluster of branches to identify crown base and calculate crown length (Gilmore et al. 1996) diminished model performance. Using SA_{bh} as the sole predictor variable (linear model 2, weighted by SA_{bh}^{-1}) worked fairly well relative to the other sapwood-based models and requires easier and less expensive data collection. However, nonsapwood-based models 10, 12, and 13 were superior to all but models 4 and 6 (additive linear and multiplicative nonlinear models using SA_{bh} and CL). Model 10 uses cross-sectional area inside the bark at crown base (ACB), while 12 and 13 use ABH or BA with a modified live crown ratio (mLCR) (Valentine et al. 1994). These equations produced results comparable with those of sapwood-based models 4 and 6 and have the advantage of not requiring coring or measurement of sapwood area.

Model 4, though best in terms of FI, does exhibit slight bias at the upper end of the data (Fig. 2). Model 2, the linear model with SA_{bh} as sole predictor, had a higher (less desirable) FI, but less bias at the upper end of the data (Fig. 3). Model 10, the best nonsapwood-based equation, yielded only a slightly higher FI than model 4 and does not exhibit any prediction bias (Fig. 4). However, this model predicts PLA from ACB and thus requires data that are more difficult to collect. Model 13, which is based on BA and mLCR, proved to be an excellent alternative. It does not require difficult data collection, has a comparable FI, and predicts PLA without bias across the range of the data (Fig. 5).

Crown parameters alone were not precise predictors. Crown length only, for example, resulted in FI values twice those of both the best sapwood- and nonsapwood-based models. This sharply contrasts results from Gilmore et al. (1996), who recommend crown length as a SA_{bh} surrogate in *A. balsamea*. Lastly, sapwood taper below the live crown (Maguire and Hann 1989; Maguire and Batista 1996) has led some authors to recommend using the distance from breast height to the center of the crown (D) as a predictor variable (Dean and Long 1986; Dean et al. 1988; Long and Smith 1989). This variable failed to contribute significantly to any of the models tested in this study, including the power function $PLA = b_1(SA_{bh}^{\,b_2})(D^{b_3})$ originally suggested by Dean and Long (1986).

Discussion

Our findings demonstrate the variability in performance of a number of similar and commonly used PLA models when applied to *T. canadensis*. This result is hardly surprising, since these models were developed for different species in different geographic areas, and optimal model form has been found to vary even within species across geographic regions (O'Hara and Valappil 1995; Gilmore et al. 1996). This variation underscores the importance of developing species- and region-specific equations.

One of the reasons for the lack of previous research on *T. canadensis* LA relationships is the difficulty in identifying the sapwood. Unlike other softwood species in the Northeast, the *T. canadensis* sapwood–heartwood boundary cannot be consistently distinguished with the "light transmittance" test (transparent sapwood, opaque heartwood), especially in increment cores. Eades (1958) noted this problem in *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and recommended iron salts as a means of colorimetrically differentiating the sapwood. Eades validated this method by applying the chemical to *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), which has a sapwood–heartwood boundary that is easily distinguished with the naked eye.

Tsuga canadensis sapwood radii determined in the field and with iron salts did not differ significantly at $\alpha = 0.05$ (paired t test for means, 39 df, $p = 0.75$). Both methods thus provide independent confirmation of the sapwood–heartwood

Table 3. Model forms, weighting factors, and fit statistics for linear and nonlinear, sapwood- and nonsapwood-based models screened for prediction of *Tsuga canadensis* projected leaf area.

