

Modeling Jack Pine (*Pinus banksiana*) Foliage Density Distribution

Robert Schneider, Mathieu Fortin, Frank Berninger, Chhun-Huor Ung, D. Edwin Swift, and S.Y. Zhang

Abstract: The vertical distribution of foliage biomass is important because it is associated with photosynthesis and is closely related to some wood quality attributes such as branch diameter and sapwood content. In this article we propose a model to predict foliage biomass distribution within the crown for jack pine trees in Eastern Canada. This model has two parts. The first one distinguishes the proportion of nodal (formed at the end of each yearly shoot) and internodal (formed during the growing season) foliage biomass. The second part of the model predicts the distribution of the biomass depending on the type of foliage (nodal or internodal). This second part is based on a two-parameter beta cumulative distribution function (cdf). The parameterization of this cdf was performed using a mixed-effects nonlinear regression. The proportion of foliage biomass found in the nodal whorls is proportional to dbh and age and inversely proportional to total height. The distribution of the foliage biomass in the nodal whorls is dependent only on tree-level variables whereas the internodal foliage biomass is influenced by both tree- and stand-level variables. The internodal foliage biomass maximum is closer to the crown base than that of nodal foliage biomass. Decomposing the distribution into whorl types leads to a better description of crown characteristics. FOR. SCI. 57(3):180–188.

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CROWN SHAPE AND STRUCTURE have been extensively studied in forest growth modeling because they are usually assumed to be good indicators of photosynthetic capacity (e.g., Landsberg 1986). Moreover, crown structure has recently been related to wood quality properties, such as sapwood content, knottiness, and juvenile wood content, which in turn affect lumber grade and tree economic value. If we take into account the fact that up to 50% of the lumber downgrade in jack pine may be due to knots (Zhang et al. 2005), predicting crown structure appears to be of utmost importance not only for tree growth but also for economic purposes. In recent years, a few studies (Mäkelä 2002, Kantola and Mäkelä 2004) have investigated the relationship between foliage biomass distribution and branch basal area of whorls. In this approach, foliage distribution is used to estimate the foliage biomass of each whorl, which in turn determines the sapwood area of the bole and branches.

The importance of the vertical distribution of crown foliage in trees has long been recognized. According to Horn (1971), suppressed trees should shift their foliage further upward and have a more equal foliage distribution to capture light more efficiently. Different species show different amounts of plasticity in shifting their foliage biomass distribution within the canopy. Close relationships have been found between foliage distribution and stand age and density and tree age, social position, and leaf area index, mainly for pine and spruce species (e.g., Maguire and Ben-

nett 1996, Gilmore and Seymour 1997, Xu and Harrington 1998, Kantola and Mäkelä 2004). However, to our knowledge, there do not seem to be any studies available on foliage distribution of jack pine (*Pinus banksiana* Lamb.), one of the most important species in the Canadian boreal forest from both an ecological and an economic point of view.

In conifers, branches are organized in whorls, defined as the point on the stem where one or more branches are placed. The branch basal areas of these whorls are roughly proportional to changes in stem basal area within the crown (Mäkelä 2002) and can thus be used to describe taper and allocation of biomass to the stem within the crown. For certain species such as Scots pine (*Pinus sylvestris*), trees produce whorls only at the end of the annual shoots (nodal whorls). Jack pine, on the other hand, produces both nodal whorls and internodal whorls, which are located within the annual shoots. In models that use the profile theory or its derivatives for allocation of carbohydrates, a different distribution of foliage biomass in trees will affect how much carbon is allocated to the stem (Perttunen et al. 1996). Changes in this allocation will in turn affect stand growth and development.

More importantly, foliage distribution will affect the light interception within the crown (Stenberg et al. 1994), where species with nodal whorls only will necessarily have different light extinction profiles within the canopy than

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those with internodal whorls. Efforts were made to distinguish nodal whorls from internodal whorls in Sitka spruce (*Picea sitchensis* [Bong.] Carr.) in a wood quality perspective (Achim et al. 2006). These results translate into different branch dynamics with regard to the type of whorl. Because the foliage biomass of a branch can be related to branch size (Valentine et al. 1994, Baldwin et al. 1997, Schneider et al. 2008), foliage distributions between the nodal and internodal whorls should also differ. There are, however, very few studies that distinguish the distribution between the different whorl types.

From a statistical perspective, prediction of foliage biomass can be challenging. Modeling of foliage biomass distribution has been performed by fitting various density functions, such as the beta or the Weibull distribution functions to field data (Maguire and Bennett 1996, Gilmore and Seymour 1997, Xu and Harrington 1998, Garber and Maguire 2005). Although the Weibull distribution function has been widely used in stand diameter distribution modeling, the beta function is usually preferred for the prediction of foliage biomass distribution. Apart from being highly flexible, one major advantage of the beta distribution is that it is bounded at the extremities (Gupta and Nadarajah 2004). This property ensures that the integration of the function from one boundary to the other is always equal to 1. In the context of foliage biomass distribution, the beta function ensures consistent mathematical behavior because the foliage biomass is systematically distributed all along the crown length.

The objective of this study was to model the biomass foliage distribution for jack pine trees in regard to tree- and stand-level variables. To do so, we used a two-part model. The first part distinguishes nodal and internodal foliage biomass proportion within the crown. Then, the second part, which is based on the beta distribution function, makes it possible to predict the biomass distribution depending on the foliage type (nodal versus internodal). Two versions of this second part of the model, one for each foliage type, were parameterized using a nonlinear mixed-model approach. This model enables a more detailed look into the way jack pine distributes its foliage.

