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Crown allometry and application of the *Pipe Model Theory* to white spruce (*Picea glauca* (Moench) Voss) and aspen (*Populus tremuloides* Michx.) in the western boreal forest of Canada

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Abstract

White spruce [*Picea glauca* (Moench)] and aspen (*Populus tremuloides* Michx.) from unmanaged stands in the boreal forest of Alberta, Canada, were examined for two of the main structural assumptions in the process-based model Crobas: 1) a constant allometric relationship between foliage mass and crown length, and 2) a constant relationship between foliage mass and sapwood area. We evaluated these relationships at both at the whole-crown and within-crown levels. Results indicated that for both species, a constant allometric relationship between foliage mass and crown length was maintained at the whole crown level over a period exceeding the peak mean annual increment of each species. Within the crowns of spruce, foliage mass accumulated faster near tree apex as total crown length increased. For aspen, the increase in foliage mass per unit crown length for any section within the crown showed greater similarity to the relationship observed at the whole crown level. The assumption of a constant relationship between foliage mass and sapwood area at crown base held rather generally for spruce but showed considerable variation for any given diameter class. For aspen, this assumption did not appear to be appropriate. For both species, there was more foliage mass per unit sapwood area with increasing height from the ground for nearly all tree size classes. This latter finding was in conflict with the pipe model theory but could not be explained by the hydraulic theory of crown architecture, which predicts a decrease in the ratio of foliage mass to sapwood area with increasing path length.

Keywords: Pipe model, crown allometry, foliage mass, *Picea glauca*, *Populus tremuloides*

39 *Introduction*

40 Crobas (Mäkelä 1997) is a process-based model which is based on the principle of carbon
41 balance, but also incorporates principles related to the functional balance (Davidson 1969;
42 Valentine and Mäkelä 2005). Among the structural regularities of trees that are assumed within
43 the Crobas model, the two which have received considerable attention are: 1) that a constant
44 allometric relationship exists between foliage mass (W_f) and crown length (Cl), and 2) that the
45 ratio of foliage mass to sapwood area at crown base (As_{cb}) is invariant across tree size, social
46 class and stand density.

47 Within Crobas, the relationship between foliage mass and crown length is used to obtain tree-
48 level estimates of foliage mass, which in turn, are used to infer As_{cb} . By inferring foliage mass
49 from crown length, the Crobas model ties the growth of the crown to the allocation of carbon
50 within the tree (Mäkelä 1997). The assumption of a constant allometric relationship between
51 foliage mass and crown length is supported by empirical observations from several tree species
52 including Silver birch (*Betula pendula* L.) (Ilomäki et al. 2003), Norway spruce (*Picea abies* (L.)
53 Karst.) (Kantola and Mäkelä 2006) and Scots pine (*Pinus sylvestris* L.) (Berninger and Nikinmaa
54 1994). Notably, Mäkelä and Sievänen (1992) postulated that the physiological basis for such a
55 relationship is that it represents the optimal balance between added photosynthetic ability from
56 increased foliage mass and the additional maintenance and respiration costs associated with a
57 longer crown. However, it is acknowledged that the assumption of a constant allometric
58 relationship between foliage mass and crown length is a generalization and findings from Mäkelä
59 and Vanninen (1998) and Schneider et al. (2008), among others, have demonstrated that
60 competition, tree size and age may influence this relationship.

Notwithstanding the effects of age, size and competition, it is postulated that the exponent parameter of the power allometric equation (Kittredge 1944) which describes the relationship between foliage mass and crown length should lie between 2 and 3 (Zeide and Pfeifer 1991). This range is an adjustment from the theoretical scaling exponent of 3, which is obtained if we assume that the crown is a fractal-like object formed by a volume filling branching network and is of constant shape (Mäkelä and Valentine 2006). The adjustment is supported by empirical observations of scaling between foliage mass and crown volume (Mäkelä and Vanninen 1998; Duursma et al. 2010).

There is sufficient evidence to suggest that the relationships described above cannot always be extended to describe scaling within the crown (Baldwin et al. 1997; Kantola and Mäkelä 2004). It is suggested that variation in the amount of foliage mass per unit crown length is related to the progressive increase in self-shading with increased distance from tree apex or increased competition from neighbouring trees; in practice, it is difficult to separate these two effects. Within Crobas, these alterations need to be taken into account if within-crown estimates of foliage mass from crown-length are desired.