Model	Model form*	Weight	R^{2}†	RMSE‡	FI§	Source‖
1	$PLA = b_0 + b_1 SA_{cb}$	SA_{cb}^{-2}	0.93	0.095 27	17.261	Marchand 1984; Coyea and Margolis 1992
2	$PLA = b_0 + b_1 SA_{bh}$	SA_{bh}^{-1}	0.95	1.090 79	15.878	Marchand 1984; Coyea and Margolis 1992
3	$\ln PLA = b_1 \ln SA_{bh}$	na	0.93	0.188 87	16.735	Espinosa Bancalari et al. 1987
4	$PLA = b_0 + b_1 SA_{bh} + b_2 CL$	SA_{bh}^{-2}	0.94	0.053 76	11.392	Coyea and Margolis 1992
5	$\ln PLA = b_1 \ln SA_{bh} + b_2 \ln CL$	na	0.92	0.161 71	14.329	Gilmore et al. 1996
6	$PLA = b_1 SA_{bh}^{b_2} CL^{b_3}$	SA_{bh}^{-2}	0.93	0.061 37	13.004	Gilmore et al. 1996
7	$\ln PLA = b_1 \ln CL$	na	0.77	0.307 96	27.287	Gilmore et al. 1996
8	$PLA = b_1 CV^{b_2}$	CV^{-1}	0.93	1.795 15	17.847	D.A. Maguire, personal communication
9	$PLA = b_0 + b_1 BA$	BA^{-1}	0.96	0.619 37	13.576	—
10	$PLA = b_1 ACB + b_2 ACB^2$	None needed	0.97	12.745 61	12.746	—
11	$PLA = b_1 ABH + b_2 ABH^2$	None needed	0.97	14.746 40	14.746	—
12	$PLA = b_0 + b_1 (ABH \times mLCR)$	ABH^{-1}	0.95	0.677 98	13.005	Valentine et al. 1994
13	$PLA = b_0 + b_1 (BA \times mLCR)$	BA^{-1}	0.95	0.589 27	12.916	—

*PLA, projected leaf area (m^2); SA_{cb}, sapwood area at crown base (cm^2); SA_{bh}, sapwood area at 1.3 m (cm^2); CL, crown length (m); CV, crown volume (0.33(CL × crown projection area); m^3); BA, basal area (cm^2); ACB, area inside the bark at crown base (cm^2); ABH, area inside the bark at 1.3 m (cm^2); mLCR, modified live crown ratio (CL/(tree height – 1.3)) (Valentine et al. 1994).

†Kvålseth's (1985) generalized R^2.

‡Root mean squared error.

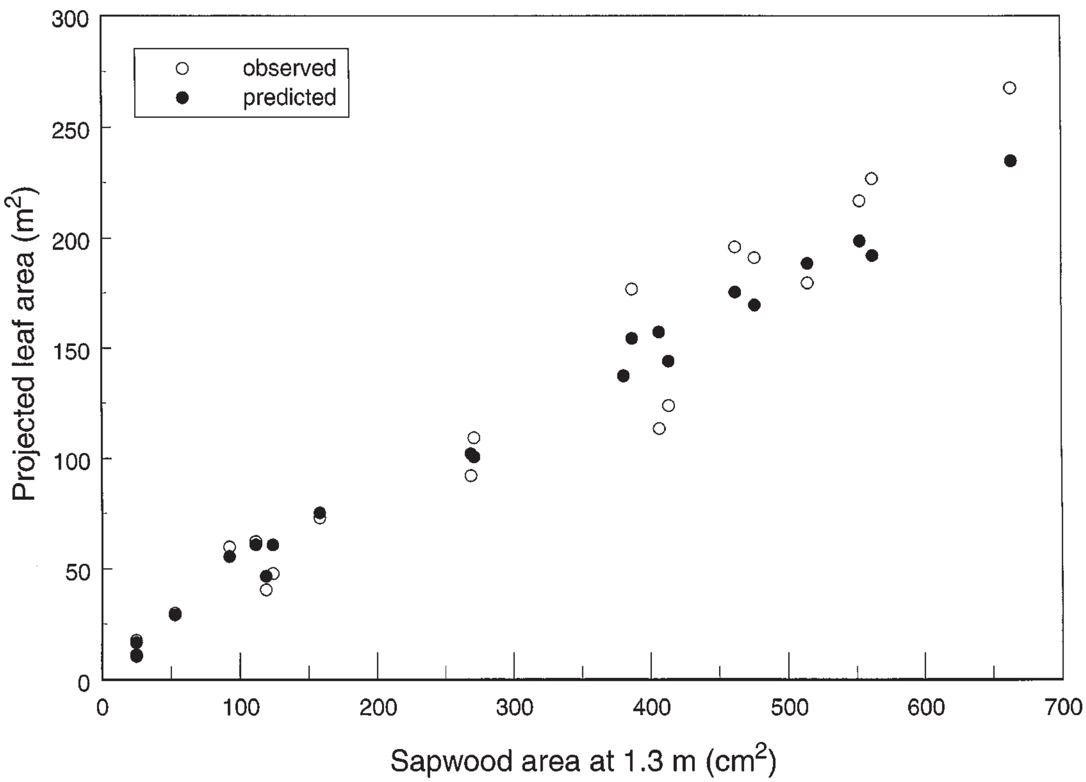
§Furnival's (1961) index of fit.

