Production ecology of *Thuja occidentalis*

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Abstract: Equations to predict branch and tree leaf area, foliar mass, and stemwood volume were developed from 25 destructively sampled northern white-cedar (*Thuja occidentalis* L.) trees, a species whose production ecology has not been studied. Resulting models were applied to a large sample of 296 cored trees from 60 sites stratified across a soil gradient throughout northern Maine. Nonlinear regression analysis was used to assess alternative forms of the relationship between volume increment (VINC) and projected leaf area (PLA); analysis of covariance was used compare stemwood growth efficiency (GE) among soil-site classes, light exposure classes, and the presence of decay. Stem volume was estimated with Honer's equation (T.G. Honer. 1967. Forest Management Research and Services Institute) with refitted parameters. PLA was best predicted with Maguire and Bennett's nonlinear model (D.A. Maguire and W.S. Bennett. 1996. Can. J. For. Res. **26**: 1991–2005) using sapwood area or crown length and the ratio of tree height to diameter at breast height. A sigmoid model form captured the relationship between VINC and PLA more precisely and with less bias than the simple power function; this implies that the relationship between GE and PLA reaches a peak rather than decreases monotonically. At PLAs >50 m^2, GE gradually declined with increasing crown size and was significantly influenced by site and light exposure. With PLA, site, and light held constant, decayed trees had a significantly lower (by 11%) GE than sound stems, a finding not previously reported for other tree species.

Résumé : Des équations de prédiction de la surface foliaire des branches et de l'arbre, de la biomasse foliaire et du volume de la tige ont été mises au point à partir d'un échantillonnage destructif de 25 thuyas occidentaux (*Thuja occidentalis* L.), une espèce dont les caractéristiques écologiques de production n'ont pas été étudiées. Les modèles ainsi élaborés ont été appliqués sur un vaste échantillon formé de 296 arbres carottés dans 60 stations réparties selon un gradient édaphique dans le nord du Maine, aux États-Unis. Une analyse de régression non linéaire a été utilisée pour évaluer les différentes formes de relation entre l'accroissement en volume (AV) et la surface foliaire projetée (SFP). Une analyse de covariance a été utilisée pour comparer l'efficacité de la croissance (EC) de la tige entre les classes de station, entre les classes d'exposition à la lumière et en présence de carie. Le volume de la tige a été estimé à l'aide des équations de Honer (T.G. Honer. 1967. Forest Management Research and Services Institute) dont les paramètres ont été recalculés. Les meilleures prédictions de la SFP ont été obtenues avec le modèle non linéaire de Maguire et Bennett (D.A. Maguire et W.S. Bennett. 1996. Res. can. rech. for. **26**: 1991–2005) en utilisant la surface d'aubier ou la longueur de la cime et le rapport entre la hauteur de l'arbre et son dhp. Une meilleure précision et un plus petit biais ont été obtenus lorsque la relation entre l'AV et la SFP était calculée par une forme de modèle sigmoïde plutôt que par la fonction simple de puissance. Cela implique que la relation entre l'EC et la SFP est caractérisée par l'atteinte d'une valeur maximale suivie d'une diminution non monotone. Pour des valeurs de SFP supérieures à 50 m^2, l'EC diminue graduellement avec l'augmentation de la taille de la cime et est significativement influencée par la station et l'exposition à la lumière. Pour des valeurs constantes de SFP, de station et de lumière, les arbres cariés avaient une EC significativement plus faible (de 11 %) que celle des arbres sains, un résultat qui n'avait encore jamais été publié pour d'autres espèces d'arbre.

[Traduit par la Rédaction]

Introduction

Northern white-cedar (*Thuja occidentalis* L.) is the fourth most abundant conifer in Maine after red spruce (*Picea rubens* Sarg.), eastern white pine (*Pinus strobus* L.), and balsam fir (*Abies balsamea* (L.) Mill) (McWilliams et al. 2005). Although considered to be shade tolerant (Johnston 1990), northern white-cedar has been observed colonizing dune sites in Michigan (Scott and Murphy 1987) and old fields in Maine (Curtis 1946); it also forms a unique, long-lived uneven-aged monoculture in cliff habitats (Larson and Kelly 1991). More commonly, this species comprises a long-lived, stable component of mixed-conifer lowlands in the Lake States (Kangas 1989) and is the most prominent component of upland mixed-species seepage forests and lowland cedar swamps in Maine's remnant presettlement forests (Fraver et al. 2009).

The concept of stemwood growth efficiency (GE), which is defined as growth per unit of leaf area (Waring et al. 1980), has been widely used in studies of forest production ecology for identifying silviculturally important patterns of tree and stand productivity. The GE is influenced by crown structure or canopy position (O'Hara 1988; Smith and Long

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1989; Long and Smith 1990; Roberts and Long 1992; Gilmore and Seymour 1996), stand structure (O'Hara 1989; Maguire et al. 1998; Mainwaring and Maguire 2004), age (O'Hara 1996; Ryan et al. 1997; Seymour and Kenefic 2002), and site resources (Binkley and Reid 1984; Vose and Allen 1988; Velazquez-Martinez et al. 1992; Jokela and Martin 2000; DeRose and Seymour 2009). Less commonly, GE has been used as an indicator of tree vigor and susceptibility to pathogens (Waring 1987; Rosso and Hansen 1998). In this regard, northern white-cedar presents a particularly interesting opportunity for study because this species is highly susceptible to heart rots (Harlow 1927; Johnston 1990) with the most severe decay (88%–97%) on well-drained upland soils (Hofmeyer et al. 2009*b*).

Recent studies of conifer production ecology in northeastern North America have quantified patterns of leaf area and growth efficiency for balsam fir (Gilmore et al. 1996; Gilmore and Seymour 1996), eastern hemlock (*Tsuga canadensis* (L.) Carr.; Kenefic and Seymour 1999; Seymour and Kenefic 2002), red spruce (Maguire et al. 1998; DeRose and Seymour 2009), and eastern white pine (Innes et al. 2005; Weiskittel et al. 2009; Guiterman et al.[2]). This study expands such knowledge to northern white-cedar, a species which has been largely overlooked in quantitative silvicultural research (Hofmeyer et al. 2009*a*). Specifically, our objectives were to develop prediction models for tree leaf area and stemwood volume increment and to test the hypotheses that tree GE varies by site class, canopy position, and presence of heartwood decay.

