Tree Physiology 31, 22–29
doi:10.1093/treephys/tpq104

Research paper

# Within crown variation in the relationship between foliage biomass and sapwood area in jack pine

Robert Schneider[1,7], Frank Berninger[2], Chhun-Huor Ung[3], Annikki Mäkelä[4], D. Edwin Swift[5] and S.Y. Zhang[6]

[1]Département de biologie, chimie et géographie, Université du Québec à Rimouski, 300, allée des Ursulines, Rimouski, QC, Canada G5L 3A1; [2]Département des Sciences Biologiques, Université du Québec à Montréal, CP 8888, Succ. Centre-ville, Montréal, QC, Canada H3C 3P8; [3]Natural Resources Canada, Canadian Wood Fibre Centre, Canadian Forest Service, PO Box 10380, Stn. Sainte-Foy, Québec, QC, Canada G1V 4C7; [4]Department of Forest Ecology, University of Helsinki, Latokartanonkaari 7, PO Box 27, FI-00014 Helsinki, Finland; [5]Canadian Wood Fibre Centre, Natural Resources Canada, Canadian Forest Service, PO Box 4000, Fredericton, NB, Canada E3B 5P7; [6]FPInnovations – Forintek Division, 2665 East Mall, Vancouver, BC, Canada V6T 1W5; [7]Corresponding author (robert_schneider@uqar.ca)

Received September 17, 2009; accepted October 27, 2010; handling Editor David Whitehead

**The relationship between sapwood area and foliage biomass is the basis for a lot of research on eco-phyisology. In this paper, foliage biomass change between two consecutive whorls is studied, using different variations in the pipe model theory. Linear and non-linear mixed-effect models relating foliage differences to sapwood area increments were tested to take into account whorl location, with the best fit statistics supporting the non-linear formulation. The estimated value of the exponent is 0.5130, which is significantly different from 1, the expected value given by the pipe model theory. When applied to crown stem sapwood taper, the model indicates that foliage biomass distribution influences the foliage biomass to sapwood area at crown base ratio. This result is interpreted as being the consequence of differences in the turnover rates of sapwood and foliage. More importantly, the model explains previously reported trends in jack pine sapwood area at crown base to tree foliage biomass ratio.**

***Keywords***: mixed-effect models, pipe model theory, sapwood taper

## Introduction

The pipe model theory views trees as an assembly of pipes that connect the leaves to the roots (Shinozaki et al. 1964*a*, 1964*b*). Through empirical evidence, the authors demonstrate that the relationship between the foliage biomass above a given point in the stem and the used pipe area at that point is linear without an intercept.

The linearity of the pipe model has been questioned by several authors by considering that the sapwood area is equivalent to the used pipe area. Moreover, results using either foliage biomass or leaf area lead to the same results (Kershaw 2001), although some authors have argued the contrary (Valentine 2001). Kershaw and Maguire (2000) found that the relationship between the cumulative foliage area above a given point and the sapwood area of the stem at that point was non-linear. The same conclusion was reached by Kantola and Mäkelä (2004). Similar results were presented by Long and Smith (1988) that related sapwood area at breast height to projected leaf area. The authors conclude that the leaf area to sapwood area ratio is directly related to tree size and stand conditions and is non-linear in form. Several studies have also shown that the pipe model ratio (i.e., cumulative foliage biomass to apex to sapwood area ratio) at crown base can vary with tree size, location, climate or stand density (Coyea and Margolis 1992, Berninger and Nikinmaa 1994, McDowell et al. 2002, Gilmore and Seymour 2004, Berninger et al. 2005, Schneider et al. 2008). Berninger and Nikinmaa (1994) postulated that the pipe model relationship might have an intercept. Modelling approaches have demonstrated that constant pipe model ratios are not necessarily ecologically meaningful (Magnani et al. 2000). Lastly, the ratio varies with the height at which sapwood area is measured. For example, the foliage area to sapwood area ratio will decrease from crown base to breast height, since the relationship between the sapwood area at crown base and that at breast height is proportional to the crown ratio (Long and Smith 1988).

Moreover, biomechanics have also questioned the validity of the pipe model theory. Farnsworth and van Gardingen (1995) demonstrated from empirical evidence that mechanical design principles were better suited to predict branch diameter. They also stated that branches constructed following the pipe model principle would use structural resources inefficiently. Further work by Taneda and Tateno (2004) also illustrated that mechanical design principles better predict biomass partitioning between shoot and foliage.

Nevertheless, the pipe model theory is extensively used in process-based tree growth models as the basis for the allometry between the foliage and the stem (Valentine 1988, Mäkelä 1997, Le Roux et al. 2001, Valentine and Mäkelä 2005). Mäkelä (2002) used the pipe model theory to introduce stem form into Crobas, a process-based model (Mäkelä 1997, Mäkelä et al. 2000). Using knowledge of the vertical foliage biomass distribution, coupled with the pipe model theory, the model is able to simulate stem taper and branchiness. The model, however, introduced a variant into the pipe model based on empirical evidence (Mäkelä and Vanninen 2001), such that the pipe model ratios within the crown varied with whorl depth, i.e., less foliage biomass per unit sapwood area at the top of the tree. Moreover, structural–functional models such as Lignum (Sievänen et al. 1997) could use more detailed information on relationships between sapwood and foliage biomass within the stems and branches.

