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RESEARCH ARTICLE

Pipe-model ratio distributions and branch foliage biomass: differences between two sympatric spruce species

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The foliage biomass–sapwood relationship (the pipe model) is critical for tree growth and is used in tree growth models for understanding the implications of this structural relationship on the allocation of resources. In this research, we compared this relationship for two commercially important and sympatric species, black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss). At locations in eastern Canada, 57 black and 50 white spruce trees were destructively sampled to obtain foliage biomass, crown structure, and tree stem measures. Using a model-based approach, we compared foliage biomass–branch basal area and foliage biomass–sapwood relationships at the tree and disk (i.e. along the tree stem) levels (i.e. pipe-model ratios) between these two species. We found that (i) branch foliage biomass–branch basal area was greater for black spruce than white spruce and (ii) pipe-model ratios along the tree stem given tree size were greater for black spruce than for white spruce. We attributed these differences to: (i) greater shade tolerance and leaf longevity of black spruce; (ii) slower growth rates of black spruce; and (iii) differing hydraulic strategies and mechanical requirements.

Keywords: boreal forest; pipe-model theory; nonlinear mixed-effects models; tree allometry; tree growth strategies; *Picea mariana*; *Picea glauca*

Introduction

Trees are the tallest terrestrial plants and main stems must provide sufficient mechanical support for branches and foliage (King 1981). The amount of foliage biomass is dependent upon leaf architecture, leaf longevity, growing space and light, as well as water and nutrient availability (Reich et al. 1995; Landsberg & Sands 2011). Furthermore, the distribution and efficiency of foliage within a tree crown dictate the capture of solar energy used for photosynthesis, thereby affecting tree growth and the ability of trees to respond to changes in competition and environmental conditions. The transport of water and nutrients to the foliage is accomplished through the sapwood, resulting in a complex allometric foliage biomass–sapwood relationship.

Shinozaki et al. (1964a, 1964b) were perhaps the first researchers to report on the relationships between foliage biomass and branch/stem cross-sectional area. They termed the allometric dependence of tree components the “pipe-model theory”. West et al. (1997) stated that sapwood within the tree stem and branches functions as an efficiently designed and predictable circulation system (i.e. a “pipe”), transporting water and nutrients from the roots to the leaves (West et al. 1997). They

further stated that this relationship is a “physiologically based allometric-scaling law”. Many researchers have used these concepts to model relationships between total leaf area or foliage biomass and stem or sapwood area at breast height (i.e. 1.3 m above ground) (e.g. Grier & Waring 1974; Whitehead 1978; Kaufmann & Troendle 1981; Albrektson 1984; Bond-Lamberty et al. 2002) and other locations within and below the living crown (e.g. Waring et al. 1982; Dean & Long 1986; Vanninen et al. 1996; Mäkelä & Vaninen 2001; Kantola & Mäkelä 2004; Stancioiu & O’Hara 2005).

The relationship between total leaf area or foliage biomass and stem or sapwood cross-sectional area was originally thought to be relatively proportional (Shinozaki et al. 1964a, 1964b). However, many researchers have found that the relationship may not be strictly proportional along the tree stem (e.g. Stancioiu & O’Hara 2005) and nonlinear models may be needed to model relationships (e.g. Kantola & Mäkelä 2004). Differences between species and also over differing stand conditions have also been found. For example, in Scots pine (*Pinus sylvestris* L.), pipe-model ratios (i.e. total foliage biomass relative to sapwood area at the crown base in this case) vary with climate (Berninger & Nikinmaa 1994), site index

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(SI, Vanninen et al. 1996), and the tree's social position (Mäkelä & Vanninen 1998).

Because of the importance of this foliage biomass–sapwood relationship to tree function, pipe-model theory has been used as a basis for allometric relationships and for tree growth predictions. As examples, this relationship has been used to predict foliage biomass by Mailly (2000) and also for carbon allocation in process-based growth models (e.g. West 1993; Mäkelä 1997; Valentine & Mäkelä 2005; Ogle & Pacala 2009).

In this research, we examined the foliage biomass–sapwood relationships of two sympatric species, black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss). These species are important commercial species that share a similar and extensive geographical distribution within the boreal forest of North America (Burns & Honkala 1990). They are closely related to Norway spruce (*Picea abies* (L.) Karsten), that occurs in the boreal forests of Europe and Russia, and also to Engelmann spruce (*Picea engelmanni* Parry), that occurs in higher elevation subalpine forests of western North America (Burns & Honkala 1990). Although the two study spruce species often occur as mixtures in the same stand, black spruce better colonizes very wet sites, whereas white spruce is more often found on richer sites (Larsen 1980). Further, although the two species appear quite similar morphologically (Marie-Victorin 1964), black spruce is considered more shade tolerant than white spruce (Burns & Honkala 1990). On similar sites, growth rates differ (Pothier & Savard 1998; Thiffault et al. 2003). In terms of crown architecture, white spruce trees have wider crowns given the same growing conditions (Power et al. 2012) but smaller foliage biomass given the same diameter outside bark at breast height (DBH) and height (Power et al. 2014). Wood properties also differ between the two species. Black spruce has higher wood density and Young's modulus, a measure of the stiffness of a material, than white spruce (Jessome 1977). Based on these previously noted differences, we hypothesized that we would find differences in the foliage biomass–sapwood relationships at the branch, tree, and disk (i.e. along the tree stem) levels. We used a model-based approach to examine these relationships while controlling for tree- and plot-level attributes.