‖Model forms, but not weighting factors, are attributed to the cited sources.

Table 4. Parameter estimates, SEs (in parentheses), and log bias correction factors (Baskerville 1972) for *Tsuga canadensis* projected leaf area models.

Model	Parameters
1	b_0 = 3.6541 (1.5968), b_1 = 0.4783 (0.027 01)
2	b_0 = 7.5432 (3.3681), b_1 = 0.3659 (0.017 87)
3	b_1 = 0.8378 (0.007 752) log bias correction factor = 1.018
4	b_0 = –9.9148 (2.7889), b_1 = 0.2688 (0.024 01), b_2 = 3.8895 (0.6440)
5	b_1 = 0.6013 (0.084 28), b_2 = 0.5406 (0.1921) log bias correction factor = 1.013
6	b_1 = 0.7587 (0.1285), b_2 = 0.5558 (0.070 75), b_3 = 0.7586 (0.1771)
7	b_1 = 1.9071 (0.028 81) log bias correction factor = 1.049
8	b_1 = 2.2109 (0.6068), b_2 = 0.8093 (0.053 47)
9	b_0 = 10.8264 (2.3662), b_1 = 0.1454 (0.006 001)
10	b_1 = 0.2862 (0.016 15), b_2 = –0.000 056 80 (0.000 018 19)
11	b_1 = 0.2471 (0.016 15), b_2 = –0.000 050 89 (0.000 014 72)
12	b_0 = 9.9455 (2.2715), b_1 = 0.2264 (0.009 060)
13	b_0 = 8.9221 (2.3341), b_1 = 0.1789 (0.007 060)

Fig. 2. Observed and predicted tree projected leaf area (PLA) relative to sapwood area at 1.3 m (SA_{bh}), as a function of SA_{bh} and crown length (CL). Predicted PLA values obtained from model 4, PLA = –9.9148 + 0.2688 × SA_{bh} + 3.8895CL.



boundary. Areas of wetwood did not react with the dye. The ferric sulfate reaction is a traditional test for tannins (Jensen 1962) and apparently highlights differences in the form of tannins between the heartwood and sapwood. Because iron salts are unspecific phenolic reagents, potentially causing a positive result because of reaction with other plant constituents (Swain 1965), we felt it necessary to confirm the validity of this test by identifying the causal mechanism. Some forms of tannins are able to reduce Fe^{3+} to Fe^{2+}. Our application of anhydrous ferric chloride (Fe^{3+}) and a Fe^{2+} reagent

Fig. 3. Observed and predicted tree projected leaf area (PLA) relative to sapwood area at 1.3 m (SA_{bh}), as a function of SA_{bh}. Predicted PLA values obtained from model 2, PLA = 7.5432 + 0.3659SA_{bh}.