Materials and Methods

Data

The measurements were obtained from three sites (eastern New Brunswick, central Quebec, and eastern Ontario). In Ontario, 16 trees were sampled in 2006 in an initial spacing trial established in 1970 with 7-foot (2,450 stems/ha, 10 trees) and 14-foot spacing (550 stems/ha, 6 trees). The New Brunswick site was a long-term precommercial thinning trial established in 1969 (Zhang et al. 2006), in which 6 trees per spacing were sampled in 2006. At the time of thinning, the stand was spaced at 4 feet (6,720 stems/ha, 6 trees), 7 feet (2,200 stems/ha, 6 trees), and 9 feet (1,320 stems/ha, 6 trees). The central Quebec sites consisted of 20-year-old operational plantations (11 plots, 28 trees, 1,100–3,200 stems/ha) and old, naturally regenerated, unmanaged jack pine stands (6 plots, 18 trees, 1,250–2,350 stems/ha, 60- and 80-year-old stands). In most plots, 3 trees

were sampled. However, 5 trees from the 20-year-old plantations were left out of the analysis because of data loss or errors in processing the needles in the laboratory.

The social position (dominant, codominant, or suppressed) was evaluated for each individual tree in each plot. To ensure a representative sample, at least one tree was randomly selected in each category of social position, when possible. Because thinning had been performed almost 40 years earlier, foliage biomass distributions were assumed to be independent of stand conditions before thinning.

Site index (SI), defined as the dominant height of the stand at age 20, was used to classify the stands. Age 20 was preferred to age 50 because some plots were young and would have required extrapolation to quantify SI. Using a reference age of 20 enabled us to interpolate the SI through stem analysis. Additional details on the sample trees and sites at time of sampling are found in Table 1.

The sample stems were felled, and all branch diameters, status (live/dead), locations along the bole, and whorl type (nodal/internodal) were noted. Nodal whorls are defined as the whorls located at the end of each annual shoot, and internodal whorls are defined as those that are located between the ends of the annual shoots. A subsample of five branches per tree was systematically collected along the crown (i.e., such that the interval between each sample branch was constant for a given tree). The sample branches were then brought back to measure the oven-dried foliage biomass. A model was developed to relate branch foliage to its characteristics. This model was then applied to the branch measurements taken in the field to estimate branch, whorl, and tree foliage biomass. Last, a model was derived to predict total stem foliage biomass from tree-level variables. Both the branch-level and tree-level foliage biomass models can be found in Schneider et al. (2008) and in the Appendix.

Model Development

The model was developed in two parts. Once the tree total foliage biomass is predicted from previously developed equations, we first need to distinguish nodal foliage biomass from internodal foliage biomass in terms of proportion of the total foliage biomass. For the second part, the different foliage biomass distribution (nodal and internodal) can be modeled separately. Consequently, we first developed a model to predict the proportion of nodal foliage biomass. Then, a distribution model was parameterized for each type of foliage biomass. For a better understanding of the data structure, let us define i , j , k , and l as the site, the plot, the tree, and the whorl indices, respectively, such that $i = 1, 2, 3$, $j = 1, 2, \dots, p_i$, $k = 1, 2, \dots, q_{ij}$, and $l = 1, 2, \dots, r_{ijk}$. Note that whorls were indexed from the stem apex to the crown base. In addition, to distinguish nodal foliage from internodal foliage, we used superscripts N and I, respectively.

Relative Foliage Biomass per Whorl Type

Let us define W_{ijk} as the total foliage biomass for tree k in plot j located in site i . The proportion of nodal foliage

Table 1. Stand and sample stem characteristics

	Ontario	New Brunswick	Quebec
Average site characteristics*			
Total precipitation (mm)	938.9	1,113.9	985.6
Mean annual temperature (°C)	4.5	5.2	1.2
Degree-days above 5°C	1,688	1,175	1,634
Average stand characteristics			
Quadratic mean dbh (cm)	21.9 (18.5–25.2) [†]	15.3 (13.6–17.7)	10.9 (6.0–17.7)
Basal area (m ² /ha)	32.4 (26.3–39.1)	29.2 (14.1–36.2)	18.3 (8.6–31.4)
Density (stems/ha)	964 (544–1,456)	1,808 (575–2,575)	2,124 (1,143–3,850)
Age (years)	36	56	38.4 (17–79)
Site index [‡]	14.0	9.0	7.5 (5.9–10.4)
Number of plots	2	3	17
Average sample tree characteristics			
dbh (mm)	208 (116–287)	163 (85–228)	159 (41–297)
Height (m)	20.04 (16.92–22.76)	15.92 (9.80–19.30)	15.06 (5.24–22.76)
Average branch diameter (mm)	19.6 (6.2–58.1)	15.8 (4.5–35.1)	12.4 (2.8–45.5)
Average foliage biomass in the nodal whorls (kg)	5.09 (0.57–10.75)	3.22 (0.21–7.75)	2.10 (0.13–10.68)
Average foliage biomass in the intermodal whorls (kg)	1.67 (0.17–3.09)	0.81 (0.003–2.08)	0.49 (0.004–2.36)
Average number of nodal whorls	15.7 (11–21)	22.2 (7–32)	20.1 (4–46)
Average number of internodal whorls	25.6 (13–38)	21.6 (1–35)	14.5 (1–30)
Number of sample trees	16	18	46

Adapted from Schneider et al. (2008).