The assumption that there is a linear relationship between foliage mass and As_{cb} is derived from the pipe model theory of plant form (Shinozaki et al. 1964). Although the original pipe model proposed by Shinozaki et al. (1964) only makes reference to a relationship between foliage mass and active xylem, this has been taken to imply that the relationship can be extended to As_{cb} , given the role of sapwood in supplying water and nutrients to foliage in the crown. Following an initial estimate of foliage mass from crown length, the pipe model relationship is used within Crobas to estimate As_{cb} . Several empirical studies support the assumption of a linear relationship between foliage mass and As_{cb} , (Kaipainen and Hari 1985; Eckmullner and Sterba

2000), while others have found the relationship to vary according to tree size, site productivity or geographic location (Gilmore et al. 1996; Berninger et al. 2005). Nevertheless, among the tree's structural relationships, the pipe model appears to be the most stable.

The relationship between foliage mass and sapwood area has also been found to be maintained at all heights within the crown (Waring et al. 1982). However, a linear relationship between foliage mass and $A_{s_{cb}}$ does not necessarily imply a linear relationship within the crown (Schneider et al. 2011). This inconsistency may be due to the re-activation of disused pipes or a lag in time between the disuse of pipes and changes in foliage mass within the crown. Hydraulic path length may also be a factor. For example, the model of hydraulic architecture described by Whitehead and Jarvis (1981) and Whitehead et al. (1984a) has been used to explain within-tree variation in the relationship between foliage area and sapwood area (Medhurst and Beadle 2002). The hydraulic model predicts that the ratio of leaf area to sapwood area should decrease with increasing distance from ground due to increasing hydraulic resistance. Substituting foliage mass for foliage area, the hydraulic model may be used to describe within-crown variations in the pipe model ratio. However, such an argument requires specific leaf area (cm^2/g) to remain stable from the tip to the base of the crown.

For the current study, we examine two main structural regularities assumed by the Crobas model for white spruce [*Picea glauca* (Moench)] and aspen (*Populus tremuloides* Michx.). These two disparate species are a major component of upland stands within the Western Canadian Boreal forest. White spruce is characterized as a shade tolerant, late successional species which maintains a large crown ratio (crown length : total tree height) throughout most of its development. Aspen, on the other hand, is a shade intolerant early successional species which maintains a relatively small crown ratio following crown closure. As a first main objective, we

test for constant allometric scaling between foliage mass and crown length for these two species. We then examine the relationship between foliage mass and crown length for sections within-crown and contrast them to the relationships seen at the whole crown level. As a second main objective, we test the assumption of a linear relationship between foliage mass and $A_{s_{cb}}$, which is derived from pipe model theory. We then test the null hypothesis that predictions of foliage mass from $A_{s_{cb}}$ under the assumption of the pipe model are dissimilar to observed values. Finally, we look at the within-crown relationship between cumulative foliage mass and sapwood area. We examine this relationship within the framework of the pipe model theory and contrast it with the relationship viewed within the framework of the hydraulic model. The results of this study will contribute to the evaluation of the Crobas model for use on white spruce and aspen within the western Canadian boreal forest. The importance of process-based models such as Crobas in directing forest management activities has been well documented (Mäkelä et al. 2000; Valentine and Mäkelä 2005).

Material and methods

Site description

The sampling of trees used in this study was performed adjacent to Permanent Sample Plots (PSPs) which had previously been installed by Alberta Sustainable Resource Development (ASRD 2005). All PSPs were situated within unmanaged stands that had been established through natural regeneration. Although the selected PSPs span approximately 500 kilometers along an east-west latitude, climatic conditions over this region are reported to be similar (Beckingham and Archibald 1996). All stands in which the sampled PSPs are located were classified to the ‘reference’ ecosite-type (i.e., upland forests with moderately well-drained, orthic-gray luvisolic soils) of the central mixedwood natural subregion of Alberta, Canada

(Beckingham and Archibald 1996). Given the common climatic conditions and ecosite-type, site index values were assumed to be relatively similar.