Due to the importance of the pipe model theory in process-based models, in particular, and the fact that it forms the basis of a lot of research in eco-physiology, in general, we want to see to what extent the pipe model theory holds for jack pine (*Pinus banksiana* Lamb.). Statistical work based on linear and non-linear mixed-effect (nlme) models is used to verify whether the relationship between foliage biomass and sapwood area is linear. In the present analysis, the proposed models relate whorl foliage biomass to sapwood area increment between two consecutive whorls. If the pipe model theory is valid, the models ought to be linear. The tested non-linear forms, however, present the best fit statistics. The non-linear models are able to capture more of the observed variability in the foliage biomass to sapwood area ratios. The model with the best fit statistics is influenced by foliage biomass distribution: the foliage biomass to sapwood area at crown base ratio increases as foliage biomass distribution is pushed towards the crown base.

## Materials

The data used for the analysis come from three jack pine sites in Eastern Canada: Petawawa Research Forest (eastern Ontario, 16 trees), Smurfit-Stone freehold (central Quebec, 47 trees) and Eel River precommercial thinning trial (eastern New Brunswick, 18 trees). Details of the measurements carried out on the stems and the stands as well as site characteristics have previously been published (Schneider et al. 2008). In summary, the diameters of all the live branches along the stem were measured as well as their location (nodal/internodal whorl, whorl height). A subsample of five branches per tree was used to parameterize a branch foliage biomass to branch diameter model, which was applied with the site, plot and tree random effects to all of the branches to estimate whorl foliage biomass. The stem diameter below each nodal whorl was also noted. Stem analysis discs were taken at regular intervals within the crown, with spacing not exceeding 1.5 m. The delimitation of the sapwood/heartwood transition was marked on the discs in the field by light transmission, with the measurements taken upon return from the field. Linear interpolation of the sapwood and heartwood areas from the discs to the stem measurements was then carried out to estimate the sapwood area at the base of each whorl. The interpolation methodology was validated using the sample discs with a maximum spacing of 3 m which lead to very little bias $-6.92e-06\ \text{m}^2$ (or $-0.18\%$) and root mean squared error ($\text{RMSE} = 5.90e-5\ \text{m}^2$) and high proportion of variance explained ($R^2 = 0.99$). One could suppose that the bias would be even smaller if the span is reduced.

## Methods

### *Foliage biomass to sapwood area ratio*

If sapwood area is considered to be used pipes, the pipe model suggests that there is a linear relationship between the foliage biomass above the given point of the stem and the sapwood area:

$$\sum_{i=1}^{k} W_i^f = \beta \cdot A_k^s \qquad (1)$$

where $W_i^f$ is the foliage biomass of whorl $i$ (in kg), $A_k^s$ is the sapwood area of whorl $k$ (in cm$^2$) and $\beta$ is the pipe model ratio.

The pipe model can also be expressed in terms of foliage biomass needed to observe a given change in sapwood area between two consecutive whorls:

$$W_k^f = \beta_0 \cdot (A_k^s - A_{k+1}^s) = \beta_0 \cdot \Delta A_k^s \qquad (2)$$

where $W_k^f$ is the foliage biomass of whorl $k$, $\Delta A_k^s$ is the difference between the sapwood area at the base of the whorl above

$A^s_{k+1}$ and just below $A^s_k$ the whorl of interest $k$ and $\beta_0$ is the model parameter.

If the active pipes of the pipe model theory can be substituted by sapwood area, the pipe model ratio ($\beta$) given in Eq. (1) and the model parameter ($\beta_0$) in Eq. (2) should have the same value.

Equation 2 was parameterized in R using the nlme function (R. Development Core Team 2008). Random effects were included in the slope to account for plot and tree hierarchical levels (Eq. (3)).

$$W^f_{ijk} = (\beta_0 + b_i + b_{ij}) \cdot \Delta A^s_{ijk} + \varepsilon_{ijk} \tag{3}$$

where $ijk$ represents the subscripts for whorl $k$ in tree $j$ of plot $i$, $b_i$ and $b_{ij}$ are the random effects for the plot and tree ($b_i \; \underset{\sim}{i.i.d.} \, \mathcal{N}(0, \sigma^2_{\text{site}}), b_{ij} \; \underset{\sim}{i.i.d.} \, \mathcal{N}(0, \sigma^2_{\text{plot}})$); $\varepsilon_{ijk}$ is the model error ($\varepsilon_{ijk} \; \underset{\sim}{i.i.d.} \, \mathcal{N}(0, \sigma^2)$).