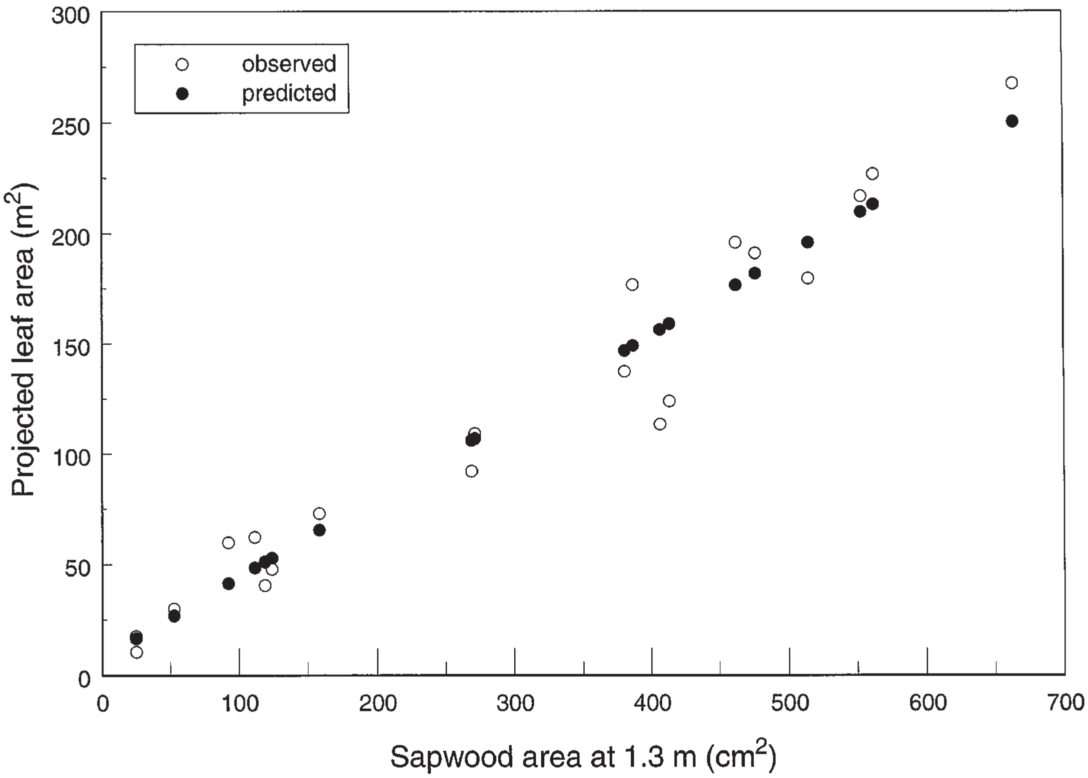
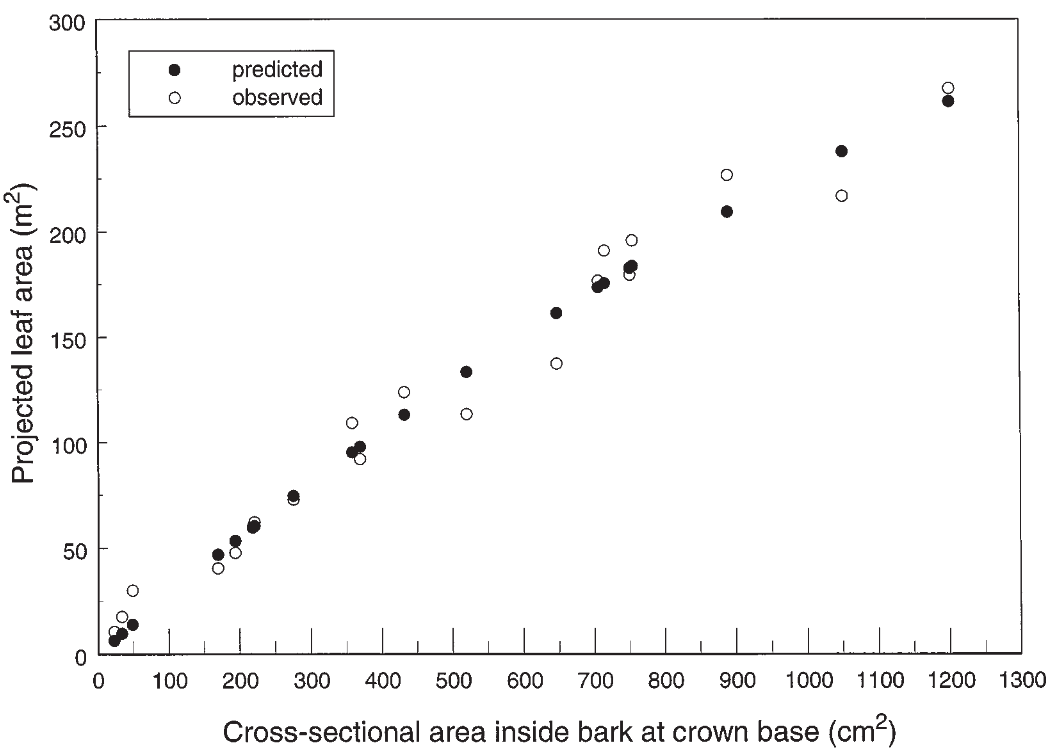