* From Canadian ecodistrict climate normals 1961–1990, Agriculture and Agri-Food Canada.

[†] Minimum and maximum values are shown in parentheses.

[‡] Site index: dominant stand height (m) at age 20.

biomass with respect to total foliage biomass can be modeled using a logistic function to ensure that the expected proportion does not exceed the range [0, 1],

$$\frac{W_{ijk}^N}{W_{ijk}^I} = \frac{1}{1 + e^{\beta_0 + \beta_1 a_{ijk} + \beta_2 h_{ijk} + \beta_3 d_{ijk}}} + \varepsilon_{ijk}, \quad (1)$$

where W_{ijk}^N is the nodal foliage biomass (kg) for tree k in plot j located in site i , a_{ijk} is the tree age (yr), h_{ijk} is the tree height (m), d_{ijk} is the tree dbh (cm), β_0 , β_1 , β_2 , and β_3 are the fixed-effect parameters, and ε_{ijk} is the residual error. The residual error term is assumed to be identically and independently distributed (iid) according to a normal distribution, such that $\varepsilon_{ijk} \sim^{iid} N(0, \sigma_{ijk}^2)$. Foliage biomass in the internodal whorls (W_{ijk}^I) was estimated to be the difference between W_{ijk} and W_{ijk}^N .

Relative Foliage Biomass Distribution

The cumulative relative foliage biomass from stem apex to whorl l (y_{ijkl}) was assumed to follow a beta cumulative density function (cdf),

$$y_{ijkl} = \sum_{l'=1}^l \frac{W_{ijkl'}^N}{W_{ijk}^N} = F(z_{ijkl}|p, q) + \varepsilon_{ijkl}, \quad (2a)$$

$$F(z_{ijkl}|p, q) = \frac{\int_0^{z_{ijkl}} x^{p-1}(1-x)^{q-1} dx}{\int_0^1 x^{p-1}(1-x)^{q-1} dx}, \quad (2b)$$

where W_{ijkl}^N is the foliage biomass for whorl l' in tree k in plot j located in site i , $F(z_{ijkl}|p, q)$ is the beta cdf with z_{ijkl} being the relative location of whorl l with respect to crown base starting from the apex and p and q being the parameters of the function, and ε_{ijkl} is the residual error term. The use of relative foliage biomass was necessary with the beta distri-

bution because it requires that the cdf be equal to 1 at the crown base.

As the beta cdf approaches both end points, i.e., when $x = 0$ and 1, the variance of the error terms converges to 0. This heteroscedastic pattern was taken into account by adding a variance function in the model (cf. Davidian and Giltinan 1995, p. 22, Pinheiro and Bates 2000, ch. 5.2) as follows:

$$\varepsilon_{ijkl} \sim N(0, \sigma^2 g^2(z_{ijkl}|\delta_1, \delta_2)), \quad (3a)$$

$$g^2(z_{ijkl}|\delta_1, \delta_2) = (\delta_1 + z_{ijkl}(1 - z_{ijkl}))^{\delta_2}, \quad (3b)$$

where σ^2 is the residual variance and δ_1 and δ_2 are two variance parameters to be estimated. Note that function 3b ensures that the variance converges to 0 as the relative location z_{ijkl} tends to 0 or 1.

To test the effects of explanatory variables, linear equations involving plot, tree, and whorl variables were substituted for parameters p and q . Different combinations of explanatory variables and interactions were tested, following a parameter prediction method. In a first step, the beta distribution was parameterized for each individual tree and whorl type, and a seemingly unrelated regression (cf. Gallant 1987) was used to relate the independent variables to both distribution parameters. The explanatory variables were kept in the model when they were significant at $\alpha = 0.05$. After each parameterization, the residuals were plotted against the explanatory variables to make sure there was no trend unaccounted for in the model. Possible multicollinearity was also assessed by studying the effect of adding or dropping one variable on the parameter estimates of the remaining variables in the model.

Note that the above developments and variable selection

process apply to the internodal relative foliage as well. Both models per whorl type were parameterized independently using the nlme package available in R software (R Development Core Team 2008, Pinheiro et al. 2009), which implements a pseudo-likelihood estimator (Pinheiro and Bates 2000, p. 312).

After several trials, the following equations were retained for the final models:

for nodal foliage,

$$p_{ijk}^N = \gamma_0 + \frac{\gamma_1}{W_{ijk}^N} + \frac{\gamma_2}{CL_{ijk}} \quad (4a)$$

$$q_{ijk}^N = \eta_0 + \eta_1 d_{ijk} + \eta_2 a_{ijk} \quad (4b)$$

for internodal foliage,

$$p^I = \gamma_3 + \gamma_4 W_{ijk}^I + \gamma_5 h_{ijk} + \gamma_6 a_{ijk} + \gamma_7 mdq_{ij} + \gamma_8 SI_{ij} \quad (4c)$$

$$q_{ijk}^I = \eta_3 + \nu_4 h_{ijk} + \eta_5 a_{ijk} + \eta_6 BA_{ij} \quad (4d)$$

where W_{ijk}^N is the total nodal foliage biomass (kg) for tree k in plot j located in site i , CL_{ijk} is the crown length (m), d_{ijk} is the tree dbh (cm), a_{ijk} is the tree age (yr), W_{ijk}^I is the total nodal foliage biomass (kg), h_{ijk} is the tree height (m), mdq_{ij} is the mean quadratic diameter (cm) for plot j in site i , SI_{ij} is the site index (m) for plot j in site i , and BA_{ij} is the basal area ($m^3 ha^{-1}$).