The first step was to determine the effect of position within the stem on the model parameter $\beta_0$ in Eq. (3). Different forms of crown depth and relative crown depth were tested, with the five best results presented in Eqs. (4a–e). In Eqs. (4a) and (4b), one unit was added to the depth measurement to ensure a logical response of the model, or else a whorl at the top of the stem would add no sapwood area to the stem, irrespective of its foliage biomass.

$$\beta_0 = (\beta_1 + b_i + b_{ij}) \cdot (1 + x_{ijk})^{\beta_2} \tag{4a}$$

$$\beta_0 = (\beta_1 + b_i + b_{ij}) \cdot (1 + d_{ijk})^{\beta_2} \tag{4b}$$

$$\beta_0 = \frac{\beta_1 + b_i + b_{ij}}{1 + \beta_2 \cdot x_{ijk}} \tag{4c}$$

$$\beta_0 = \frac{\beta_1 + b_i + b_{ij}}{1 + \beta_2 \cdot d_{ijk}} \tag{4d}$$

$$\beta_0 = \frac{\beta_1 + b_i + b_{ij}}{1 + \beta_2 \cdot x_{ijk} + \beta_3 \cdot H^c_{ij}} \tag{4e}$$

where $\beta_1$, $\beta_2$ and $\beta_3$ are the fixed effect parameters; $d_{ijk}$ is the crown depth (in m) of whorl $k$ of stem $j$ in plot $i$, defined as the distance from stem apex; $H^c_{ij}$ is the crown length (in m) and $x_{ijk}$ is the relative crown depth of whorl $k$ of stem $j$ in plot $i$, defined as $d_{ijk} / H^c_{ij}$.

The linearity of the pipe model was tested by placing an exponent on the sapwood area increment (Eq. (5)).

$$W^f_{ijk} = \beta_0 \cdot \Delta A^{s,\beta_4}_{ijk} + \varepsilon_{ijk} \tag{5}$$

where $\beta_0$ is defined in Eqs 4a–e; $\beta_4$ is the exponent fixed effect parameter.

### *Scaling from whorl to crown base*

The models presented in the previous section present whorl foliage biomass as a function of the stem sapwood increment from one whorl to the next. By inverting the model, it is possible to estimate the change in sapwood area as a function of foliage biomass. In this perspective, sensitivity of the best model to different foliage biomass distributions was evaluated using the methodology proposed by Mäkelä (2002). The foliage between two points in the stem is given by multiplying beta density distribution by the foliage biomass of the stem (Eq. (6)).

$$W^f_{ijk} = W^f_{ij} \cdot \frac{\int_{x_{ijk}}^{x_{ijk+1}} x^p (1-x)^q \, dx}{\int_0^1 x^p (1-x)^q \, dx} \tag{6}$$

where $W^f_{ij}$ is the total stem foliage biomass; $k$ is the index of the whorl of interest; $p$ and $q$ are the beta function parameters.

Model sensitivity to foliage distribution was studied using three different sets of $p$ and $q$ parameters: skewed distribution to stem apex ($p = 1$ and $q = 2$), symmetric distribution ($p = 1.5$ and $q = 1.5$) and skewed distribution to crown base ($p = 2$ and $q = 1$). The changes in the pipe model ratio were then observed. Previously published work was used to predict stem foliage from crown length and stem characteristics (Schneider et al. 2008) ($R^2 = 0.72$):

$$w^f_{ij} = (0.1211 + 0.0009 \cdot \text{age}_{ij}) \cdot H_{ij}^{c, 2.6732 - 0.0126 \cdot H^{\text{tot}}_{ij} / dbh_{ij}} \tag{7}$$

Average stem age (40 years), average height to diameter at beast height (dbh) ratio (100) and crown length ($H^c = 6$ m) in the database were inserted in Eq. (7). To study the influence of foliage distribution on sapwood area, the sapwood taper was predicted by keeping crown length constant ($H^c = 6$ m, mean crown length in data) and using different beta functions to induce distributions skewed to the top (Eq. (9) with $p = 1$ and $q = 2$), symmetrical distributions (Eq. (9) with $p = 1.5$ and $q = 1.5$) and distributions skewed towards the crown base (Eq. (5) with $p = 2$ and $q = 1$).

## Results

The models show that whorl position within the crown significantly improves the fit as indicated by the lower Akaike information criteria (AIC) of Model 2 when compared with Model 1 (Table 1). Model 2 predicts foliage biomass from the sapwood