Materials and methods

Plot and tree measures

For this study, foliage biomass and sapwood measures were obtained for 57 black spruce and 50 white spruce trees following sampling and measurement protocols used in similar studies for other species (e.g. Waring et al. 1982; Kantola & Mäkelä 2004). The white spruce trees were obtained from the Petawawa Research Forest in Ontario, Canada, whereas the black spruce trees were

collected in the region of Lac-St-Jean and Témiscamingue in the province of Québec, Canada. Several stands were included at each location and one sample plot was established in each stand (Table 1). Sampling at the various sites took place during the growing season (May–September) from 2008 to 2010.

White spruce trees from Ontario were sampled from existing plantations that received spacing or thinning treatments; however, the last thinning was conducted in 1982 and growth would be expected to be similar to that of naturally regenerated, white spruce-dominated stands. Sample trees were taken inside or from the periphery of existing permanent sample plots (PSPs) ranging in size from 0.03 to 0.08 ha. For all live trees ≥ 1.1 cm diameter outside bark (DBH; 1.3 m above ground) in the PSP, species was recorded and DBH was re-measured; heights of previously measured trees were also re-measured. The measures of all live trees located in each PSP were used to calculate the plot-level variables as later described. Stand age was based on the plantation age adjusted to 1 m above ground (i.e. circa age at breast height), using adjustments provided in Pothier and Savard (1998). For each plot, all trees with undamaged crowns were divided into small, medium, and large DBH classes, where class limits varied by plot. One small, two medium, and two large DBH trees were randomly selected for detailed crown measures, resulting in four sample trees per plot.

Black spruce trees from Québec were selected from stands naturally regenerated following a regeneration cut (i.e. clear-felling) or a stand-replacing fire. Stands of different ages, densities (i.e. trees per hectare) and site indices were selected using forest stand maps. For each selected stand, a variable-radius plot (Husch et al. 1982) with a basal area factor of $1 \text{ m}^2 \text{ ha}^{-1}$ was established at a location previously determined on the forest map. Species was recorded and DBH was measured for all live trees ≥ 1.1 cm DBH. Height was measured for 20–90 trees across the range of DBHs. These measures were used to calculate the plot-level variables. Age at 1 m above ground for three dominant black spruce trees with undamaged crowns was determined using increment cores. The mean age of the three dominant trees was used as stand age. As with white spruce, trees with undamaged crowns in the plot were divided into small, medium, and large DBH classes. For each plot, one sample tree was selected for detailed crown measures from each DBH class, resulting in three sample trees per plot.

All selected sample trees were felled. The total height and height to live crown were measured after felling. Height to live crown was considered to be the height from ground to the lowest branch that presented green foliage and above which all the whorls included at least one living branch. The vertical position of each live branch along the tree stem was recorded, along with the measured branch basal diameter and branch insertion angle.

Table 1. Characteristics and locations of the sample sites.

| Characteristics | Petawawa, Ontario | Lac-St-Jean, Quebec | Témiscamingue, Quebec |
|-----------------------------------|-------------------|---------------------|-----------------------|
| Location | 45°59'N, 77°25'W | 49°00'N, 72°40'W | 46°45'N, 78°20'W |
| Species | White spruce | Black spruce | Black spruce |
| Mean Annual Temperature (°C) | 4.3 | 1.7 | 2.7 |
| Mean Annual Precipitation (mm) | 853 | 937 | 887 |
| Number of plots | 12 | 12 | 7 |
| Age (year) | 40–75 | 30–120 | 30–120 |
| Density (stems ha ⁻¹) | 130–2500 | 900–11,300 | 1500–4500 |
| Number of plots | 12 | 12 | 7 |
| Number of Sample Trees | 56 | 36 | 21 |

The crown of each felled tree was then divided into five sections of equal lengths. In each section, one branch was randomly selected for foliage biomass measurement. Sampled branches were placed into paper bags and transported to the laboratory. After drying at room temperature for several weeks, foliage was removed from each sample branch and oven-dried at 60°C for 24 hours. After being dried, the foliage was weighed to the nearest 0.01 g.

Following selection of branches for biomass measurement, 1–2 cm long segments of each sample tree stem (hereafter termed “disks”) were extracted for a number of points along the stem, specifically: at stump height (0.3 m above ground); at crown base; at 1 m intervals between the crown base to the tree stem apex; and at several other positions between the crown base and the stump height (intervals less than 2.5 m) (Figure 1). Immediately after extracting each disk, the sapwood was delimited from the heartwood using the light transmission

technique (Grier & Waring 1974) on the side of the disk closest to the tree apex. Diameter inside bark and heartwood diameter were each measured on two perpendicular axes.

Plot-level variables

Sample data were compiled to obtain plot-level variables (Table 2). First, unmeasured heights of trees in each plot were imputed using plot-specific models described in Power et al. (2012). Once all unmeasured heights were imputed, the dominant height (DH, m) for each plot was calculated by averaging the height of the 100 largest trees per hectare. Quadratic mean DBH (QDBH, cm), density (Dens, stems ha⁻¹), and basal area (G, m² ha⁻¹) were calculated using only the trees that comprised the main cohort of the stand. We excluded saplings that belonged to the regeneration cohort except for three stands of black spruce 20–30 years old, where the saplings were considered to be part of the main cohort. SI (DH at 50 years total age) was calculated using the SI equations developed by Pothier & Savard (1998) with DH and stand age as input variables.

Calculations of tree- and disk-level variables

For each stem section on sampled trees, geometric means of the diameter inside bark measures and of the heartwood diameter measures were used to calculate the inside bark disk area, heartwood area and, by subtraction, sapwood area. These were linked with the position along the stem (i.e. height from ground).