Results

Relative Foliage Biomass per Whorl Type

The parameterization of the first part (submodel 1) yielded parameter estimates (Table 2) that were used in turn to generate simulated relative foliage biomasses. Some of these are shown in Figure 1. On average, the nodal foliage is more abundant than the internodal foliage; i.e., the predicted proportions for nodal foliage are generally greater than 0.5. The proportion of foliage found in the nodal whorls increases with tree dbh. Furthermore, as stem age increases, it shifts upwards and flattens out. On the other

Table 2. Model information for determining the proportion of foliage biomass found in the nodal whorls (Equation 3)

	Parameter estimates (SE)
Parameters	
β_{30}	-0.4096 (0.1676)*
β_{31}	-0.0276 (0.0056)**
β_{32}	0.0751 (0.0288)***
β_{33}	-0.0490 (0.0232)*
σ_{3ijk}	0.0099
Fit statistics	
$R^{2\dagger}$	0.39
Root mean square error [‡]	0.09

* $P < 0.05$.

** $P < 0.0001$.

*** $P < 0.01$.

† Calculated as $1 - \frac{\sum_{ij}(y_{ij} - \hat{y}_{ij})^2}{\sum_{ijk}(y_{ij} - \bar{y})^2}$.

‡ Calculated as $(\sum_{ij}(y_{ij} - \hat{y}_{ij})^2/n)^{0.5}$ where n is the number of measurements.

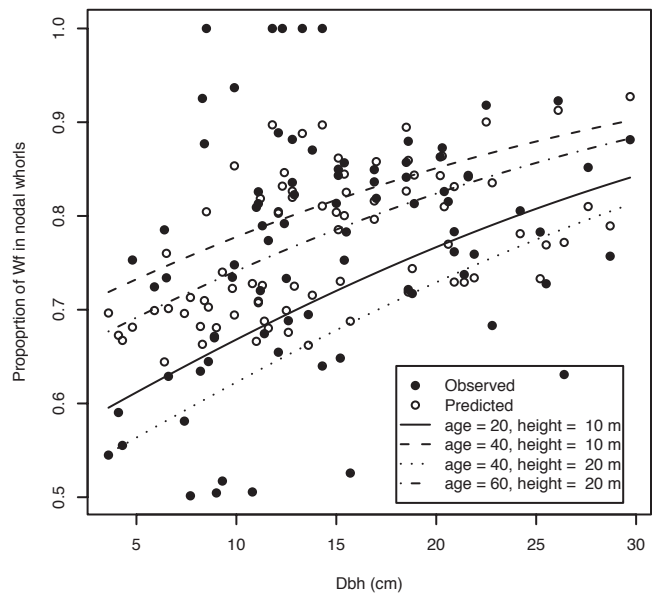


Figure 1. Observed and predicted proportions of foliage biomass found within the nodal whorls.

hand, the proportion of foliage biomass in nodal whorls tends to decrease as total stem height decreases.

Relative Foliage Biomass Distribution

The parameterization of the second part (submodel 2a) with parameters set as shown in Equations 4a–4d was possible using the nlme package, and the resulting parameter estimates are shown in Table 3. The estimated values for the parameters of the beta distribution (Equation 2b) should be interpreted as follows: higher values of p indicate a shift of the probability density function toward the crown base, whereas an increase in q results in a skewed distribution toward the upper crown.

As nodal foliage biomass increases, the inverse value, i.e., $1/\text{nodal foliage biomass}$, decreases. The negative value of parameter estimates associated with this variable ($\gamma_1 = -0.0901$) indicates that increases in nodal foliage biomass also increases the value of p , resulting in nodal biomass being more concentrated toward the crown base. Crown length has the opposite effect ($\gamma_2 = 1.7965$). As it increases, the inverse value decreases, as does the value of p . As dbh decreases ($\eta_1 = -0.0446$) and age increases ($\eta_2 = 0.0277$), the value of the q parameter increases and the nodal foliage biomass concentrates in the upper crown.

As the internodal foliage biomass increases, the p parameter increases as well and the distribution shifts toward the crown base ($\gamma_1 = 0.3458$). Increases in the site index ($\gamma_5 = 0.1216$) and decreases in the mean quadratic diameter ($\gamma_4 = -0.0481$) induce similar effects. Increases in stand basal area increase the value of the q parameter, and, consequently, the biomass distribution shifts toward the upper crown. The effects of stem age and height are more complex because these two variables act on both the p and q parameters.

To better understand the effect of the different explanatory variables on relative foliage biomass distribution, we chose a reference tree with the average values found in the

Table 3. Model information for the nodal and internodal foliage biomass

	Nodal whorls (Equations 4a and 4b)		Internodal whorls (Equations 4c and 4d)	
	p^N	q^N	p^I	q^I
Parameter estimates (SE)				
Intercept	1.4335 (0.0436)*	1.2124 (0.0466)*	0.7596 (0.1159)*	0.7872 (0.1037)*
Tree level				
1/nodal foliage biomass	-0.0901 (0.0140)*			
Internodal foliage biomass			0.3458 (0.0366)*	
dbh		-0.0446 (0.0027)*		
Total stem height			-0.0706 (0.0125)*	-0.0579 (0.0115)*
1/crown length	1.7965 (0.2272)*			
Age		0.0277 (0.0010)*	0.0125 (0.0033)*	0.0251 (0.0039)*
Stand level				
Stand basal area				0.0228 (0.0033)*
Mean quadratic diameter			-0.0481 (0.0069)*	
SI			0.1216 (0.0138)*	
Fit statistics				
R^2		0.96		0.90
Root mean square error		0.0716		0.1021
Kolmogorov-Smirnov statistics		0.14 (0.06)		0.14 (0.06)
Variance function parameters				
δ_1		1.25508e-15		6.590151e-16
δ_2		0.1494		0.2319
σ^2		0.0127		0.0376