Table 1. Fit statistics, parameter estimates and variance–covariance estimates of the best models (all parameter estimates are highly significant, i.e., $P < 0.0001$)

| Model | Model form | AIC | $\beta_1$ | $\beta_2$ | $\beta_3$ | $\beta_4$ | $\sigma_{\text{site}}$ | $\sigma_{\text{plot}}$ | $\sigma$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | $W^f_{ijk} = \beta_1 \cdot \Delta A^s_{ijk}$ | – 3170 | 0.0314 | | | | 0.010 | 0.011 | 0.135 | 0.28 |
| 2 | $W^f_{ijk} = (\beta_1 \cdot \Delta A^s_{ijk})/(1 + \beta_2 \cdot x_{ijk})$ | – 3202 | 0.0396 | 0.3931 | | | 0.012 | 0.013 | 0.134 | 0.29 |
| 3 | $W^f_{ijk} = (\beta_1 \cdot \Delta A^s_{ijk},\beta_4)/(1 + \beta_2 \cdot x_{ijk} + \beta_3 \cdot H_{ij}{}^c)$ | – 3513 | 0.0268 | – 0.0858 | – 0.0909 | 0.5130 | 0.006 | 0.009 | 0.126 | 0.37 |

area increment and relative position of the whorl within the crown. The insertion of an exponent on the sapwood area increment also contributes to improving the fit (Model 3), where foliage biomass is predicted using sapwood area increment, relative position within the crown and crown length. More importantly, the exponent is statistically different from 1.

The pipe model ratio shows an interesting trend with respect to distance from stem apex (Figure 1). It either increases or decreases asymptotically from stem apex to crown base. When the predicted pipe model ratio for each model is observed, calculated by summing from stem apex the increase in sapwood area of each whorl, the non-linear form is the only one that is able to capture the observed trends. The original pipe model predicts a constant ratio throughout the crown. The model, which includes whorl location but is linear with respect to foliage biomass, indicates a constant decrease within the crown.

No trends within the residuals for the non-linear model can be observed (Figure 2). Stand level (stand density, stand basal area), tree level (stem foliage biomass, crown length, total

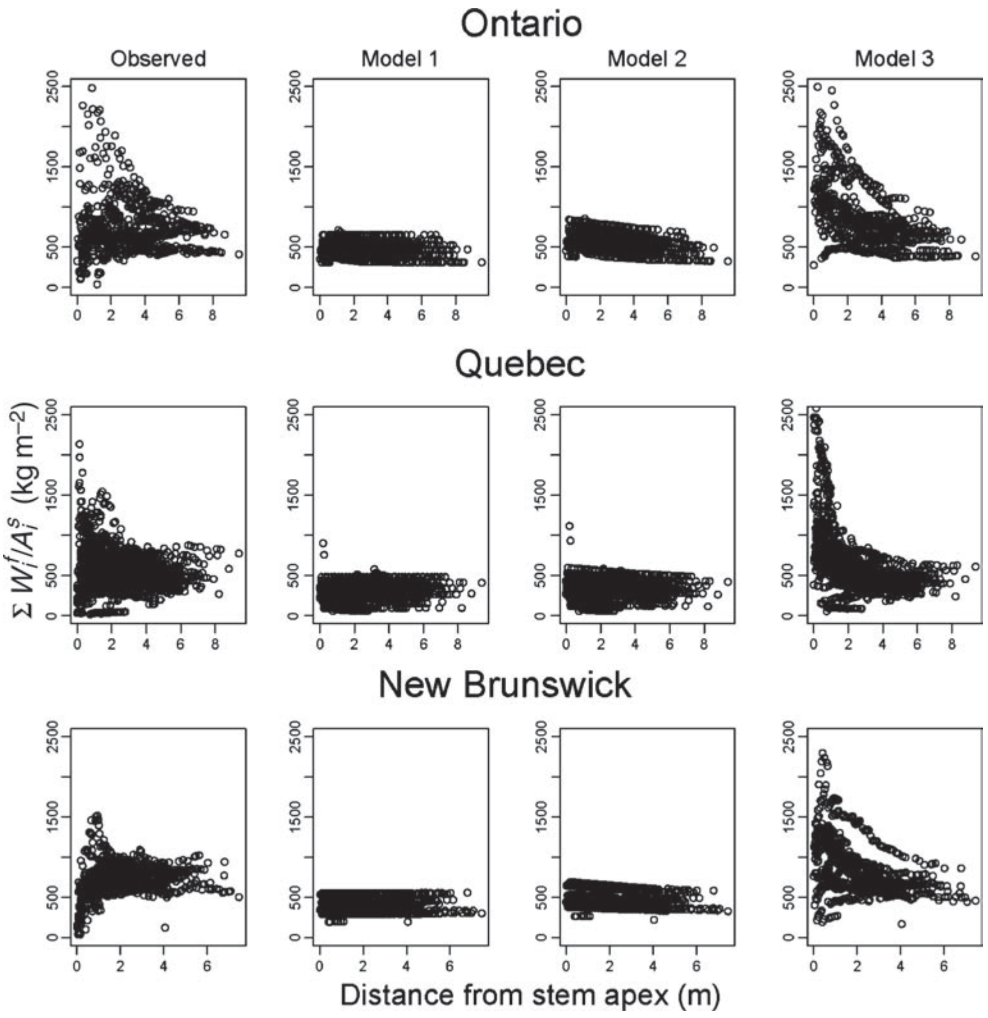

Figure 1. Observed and predicted pipe model ratios versus distance from stem apex per site. Predicted values are obtained by inverting the models (i.e., sapwood area increments as a function of foliage biomass) and summing the increments.