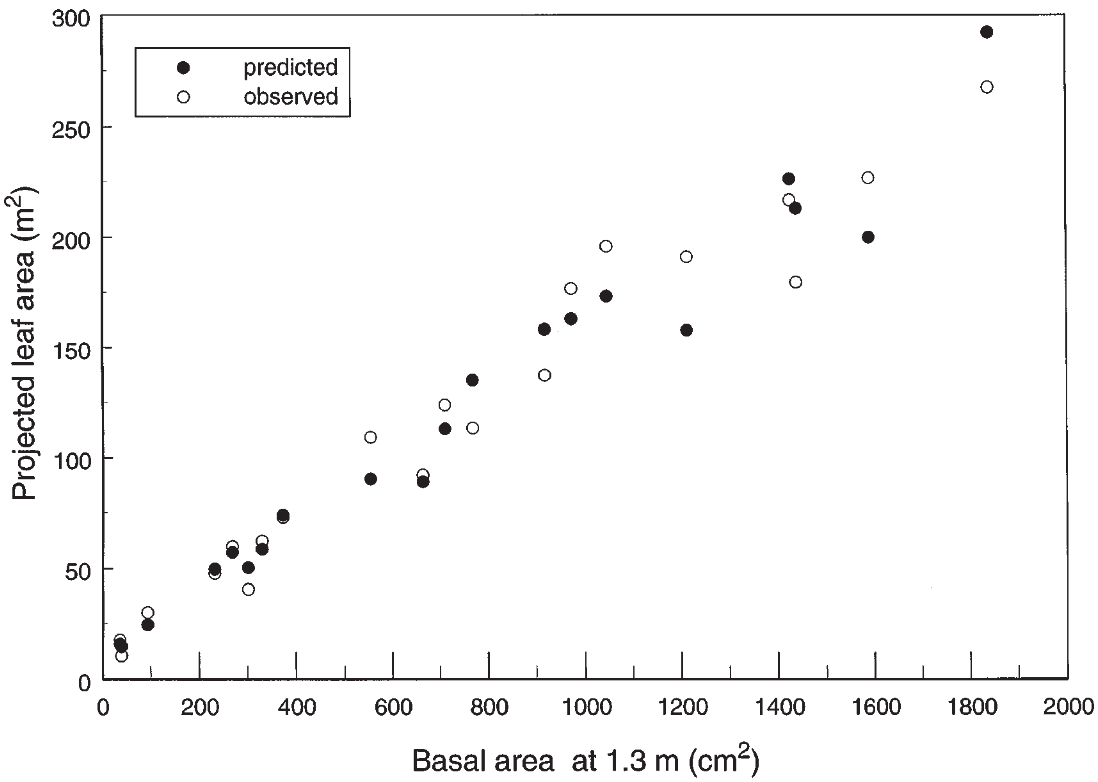
Fig. 4. Observed and predicted tree projected leaf area (PLA) relative to cross-sectional area inside the bark at crown base (ACB), as a function of ACB. Predicted PLA values obtained from model 10, PLA = 0.2862ACB – 0.000 050 89 ACB^2.