* $P < 0.0001$.

data set. The mean tree was 50 years old, with 3.4 kg of nodal foliage biomass, 0.8 kg of internodal foliage biomass, a dbh of 13.4 cm, a crown length of 5.7 m, a total height of 14.8 m in a stand with 25.5 m²/ha of basal area, with a mean quadratic diameter of 14.7 cm and a site index of 9.3 m (dominant height at age 20). Then, we changed the value of one explanatory variable (increase or decrease of 50%) at a time while keeping the other variables at their reference points. Simulated relative foliage biomasses were then obtained using the aforementioned parameter estimates. These predictions are shown in Figures 2 and 3 for the tree- and stand-level explanatory variables, respectively.

Nodal foliage biomass tends to shift upward as trees get older. For younger trees, nodal foliage biomass is largely concentrated at the crown base, whereas internodal biomass is more or less evenly distributed all along the crown length. Increases in dbh make the nodal foliage biomass shift slightly downward, whereas internodal foliage seems to be unaffected. Decreases in crown length have a similar effect. Finally, changes in terms of height affect internodal foliage biomass, with taller trees having more evenly distributed biomass than smaller trees.

At the stand level, internodal foliage biomass tends to shift slightly upward as basal area increases. Increases in stand mean quadratic diameter result in a similar effect. As a matter of fact, trees growing with bigger trees tend to have their internodal foliage biomass concentrated in the upper crown. Finally, decreases in site index cause internodal foliage biomass to shift upward.

The simulated foliage biomass distributions shown in Figures 2 and 3 are presented to provide an idea of the magnitude of the different effects. Different reference points for the explanatory variables would yield different simulated foliage biomass. However, the differences are roughly the same in terms of magnitude.

In terms of parameterization, the variance function (Equation 3a) made it possible to capture the heteroscedastic trend of the error terms. The variance actually tends toward 0 as the location within the crown gets closer to the tip of the tree or the crown base. An example of how this trend is accounted for in the model is shown in Figure 4. When the variance function was included in the model, the fit increased in both cases. For the nodal biomass distribution, the Akaike information criterion and Bayesian information criterion decreased from -3,832 to -3,795 and from -9,426 to -9,378, respectively. For the internodal biomass distribution, the same criteria decreased from -2,446 to -2,388 and from -7,766 to -7,697, respectively. The parameter estimates of the variance function can be found in Table 3.

Discussion

Jack pine foliage biomass is divided into nodal and internodal whorls. In this study, we managed to parameterize a two-part model that may serve to predict the biomass distribution for each type of foliage. The first part of the model predicts how the foliage biomass splits into nodal and internodal biomasses. Then, the second part predicts the distribution of the biomass depending on the type of foliage. The two versions of the second part (one for each foliage type) are based on the cdf of the beta distribution. To our knowledge, there has been no reported work on the differences between nodal and internodal whorls in terms of foliage biomass modeling for jack pine. This model in our study makes it possible to better understand foliage distribution and better characterize crown shape.

As the stem ages, the proportion of internodal foliage biomass decreases. We hypothesize that the explanation for this result is related to shading effect. Internodal whorls are