Field and laboratory measurements

In total, 65 white spruce trees from 15 PSPs and 46 aspen trees from 12 PSPs were felled (Table 1). The process of selecting trees to be felled for biomass sampling is described in Sattler et al. (2014). Briefly, however, trees were selected in order to provide a range in sizes (*DBH*) and tree ages (cambial age at *BH*) for the given plot. Once felled, all live branches greater than 0.3 cm in diameter at the point of insertion with the main stem (9332 branches) were measured for branch diameter, branch angle, and location along the main stem. A subsample of 6 branches on each felled tree was then randomly selected after first dividing the live crown in two equal halves (3 in the upper half and 3 in the lower half). Subsampled branches were first measured for total branch length (H_b (cm)) and then collected in bags and brought to a lab for further processing. At the lab, foliage was separated from woody components. From each of the sampled branches, an estimate of specific leaf area (cm^2/g) was calculated by scanning a subsample of the foliage using WinSeedle (for spruce) and WinFolia (for aspen) (Regent Instruments Inc. 2003, Québec, Canada). All foliage was then oven dried (minimum 72hours @ 70C) and weighed. Sapwood in the tree bole was measured on discs cut at crown base, mid-crown, half-way between crown base and mid-crown and finally half-way between mid-crown and the apex of the crown. Sapwood widths were measured at four orthogonal points after holding the discs up to a light source and tracing around the darkened heartwood centre.

Table 1

Scaling up from branch to tree

To scale-up measurements of foliage mass (see Table 2 for variable descriptions) from branch to tree, we developed a nonlinear mixed effect model which included both plot and tree-level random effects. The species-specific models were fitted using data collected from individual branches. For white spruce and aspen, the models performed quite well with adjusted- R^2 values (68% for spruce; 86% for aspen) comparable to those reported by (Kantola and Mäkelä 2004) and (Ceulemans et al. 1990). Details of the model construction and associated fit statistics are provided in Appendix 1. For each species, the fitted model was used to calculate foliage mass for all live branches ≥ 3 mm. Tree-level totals for foliage mass were obtained by summing across all branches within a tree.

Table 2

Whole crown allometry

Tests for a constant or variable allometric relationship (CAR or VAR, respectively) between W_f and Cl were performed using the following two equations:

$$[1] \quad \hat{W}_f = \delta_0 Cl^{\delta_1} + \varepsilon_1$$

$$[2] \quad \hat{W}_f = \delta_0 Cl^{\delta_1} \exp^{Cl\delta_2} + \varepsilon_2$$

Where $\hat{W}_f$ and Cl are as previously defined and δ_0 , δ_1 and δ_2 are parameters to be estimated from the data. For both Equation 1 and Equation 2, δ_0 is the rate parameter, while δ_1 is the scale parameter. Equation 1 assumes constant allometry, while Equation 2 is formulated following Ruark's variable allometric equation (VAR) (Ruark et al. 1987). If the relationship is constant, then there should be no improvement in model performance between Equation 1 and Equation 2. Furthermore, estimates resulting from Equation 1 should be unbiased across Cl . Since the

competitive status of the tree may influence scaling between $\hat{W}_f$ and Cl , residuals were also examined across the basal area of larger trees (Bal). Equations 1 and 2 were fitted using a power variance weighting structure that was a function of Cl . Comparisons between Equations 1 and 2 were performed using likelihood ratio tests and adjusted- R^2 values.

Within-crown allometry

To contrast within-crown scaling between foliage mass and crown length with that observed at the whole crown level, we first dividing total Cl into four equal sections ($k=1, 2, 3, 4$); where 1 is the top section and 4 is the section at the base of the live crown. Under the assumption that scaling at the whole crown level follows Equation 1, then one should be able to estimate foliage mass for the k -th crown section as:

$$[3] \quad \hat{W}_{f_k} = \varphi_k (Cl_k^{\delta_1} - Cl_{k-1}^{\delta_1})$$

where $\hat{W}_{f_k}$ is the foliage mass of the k -th crown section, Cl_k is the crown length from the crown apex to the base of section k , and Cl_{k-1} is the crown length from the crown tip to the base of section $k-1$. The parameter φ_k is to be estimated while δ_1 is derived from Equation 1, assuming constant allometry. Thus, moving from the top crown section to the bottom of the crown, foliage mass for each section was estimated by fitting the following set of equations:

$$[3a] \quad \hat{W}_{f_1} = \varphi_1 Cl_k^{\delta_1}$$

$$[3b] \quad \hat{W}_{f_2} = \varphi_2 (Cl_2^{\delta_1} - Cl_1^{\delta_1})$$

$$[3c] \quad \hat{W}_{f_3} = \varphi_3 (Cl_3^{\delta_1} - Cl_2^{\delta_1})$$

$$[3d] \quad \hat{W}_{f_4} = \varphi_4 (Cl_4^{\delta_1} - Cl_3^{\delta_1})$$

If constant allometric scaling is observed at the whole crown-level, then we should see $\varphi_k = \delta_0$ for all k . Summing across Equations 3a to 3b should, therefore, yield:

$$[3e] \quad \hat{W}_f = \delta_0 C l_4^{\delta_1} = \varphi_4 C l_4^{\delta_1}$$

A power variance weight function was used to fit Equations 3a to 3d, while residual plots were used to identify bias. Model performance was assessed with adjusted- R^2 .