(Ferrozine) indicated the presence of Fe^{2+} in the sapwood, but not in the heartwood. This confirmed that $Fe^{3+} \rightarrow Fe^{2+}$ reducing tannins are not present in the heartwood, and provided evidence that a difference in the forms of tannins is the mechanism for the ferric sulphate reaction.

Our results confirm the value of SA as a LA surrogate, as

Fig. 5. Observed and predicted tree projected leaf area (PLA) relative to basal area at 1.3 m (BA), as a function of BA and a modified live crown ratio (mLCR). Predicted PLA values obtained from model 13, PLA = 8.9222 + 0.1789(BA × mLCR).



is suggested by the functional relationship between conducting xylem and foliage. This supports the findings of Waring et al. (1982), who recommended linear models with SA_{bh} or SA_{cb} for *T. heterophylla* and *Tsuga mertensiana* (Bong.) Sarg. (mountain hemlock). However, Waring et al. (1982) did not test other predictor variables. Our findings indicate that models with SA alone are not optimal for *T. canadensis*. The significance of CL as a second predictor variable may be attributed to the fact that it reflects tree height, the arrangement of foliage in space, or light environment. Unlike Gilmore et al. (1996), we found that crown parameters alone (either CL or conic crown volume) did not perform well as PLA predictors. This may be due to the fact that *A. balsamea*'s growth pattern results in a consistent, geometric crown shape, while *T. canadensis* crowns are more irregular. Additionally, model 4, with SA_{bh} and CL as predictor variables, performed well across most of the range of the data but underestimated PLA of our largest trees. This model could lead to overestimation of growth efficiency for large trees and should not be applied to trees at the upper range of our data. Model 2 based on SA_{bh} alone is a less biased alternative.

The equation with SA_{cb} (model 1, weighted by SA_{cb}^{-1}) did not perform as well as the model using SA_{bh}. This is surprising since, in theory, SA_{cb} is more closely associated with leaf area, given the taper in sapwood from breast height to crown base (Waring et al. 1982; Maguire and Hann 1989). Gilmore et al. (1996) also found SA_{bh} to be a better predictor than SA_{cb} for *A. balsamea* PLA, but the magnitude of difference in model performance was much greater in their study. Their results may be explained by the fact that SA_{cb} was measured at the lowest whorl in their study, excluding isolated branches below this height.

Perhaps the most interesting result was the performance of models 10, 12, and 13 based on stem cross-sectional area at crown base and breast height with and without mLCR. There is no evidence that the superior performance of these nonsapwood-based models was due to the difficulty of identifying the sapwood in this species (i.e., errors in sapwood identification). The agreement between optical and colorimetric identification of the sapwood–heartwood boundary in this study suggests that the sapwood radius was correctly identified. Model 10, using ACB alone, had the highest R^2, a FI value comparable with that of the best sapwood-based model, and no prediction bias. The superior performance of this model relative to models based on breast height measurements was not surprising, since sapwood taper below the base of the live crown weakens the correlation between stem cross-sectional area and sapwood area (Maguire and Bennett 1996). Despite the superior performance of this model, practical application is limited by the difficulty of measuring area inside the bark at crown base.

Models 12 and 13, nonsapwood-based approaches to PLA estimation suggested by Valentine et al. (1994), produced results comparable with those of the best sapwood-based equations and were free of bias. It has been proposed that mLCR is a surrogate for a taper model (Maguire and Bennett 1996). The approach suggested by Valentine et al. (1994) is thus effective because it approximates estimating LA from stem cross-sectional area at crown base. There was no detectable advantage to using ABH, which requires bark thickness, instead of the easy-to-measure BA, presumably because the two are highly correlated. The ability to substitute BA for inside-bark cross-sectional area at breast height means that standard nondestructive measurements of DBH, tree height, and crown length can be used when coring is undesirable. Additionally, these findings suggest that recent theoretical advances made in the understanding of growth dynamics through assessment of leaf area can be implemented via manipulation of trees based on their size and crown ratio. Application of nonsapwood-based models, such as the one proposed by Valentine et al. (1994), may prove valuable for bridging the gap between theoretical and actual manipulations of stand structure based on leaf area distribution.

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