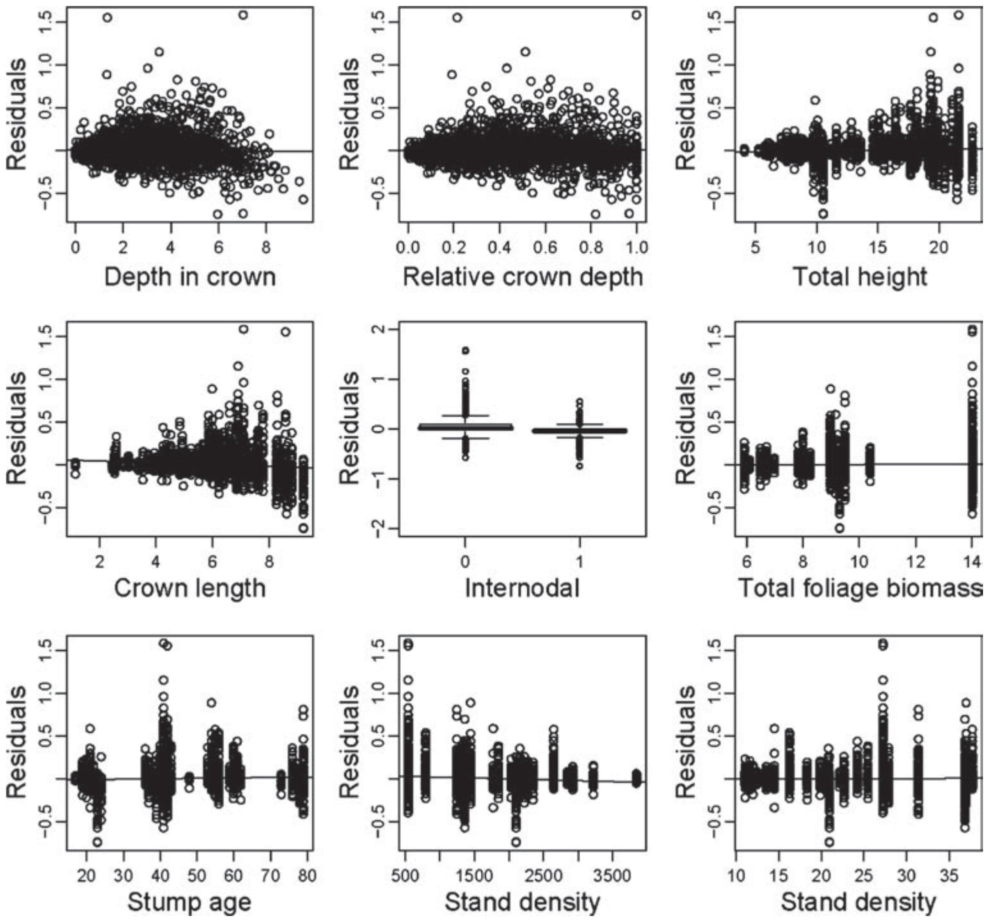

Figure 2. Residuals of the best model.

height) and whorl level variables (depth in crown, whorl type: nodal/internodal) do not show important trends within the residuals.

Model sensitivity analysis shows that the pipe model ratio is dependent on the foliage biomass distribution, with all the other factors kept constant (Figure 3), where the $W^f$ to $A^s$ ratio is proportional to the amount of foliage biomass that is present at the bottom of the crown. In other words, according to the model, trees that have the majority of their foliage near the crown base will have less sapwood area when compared with trees that have their foliage biomass near the top of the tree.

## Discussion

At first glance, the pipe model seems to adequately describe the changes in foliage biomass for a given sapwood increment in jack pine crowns. Upon more detailed inspection, important deviations from the pipe model appear. Other factors such as whorl position within the crown improve the predictions of the pipe model. The trends with respect to whorl position are similar to those presented by Berninger and Nikinmaa (1994) and Mäkelä and Vanninen (2001).

The different models give similar fit statistics because several of the explanatory variables are closely related. Figure 1, however, shows that the non-linear model has more realistic behaviour: it is able to predict the peak in the foliage biomass-to-stem area ratio in the upper crown. By using different foliage biomass distributions which represent tree social status and stand conditions (Schneider et al. 2010), it can reproduce observed foliage biomass to sapwood area changes in jack pine (Schneider et al. 2008). Moreover, such changes are also observed for Scots pine (Berninger et al. 2005).