Whole-crown foliage mass from pipe model theory

Using pipe model theory, the following equation was fitted to the spruce and aspen data:

$$[4] \quad \hat{W}_f = \alpha_0 A_{s_{cb}} + \varepsilon_4$$

where $\hat{W}_f$ is as previously defined, $A_{s_{cb}}$ (cm^2) is sapwood area at the base of the live crown and α_0 is the pipe model ratio. Our evaluation of the pipe model for use on spruce and aspen was conducted using equivalence testing as described by Robinson et al. (2005). The equivalence tests were performed for the whole dataset as well as by diameter class. Tests of the null hypothesis of dissimilarity on the intercept were used to test for lack of bias, while tests of the null hypothesis of dissimilarity on the slope was used to test for appropriate association between measured and predicted values. As a region of equivalence, we began with $\pm 10\%$ for the intercept and $\pm 10\%$ for the slope, and increased the region in increments of 5% until we could reject the null hypothesis of dissimilarity. As a point of comparison for the pipe-based models, we calculated $\hat{W}_f$ using *DBH* and height-based equations from the parameters provided by Manning (1984; for white spruce) and Alemdag (1984; for aspen); in both cases, the published parameters were suitable for the range of tree sizes in the current study. The same equivalence tests were then performed on the resulting predictions.

214 Within-crown foliage mass from pipe model theory

215 To examine within-crown scaling between cumulative $\hat{W}_f$ and sapwood area along the stem,
216 the ratio of these two variables at the base of the k -th crown section was calculated as:

217 [5]
$$Rp_k = \frac{\sum_{1}^k \hat{W}_{f_k}}{As_k}$$

218 where Rp_k is the ratio between cumulative $\hat{W}_{f_k}$ and As_k at the base of the k -th crown quarter
219 section. To test the assumption that the pipe model ratio remains constant within the crown, Rp_k
220 was plotted against the relative position within the crown ($Rdinc$; 0=tree apex, 1=crown base),
221 with the relationship fitted using a linear regression. Potential effects of size class on the
222 relationship were addressed by fitting a separate regression for each diameter class. As a
223 complimentary tests, the relative position within the crown was replaced with the height (m) to
224 the base of the k -th crown quarter section (H_k) and regression equations again fitted for each
225 diameter class. For each independent variable, the linear regression used was:

226 [6]
$$Rp_k = \lambda_{0,dclass} + X_k \lambda_{1,dclass} + \varepsilon_6$$

$$X = Rdinc, H_k$$

227 Under the assumption of a constant pipe model ratio, λ_1 should be zero, regardless if Equation 6
228 is fitted using $Rdinc$ or H_k . However, support for the hydraulic model may be found if λ_1 is
229 negative and significant when Equation 6 is fitted using H_k given that Rp_k is said to decrease
230 with increasing hydraulic path length (represented here by H_k). As was done in previous
231 equations, heteroskedasticity and correlation between observations were addressed when fitting
232 Equation 6.

As final step, trends in specific leaf area from tree top to crown base for both spruce and aspen were examined using a set of linear regressions. The analysis of vertical trends for specific leaf area was included since an increase in specific leaf area from tree apex to crown base would impact our ability to draw comparisons between expected trends under the pipe model ratio (which uses foliage mass) and those expected under the hydraulic model (which uses foliage area).

Following Marshall and Monserud (2003), specific leaf area was modelled as:

$$[7] \quad SLA = \eta_0 + Crdpth * \eta_1 + \varepsilon_7$$

where SLA is the specific leaf area (cm^2/g), $Crdpth$ is crown depth from tree apex, and η_0 and η_1 are parameters to be estimated. For both spruce and aspen, Equation 7 was fitted separately for each diameter class. Parameters for Equation 7 and all previous equations were estimated using the `gnls` function (generalized nonlinear least squares) in the `nlme` package (Pinheiro et al. 2015) for R (R Core Team 2013).