Total and heartwood volumes were calculated for each tree by summing volumes for each stem section delimited by two consecutive disks. First, the volume of the stump section was calculated assuming a cylinder using the stump disk and the distance from the disk to the ground (i.e. 0.3 m). Following Hush et al. (1982), the volume of the next stem section delimited by the stump disk and the next disk toward the tree apex was calculated assuming a frustum of neiloid. All other section volumes were calculated assuming a paraboloid frustum shape and the adapted Smalian's equation (Hush et al. 1982), with

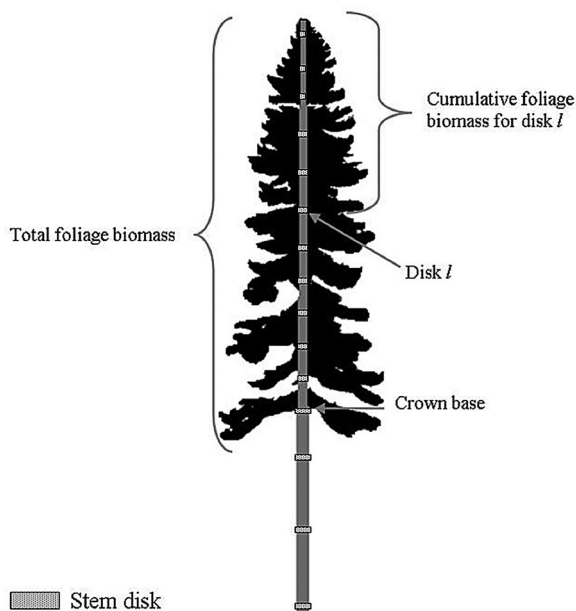


Figure 1. Sample tree representation with disks along the stem, and total versus cumulative foliage biomass.

Table 2. Summary statistics for plot-, tree- and branch-level variables (50 white spruce trees in 12 plots, 57 black spruce trees in 19 plots).

| Variable | Black spruce | | | | White spruce | | | |
|--|--------------|-------|--------|-----------|--------------|-------|------|-----------|
| | Min. | Mean | Max. | Std. Dev. | Min. | Mean | Max. | Std. Dev. |
| Branch basal area (mm ²), Gb | 0.8 | 130.0 | 615.0 | 115.7 | 3.1 | 428.8 | 2124 | 393.1 |
| Diameter at breast height (cm), DBH | 5.4 | 14 | 26.8 | 5.6 | 10.8 | 27.7 | 42.2 | 7.5 |
| Diameter at breast height/total height, <i>D/H</i> | 0.64 | 1.05 | 1.48 | 0.17 | 0.79 | 1.44 | 2.20 | 0.31 |
| Total tree height (m), Ht | 5.5 | 13.2 | 20.8 | 4.4 | 13.3 | 19.3 | 26.9 | 4.0 |
| Dominant Height (m), DH | 9.2 | 15.6 | 20.5 | 3.6 | 15.6 | 21.9 | 26.2 | 4.0 |
| Stand age (age at 1 m height), | 20 | 70 | 120 | 28.4 | 43 | 61 | 71 | 13 |
| Quadratic mean DBH (cm), QDBH | 5.8 | 11.4 | 26.8 | 3.7 | 15.4 | 26.8 | 35.2 | 5.8 |
| Stand basal area (m ² ha ⁻¹), G | 10.0 | 29.8 | 47 | 9.8 | 13.2 | 24.3 | 68.2 | 12.3 |
| Site index (height in m at 50 year), SI | 9.5 | 14.6 | 17.7 | 2.1 | 15.8 | 19.53 | 22.1 | 2.2 |
| Stand density (stems ha ⁻¹), Dens | 921 | 3697 | 11,263 | 2478 | 136 | 661 | 3657 | 852 |

Notes: NA, not applicable; Min., minimum; Max., maximum; St. Dev., standard deviation.

the exception of the topmost segment for which volume was calculated assuming a conical shape. The sapwood volume of the tree was calculated by subtracting the heartwood volume from the total volume of the tree, and this was then divided by the tree height, giving a proxy for the mean sapwood surface area, hereafter termed “mean sapwood area”.

Branch-level foliage biomass–sapwood relationship

To examine the foliage biomass–sapwood relationship at the branch level, we compared branch foliage biomass (Wfb) versus branch basal area (Gb) relationships between the two species while controlling for tree- and plot-level variables that affect branch length and foliage density. The branch basal area was used rather than branch sapwood area, since branch basal area heartwood in these two species is often very small. First, a simple nonlinear power model was selected as the base model, following Berninger & Nikinmaa (1994). Since the relative position of the branch inside the crown (*Cd*) is expected to relate to both branch basal area and branch foliage biomass, *Cd* was added to the model, along with the interaction between *Gb* and *Cd*, where *Cd* was defined as being 0 at the top of the tree and 1 at the crown base. Finally, the hierarchy of errors (i.e. random effects) at the site (i.e. stand), plot, tree, and branch levels was added, resulting in the following nonlinear mixed-effects model for branch foliage biomass:

$$\begin{aligned} \text{Wfb}_{ijkrl} = & \beta_1 \text{Gb}_{ijkrl}^{\beta_2} + \beta_3 \text{Cd}_{ijkrl} + \beta_4 \text{Gb}_{ijkrl} \text{Cd}_{ijkrl} \\ & + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{r(ijk)}, \end{aligned} \quad (1)$$

where β_1 to β_4 are fixed-effects parameters; *ijkrl* are subscripts for branch *r* in tree *k* in plot *j* in site *i*; and ε represents the error terms of the model at the site (ε_i), plot within site ($\varepsilon_{j(i)}$), tree within plot ($\varepsilon_{k(ij)}$) and branch within tree ($\varepsilon_{r(ijk)}$) levels.