We first thought that differences in leaf-specific transpiration rates were responsible for the reduction in foliage biomass to sapwood area ratios with distance from stem apex. Crowns are subject to large gradients of shading. Foliage at the top of the tree will have higher photosynthetic output per leaf area than that at crown base and have, therefore, higher requirements in terms of water to be transpired. This is particularly true since pine canopies are well coupled to the atmosphere. Also, gradients in water vapour pressure deficit will be small compared with gradients in light (Stewart 1988). This does not, however, explain that foliage mass per change of stem sapwood area

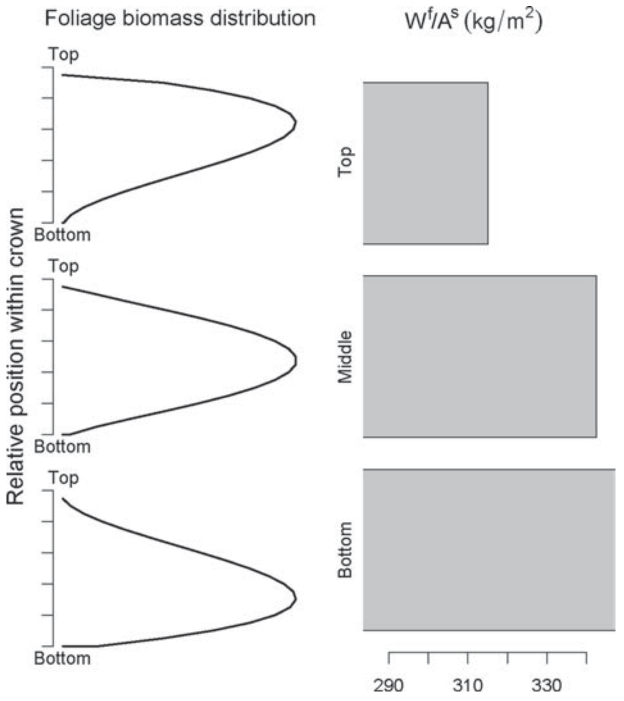

Figure 3. Influence of foliage biomass distribution on the pipe model ratio at the crown base ratio. Foliage biomass is estimated through a beta distribution (shown on the left) and used with the summation to crown base of the inverted Model 3.

increases in the lower parts of the crown, but would lead to the opposite prediction.

Moreover, potential changes in specific conductivity of the sapwood along the stem might explain the presented results (Spicer and Gartner 2001): specific conductivity usually increases from pith to bark and reaches a maximum at crown base. Hydraulic conductivity of branches is much lower than that of the stem, where hydraulic segmentation may lead to lower water potentials in the branches of the lower crown (e.g., Zimmermann 1978, Joyce and Steiner 1995). Altogether, it seems that changes in leaf-specific transpiration rates cannot be used solely to explain the observed deviations from the pipe model theory.

We hypothesize that our results may be explained by differences between the turnover rates of sapwood and foliage. The non-linear relationship and the lower foliage mass-to-sapwood area ratios in the lower crown could indicate that heartwood is produced in the larger and older branches. Branch junctions are usually less efficient than they should be according to hydraulic theories (Schulte and Brooks 2003). Moreover, the need to reconnect foliage to older sapwood in the lower crown (Maton and Gartner 2005) could increase the branch/stem junction inefficiency. Experimentally, sapwood turnover is very hard to measure and few theories can explain it. Process-based modellers usually predict that sapwood turnover is linked to crown progression or foliage shedding (Hari et al. 1985, Sievänen et al. 1997). There is also evidence that links sapwood turnover to branch age or to mechanical stress (Stokes and Berthier 2000). Simulation methods have been used to verify whether sapwood senescence is either foliage controlled or age induced (Sievänen et al. 1997). Foliage-controlled senescence fared only slightly better than the age-induced alternative, when simulation results were compared with field data. Nevertheless, the increase in sapwood area by a whorl close to the crown base will be higher than for a whorl with the same amount of foliage biomass near the tree top, which favours hypotheses based on sapwood senescence.

The pipe model theory is based on used and disused pipes (Shinozaki et al. 1964*a*), and is often interpreted by sapwood and heartwood area (Whitehead 1978). This interpretation leads to differences in observed and simulated sapwood areas (Mäkelä 2002). Moreover, modelling approaches need to integrate turnover and/or reuse rates to translate the static pipe model theory to a dynamic growth model (Valentine 2001). The observed non-linearity might be explained by slower turnover rates, i.e., shed foliage does not directly translate into sapwood senescence. In other words, there is a substantial lag between the point in time when foliage dies and heartwood formation. This seems to be especially true when the foliage biomass is concentrated at the top of the stem, i.e., when there is high foliage shedding towards the crown base.

It is noteworthy to add that there are various definitions of sapwood in the literature and that these can have important differences (Rust 1999). The definition we used, based on light transmission in thin sawn stem discs, is probably relatively close to a hydraulic definition of sapwood, but does not provide information on changes in hydraulic conductivity between tree rings.

Some evidence points to inefficient tree design when hydraulic theories are used (Farnsworth and Van Gardingen 1995, Taneda and Tateno 2004), while other studies have shown that the pipe model theory can be used to adequately predict stem taper (Mäkelä 2002). This shows that the tradeoffs between hydraulic and mechanical design of trees are modulated by the turnover rates of sapwood. Moreover, the results show that the linearity of the relationship between sapwood area and foliage biomass of the pipe model theory is not necessarily valid. The non-linear model predicts that less foliage is needed for changes in sapwood area increments. From a biological stand point, stem sapwood would rapidly change into heartwood when foliage is shed from a branch for whorls which are at the base of the crown.