Results

Foliage mass and crown length: whole crown allometry

The estimated parameters and fit statistics for the CAR (Equation 1) and VAR (Equation 2) models for spruce and aspen are presented in Table 3. Likelihood ratio tests and values for the RMSE indicated that for both spruce and aspen, the VAR model was not superior to the CAR. Thus, for both spruce and aspen, scaling between foliage mass and crown length appeared to be constant over increasing crown length. For spruce, the CAR model indicated that foliage mass scaled with crown length with an exponent of 1.45 (Figure 1a), while for aspen the exponent was 1.29 (Figure 1b). For both species, the residuals resulting from the CAR model showed no trends

across crown length. However, for spruce, there was noticeable bias when the residuals were plotted against *Bal*. Specifically, the CAR model under-estimated foliage mass on trees in a dominant position and over-estimated foliage mass for trees in a suppressed position. For aspen, there were no trends in the residuals when plotted across *Bal*.

Table 3

Figure 1.

Foliage mass and crown length: within-crown allometry

For spruce, the results of Equation 3a to 3b suggest that the constant allometry observed at the whole crown level is not observed for individual sections within the crown. For the section 75% to crown base, φ_4 was significantly lower than the value for δ_0 observed at the whole crown level (Table 4). With increasing crown length, the increase in foliage mass near to base of the crown was lower than all other sections of the crown (Figure 2). In the top half of spruce crowns, values for φ_k were significantly greater than that observed at the whole crown level indicating that as the crown length increased, the increase in foliage in these sections was higher than in other parts of the crown. At 50% to 75% from the crown apex, the increase in foliage mass with increasing crown length was closest to that observed at the whole crown level. However, there was considerable variability between trees as indicated by the low adjusted- R^2 value (Table 4). Analysis of the residuals revealed that there was minimal bias across *Bal* in the top quarter section of the crown. Bias in relation to *Bal*, however, was evident within all three lower crown quarter sections, with trends in the residuals mirroring those from the CAR model fitted to the whole-crown (Figure 3).

Table 4

For aspen, constant allometric scaling in individual crown sections generally seemed to hold. For the section 75% to crown base, foliage mass increased with increasing crown length at a rate similar to that at the whole crown level given that $\phi_4 = \delta_0$. The middle crown sections (25-50% and 50-75%) displayed the greatest increase in foliage mass with increasing crown length, while the rate of increase was much lower in the top crown section (Figure 2). For each crown section, the estimates of foliage mass did not appear to be biased with respect to *Bal* (Figure 4).

Figure 2.

Figure 3.

Figure 4.

Pipe model ratio: whole-crown allometry

The estimated pipe model ratio in Equation 4 (α_0) was 0.14 (SE=0.005) for spruce and 0.03 (SE=0.001) for aspen. The pipe model explained a far greater proportion of the variability in foliage mass for spruce (Adj.- R^2 =69%; RMSE=7.48 Kg; bias=-0.11) than for aspen (Adj.- R^2 =25%; RMSE=1.09 Kg; bias=-0.19). When fitted to the dataset containing all diameter classes, equivalence tests on the intercept (test of bias) and the slope (test of accuracy) had a smaller minimum region to reject the null hypothesis of dissimilarity for spruce than for aspen (Table 5). For individual diameter classes, equivalence tests on the intercept for spruce showed comparable results to that found for aspen, with minimum regions of rejection between 15 and 40%. However, tests on the slope indicated that the pipe model tended to provide greater accuracy in estimates of foliage mass for spruce than for aspen. For any one diameter class, we judged the regions of equivalence required to reject the null hypothesis for the slope to be quite large for both spruce and aspen. Nevertheless, there was stronger evidence in favour of the pipe

model than the regionally calibrated *DBH* and height-based equations provided by Manning et al. (1984) and Alemdag (1984) (Table 5).

Table 5

Pipe model ratio: within-crown allometry

For spruce, the pipe model ratio (Rp_k) showed some variation over relative position within the crown (Figure 5). However, the linear regressions for each diameter class revealed that the slope of the relationship was not significant (Equation 6; Table 6), thus, lending support to the assumption that the pipe model ratio remains more-or-less constant within the crown, regardless of tree size. Similarly, the pipe model ratio within the crowns of small trees appeared unchanged with increasing distance from ground (Figure 5). However, regression analysis revealed that the pipe model ratio increased with increasing distance from the ground within the crowns of trees from all other diameter classes. This latter finding, therefore, suggested that the ratio was affected by increasing hydraulic path length.

Table 6

With Equation 6 fitted to the aspen data using relative position in the crown as the independent variable in Equation 6, there was a tendency for the pipe model ratio to decrease from crown apex to crown base in the smallest two diameter classes. No significant trends were noted in the larger two diameter classes (Table 6). When relative position was replaced by absolute distance from the ground in Equation 6, there was a clear tendency for the pipe model ratio to increase with increasing height in all but the smallest diameter class. As with spruce, the variability in the ratio was high with the significant fitted regressions explaining only 8% and 18% of the within-crown variability for the two largest diameter classes.