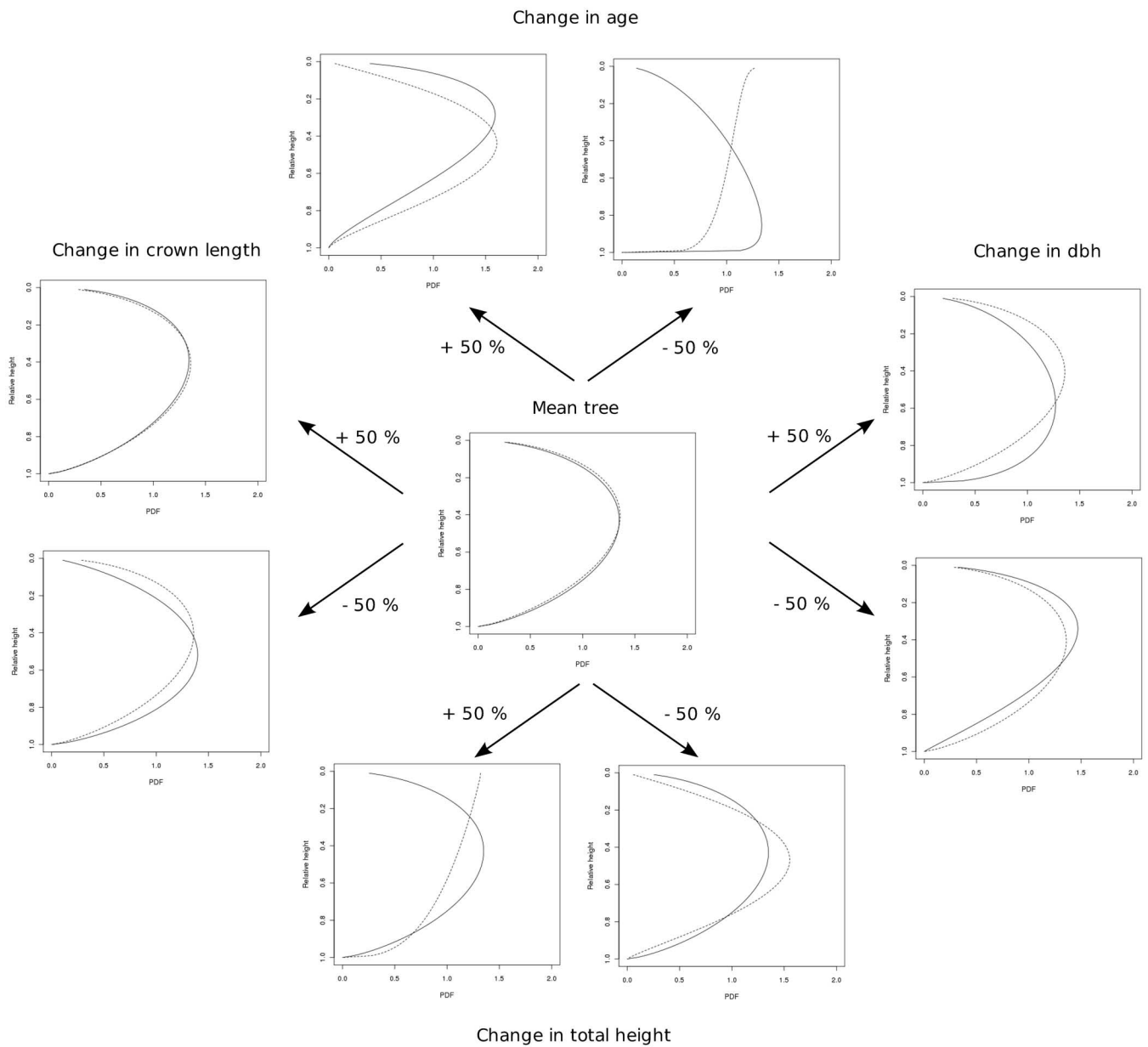


Figure 2. Simulated effects in changes of tree-level variables on the nodal (full line) and internodal (dotted line) foliage biomass probability density functions based on mean tree dimensions.

shaded by the nodal whorls, even during their early development. The shading effect (by stand closure through age and crown length) seems to have a greater impact. A second hypothesis is that the cones inserted along the stem seem to prefer the internodal position, as observed in the field. This explanation could not be confirmed by our data because cone measurements were not taken during fieldwork. Nevertheless, the proportion of internodal whorls to nodal whorls is inversely proportional to stem age.

Our results, however, support those reported by Achim et al. (2006), who found different branch dynamics in Sitka spruce with regard to whorl type. Branches located on internodal whorls had higher probabilities of dying compared with nodal branches. Moreover, nodal whorl branches were larger than those of the internodal whorls. For younger trees, our models indicate that the internodal foliage is more concentrated in the lower crown than in the nodal foliage.

The situation reverses as the tree ages. The shedding of the internodal branches could be more important in older trees. In addition, nodal branches could grow faster in taller trees. The real explanation could be an interaction between these two phenomena. The literature on branch dynamics with regard to whorl type is rather scarce, and we cannot confirm any of these two hypotheses with our data.

Many studies have reported that stand density directly controls foliage biomass distribution (Maguire and Bennett 1996, Gilmore and Seymour 1997, Xu and Harrington 1998, Kershaw and Maguire 2000, Garber and Maguire 2005). For jack pine, our results show that nodal foliage biomass distribution is mainly dictated by tree-level variables, whereas internodal foliage biomass is influenced by stand-level variables.

Unlike in Scots pine (Mäkelä and Vanninen 2001), the relative foliage biomass distribution in jack pine tends to