Methods

Field methods

Sixty sites were selected throughout central and northern Maine for a companion investigation of northern white-cedar growth and decay (Hofmeyer et al. 2009*b*). Two soil pits were excavated at each site down to the depth of root restriction to determine the Briggs (1994) site class. Soil pits were located at the edge of the widest portion of the cedar stand and along a topographic gradient where possible (e.g., one uphill and one downhill or one pit and one mound sampled). Depth to redoxymorphic features, depth of root restriction, and percentage of coarse fragments were recorded for each pit. Sites with soil pits varying by more than one site class were rejected because of soil variability that would complicate interpretation of the results. Initial screening of the data suggested that Briggs' (1994) site classes were too specific. Based on soil drainage, sites were grouped into "good", "poor", and "wet" sites. Good sites fall into Brigg's site classes 1–3, poor sites were site class 4, and wet sites were site class 5 and organic soils with no redoxymorphic features.

On all but one site, five trees were double cored to the pith (perpendicular to one another) at breast height (1.3 m). Cores were held to the sky to identify the boundary of translucent sapwood and opaque xylem prior to mounting. Cores were mounted in the field and tree number, canopy position, sapwood thickness, and point of decay (if present) were marked on the core board. Bark thickness was measured with a bark gauge to the nearest millimetre at each core location on the bole. Tree diameter was measured at breast height to the nearest millimetre. Total height, height of the live crown base, and height of the lowest live branch were measured with a Haglof Vertex III hypsometer. Live crown base was defined as the point on the bole with living branches covering ≥50% of the circumference of the bole.

Light exposure classes (LECs) were identified following Bechtold's (2003) protocol to reduce errors associated with assigning traditional crown classes in stratified or multicohort stands (Nicholas et al. 1991). Light exposure was rated on a 1 to 5 scale for each tree: class 5 is analogous to a dominant tree (light on the top and four sides), and class 1 is analogous to an intermediate (light on the top or one side only). Only trees in the continuous upper canopy with an LEC ≥1 were sampled; no overtopped or outwardly defective trees were sampled. For later analysis, LECs were combined to form "high", "moderate", and "low" levels of light exposure, where low includes class 1, moderate includes classes 2 and 3, and high includes classes 4 and 5.

Twenty-five northern white-cedar trees from 13 sites were selected for destructive sampling from the 296 trees cored in the growth and decay study (Table 1, Fig. 1). Briggs' (1994) site classes formed the sampling strata, with sample trees distributed in proportion to the overall site-class distribution of the 60 plot sample. Attempts were made to stratify the sample over LEC 1 through LEC 5; however, only a single observation of LEC 5 was obtained. Ideal sample trees were selected when possible (i.e., free from heart rot, no forking of the bole, and no obvious crown damage). Because of the high incidence of decay and poor crown form, several sample trees had some crown or bole defect. Trees were destructively sampled between 18 July and 17 August 2006.

Crown projection was measured along six crown radii before felling. Stump height (0.3 m) and breast height were marked on the bole and diameter was measured to the nearest millimetre. Distance to the lowest live branch, base of the live crown, and total height were measured (to the nearest 0.01 m). The tree crown was divided into three unequal sections: the top one-half, the middle quartile, and the lower quartile (after DeRose and Seymour 2009). A branch from each section was chosen at random based on distance within the crown section. If the randomly chosen branch was damaged during felling, the branch was replaced by a second random sample. Distance along the bole and diameter just beyond the branch collar were recorded for each sample branch. Five subdominant foliar sprays (cedar leaf formations) were selected from each sample branch. Sprays were selected from throughout the total range of foliage locations and morphologies on each sample branch because aging northern white-cedar foliage is difficult owing to the lack of bud scars (Reiners 1974). Sprays were placed in plastic freezer bags and stored in a cooler on ice. Remaining portions of sample branches were sectioned and placed in paper bags for air drying. All remaining live branches were measured for their distance along the bole and basal diameter above the branch collar (nearest 0.1 mm).

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[2] Guiterman, C.H., Seymour, R.S., and Weiskittel, A.W. Influence of contrasting thinning regimes on leaf area index of *Pinus strobus*: long-term trends predicted from allometric equations and litterfall data. Submitted to Forest Science.

Table 1. Descriptive attributes of 25 destructively sampled northern white-cedar trees by site class.

	Mean (SE)	Range
"Good" sites (N = 8)		
DBH (cm)	34.0 (3.01)	23.7–46.3
Height (m)	16.7 (0.93)	12.3–19.7
CL (m)	11.3 (0.97)	8.2–16.1
Age (years)	127.1 (9.51)	101–176
"Poor" sites (N = 4)		
DBH (cm)	29.8 (4.93)	19.1–41.2
Height (m)	13.4 (1.52)	10.6–16.2
CL (m)	8.3 (1.11)	5.5–10.7
Age (years)	162.5 (31.04)	107–228
"Wet" sites (N = 13)		
DBH (cm)	27.5 (2.48)	14.1–42.7
Height (m)	15.5 (0.74)	10.5–20.0
CL (m)	10.6 (0.95)	6.2–16.3
Age (years)	125.5 (10.76)	75–202

Note: Age was calculated as the number of annual rings at breast height. DBH, diameter at breast height; CL, length of the live crown.

Sample trees were then limbed, and each successive 1 m interval was marked on the bole starting at 1.3 m. Cross-sectional discs (approximately 2 cm thick) were removed at each 1 m interval marked on the bole. An additional disc was taken just beneath the lowest live branch if this location did not coincide with the standard sampling interval. Bark thickness of each disc was measured in the field along two radii. Sapwood thickness was measured in the field along six radii on the lowest live branch and breast height discs. The interface of the opaque heartwood and the translucent sapwood was readily observed by holding the disc toward the sky.