Figure 5.

Figure 6.

For both spruce and aspen, the variability in specific leaf area from tree apex to crown base was quite large for any one diameter class. Results from Equation 7 revealed that for white spruce, there was no significant relationship between specific leaf area and crown depth ($Crdpth$) (Table 7). For aspen, there was a significant increase in specific leaf area from crown apex to crown base for all diameter classes.

Table 7.

Discussion

Foliage mass – crown length allometry

That whole-crown foliage mass in spruce showed constant allometric scaling with crown length was unexpected. Given the low self-pruning of branches, high needle retention and a reduction in height growth with age, our prior expectation was that the largest and most mature spruce trees within the sample dataset would accumulate more foliage mass for a given increase in crown length, leading to variable allometric scaling. For aspen, we also expected whole crown foliage mass to show variable scaling with crown length. This was based on the general understanding that age-related decline in foliage mass usually appears soon after the peak in mean annual increment for shade intolerant species (Sato 1962), and was previously used to explain a reduction in foliage area in aspen (Lieffers and Stadt 1994).

For spruce, the finding contrary to our expectations suggests that this species employs a strategy of carbon allocation which accounts for the retention of old needles and adjusts the rate of production of new foliage in order to maintain a constant relationship with the vertical growth of the crown. Moreover, this strategy of carbon allocation appears to be maintained beyond the

peak mean annual growth of spruce given that the oldest trees we sampled were approximately 150 years old. Although the findings are contrary to our expectations, similar trends were found in Norway spruce, a species which displays a shade-tolerance similar to that of white spruce (Kantola and Mäkelä 2004). However, it should be noted that Kantola and Mäkelä (2004) did not explicitly test the possibility that a VAR model would have better suited their data.

As was the case for spruce, aspen showed a constant allometric relationship between foliage mass and crown length. For aspen, it appears that despite age-related effects such as increased incidence of disease and reduced stomatal conductance (Smith et al. 2011), carbon continues to be allocated in a manner which maintains the same amount of foliage production for a given increase in crown length. Similarly, Ilomäki et al (2003) reported a constant allometric relationship between foliage mass and crown length for silver birch. However, as was previously noted, there was no indication that Ilomäki et al. (2003) explicitly tested for a variable allometric relationship.

Supposing that the full crown of both spruce and aspen are exposed to sunlight, then the relative rates of growth for foliage mass and crown length should, in theory, be in response to the need to regulate self-shading (Okerblom and Kellomäki 1982). In such a case, a constant allometric relationship between foliage mass and crown length will be one that provides the optimal compromise between the benefits of increased foliage mass (i.e., increased photosynthesis) and the increased respiration costs that come with maintaining the structures to support a larger crown (Mäkelä and Sievänen 1992). For aspen, one can argue in support of this supposition given that its growth strategy is to maintain the near entirety of the crown above that of competing vegetation. It is less defensible for white spruce, however, where a large proportion of the crown lies within the shade cast by competitors and is therefore, less

photosynthetically active (Schoonmaker et al. 2014). Consequently, competition from neighbouring trees is also likely to be an important factor driving size-related changes in foliage growth. Indeed, bias across Bal in the residuals resulting from the CAR model in spruce indicated that competition from neighbouring trees had an effect on the relationship between whole crown foliage mass and crown size beyond that posed by self-shading.

In comparison to other boreal tree species, the estimated exponent parameter for Equation 1 was low for both spruce and aspen. For the shade tolerant Norway spruce, Kantola and Mäkelä (2006) reported a value of 1.78. A value of in the range of 2-3 was reported by Mäkelä and Sievänen (1992) for open grown Scots pine and red pine, both shade-intolerant species. For Silver birch, also a shade intolerant species, Ilomäki et al. (2003) reported an exponent parameter of 2.62. It is likely that differences in site fertility and local climate are at least partially responsible for the observed discrepancies and thus, direct comparison is not possible. Nevertheless, it was interesting to note that the aforementioned studies used trees from either open grown or evenly spaced, single-species, managed stands. Within the unmanaged mixed-species stands sample for the current study, greater heterogeneity of within canopy light levels and increased competition for light may possibly explain why the allometric exponents we found were low relative to those reported in other studies.