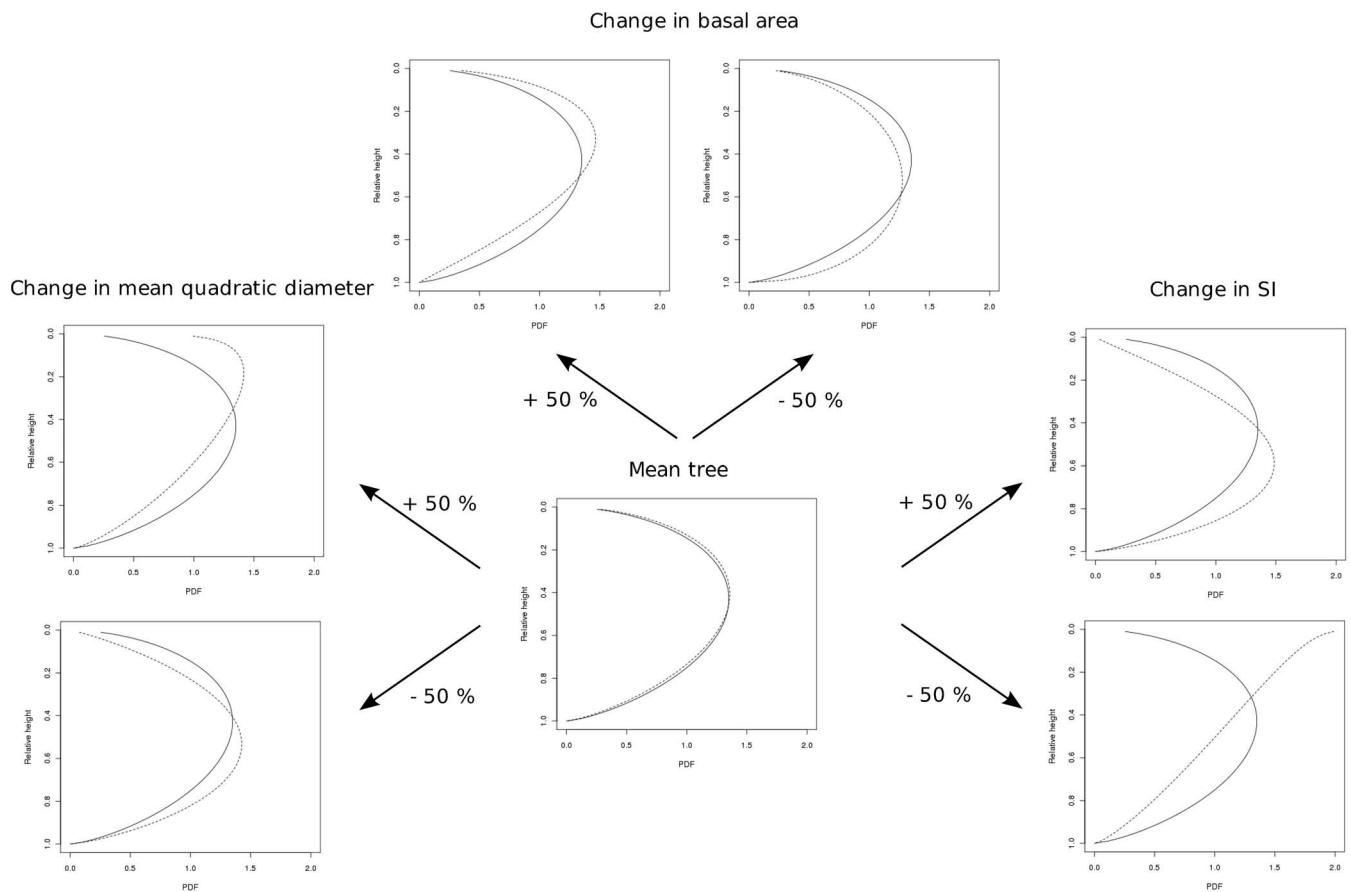


Figure 3. Simulated effects of changes in stand-level variables on the nodal (full line) and internodal (dotted line) foliage biomass probability density functions based on mean tree dimensions.

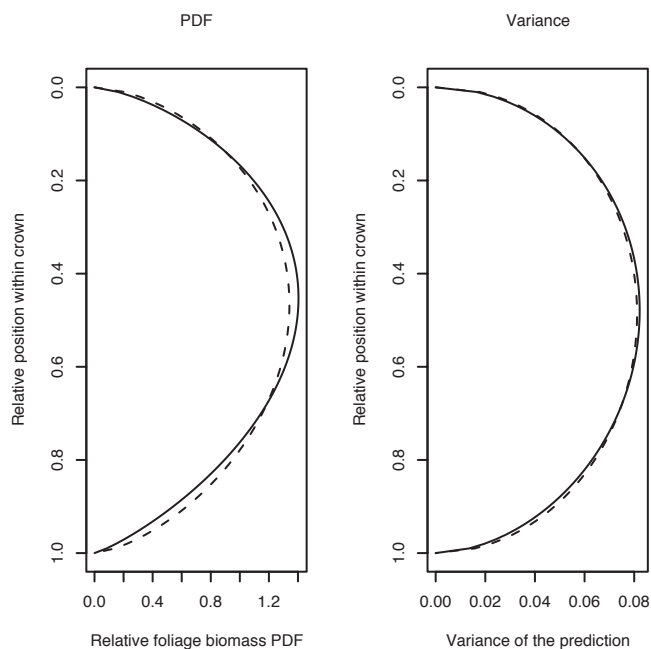


Figure 4. Simulated probability density plot and variance.

shift upward as the stem ages. Because jack pine stands are even-aged, the effect of tree age could be interpreted as the effect of stand closure and greater clustering of foliage within the crown. This makes it harder for the stems to support foliage at the bottom of the crown. Species shade

tolerance has also been proposed as an explanation for the differences between the age effect in Norway spruce (*Picea abies*) and Scots pine (Kantola and Mäkelä 2004), shade-tolerant species trees having the ability to change their foliage biomass distribution. Because jack pine is shade-intolerant like Scots pine, this age effect is more likely to be the result of the stand closure effect. We cannot confirm this assumption because the age and the stand closure effects cannot be distinguished in our data set.

The observed changes in distribution of foliage biomass and the responses of foliage biomass distributions to the relative position of the trees within the stand fit quite well with the pattern that Horn (1971) put forth: early succession species have a wide foliage distribution over several layers, whereas the foliage of suppressed and understory trees is distributed in a monolayer at the top of their crowns. Although shade tolerance has already been used to explain differences in foliage biomass flexibilities between Norway spruce and Scots pine, one could argue that it might be attributable to the different tree architectures. The foliage biomass of species with internodal whorls (jack pine, Norway spruce, and Douglas fir [*Pseudotsuga menziesii*]) shows distribution shifts with regard to certain tree and stand variables. Species with nodal whorls only, such as Scots pine, have foliage biomass distributions that are less flexible. These differences could be due to the fact that species with internodal whorls are able to better allocate their photosynthetic centers to areas that maximize light

capture by varying the growth, formation, and survival rates of the internodal whorls.