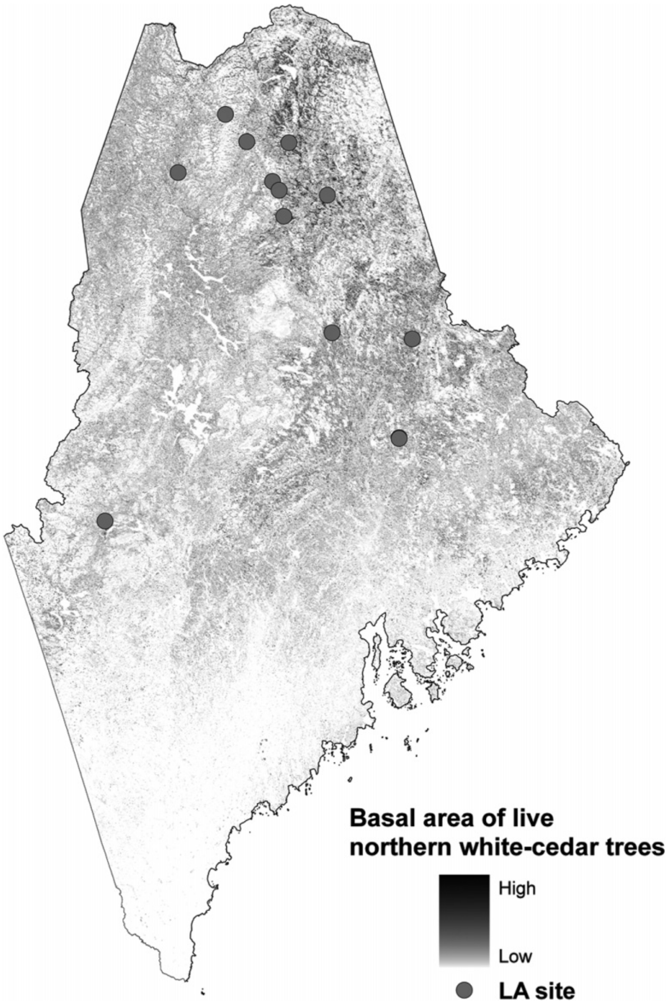
Foliage samples were transferred from coolers to a freezer (–15 °C) immediately after returning from the field. Branch sections stored in paper bags were placed in a drying room at 60 °C for 5 weeks and dried to a constant mass.

Laboratory procedure

Dried branch samples were sorted into cones, photosynthetic, and nonphotosynthetic tissues. Drying did not appear to alter branch tissue color. Because northern white-cedar does not have discrete foliage and woody tissue junctions (Briand et al. 1992), separation of these parts involved some judgment. Main axes on a few higher order branches that were predominantly brown woody tissue with few green foliage scales were classified as woody tissue. Dry mass of cones, foliage, and woody tissue was determined to the nearest 0.01 g on a digital balance.

Frozen foliage samples were scanned using Regent WinSeedle software within 15 min of removal from ice. One-sided projected leaf area (mm^2) was determined with a flatbed scanner at 800 dpi resolution. After scanning, the samples were placed into a paper envelope and dried at 60 °C for 72 h. Mass of dried foliage was determined on a digital balance to the nearest 0.0001 g within 30 s of removal from the oven. Specific leaf area (SLA) was determined for each foliage sample as the fresh foliage area per unit dry foliage mass (cm^2/g). Dried foliage mass from the SLA sample was added to the dried branch foliage mass to determine the branch foliage mass (BFM; g) for each branch sample. Branch SLA was multiplied by BFM to determine branch leaf area (BLA) (Table 2).

Fig. 1. Site locations of the 25 destructively sampled northern white-cedar trees. See Hofmeyer et al. (2009*b*) for the locations of the 60 cored-tree sample sites.



Cross-sectional discs were ground to a uniform thickness using a drum sander and then sanded repeatedly with progressively finer grit sandpapers. Two radii were analyzed on each disc using Regent WinDendro software and a flatbed scanner at 1200 dpi resolution, except the breast height disc where six radii were used to determine past growth and sapwood area. Data files from WinDendro were imported into Regent WinStem software for incremental diameter, incremental height, and volume analysis.

Statistical analysis

The BLA and BFM were estimated using the following modified Weibull function:

$$[1] \qquad \sqrt{y} = (b_1 D^{b_2})(\mathrm{RD}^{b_4-1})[\exp\, -(b_3 \mathrm{RD}^{b_4})]$$

where y is either estimated projected BLA (cm^2) or estimated BFM (g), D is the branch basal diameter (mm), and

Table 2. Specific leaf area, branch foliage mass, and branch leaf area for the lower, middle, and top crown sections of 25 northern white-cedar sample trees.

Tree characteristic and crown section	Mean (SE)	Range
Specific leaf area (cm^2/g)		
Lower	61.68 (1.86)	41.62–79.44
Middle	55.59 (1.44)	41.76–68.53
Top	46.02 (1.94)	31.81–68.85
Branch foliage mass (g)		
Lower	230.28 (32.78)	29.45–657.02
Middle	170.30 (31.90)	10.80–559.61
Top	100.77 (17.61)	1.55–369.17
Branch leaf area (cm^2)		
Lower	14 257.02 (2187.72)	2041.59 – 42 765.61
Middle	9313.18 (1698.85)	538.37 – 29 656.56
Top	4549.61 (770.93)	55.79 – 17 083.46

RD is the relative distance of the branch from the top of the tree. The values of RD range from 0 to 1: 0 is the terminal shoot, and 1 is the lowest live branch. The sum of predicted BLA for all branches of each tree is the estimated tree-level projected leaf area (PLA; m^2). The sum of predicted BFM for all branches is the estimated tree-level total crown foliage mass (CFM; kg). Equation 1 (without the square-root transformation) was first used by Maguire and Bennett (1996) for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and, subsequently, by DeRose and Seymour (2009) Weiskittel et al. (2009), and Guiterman et al.[2] for northeastern conifers. In these data, eq. 1 with the square-root transformation exhibited less prediction bias and a more normal distribution of residuals than the untransformed model.

Using data for the stem-analyzed trees, many allometric equations were screened to predict PLA and CFM from tree dimensions and sapwood area (Hofmeyer 2008). The best models were equations first published by Maguire and Bennett (1996):

$$[2] \qquad y = b_1 \mathrm{CL}^{b_2} \exp(b_3 \mathrm{DBH}/H)$$

$$[3] \qquad y = b_1 \mathrm{SA}^{b_2} \exp(b_3 \mathrm{DBH}/H)$$

where y is estimated PLA (m^2) or CFM (kg), CL is the live crown length (m), SA is the sapwood area (cm^2) at breast height, DBH is the diameter at breast height (1.3 m; cm), H is the total tree height (m), and the b_i's are regression coefficients. One outlier with aberrant sapwood measurements was dropped from the fitting model (eq. 3). Equation 3 was then used to estimate PLA and CFM for the 296 cored trees.

Stemwood volumes of the cored trees were calculated from Honer's (1967) equation, which was refitted by nonlinear regression to the WinStem data (in metric units) for the 25 stem-analyzed trees:

$$[4] \qquad V = \frac{\mathrm{DBH}^2}{0.696\,28 + (20.6105/H)}$$

where V is the total stemwood volume inside bark in cubic decimetres and the other variables are as previously defined.