The branch biomass model was fitted using the version 2.13.2 of the nlme package (Pinheiro et al. 2012) implemented in the software R version 2.14.1 (R Development Core Team 2011) and using data on sampled branches for both species combined. All random effects were assumed to follow normal distributions. The hierarchy of errors at the site, plot, tree, and branch levels accounted for common correlations of plots within sites, trees within plots, and branches within trees, and also heteroscedasticity resulting from this hierarchy. However, the level-1 errors (i.e. branch-level errors, often termed “white-noise” errors) were checked for homogeneity of variances using residual plots and for normality using normality plots. Where heteroscedasticity of the level-1 errors was detected, a function to model the variance of the level-1 errors was added to the model (Pinheiro & Bates 2000).

Once this base model was fitted (Equation (1)), the residuals combined over all levels were then plotted against plot- and tree-level explanatory variables that represented growth conditions (Table 2). The variables that showed relationships with the residuals were selected as candidate explanatory variables, and these were then added individually or in combination, in additive or multiplicative form to the base model. Likelihood ratio tests were performed using the augmented versus the base models to decide whether to retain or reject the additional explanatory variables using $\alpha = 0.05$. A number of candidate models resulted using this process; of these, the model with the lowest AIC was selected as the branch foliage biomass model. Also, 10-fold cross-validation was performed on the selected model and used to obtain root mean squared prediction error (RMSPE) as a measure of model accuracy calculated as

$$\text{RMSPE} = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n - p}}, \quad (2)$$

where y_i and \hat{y}_i are the observed and estimated values, respectively, for i th observation when excluded from the model fit, n is the number of observations, and p is the number of parameters in the model.

To test for differences between species, the selected branch foliage biomass model was altered by using a species-specific dummy variable (Dm equal 0 for black spruce and 1 for white spruce) to alter each fixed-effects parameter. This species-specific model was then fitted, again using the pooled-species data, and compared to the model without the species dummy variable using a likelihood ratio test ($\alpha = 0.05$). If differences between the two species were detected, but one or more alterations were not significant, the alteration with the highest p -value was removed and the model was fit again. Using this iterative process, a final species-specific branch foliage biomass model was obtained. The branch foliage biomass versus branch basal area relationship was then examined using the final model. In particular, predicted population-averaged (i.e. using fixed-effects only) branch foliage biomass versus branch basal area for different crown depths was graphed and compared between the two species.

As well as using the branch foliage model to examine species differences, the fitted models were used to estimate the foliage biomass on non-sampled branches of each tree, again following the approaches used in studies of other species. However, for this purpose, subject-specific predictions at the tree level were obtained by adding the estimated random effects at the site, plot, and tree levels to the population-averaged predicted values. From this, total foliage biomass for the entire crown was calculated, along with foliage biomass above all vertical positions on the tree stem at which the sapwood area had been measured. These biomass values were used in the subsequent pipe-model ratio explorations.

Tree-level pipe-model ratios

We examined how the foliage biomass–sapwood relationship varies with tree- and stand-level variables and with species. For this purpose, the pipe-model ratio at the tree level (Rt) was defined as total foliage biomass divided by the mean sapwood area. First, Rt was plotted against the plot- and tree-level variables (Table 2) as an aid for selecting candidate explanatory variables. Then, each candidate variable was entered into a basic power function:

$$Rt_{ijk} = \beta_1 x^{\beta_2} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}, \quad (3)$$

where x is an explanatory variable at the plot or tree level; β_1 and β_2 are fixed-effects parameters; ijk are the subscripts for tree k in plot j in site i ; and ε represents the error terms of the model at the site (ε_i), plot within site ($\varepsilon_{j(i)}$) and trees within plot ($\varepsilon_{k(ij)}$) levels.

Assumptions for random-effects errors of Equation (3) were similar to those for the branch foliage biomass model, except that the level-1 errors were at the tree level. Using the nlme package of R, v.2.14.1 software (Pinheiro et al. 2012) and data pooled for both species, models using each candidate variable were fitted and the variable that produced the lowest model AIC was retained as the base model. Following the same process as for the branch-level foliage biomass model: (i) additional explanatory variables were added to the base model and a model was selected; (ii) this model was altered using the species-specific dummy variable and compared to the model without species to test species differences; and (iii) the species-specific model was simplified, if possible. The final tree-level pipe ratio model was then used to graphically compare the pipe-model ratio between the two species given similar tree- and stand-level conditions.

Pipe-model ratios along the tree stem

To examine how the foliage biomass–sapwood relationship varies along the tree stem, first, the pipe-model ratio at a point on the tree stem (Rd) was defined as the cumulative foliage biomass between any position l on the stem and the apex of the tree divided by the sapwood area at position l (Figure 1). A similar modeling approach was used as for the pipe-model ratio at the tree level, starting with a basic power function fitted using candidate plot- and tree-level explanatory variables (Table 2) and the pooled data for both species. Since the cumulative foliage biomass is the same for all positions below the live crown, the base model was a segmented model joined at the base of the live crown. The random effects included errors at the four levels, namely the site, plot, tree, and position within tree levels. Following a similar process to select explanatory variables for both components of the segmented model, a model was selected for the pooled-species data. Each fixed-effects parameter of the segmented model was then modified using a dummy variable to represent black versus white spruce. Likelihood ratio tests were used to systematically remove any modifications that were not significant at $\alpha = 0.05$. All models were fitted using the nlme package of R, v.2.13.2 software (Pinheiro et al. 2012). The final model was used to test differences in pipe-model ratios along the tree stem for the two species, given similar tree- and stand-level variables.