Although the non-linear form is statistically better, the pipe model still offers a very good approximation of the sapwood area when expressed as a function of foliage biomass. The evidence points to the role of sapwood turnover rates in determining the sapwood area of a whorl. While differences in hydraulic conductivity and transpiration of foliage have received much attention (e.g., Mencuccini and Grace 1996), our knowledge of the mechanisms that lead to changes from sapwood to heartwood are not well understood. A pipe model that does not allow for the reuse of old sapwood by new foliage presumes identical turnover rates of foliage and sapwood. As pointed out by Valentine (2001), however, the pipe model does accommodate differing turnover rates. To wit, one can think of new foliage attaching to the sapwood pipes that elongate through terminal buds, so different rates of sapwood and foliage turnover—as indicated by more annual rings of sapwood than annual cohorts of foliage—neither negate the pipe model nor render it inaccurate.

Our data indicate that turnover rates of foliage and sapwood are far from identical and have to be taken into account when modelling the tree structure in conifers. The fact that the turnover rates are different does not necessarily mean that the pipe model theory does not hold exactly, as suggested by Valentine (2001). The conductivity profile from pith to bark of the stem could probably be used to extend the pipe model theory from the theoretical view of used pipes to sapwood areas which can be measured, as suggested by Mäkelä (2002).

In this article, we describe the pipe model in terms of increments of foliage mass and sapwood area throughout the stem. This approach was chosen to better understand the allocation to and taper of sapwood within the crown. In physiological terms, we assume that a change in sapwood area from one whorl to the next is related to the foliage mass of that whorl. Since most of the wood in the crown is sapwood, the changes in sapwood area are mostly caused by the increase in the number of sapwood rings when going down the crown. Our formulation of the pipe model is distinct from the 'classical pipe model theory' (Shinozaki et al. 1964*a*) (which uses a theoretical used pipe area and total leaf biomass from stem apex) and from the approach of Kershaw and Maguire (2000) (which uses sapwood area and foliage area increments). These different approaches to modify the pipe model are discussed in Valentine (2001) and Kershaw and McGuire (2001). As can be seen, there is no consensus on how to modify the pipe model theory for within-tree variations or to link the pipe model. However, two recent publications support our model based on changes in foliage biomass as a function of sapwood area. Fiora and Cescatti (2008) show that tree pruning reduces sapflow in the inner part of the stem, suggesting that the sapflow of lower canopy branches occurs preferentially in the inner sapwood. Domec et al. (2006) demonstrate that low sapwood conductivity in the radial direction creates high pressure gradients in the sapwood of trees. Finally, according to Maton and Gartner (2005), new foliage can reconnect itself to older sapwood. Altogether, these publications indicate that our approach might be physiologically justified. Nevertheless, further work would be needed to determine the exact reasons for the differences between the active pipes of the pipe model theory and observed sapwood area in the stem.

## Acknowledgments

The authors would like to acknowledge the support of Robert Allard, Steve D'eon, Gestion foretière du Saint Maurice Inc. and the Petawawa Research Forest. Finally, reviews, editorial comments and suggestions of Pamela Cheers, Mathieu Fortin, Harry Valentine and the two anonymous reviewers were much appreciated.

## Funding

The authors would like to thank the Fonds québécois pour la recherche sur la nature et les technologies and the NSERC Strategic Network on forest management for value-added products for financial support.

## References

Berninger, F. and E. Nikinmaa. 1994. Foliage area-sapwood area relationships of Scots pine (*Pinus sylvestris*) trees in different climates. Can. J. For. Res. 24:2263–2268.

Berninger, F., L. Coll, P. Vanninen, A. Mäkelä, S. Palmroth and E. Nikinmaa. 2005. Effects of tree size and position on pipe model ratios in Scots pine. Can. J. For. Res. 35:1294–1304.

Coyea, M.R. and H.A. Margolis. 1992. Factors affecting the relationship between sapwood area and leaf area of balsam fir. Can. J. For. Res, 22:1684–1693.

Domec, J.-C., B. Lachenbruch, and F.C. Meinzer. 2006. Bordered pit structure and function determine spatial patterns of air-seeding thresholds in xylem of Douglas-fir (*Pseudotsuga menziesii*; Pinaceae) trees. Am. J. Bot. 93:1588–1600.

Farnsworth, K.D. and P.R. van Gardingen. 1995. Allometric analysis of Sitka spruce branches: mechanical versus hydraulic design principles. Trees 10:1–12.

Fiora, A. and A. Cescatti. 2008. Vertical foliage distribution determines the radial pattern of sap flux density in *Picea abies*. Tree Physiol. 28:1317–1323.

Gilmore, D.W. and R.S. Seymour. 2004. Foliage-sapwood area equations for balsam fir require local validation. For. Sci. 50:566–570.

Hari, P., L. Kaipiainen, E. Korpilahti, A. Mäkelä, T. Nilsson, P. Oker-Blom, J. Ross and R. Salminen. 1985. Structure, radiation and photosynthetic production in coniferous stands. University of Helsinki, Department of Silviculture, Research Notes No. 54, 1–233.