Two alternative nonlinear models were screened to describe the relationship between the estimated mean annual volume increment (VINC; dm^3) for the 2004 and 2005 growth years and both PLA and CFM:

$$[5] \qquad \mathrm{VINC} = b_1 x^{b_2}$$

$$[6] \qquad \mathrm{VINC} = b_1 \left\{ 1 - \exp\left[-\left(\frac{x}{b_2} \right)^{b_3} \right] \right\}$$

where x is PLA (m^2) or CFM (kg), and the b_is are regression coefficients. Equation 5 is a simple power function that corresponds to a monotonically declining GE with increasing crown size (where $b_2 < 1$), whereas eq. 6 corresponds to a peaking GE pattern (Seymour and Kenefic 2002). Models were weighted by x^{-2} to improve homoscedasticity, which resulted in a better fit as judged by the lowest Furnival's (1961) index.

Stem volume at the end of the 2004 growing season was estimated for the 296 cored northern white-cedar trees with eq. 4. Diameter outside bark and total height were calculated for the year of sampling and the previous two growing seasons. Diameter increment was analyzed in WinDendro and a constant proportion of tree-specific bark thickness to diameter was assumed to estimate inside-bark volume. Several regression models were screened to predict height growth by diameter, height, live crown ratio, LEC, and (or) site class from the stem-analyzed trees, but none yielded significant patterns. Therefore, the simple mean annual height increment for the top metre of the destructively sampled stems (0.08 m) was used to calculated height growth for the previous 2 years in all cored sample trees. Volume for the previous 2 years was estimated for the cored trees with eq. 4. VINC was determined by subtracting the previous years' volumes from the most recent full year's volume and dividing by 2 to get periodic annual VINC. Actual VINCs as calculated from the 25 stem-analyzed trees by WinStem were compared with the VINCs based on increment cores to assess the accuracy of this common growth reconstruction procedure.

The GE of cored trees was defined as the ratio of calculated VINC to PLA estimated from eq. 3. Here, we assume that crown attributes did not change between 2004 and the

Table 3. Parameter estimates and fit statistics for branch leaf area (BLA; cm^2) and branch foliage mass (BFM; g) using eq. 1.

	Parameter estimate					
Branch characteristic	b_1	b_2	b_3	b_4	R^2	RMSE
BLA	6.457 (2.013)	0.876 (0.079)	0.340 (0.230)	1.239 (0.107)	0.838	0.7116
BFM	0.750 (0.213)	0.948 (0.074)	0.553 (0.203)	1.171 (0.088)	0.842	0.09143

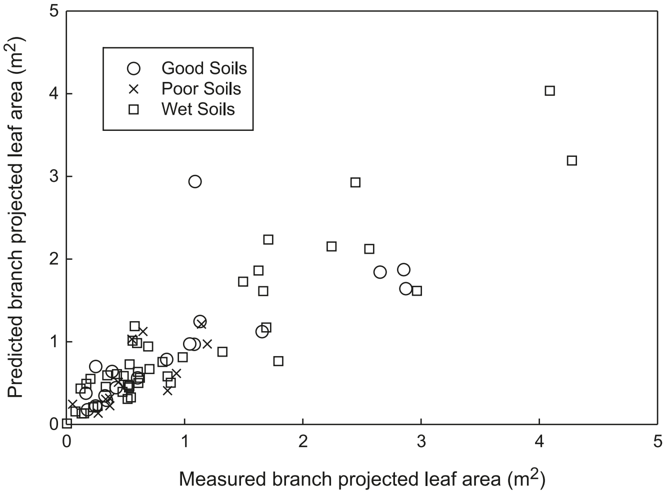
Note: Parameter SEs are given in parentheses.

Table 4. Parameter estimates and fit statistics for tree-level projected leaf area (PLA) and crown foliage mass (CFM), calculated using crown length (eq. 2) and sapwood area (eq. 3).

Equation and parameter	b_1	b_2	b_3	R^2	RMSE
Equation 2					
PLA	2.479 (0.976)	0.516 (0.148)	0.977 (0.142)	0.832	11.193
CFM	0.370 (0.132)	0.681 (0.133)	0.942 (0.128)	0.877	2.066
Equation 3					
PLA	1.024 (0.587)	0.568 (0.155)	0.664 (0.185)	0.835	11.100
CFM	0.167 (0.099)	0.629 (0.160)	0.636 (0.191)	0.835	2.389

Note: Parameter SEs are given in parentheses.

Fig. 2. Predicted versus observed projected branch leaf area, showing lack of bias by site class.



sampling date. Analysis of covariance was used to test for differences in GE among light exposure classes, soil site classes, and presence of central decay (eq. 7):

$$[7] \quad GE = b_0 + b_1\text{PLA} + (d_1 + d_2)\text{SITE} + (d_3 + d_4)\text{LITE} + d_5\text{Decay}$$

where the covariate PLA allows GE to vary by crown size, SITE is one of three combined soil classes, LITE is one of three combined LECs. Decay represents the presence–absence of heart rot as detected by increment coring, the b_i's are regression coefficients, and the d_i's are coefficients of [0,1] dummy variables. All analyses were conducted in SYSTAT version 12 (SYSTAT Inc., Chicago, Illinois) using a significance level of $\alpha = 0.05$. GE based on CFM was also analyzed; the results were identical and, thus, were not reported.

Results

Branch leaf area and foliage mass

Mean SLA differed ($p < 0.001$) by location within the crown (Table 2); furthermore, this pattern was not affected by site class ($p = 0.278$) or LEC ($p = 0.095$). Equation 1 explained >80% of the variation in both BLA and BFM (Table 3) and was unbiased by site class (Fig. 2). For a given branch diameter, eq. 1 predicts a maximum BLA at 0.65 RD, and BFM is estimated to peak at RD = 0.3 (Fig. 3).

Projected leaf area and crown foliage mass

Both eqs. 2 and 3 had nearly identical fit statistics (Table 4). Thorough analyses of VINC and GE using these and other PLA-prediction models (Hofmeyer 2008) yielded identical conclusions regardless of the model chosen; therefore, for brevity, subsequent analyses are based on the sapwood-based eq. 3. Equation 3 predictions based on increment cores of the stem-analyzed trees compare favorably, with no bias, to the measured sapwood areas and PLAs calculated from branch summation (Fig. 4). Equation 2 seriously overpredicted PLA for a few very long-crowned trees that were well outside the range found in the stem-analyses sample, whereas the sapwood-based model was more robust upon such extrapolation.