Results

Branch-level foliage biomass – sapwood relationship

Using the modelling process as explained, no other candidate explanatory variables were added to the base branch foliage biomass–branch basal area model

(Equation (1)). The likelihood ratio test of the base model versus the base model altered using a dummy variable for species indicated significant differences between species (likelihood ratio test, p -value $< .01$). However, not all modifications of fixed-effects parameters were needed. Following further testing only the modification of the β_2 parameter of Equation (1) was retained, resulting in the following simplified species-specific model:

$$\begin{aligned} Wfb_{ijk} &= \beta_1 Gb_{ijk}^{(\beta_2 + \beta_5 Dm)} + \beta_3 Cd_{ijk} \\ &+ \beta_4 Gb_{ijk} Cd_{ijk} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} \\ &+ \varepsilon_{r(ijk)}, \end{aligned} \tag{4}$$

where Dm is a dummy variable for species (0 for black spruce and 1 for white spruce); β_1 – β_5 are fixed-effects parameters; and all other terms are as previously defined for Equation (1).

Estimated parameters for Equations (1) and (4) are given in Table 3. The log-likelihood for the model without species (Equation (1), $\log L = -2495$) was lower than for the species-specific model (Equation (4), $\log L = -2477$) with a likelihood ratio of 35.76 ($p < .0001$). The RMSPE values decreased from 64.8 g for Equation (1) to 63.9 g for Equation (4), further indicating an improvement using the species-specific parameters of Equation (4).

For both species, the foliage biomass per unit of branch basal area decreases from the top of the tree to the crown base except for the smaller branches (less than 5 mm diameter) (Figure 2). Using the fitted species-specific model, black spruce branches support a larger amount of foliage biomass for a given branch basal area, and these differences also increase with increasing branch basal area (Figure 2).

Tree-level pipe-model ratios

The final model for the tree-level pipe-model ratio included only DBH over height as an explanatory variable (Equation (5)). Adding in a species-specific dummy variable to alter the fixed-effects parameters resulted in a better model (likelihood ratio test, p -value $\leq .01$) indicating differences between species. However, as with the branch-level model, only one alteration (for β_1) was significantly different from 0 (Equation (6))

$$Rt_{ijk} = \beta_1 \left(\frac{D_{ijk+}}{H_{ijk}} \right)^{\beta_2} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}, \tag{5}$$

$$\begin{aligned} Rt_{ijk} &= (\beta_1 + \beta_3 Dm) \left(\frac{D_{ijk+}}{H_{ijk}} \right)^{\beta_2} + \varepsilon_i + \varepsilon_{j(i)} \\ &+ \varepsilon_{k(ij)}, \end{aligned} \tag{6}$$

where D/H is the ratio of DBH over height; Dm is a dummy variable for species with a value of (0 for black

Table 3. Parameter estimates for branch foliage biomass–branch basal area (Equations (1) and (3)), tree-level pipe-model ratio (Equations (4) and (5)), and disk-level pipe-model ratio (Equations (6) and (8) including (8a)).

| Model | Parameter estimate p -values | | | | | | | | Variance components | | | | |
|---------------|--------------------------------|--------------|----------------|---------------|---------------|--------------|--------------|---------------|---------------------|-----------------|-----------------|------------------------|-------|
| | β_1 | β_2 | β_3 | β_4 | β_5 | β_6 | β_7 | β_8 | σ^2 site | σ^2 plot | σ^2 tree | $\sigma^2 \varepsilon$ | RMSPE |
| Equation (1) | 0.695 < 0.01 | 0.941 < 0.01 | 3.828 0.30 | -0.266 < 0.01 | NA | NA | NA | NA | 0.0005 | 0.0479 | 31.074 | 1.077 | 64.8 |
| Equation (4) | 0.417 < 0.01 | 1.08 < 0.01 | 6.105 0.09 | -0.351 < 0.01 | 0.049 < 0.01 | NA | NA | NA | 0.0644 | < 0.0001 | 5.8783 | 1.0901 | 63.9 |
| Equation (5) | 138.9 < 0.01 | 0.551 < 0.01 | NA | NA | NA | NA | NA | NA | 2998 | 185.2 | NA | 307.6 | 71.0 |
| Equation (6) | 166.2 < 0.01 | 1.14 < 0.01 | -1116.9 < 0.01 | NA | NA | NA | NA | NA | 1246 | 177.9 | NA | 303.7 | 49.0 |
| Equation (7) | 44.823 < 0.01 | 0.575 < 0.01 | 0.072 < 0.01 | 2.150 < 0.01 | 106.61 < 0.01 | 1.058 < 0.01 | -0.055 0.22 | NA | 1507 | 320.6 | 270.9 | 141.6 | 62.7 |
| Equation (8a) | 37.617 0.02 | 0.433 < 0.01 | -0.027 0.523 | 2.925 < 0.01 | 0.213 < 0.01 | NA | NA | NA | NA | NA | NA | NA | NA |
| Equation (8) | 977.1 0.05 | 0.363 < 0.01 | -0.283 < 0.01 | 3.231 < 0.01 | -905.6 < 0.01 | 0.641 < 0.01 | 0.254 < 0.01 | -2.354 < 0.01 | 503.1 | 155.5 | 214.3 | 123.9 | 47.6 |

Notes: NA, not applicable; RMSPE, root mean squared prediction error based on prediction errors (10-fold cross-validation).