Within-crown scaling between foliage mass and crown length

Although whole crown scaling between foliage mass and crown length was constant, there were significant shifts in the allocation of foliage within the crown. For example, within-crown scaling in spruce revealed that the top sections of the crown accumulate foliage mass faster with increasing tree size than sections in the lower half of the crown. As suggested by Mäkelä and

383 Vanninen (1998), this implies that there is a shift in the allocation of growth higher up the tree as
384 trees get bigger.

385 In the top 25% of the crown, the accumulation of foliage with increasing crown length was
386 largely unrelated to the competitive status of the tree (*Bal*). Shade cast by neighbouring
387 competitors, therefore, appears has little effect on the tops of spruce trees. Similar results were
388 reported by Kantola and Mäkelä (2004), where the allometric relationship between foliage mass
389 and crown length in the top 5m of Norway spruce crowns was unaffected by tree age or
390 competition.

391 For aspen, the within-crown sections showed greater similarity in terms of how foliage mass
392 accumulated with increasing crown length. Although foliage mass accumulated slightly faster in
393 the middle section of aspen crowns, competition from neighbouring trees appeared to have little
394 effect on all crown sections. This seems to confirm our earlier suggestion that scaling of foliage
395 mass with crown length in aspen is largely driven by the need to control self-shading. It remains
396 unclear, however, why the allometric scaling exponents for all crown sections were much lower
397 than the expected value for open grown trees. Greater investment into branch wood production
398 and a decreased foliage production during drought years may be at least partially responsible for
399 this discrepancy.

400 Whole crown foliage mass from pipe model theory

401 Mäkelä (1997) notes that the assumption of a linear relationship between whole crown
402 foliage mass and As_{cb} will hold on average, but is expected to show some deviation. Deviations
403 may arise through differences in tree size, competition or other environmental factors (Mäkelä
404 and Vanninen 1998). For the current study, we accounted for potential effects of tree size by
405 examining the relationship between foliage mass and As_{cb} separately for different diameter

classes. While our use of diameter classes would have also captured some competition-related effects, one would need to examine the relationship across different measures of competition (e.g. crown ratio or *Bal*) in order to fully account for such effects.

Viewed within context described by Mäkelä (1997), the results of the equivalence testing on white spruce are in line with expectations. That is, for the full dataset, the regions of equivalence to reject the hypothesis that model predictions are both biased and dissimilar, were within the 25% limit suggested by Wellek (2003). However, for any one diameter class, we can expect considerable dissimilarity between observed and predicted values. While this latter point raises questions regarding the robustness of the pipe model, it must be weighed against the superior performance of the pipe model relative to the regionally calibrated DBH and height based equations. This finding is in accordance with Lehtonen (2005) where it was reported that the basal area of the stem at crown base was a better predictor of foliage mass than DBH or DBH and height-based equations for Norway spruce and Scots pine. Therefore, we conclude that further efforts to validate the pipe model theory for use on white spruce appears to be warranted.

For aspen, the large regions of equivalence required to reject the null hypothesis of dissimilarity for the full dataset as well as for any given diameter class suggest that the pipe model, as was tested here, is not appropriate for this species. That being said, using a pipe-based model to predict foliage mass in aspen should still be considered given its performance relative to that of the regionally calibrated DBH and height-based equations. Mäkelä (2002) proposed a modification of the pipe model which accounts for the gradual transition of heartwood to sapwood, and should be considered at a 'next step' in the evaluation of the pipe model for use on aspen. Alternatively, issues related to the measurement of sapwood in aspen may have influenced our results. For example, swelling of the main stem near the crown base of aspen we

sampled may be a source of bias. Additionally, the visual delineation of sapwood area in aspen was hampered by the frequent occurrence of isolated pockets of sapwood within the heartwood, which were absent in spruce. Similar considerations were also discussed by Mäkelä and Vanninen (2001), who suggest that an examination of the hydraulic capabilities would help explain such discrepancies.

Within-crown foliage mass from pipe model theory

Our examination of the pipe model ratio within the crowns of spruce and aspen trees provided conflicting results. On the one hand, the ratio was found to be moderately stable over relative position within the crowns of spruce and in the two larger size classes for aspen. One could, therefore, argue that there is evidence to suggest that the pipe model is generally unaffected by factors such as whorl age and light conditions. However, potential effects of hydraulic path length on the pipe model ratio are not well accounted for when using relative position within the crown. The influence of this latter factor on the pipe model ratio is more clearly addressed through an examination of the ratio as a function of absolute height from the ground. That the pipe model ratio did not remain constant with increasing absolute height from the ground, therefore, suggests that hydraulic path length may influence the amount of foliage mass supported by a given area of sapwood.