Volume increment and growth efficiency

Weighted nonlinear regression produced very similar fit statistics for both VINC prediction models (eqs. 5 and 6; Table 5). For both PLA and CFM, the sigmoid eq. 6 slightly outperformed the power function, which is effectively a simple linear equation because the exponents do not differ from 1.0. For a given model form, CFM was a marginally better predictor than PLA, although this difference is negligible. Predictions are essentially identical for PLAs ≤120 m^2 but diverge above this point, where eq. 6 has a clear advantage (Fig. 5). For PLA >150, the power function overpredicts all

Fig. 3. (A) Branch leaf area and (B) branch foliage mass as a function of relative distance into the crown and branch diameter, as predicted using eq. 1.

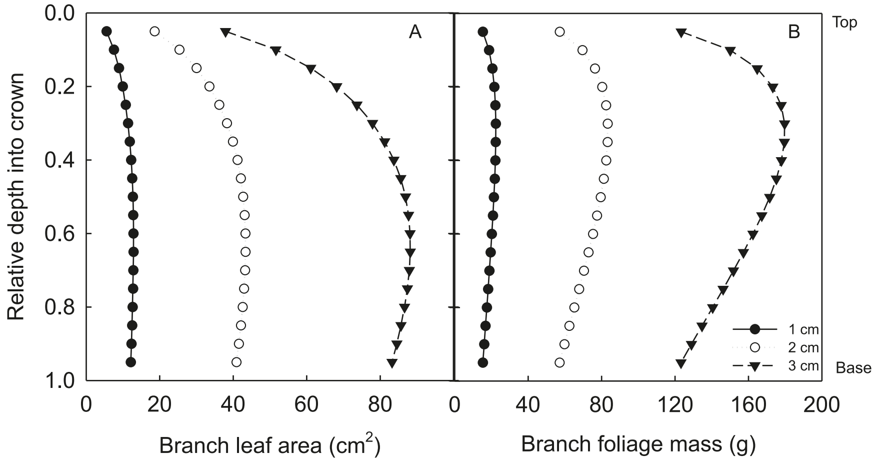


Table 5. Parameter estimates and fit statistics of VINC prediction eqs. 5 and 6.

Dependent variable and equation No.	b_1	b_2	b_3	R^2	FI (dm^3)	Unweighted RMSE
PLA						
5	0.139 46 (0.023 62)	0.985 43 (0.041 17)	—	0.652	2.8075	3.5475
6	24.366 (7.1186)	123.718 (45.084)	1.239 (0.114 33)	0.658	2.7862	3.518
CFM						
5	0.6941 (0.069 09)	0.96456 (0.03908)	—	0.665	2.7763	3.4791
6	25.912 (8.4728)	28.286 (11.780)	1.1855 (0.108 12)	0.670	2.7591	3.4566

Note: All models are weighted by x^{-2}. Parameter SEs are given in parentheses. FI, Furnival index, which is comparable with the root mean square error of the unweighted model, which is given for reference.

Fig. 4. Sapwood area and projected leaf area of the stem-analyzed trees, showing close correspondence between actual values with those estimated from increment cores (sapwood) and regression eq. 3. Lines are simple least-squares linear regressions fit to each data set.

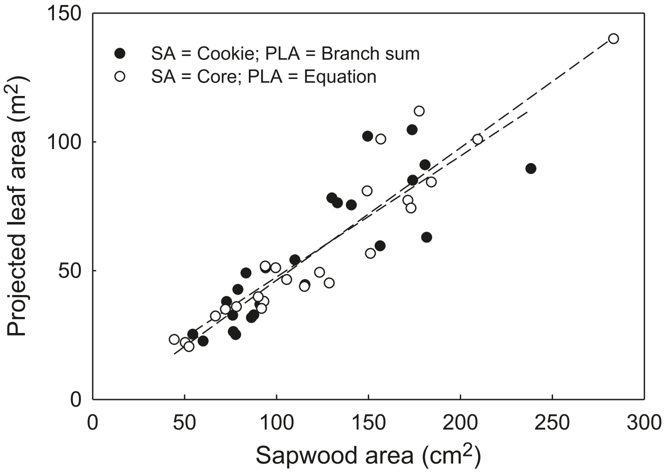
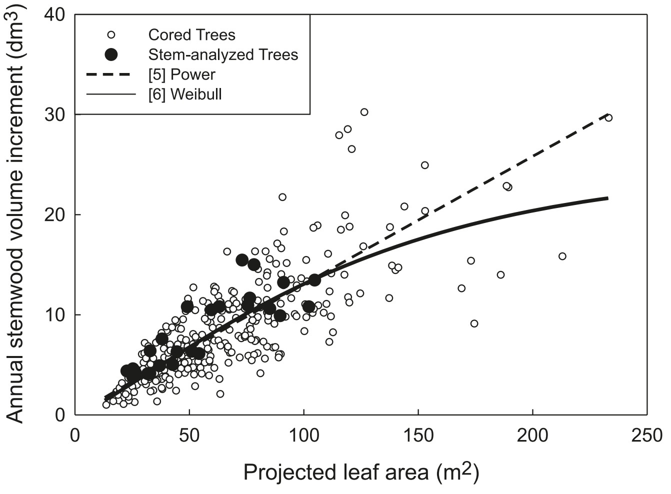


Fig. 5. Comparison of eqs. 5 and 6, showing bias of eq. 5 at PLA >150. Measured values from stem-analyzed trees are shown for reference.



eight observations, whereas the sigmoid Weibull function is much less biased. The finding that the relationship between VINC and PLA is not linear demonstrates that GE is affected by crown size and, thus, must be included in any analysis of GE effects.

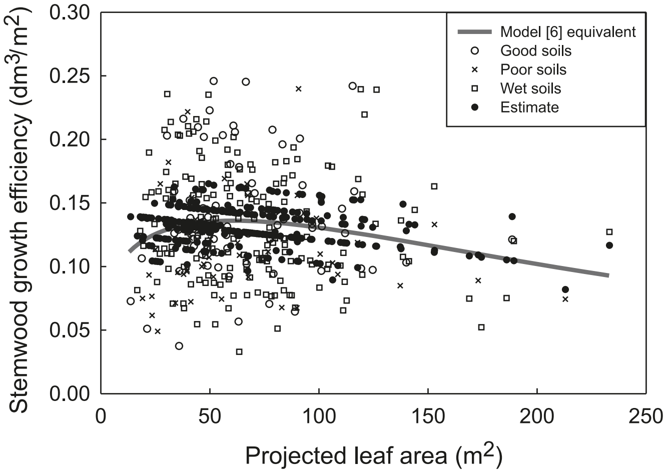
When PLA is added as a covariate in the linear eq. 7 designed to test whether soil classes, light environment, and decay are related to stemwood GE, all main effects are significant (Table 6). Contrasts are largely in the expected direction: trees in high light conditions grew more wood per

Table 6. Covariance analysis of growth efficiency using eq. 7 fit with dummy variable coding.