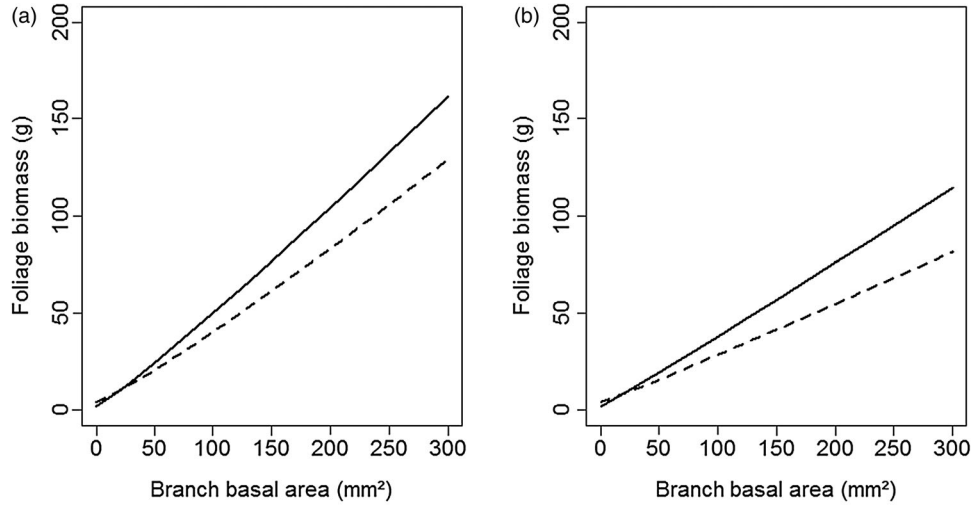


Figure 2. Black and white spruce foliage biomass versus branch basal area relationship for: (a) black spruce for relative crown depth of 0.33 (solid line) and 0.66 (dashed line) and (b) white spruce for relative crown depth of 0.33 (solid line) and 0.66 (dashed line).

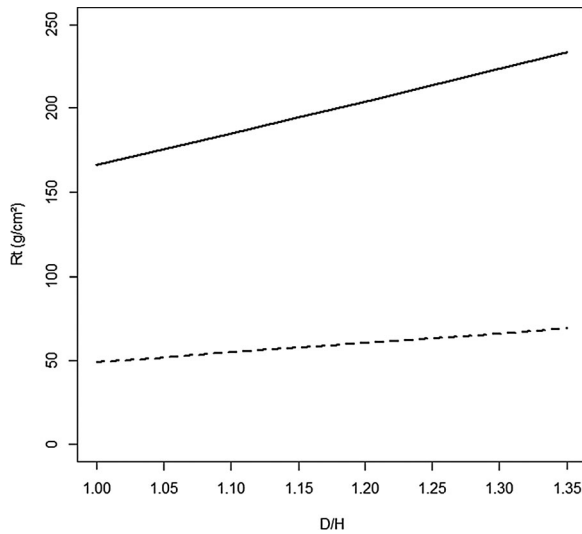


Figure 3. Tree-level pipe-model ratio (R_t) plotted against DBH over total height ratio (D/H) for black spruce (solid line) and white spruce (dashed line).

spruce and 1 for white spruce); β_1 to β_3 are fixed-effects parameters; and all other terms are as previously defined for Equation (3).

Parameter estimates for Equation (5) and (6) are given in Table 3. The log-likelihood for the pooled-species model (Equation (5)) was -773 , whereas the species-specific model (Equation (6)) had a higher log-likelihood of -765 . Moreover, the RMSPE values were 71.0 g/cm^2 for Equation (5) versus 49.0 g/cm^2 for Equation (6). Using Equation (6), R_t is higher for black spruce than for white spruce given the same tree attributes. Moreover, R_t increases faster with D/H for black spruce than for white spruce.

Pipe-model ratios along the tree stem

The final segmented model for pipe-model ratios along the tree stem was

$$\begin{aligned} Rd_{ijkl} = & \beta_1 Sd_{ijkl}^{\beta_2} \text{Dens}_{ij}^{\beta_3} + \beta_4 \text{DBH}_{ijk} \\ & + C(\beta_5 \text{Cd}_{ijkl}^{\beta_6} \text{Dens}_{ij}^{\beta_7}) + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} \\ & + \varepsilon_{l(ijk)}, \end{aligned} \quad (7)$$

where Dens is in stems per hectare; Sd the relative location below crown base with a value of 0 at the base of the tree up to 1 at and above crown base; C is a dummy variable equal to 0 (below crown base) or 1 (above crown base); Cd is the relative location within the living crown with a value of 0 below and at crown base up to 1 at tree stem apex; β_1 to β_7 are fixed-effects parameters; $ijkl$ are the subscripts for the position l in tree k in plot j in site i ; and ε represents the error terms of the model at the site (ε_i), plot within site ($\varepsilon_{j(i)}$), tree within plot ($\varepsilon_{k(ij)}$) and disks within trees ($\varepsilon_{l(ijk)}$) levels.

This model gave better results based on the log-likelihood than any other model tested. Further, since the foliage biomass is the same for all points below the live crown, this segmented model was considered biologically tractable. To examine differences between species, the selected segmented model was modified using the species-specific dummy variables to alter all fixed-effects parameters. However, not all alterations were significantly different from 0. The final species-specific segmented model was as follows:

$$\begin{aligned} Rd_{ijkl} = & (\beta_1 + \beta_5) Sd_{ijkl}^{(\beta_2 + \beta_6 \text{Dm})} \text{Dens}_{ijkl}^{(\beta_3 + \beta_7 \text{Dm})} \\ & + (\beta_4 + \beta_8 \text{Dm}) \text{DBH}_{ijk} + C(\delta a) \\ & + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{l(jik)}, \end{aligned} \quad (8)$$

where (8a) is $\beta_1 C d_{ijkl}^{(\beta_2 + \beta_4 Dm)} \text{Dens}_{ij}^{(\beta_3 + \beta_5 Dm)}$, Dm is a dummy variable for species (0 for black spruce and 1 for white spruce); β_1 to β_8 are fixed-effects parameters; and all other terms are as defined for Equation (7).