Joyce, B.J. and Steiner, K.C. 1995. Systematic variation in xylem hydraulic capacity within the crown of white ash (*Fraxinus americana*). Tree Physiol. 15:649–656.

Kantola, A. and A. Mäkelä. 2004. Crown development in Norway spruce [*Picea abies* (L.) Karst.]. Trees 18:408–421.

Kershaw, J.A. 2001. Reply. Influence of vertical foliage structure on the distribution of stem cross-sectional area increment in western hemlock and balsam fir. For. Sci. 47:117–118.

Kershaw, J.A. and D.A. Maguire. 2000. Influence of vertical foliage structure on the distribution of stem cross-sectional area increment in western hemlock and balsam fir. For. Sci. 46:86–94.

Le Roux, X., A. Lacointe, A. Escobar-Gutiérrez and S. Le Dizès. 2001. Carbon-based models of individual tree growth: a critical appraisal. Ann. For. Sci. 58:469–506.

Long, J.N. and F.W. Smith. 1988. Leaf area–sapwood area relations in lodgepole pine as influenced by stand density and site index. Can. J. For. Res. 18:247–250.

Magnani, F., M. Mencuccini, and J. Grace. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant Cell Environ. 23:251–263.

Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. For. Sci. 43:7–24.

Mäkelä, A. 2002. Derivation of stem taper from the pipe theory in a carbon balance framework. Tree Physiol. 22:891–905.

Mäkelä, A. and P. Vanninen. 2001. Vertical structure of Scots pine crowns in different age and size classes. Trees 15:385–392.

Mäkelä, A., R. Sievänen, M. Lindner and P. Lasch. 2000. Application of volume growth and survival graphs in the evaluation of four process-based forest growth models. Tree Physiol. 20:347–355.

Maton, C. and B.L. Gartner. 2005. Do gymnosperm needles pull water through the xylem produced in the same year as the needle? Am. J. Bot. 92:123–131.

McDowell, N., H. Barnard, B. Bond, et al. 2002. The relationship between tree height and leaf area: sapwood area ratio. Oecologia 132:12–20.

Mencuccini, M. and J. Grace. 1996. Developmental patterns of aboveground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. Plant Cell Environ. 19:939–948.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. http://www.r-project.org/ (10 July 2009, date last accessed).

Rust, S. 1999. Comparison of three methods for determining the conductive xylem area of Scots pine (*Pinus sylvestris*). Forestry 72:103–108.

Schneider, R., F. Berninger, C.H. Ung, P.Y. Bernier, D.E. Swift, and S.Y. Zhang. 2008. Calibrating jack pine allometric relationships with simultaneous regressions. Can. J. For. Res., 38:2566–2578.

Schneider, R., M. Fortin, F. Berninger, C.H. Ung, D.E. Swift, and S.Y. Zhang. 2010 Modeling jack pine (*Pinus banksiana*) foliage density distribution. For. Sci. (in press).

Schulte, P.J. and J.R. Brooks. 2003. Branch junctions and the flow of water through xylem in Douglas-fir and ponderosa pine stems. J. Exp. Bot. 387:1597–1605.

Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964*a*. A quantitative analysis of plant form-the pipe model theory. I. Basic analyses. Jpn. Ecol. 14:97–105.

Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964*b*. A quantitative analysis of plant form- the pipe model theory: II. Further evidence of the theory and its application in forest ecology. Jpn. Ecol. 14:133–139.

Sievänen, R., E. Nikinmaa, and J. Perttunen. 1997. Evaluation of importance of sapwood senescence on tree growth using the model LIGNUM. Silva Fenn. 31:329–340.

Spicer, R. and B.L. Gartner. 2001. The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. Trees 15:222–229.

Steward, J.B. 1988. Modelling surface conductance of pine forests. Agri. For. Meteorol. 43:19–35.

Stokes, A. and S. Berthier. 2000. Irregular heartwood formation in *Pinus pinaster* Ait. is related to eccentric, radial, stem growth. For. Ecol. Manag. 135:115–121.

Taneda, H. and Tateno, M. 2004. The criteria for biomass partitioning of the current shoot: water transport versus mechanical support 1. Am. J. Bot. 91:1949–1959.

Valentine, H.T. 1988. A carbon-balance model of stand growth: a derivation employing pipe-model theory and the self-thinning rule. Ann. Bot. 62:389–396.

Valentine, H.T. 2001. Influence of vertical foliage structure on the distribution of stem cross-sectional area increment in western hemlock and balsam fir. For. Sci. 47:115–116.

Valentine, H.T. and A. Mäkelä. 2005. Bridging process-based and empirical approaches to modeling tree growth. Tree Physiol. 25:769–779.

Whitehead, D. 1978. Estimation of foliage area from sapwoodbasal area in Scots pine. Forestry 51:137–149.

Zimmermann, M.H. 1978. Hydraulic architecture of some diffuse porous trees. Can. J. Bot. 56:2286–2295.