Parameter description	Parameter in eq. 7	Parameter estimate	ANOVA p value	Least-squares mean GE	Sample size
Intercept	b_0	0.138 79			
PLA	b_1	0.000 180 71	0.038		
SITE			0.0007		
Good	d_1	0.014 603		0.1515a	72
Poor	d_2	–0.018 384		0.1185b	50
Wet	—	—		0.1369c	175
LITE			0.004		
High	d_3	0.019 934		0.1529a	50
Moderate	—	—		0.1329b	182
Low	d_4	–0.011 794		0.1212b	65
DECAY		—	0.019		
Not decayed	d_5	0.015 322		0.1433a	72
Decayed	—	—		0.1280b	225

Note: Least-squares means followed by the same letter do not differ at $\alpha = 0.05$ using Tukey's honest significant difference test. GE, growth efficiency; LITE, one of three combined LECs.

Fig. 6. Observed growth efficiency (GE) versus eq. 7 estimates. The GE predicted from eq. 6 is shown for reference.



unit PLA than those in moderate or low conditions (p = 0.004); decayed trees had a lower GE than sound ones (p = 0.019); and trees on good and wet soils outgrew those on poor soils (p = 0.0007; Table 6). Interestingly and unexpectedly, wet soils (which are mostly organic soils consisting of several metres of muck in this study) had significantly higher GEs than poor soils, which are very shallow poorly drained glacial tills. The contrast between good and wet soils was only marginally nonsignificant (p = 0.064). The sign of the covariate PLA coefficient is negative, suggesting declining GE with increasing crown size, as expected. This is clearly evident in Fig. 6, where the eq. 7 estimates show a declining GE with increasing PLA. For reference, we also show the predicted GE obtained by dividing the VINC model (eq. 6) predictions by their corresponding PLA as was done by DeRose and Seymour (2009). This equation corresponds closely to the eq. 7 predictions at PLAs >60 m^2, the point at which eq. 6 peaks, but departs below this point as the sigmoid VINC model (eq. 6) again declines for very small-crowned trees.

Discussion

Leaf area prediction

Mean SLA in this study (54.4 cm^2/g) suggests northern white-cedar foliar sprays have more surface area per unit mass than red spruce (44.9 cm^2/g; Maguire et al. 1998) or balsam fir (32.7 cm^2/g; Gilmore and Zenner 2005) but less than eastern hemlock (58.4 cm^2/g; Kenefic and Seymour 1999) or eastern white pine (68.8 cm^2/g; Guiterman et al.[2]). The SLA patterns indicate a high degree of within-tree plasticity in foliar morphology. Northern white-cedar shade foliage in the lower crown tends to be thin with a high surface area per unit mass, whereas sun foliage in the upper half of the crown is relatively more massive. Higher SLA values in shade foliage often describe morphological responses to low-light conditions, lower temperatures, and less moisture stress than sun foliage (Barnes et al. 1998).

The high variability in crown architecture and foliar morphology of northern white-cedar is evident in the fact that our leaf-area predictors for branches (eq. 1) and whole trees (eqs. 2 and 3) exhibit somewhat lower precision than comparable studies of other northern conifers, in which R^2 values are typically >0.9 (Kenefic and Seymour 1999; DeRose and Seymour 2009; Guiterman et al.[2]). Because the sapwood of northern white-cedar is readily distinguished as a distinct color change at the heartwood boundary, eq. 3 could be applied to both freshly obtained increment cores as well as archived samples. If wood samples are not available, eq. 2 should provide unbiased PLA estimates, although we urge caution in extrapolating this equation beyond a CL of 16 m, the longest crowns in our stem-analyzed data set (Table 1).

Volume increment and growth efficiency

Although the procedure of reconstructing stemwood growth and PLA from increment cores has been commonly used in production ecology studies to obtain a large sample over environmental and structural gradients (e.g., Long and Smith 1992; Kollenberg and O'Hara 1999; DeRose and Seymour 2009), we are unaware of a case where this procedure has been shown to be unbiased using actual measured

VINCs and PLAs obtained from detailed stem dissections from the same study population. We offer such a validation in Fig. 4, where the simple allometric relationships between PLA and sapwood area are statistically identical using both coring and stem dissection. Furthermore, Fig. 5 shows that VINCs determined by stem analysis at 1 m intervals and PLAs estimated from sapwood areas determined from six radii on breast-height discs follow the same relationship as the large sample of VINCs and PLAs estimated from two increment cores.

The superiority of the sigmoid VINC prediction model over the simple power function has been observed in other studies of shade-tolerant species (Roberts and Long 1992; Gilmore and Seymour 1996; Seymour and Kenefic 2002). Being asymptotic, this model also predicts a declining GE as with increasing crown size, which is a very common pattern first described by Assmann (1970) and subsequently observed in most comparable studies. The power function can also produce this declining pattern if the fitted exponent is significantly <1.0 (e.g., Maguire et al. 1998; DeRose and Seymour 2009). However, in this study, the power function was unable to capture this declining GE pattern (the exponent did not differ from 1.0; Table 5), likely because the optimum inverse-square weights used to homogenize residual variance deemphasized the largest crowned trees, which control the upper-end fit. The strongest evidence for declining GE with increasing PLA lies in the significance ($p = 0.038$; Table 6) of the PLA covariate in eq. 7, although this simplified linear model cannot account for any peaking pattern.

Although northern white-cedar has a reputation for being slow growing and, thus, less productive than its common conifer associates, the predicted VINC for a PLA of 100 m^2 is about 13 dm^3 (Fig. 5), which is similar to eastern hemlock and red spruce in multiaged stands (Seymour and Kenefic 2002) but lower than red spruce (16 dm^3) and balsam fir (18 dm^3) in younger, even-aged stands (DeRose and Seymour 2009). A stand of such cedars with a projected leaf area index of 4 would produce 5.2 m^3/ha of stemwood annually, an impressive value considering the generally poor quality of the soils and the low site index (barely over 10 m at breast height age of 50 years; Hofmeyer et al. 2009*b*).