Parameter estimates for Equations (6) and (8) (including (8a)) are given in Table 3. The species-specific model (Equation (8), including (8a)) resulted in increased likelihood (−6317 versus −6432 for Equation (7)), and the likelihood ratio test indicated significant differences between black and white spruces (p -value < .01). Also, the RMSPE value was smaller for Equation (8) (47.6) than for Equation (7) (62.7) further indicating differences in Rd relationships between black and white spruces. Using the species-specific segmented model, the pipe-model ratios increase from the base of the tree to the crown base for both species (Figure 3). Also, the pipe-model ratios increase with DBH and decrease with stand density. However, the Rt values were larger for black spruce than for white spruce given the same DBH, stand density, and locations on the tree stem; the estimated parameter associated with stand density was nearly zero for white spruce. For locations within the crown, pipe-model ratios increase slightly from the crown base to the top of the tree for black spruce (Figure 3). For white spruce, the ratio also slightly increases from crown base to mid-crown but then rapidly increases from the mid-point of the crown to the top of the tree.

Discussion

Our results indicate that black spruce has more branch-level foliage biomass given the same branch basal area than white spruce. Moreover, black spruce tends to maintain higher pipe-model ratios (i.e. more foliage per unit sapwood area) along the tree stem than white spruce. These differences were consistent across the sampled growth conditions. Why do these differences occur? We propose here that the differences between these two sympatric species could be partly explained by the combination of differential adaptations of leaves to shading, growth rates, hydraulic support strategies, and mechanical support requirements.

As with many studies of allometric relationships within trees, sampling for our study was limited due to the extensive cost and destructive nature of foliage measures. However, we sampled trees from a range of site indices, densities, and stand ages. Further, we used a model-based approach to control for differences in tree and stand characteristics by including tree- and stand-level attributes as explanatory variables before adding species to the models. Moreover, our results were consistent with our understanding of the ecophysiology of these species and with prior research on other coniferous species in the northern hemisphere.

As noted earlier, black spruce is more shade tolerant than white spruce (Burns & Honkala 1990), resulting in a greater ability to regenerate and survive under lower light levels. Specifically, black spruce seedlings have been shown to have high stomatal conductance and higher specific leaf area showing better adaptation to shade than white spruce (Dang & Cheng 2004). Shade tolerance affects the distribution of the foliage inside the living crown (Zeide & Pfeifer 1991; Mäkela & Vaninen 2001). Black spruce has longer leaf longevity and, also, higher photosynthetic nitrogen-use efficiency in older needles than white spruce (Kayama et al. 2007). As a result, since needles can be retained longer under shade conditions, black spruce can support foliage deeper inside the living crown, partly explaining why branch-level foliage biomass is greater than for white spruce given the same branch basal area (Figure 2).

Shade tolerance differences between black and white spruces also contribute to differences in tree-level pipe-model ratios and in pipe-model ratios along the tree stem. Kaufmann and Troendle (1981) reported that the shade-intolerant lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) and aspen (*Populus tremuloides* Michx.) have smaller tree-level pipe-model ratios (i.e. total biomass/sapwood area at breast height) than the shade-tolerant Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). They suggest that more tolerant species may have lower water losses per unit leaf area, and consequently, a larger crown biomass per unit sapwood area. A similar result was observed by Waring et al. (1982) who compared total leaf area per unit sapwood area at breast height for 10 gymnosperm species varying in shade tolerance. Consistent with prior research, we found higher tree-level pipe-model ratios and higher pipe-model ratios along the tree stem in the more shade-tolerant black spruce. We also found a more rapid increase in pipe-model ratios along the stem from mid-crown to the top of the tree in white spruce, likely due to minimal foliage shedding in the upper crown where light levels are higher.

In terms of differences in growth rates, Bond-Lamberty et al. (2002) found larger sapwood to heartwood proportions in stems of fast-growing species. White spruce has been shown to have higher growth rates than black spruce (Pothier & Savard 1998; Thiffault et al. 2003) and black spruce is known to have a lower transpiration rate per unit of leaf area than other boreal tree species (Ewers et al. 2005). The higher pipe-model ratio may also explain the lower growth of black spruce since modeling studies suggest that a higher pipe-model ratio may result in lower allocation to the stem and consequently lower growth (Berninger & Nikinmaa 1997). Overall, the observed larger tree-level pipe-model ratios in black spruce given the same tree sizes are consistent with expected results for slower growing species.