Relative foliage biomass distribution studies generally standardize foliage biomass per unit length of crown (Maguire and Bennett 1996, Xu and Harrington 1998, Mäkelä and Vanninen 2001, Kantola and Mäkelä 2004, Garber and Maguire 2005). Some discussions on the use of this standardization have, however, arisen in the literature (Mizunaga and Umeki 2001): use of more precise models yields a better picture of foliage distribution and of the forces at work. The two versions of the second part of our model rely on the same approach, a nonlinear parameterization of the beta cdf, which includes a variance function to account for heteroscedasticity. Similar studies for parameterization of the Weibull distribution to diameter distribution have already been published (Liu et al. 2004).

The assumption of an additive independent and homogeneous error term in the nonlinear approach is a strong one. In fact, it can reasonably be assumed that the variances of the error terms are not homogeneous. The cumulative beta function has $[0, 0]$ for starting point and $[1, 1]$ for end point, which leads to very small errors at the tail end of the distribution. In contrast, the variance in prediction will peak at, or very close to, the maximum of the relative foliage biomass. In this case study, the proposed variance function makes it possible to relax the assumption of homogeneous error terms, and it increased the goodness of fit of both models.

On the other hand, the within-tree error terms are unlikely to be independent from each other. In fact, a positive error term for a particular whorl is likely to result in a negative error term for another whorl because the cumulative sum of the relative biomasses converges to 1. In this study, these possible negative correlations were not considered and remain to be tested. Because most correlation structures in the statistical literature are designed to account for positive correlations (cf. Pinheiro and Bates 2000, Littell et al. 2006), some developments might be needed. Because the dependence among the error terms was not considered in this study, the coverage of confidence intervals for the parameter estimates might not be nominal (Gregoire et al. 1995). However, empirical correlations calculated from the model residuals showed that these correlations were small and, consequently, we expect these biases in the statistical inferences to be small or even negligible.

Other methods based on the prediction of the moments (parameter recovery) or the prediction of the parameter (parameter prediction) of the biomass distribution could have been used instead of a nonlinear model. These methods are thought to provide more reliable results because they depend on the probability density function itself and not on a nonlinear model based on a probability density function or a cdf. We first compared these two approaches (parameter recovery and parameter prediction) with the one we used in this study, and the nonlinear model proved to have the best fit. With diameter distribution modeling, Zhang et al. (2003) also came to the conclusion that maximum likelihood estimation methods seemed to offer the best results when distribution functions were parameterized to diameter distributions. Implementation of the parameter recovery and

parameter prediction methods in the modeling of jack pine foliage biomass remains to be improved and tested.

Conclusions

The proposed method first decomposes the foliage into nodal and internodal whorls and then applies distinct distributions to each whorl type. This detail yields an insight into the crown characteristics whereby the nodal distribution peaks closer to the crown base than the internodal distribution as stem age increases. Moreover, the nodal foliage distribution is influenced solely by tree-level variables, whereas the internodal foliage distribution is affected by both tree- and stand-level variables. Further work on jack pine branch dynamics would, however, be needed to better understand the physiological processes responsible for the observed trends.

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Appendix: Previously Published Models

Branch foliage biomass is predicted by branch diameter and location within the crown (Equation A1),

$$W_{ijklm} = (0.0003257 + b_{1i} + b_{1ij} + b_{1ijk}) \cdot d_{ijklm}^2 \cdot (1 + x_{ijklm})^{0.94} + \varepsilon_{1ijklm}, \quad (\text{A1})$$

where i, j, k, l , and m are subscripts to indicate hierarchical level; branch m in whorl l of stem k in plot j in site i ; W_{ijklm} is foliage biomass of branch m (kg); d_{ijklm} is branch diameter (cm); x_{ijklm} is the relative position of branch m within the crown (stem apex: $x = 0$; crown base: $x = 1$); $b_i, b_{ij},$ and b_{ijk} are site, plot, and tree random effects, where $b_{1i} \sim \mathcal{N}(0, 6.96 \times 10^{-10})$, $b_{1ij} \sim \mathcal{N}(0, 6.08 \times 10^{-5})$, and $b_{1ijk} \sim \mathcal{N}(0, 4.90 \times 10^{-5})$; and ε_{1ijklm} is residual error, where $\varepsilon_{1ijklm} \sim \mathcal{N}(0, 0.0403)$.

This relationship was applied to the branch measurements with the site, plot, and tree random effects to yield the estimated whorl foliage biomass. On average, there were 1.16 internodal whorls per annual shoot (ranging from 0 to 5 internodal whorls). However, these only accounted for 23% of the total foliage biomass of the tree (ranging from 1 to 49%).

As presented in Schneider et al. (2008), the total tree foliage biomass can be estimated from crown length, stem age, dbh, and total height (Equation A2).

$$W_{ijk} = (0.1211 + b_{2i} + 0.0009 \cdot a_{ijk}) \cdot l^{2.6732 - 0.0126 \cdot (h_{ijk}/d_{ijk})} + \varepsilon_{2ijk} \quad (\text{A2})$$

where W_{ijk} is tree foliage biomass (kg), a_{ijk} is stem age (yr), h_{ijk} is stem height (m), d_{ijk} is dbh (cm), b_{2i} is site random effect, where $b_{2i} \sim \mathcal{N}(0, 0.0406)$, and ε_{2ijk} is residual error, which can be calculated from the seemingly unrelated regression parameters presented in Schneider et al. (2008).