The very high significance of SITE in the GE analysis ($p = 0.0007$; Table 6) indicates that Briggs' 1994 site classes are meaningful indicators of white-cedar productivity, as they are predictors of heart rot (Hofmeyer et al. 2009*b*). Although one would logically expect GE to be higher on better sites, clear demonstrations of such a pattern in natural stands are surprisingly rare (Groot and Saucier 2008; DeRose and Seymour 2009), especially if fertilization studies are excluded. We have no obvious explanation for why completely saturated and organic soils have higher GE than very shallow till soils, because this suggests that something other than a simple drainage gradient is at work. It is possible that some saturated mineral soils, as well as the organic soils, are enriched by subsurface water movement, which could be better oxygenated and carry more nutrients, than the completely stagnant poorly drained tills; however, we did not measure these factors.

This study is the first to use Bechtold's 2003 LECs as an objective alternative to conventional crown classes for assessing GE, and the results are promising, especially once the classes are combined as in Table 6. One problem with using conventional crown classes is that they are unavoidably confounded with crown size (PLA) itself, which may disguise offsetting patterns. For example, dominant trees tend to have the highest PLAs in any given stand; as a result, they typically exhibit slightly lower GE than smaller crowned codominants owing to a less efficient crown architecture (O'Hara 1988; Roberts et al. 1993), thereby offsetting any advantage gained by their superior crown position. Bechtold's classes separate this illumination effect from crown size, allowing both to be analyzed simultaneously yet independently.

Clearly, the most growth-efficient cedars are well-illuminated trees on well-drained upland soils with relatively small crowns (PLA optimum = 60 m^2, Fig. 6), as has been found in virtually all similar studies.

This study is also the first to our knowledge to demonstrate an association between heart rot and GE ($p = 0.019$; Table 6); on average, decayed trees had 11% lower GE than sound ones with site, light, and crown size held constant. Perhaps, this result should not be surprising because early applications of the GE concept involved assessing resistance to forest pests (Waring et al. 1980; Waring 1987). Interestingly, this effect of decay is not apparent if analyzed in isolation of the other variables which also influence GE — most importantly site quality, which strongly influences the probability of a stem being decayed (Hofmeyer et al. 2009*b*). Although this result suggests that decayed cedars may allocate resources to defense mechanisms at the expense of stemwood production, future research of an entirely different design would be required to elucidate such a mechanism.

We remind readers that our large study population was not completely random; we sampled only trees that were outwardly sound, and we did not sample trees in Bechtold's (2003) LEC class 0 (overtopped stems). Unlike previous GE studies, it was not always possible to select trees with ideal crown architecture to estimate leaf area, foliage mass, and stem volume. Northern white-cedar has weak apical control that frequently results in main stem forking (Curtis 1946). Nearly 80% of the outwardly sound trees cored prior to selecting the sound stem-analysis sample trees had internal decay. Thus, tree selection for PLA and VINC analysis included some stems with small forks and some trees with small volumes of central decay.

Finally, we believe that this study highlights the value of combining intensive stem-analysis sampling with a large, stratified increment-core sample stratified over resource gradients. Meticulous tree-dissection methods are essential to develop tree-level prediction equations but are so cost- and labor-intensive that sample sizes are rarely large enough to identify silviculturally relevant patterns on the landscape. Applying these equations to a large, one-time sample using consistent and robust methods of growth reconstruction can reveal such patterns, as they have in this study.

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References

Assmann, E. 1970. Principles of forest yield study. Pergamon Press Ltd., Oxford, UK.

Barnes, B.V., Zak, D.R., Denton, S.R., and Spurr, S.H. 1998. Light. *In* Forest ecology. 4th ed. Ch. 8. John Wiley & Sons, New York. pp. 182–205.

Bechtold, W.A. 2003. Crown position and light exposure classification — an alternative to field-assigned crown class. North. J. Appl. For. **20**(4): 154–160.

Binkley, D., and Reid, P. 1984. Long-term responses of stem growth and leaf area to thinning and fertilization in a Douglas-fir plantation. Can. J. For. Res. **14**(5): 656–660. doi:10.1139/x84-118.

Briand, C.H., Posluszny, U., and Larson, D.W. 1992. Differential axis architecture in *Thuja occidentalis* (eastern white cedar). Can. J. Bot. **70**(2): 340–348. doi:10.1139/b92-045.

Briggs, R.D. 1994. Site classification field guide. Technical Note 6. Cooperative Forestry Research Unit, University of Maine, Orono, Maine. Maine Agric. For. Exp. Stn. Misc. Publ. 724.

Curtis, J.D. 1946. Preliminary observations on northern white cedar in Maine. Ecology, **27**(1): 23–36. doi:10.2307/1931014.

DeRose, R.J., and Seymour, R.S. 2009. The effect of site quality on growth efficiency of upper crown class *Picea rubens* and *Abies balsamea* in Maine, USA. Can. J. For. Res. **39**(4): 777–784. doi:10.1139/X09-012.

Fraver, S., White, A.S., and Seymour, R.S. 2009. Natural disturbance in an old-growth landscape in northern Maine, USA. J. Ecol. **97**(2): 289–298. doi:10.1111/j.1365-2745.2008.01474.x.

Furnival, G.M. 1961. An index for comparing equations used in constructing volume tables. For. Sci. **7**: 337–341.

Gilmore, D.W., and Seymour, R.S. 1996. Alternative measures of stem growth efficiency applied to *Abies balsamea* from four canopy positions in central Maine, USA. For. Ecol. Manage. **84**(1–3): 209–218. doi:10.1016/0378-1127(96)03728-0.

Gilmore, D.W., and Zenner, E.K. 2005. Foliage–sapwood area relationships for balsam fir in north-central Minnesota. North. J. Appl. For. **2**(3): 203–210.

Gilmore, D.W., Seymour, R.S., and Maguire, D.A. 1996. Foliage–sapwood area relationships for *Abies balsamea* in central Maine, USA. Can. J. For. Res. **26**(12): 2071–2079. doi:10.1139/x26-235.

Groot, A., and Saucier, J.P. 2008. Volume increment efficiency of *Picea mariana* in northern Ontario, Canada. For. Ecol. Manage. **255**(5–6): 1647–1653. doi:10.1016/j.foreco.2007.11.024.

Harlow, W.M. 1927. The effect of site on the structure and growth of white cedar *Thuja occidentalis* L. Ecology, **8**(4): 453–470. doi:10.2307/1930153.

Hofmeyer, P.V. 2008. Ecology and silviculture of northern white-cedar (*Thuja occidentalis* L.) in Maine. Ph.D. dissertation, The University of Maine, Orono, Maine.

Hofmeyer, P.V., Kenefic, L.S., and Seymour, R.S. 2009*a*. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: a synthesis of knowledge. North. J. Appl. For. **26**(1): 21–27.