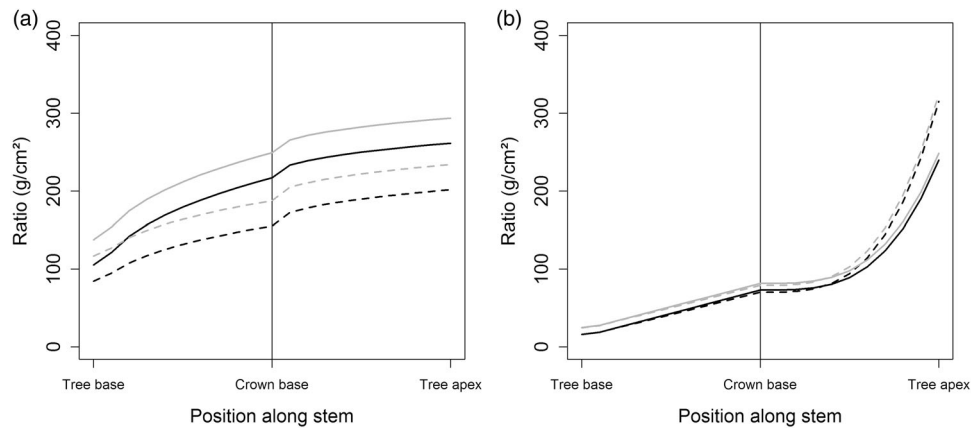


Figure 4. Pipe-model ratio along the stem (R_d) plotted against relative position in the stem for: (a) black spruce and (b) white spruce; 500 stems/ha, DBH = 15 (solid black line) and DBH = 25 (solid grey line), 2500 stems/ha, DBH = 15 (dashed black line) and DBH = 25 (dashed grey line).

An interesting result was that both species showed an increase in the tree-level pipe-model ratios with increasing tree taper (i.e. DBH over height ratios) (Figure 4). Trees with greater taper have differentially greater DBH growth than height growth, resulting in a greater proportion of earlywood to latewood. Earlywood has been shown to have higher hydraulic conductivity than latewood (Tyree & Zimmerman 2002). This differential DBH versus height growth is more pronounced in older trees, since height growth rates decline at younger ages than DBH growth rates (Wang et al. 1998). Furthermore, these older trees have longer tracheids, also associated with increased sap conductivity (Pothier et al. 1989). Overall, trees with higher taper require less sapwood area to transport a given amount of sap leading to lower tree-level pipe-model ratios. This was more pronounced for black spruce than for white spruce indicating higher foliage per unit sapwood area given the same taper.

For both spruce species, we found less branch-level foliage biomass per unit branch basal area from the tree apex to the crown base as branch lengths increased (Figure 2). The loss of hydraulic conductivity over longer branch lengths contributes to a decrease in foliage density from upper to lower branches (Protz et al. 2000). However, black spruce had greater branch-level foliage biomass per unit branch basal area, likely due to leaf longevity as noted earlier.

Differences in strategies between the two species with regards to moisture stress also partially explain the tree-level pipe-model differences. First, black spruce trees are often shorter than white spruce trees given the same growing conditions resulting in less water stress (McDowell et al. 2002) primarily due to decreased gravitational force (Koch et al. 2004). Conversely, to compensate for greater moisture stress, white spruce must increase the

sapwood area and/or conductive capacity per unit area (Becker et al. 2000). Also, black spruce may have a different response to moisture stress than white spruce. Pepin et al. (2002) found that black spruce was sensitive to top soil layer water deficits by closing stomata even when underlying soil layers were moist. This behaviour may reduce the impacts of even moderate moisture stress on the xylem water potential, resulting in a decreased need for large sapwood areas.

Mechanical support requirements also contribute to the differences in foliage attributes between the two species. White spruce has a wider crown than black spruce (Power et al. 2012) with correspondingly larger branch basal areas needed to mechanically support these longer branches. However, the larger branch basal area does not necessarily result in directly proportional increases in foliage. Foliage biomass is often concentrated towards branch tips with greater light availability (Baldwin & Peterson 1997). This would be more pronounced in shade-intolerant species with shorter leaf longevity and lower leaf efficiency. As a result, white spruce has less branch-level foliage per unit branch basal area. Since black spruce has a higher wood density and a larger Young's modulus than white spruce (Jessome 1977), black spruce branches may be able to mechanically support a larger amount of foliage biomass than white spruce given the same branch basal area. Collectively, these characteristics contribute to a larger amount of branch-level foliage biomass per unit branch basal area in black spruce.

Mechanical support requirements may also help explain differences in the tree-level pipe-model ratios between black and white spruces. As with tree branches, the higher wood density and a larger Young's modulus of black spruce (Jessome 1977) indicates that less wood is

needed to support the tree crown. Also, support at the tree base must increase to support the increased weight of taller trees and also the increased effects of wind and other forces (King 1981). Given that white spruce grows taller than black spruce, the need for mechanical support results in greater tree taper, which, as noted earlier, is associated with greater sapwood area. Overall, the need for mechanical support contributes to lower tree-level pipe-model ratios in white spruce.

These research results on foliage biomass–sapwood relationships can be used in forecasting growth including biomass and wood properties of these two species. Maily (2000) used the pipe-model ratios to estimate foliage biomass in DRYADE. Other authors used the functional link between sapwood and foliage biomass to allocate carbon in tree growth models. As a notable example, the pipe-model theory was used as the basis for CROBAS and Pipe-Qual (Mäkelä 1997; Mäkelä & Mäkinen 2003), Ogle and Pacala (2009) used the pipe-model allometric relationship in ACGCA, a semi-functional model that describes growth of red maple (*Acer rubrum* L.) and loblolly pine (*Pinus taeda* L.) under different physiological states. Collectively, these models use a more process-based approach to better reflect growth processes, and foliage biomass–sapwood relationships provide the foundation for these models.

In conclusion, we found differences in foliage biomass–sapwood relationships at the branch-, tree- and disk levels for these two geographically overlapping, extensive, and commercially important spruce species. Overall, we found that shade-tolerant black spruce with lower growth rates and narrower crowns had higher branch-level foliage biomass and larger pipe-model ratios along the tree stem than the less shade tolerant, faster growing white spruce. To our knowledge, this is the first paper comparing foliage biomass–sapwood relationships between white and black spruces

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