Hofmeyer, P.V., Seymour, R.S., and Kenefic, L.S. 2009*b*. Influence of soil site class on growth and decay of northern white-cedar and two associates in Maine. North. J. Appl. For. **26**(2): 68–75.

Honer, T.G. 1967. Standard volume tables and merchantable conversion factors for the commercial tree species of central and eastern Canada. Forest Management Research and Services Institute, Ottawa, Ont.

Innes, J.C., Ducey, M.J., Gove, J.H., Leak, W.B., and Barrett, J.P. 2005. Size–density metrics, leaf area, and productivity in eastern white pine. Can. J. For. Res. **35**(10): 2469–2478. doi:10.1139/x05-174.

Johnston, W.F. 1990. *Thuja occidentalis* L. — northern white-cedar. *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Handb. 654. pp. 1189–1209.

Jokela, E.J., and Martin, T.A. 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. Can. J. For. Res. **30**(10): 1511–1524. doi:10.1139/cjfr-30-10-1511.

Kangas, P. 1989. Comparison of two northern white cedar (*Thuja*) forests. Mich. Bot. **28**(2): 59–66.

Kenefic, L.S., and Seymour, R.S. 1999. Leaf area prediction models for *Tsuga canadensis* in Maine. Can. J. For. Res. **29**(10): 1574–1582. doi:10.1139/cjfr-29-10-1574.

Kollenberg, C.L., and O'Hara, K.L. 1999. Leaf area and tree increment dynamics of even-aged and multiaged lodgepole pine stands in Montana. Can. J. For. Res. **29**(6): 687–695. doi:10.1139/cjfr-29-6-687.

Larson, D.W., and Kelly, P.E. 1991. The extent of old-growth *Thuja occidentalis* on cliffs of the Niagara Escarpment. Can. J. Bot. **69**: 1628–1636.

Long, J.N., and Smith, F.W. 1990. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: the influence of site quality and stand structure. J. Appl. Ecol. **27**(3): 847–856. doi:10.2307/2404381.

Long, J.N., and Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. For. Ecol. Manage. **53**(1–4): 53–64. doi:10.1016/0378-1127(92)90033-6.

Maguire, D.A., and Bennett, W.S. 1996. Patterns in vertical distribution of foliage in young coastal Douglas-fir. Can. J. For. Res. **26**(11): 1991–2005. doi:10.1139/x26-225.

Maguire, D.A., Brissette, J.C., and Gu, L. 1998. Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine. Can. J. For. Res. **28**(8): 1233–1240. doi:10.1139/cjfr-28-8-1233.

Mainwaring, D.B., and Maguire, D.A. 2004. The effect of local stand structure on growth and growth efficiency in heterogeneous stands of ponderosa pine and lodgepole pine in central Oregon. Can. J. For. Res. **34**(11): 2217–2229. doi:10.1139/x04-108.

McWilliams, W.H., Butler, B.J., Caldwell, L.E., Griffith, D.M., Hoppus, M.L., Laustsen, K.M., Lister, A.J., Lister, T.W., Metzler, J.W., Morin, R.S., Sader, S.A., Stewart, L.B., Steinman, J.R., Westfall, J.A., Williams, D.A., Whitman, A., and Woodall, C.W. 2005. The forests of Maine: 2003. USDA For. Serv. Northeast. Res. Stn. Resour. Bull. NE-164.

Nicholas, N.S., Gregoire, T.G., and Zedaker, S.M. 1991. The reliability of tree crown position classification. Can. J. For. Res. **21**(5): 698–701. doi:10.1139/x91-095.

O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can. J. For. Res. **18**(7): 859–866. doi:10.1139/x88-132.

O'Hara, K.L. 1989. Stand growth efficiency in a Douglas-fir thinning trial. Forestry, **62**(4): 409–418. doi:10.1093/forestry/62.4.409.

O'Hara, K.L. 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. For. Sci. Monogr. 33.

Reiners, W.A. 1974. Foliage production by *Thuja occidentalis* L. from biomass and litter fall estimates. Am. Midl. Nat. **92**(2): 340–345. doi:10.2307/2424299.

Roberts, S.D., and Long, J.N. 1992. Production efficiency of *Abies lasiocarpa*: influence of vertical distribution of leaf area. Can. J. For. Res. **22**(9): 1230–1234. doi:10.1139/x92-164.

Roberts, S.D., Long, J.N., and Smith, F.W. 1993. Canopy stratification and leaf area efficiency: a conceptualization. For. Ecol. Manage. **60**(1–2): 143–156. doi:10.1016/0378-1127(93)90028-L.

Rosso, P., and Hansen, E. 1998. Tree vigour and the susceptibility of Douglas fir to *Armillaria* root disease. Eur. J. For. Pathol. **28**(1): 43–52. doi:10.1111/j.1439-0329.1998.tb01164.x.

Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. **27**: 213–262. doi:10.1016/S0065-2504(08)60009-4.

Scott, M.L., and Murphy, P.G. 1987. Regeneration patterns of northern white-cedar, an old-growth forest dominant. Am. Midl. Nat. **117**(1): 10–16. doi:10.2307/2425702.

Seymour, R.S., and Kenefic, L.S. 2002. Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multiaged northern conifer stands. Can. J. For. Res. **32**(11): 2032–2042. doi:10.1139/x02-120.

Smith, F.W., and Long, J.N. 1989. The influence of canopy architecture on stemwood production and growth efficiency of *Pinus contorta* var. *latifolia*. J. Appl. Ecol. **26**(2): 681–691. doi:10.2307/2404092.

Velazquez-Martinez, A., Perry, D.A., and Bell, T.E. 1992. Response of aboveground biomass increment, growth efficiency, and foliar nutrients to thinning, fertilization, and pruning in young Douglas-fir plantations in the central Oregon Cascades. Can. J. For. Res. **22**(9): 1278–1289. doi:10.1139/x92-170.

Vose, J.M., and Allen, H.L. 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. For. Sci. **34**(3): 547–563.

Waring, R.H. 1987. Characteristics of trees predisposed to die. Bioscience, **37**(8): 569–574. doi:10.2307/1310667.

Waring, R.H., Thies, W.G., and Muscato, D. 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci. **26**(1): 112–117.

Weiskittel, A.R., Kershaw, J.A., Jr., Hofmeyer, P.V., and Seymour, R.S. 2009. Species differences in total and vertical distribution of branch- and tree-level leaf area for the five primary conifer species in Maine, USA. For. Ecol. Manage. **258**(7): 1695–1703. doi:10.1016/j.foreco.2009.07.035.