Our findings with respect to hydraulic path length, however, were not consistent with the hydraulic model of crown architecture. The hydraulic model predicts that the ratio of whole crown foliage area to sapwood area at breast height should decrease with increasing tree height (Whitehead and Jarvis 1981; McDowell et al. 2002). It is postulated that in order to maintain leaf-specific hydraulic sufficiency, taller trees require greater sapwood area per foliage area given the longer hydraulic path length and associated gravitational constraints. Whitehead et al.

(1984b), Coyea and Margolis (1992), McDowell et al. (2002) and Mencuccini (2002) all reported decreasing ratios of leaf area to sapwood area with increasing tree size. Furthermore, the hydraulic model predicts that there should be progressively less foliage area per unit sapwood area with increasing distance from the ground. Medhurst and Beadle (2002), for example, found the leaf area to sapwood area ratio to decrease with increasing distance from crown base in *Eucalyptus* (*Eucalyptus nitens*). These finding, however, do not necessarily imply that similar trends should be observed if foliage area is replaced by foliage mass (i.e., the pipe model ratio). This is because specific leaf area may increase by a factor of 2 from tree top to crown base. Consequently, using foliage mass in place of foliage area can smooth out the variation of the pipe model ratio along the stem (Valentine 2001). However, for the spruce we examined, specific leaf area did not appear to change significantly within the crown. Therefore, one may argue that the within-crown trends for the pipe model ratio should be similar to those predicted by the hydraulic model. Indeed, Mäkelä and Vanninen (2001) found the pipe model ratio to decrease from crown base to tree apex for Scots pine. In contrast, for the current study we found the pipe model ratio to increase with increasing distance from the ground for spruce. For aspen, specific leaf area was found to increase with increasing depth from crown apex for all diameter classes. If anything, this should have reduced our ability to detect any significant within crown trends in the pipe model ratio (Valentine 2001). To the contrary, we detected an increasing trend in the pipe model ratio over increasing distance from the ground.

An increasing pipe model ratio with increasing distance from the ground tree is not without precedence. At the whole-crown level, Mokany et al. (2003) and Schneider et al. (2008) both reported an increase in the pipe model ratio with increasing tree size for alpine ash (*Eucalyptus delegatensis* R.T. Baker) and jack pine, respectively. Furthermore, McDowell et al. (2002) noted

an increasing pipe model ratio with increasing tree height in Norway spruce and Balsam fir [*Abies balsamea* (L.) Mill.]. Within the crown, Schneider et al. (2011) found that the pipe model ratio decreased with increasing distance from tree apex in Jack pine sampled at three different sites in eastern Canada. They rationalized that differences in the turnover rates of sapwood and foliage could explain the trends they observed. Specifically, they argued that the presence of heartwood in older branches and the re-activation of disused sapwood near crown base leads to greater hydraulic inefficiency lower in the crown, which in turn causes the pipe model ratio to be lower near crown base. However, under this hypothesis we would have expected trends for the within-crown pipe model ratio to show a significant nonlinear relationship with relative depth into the crown for trees in the larger diameter classes. Increased sapwood permeability and soil-to-leaf water potential difference have been cited as possible mechanisms that could explain an increase in pipe model ratio with tree size, although the current set of arguments in favour of these mechanisms is not convincing (McDowell et al. 2002). Leaf specific conductivity, which measures the ability to supply water to unit of foliage, is assumed to be constant across increasing tree size according to the hydraulic path length theory. However, Mokany et al. (2003) found that leaf specific conductivity increased with tree size and, therefore, could explain increases in the pipe model ratio with increasing tree height. Despite the findings that lend support to our current set of results, an examination of leaf specific conductivity in spruce and aspen would be needed to explore the potential link to the within-crown trends for the pipe model ratio we observed.

We found the relationship between the pipe model ratio and distance from ground varied by diameter class for spruce but not for aspen. This suggests that for spruce, there is greater size dependency in the relative rates of increase between foliage mass and sapwood area within the

crown. A second point separating the two species was the relationship between the pipe model ratio and the relative depth into the crown (Figure 5 and 6). For spruce, it appears that the relative position within the crown does not account for the effect of increasing hydraulic path length on the pipe model ratio given that there was bias in the residuals when plotted against distance from pith. Conversely, for aspen, using relative position in the crown produced unbiased estimates with respect to both relative position in the crown and distance from ground (Figure 6). This finding could be related to differences in hydraulic conductance between coniferous and diffuse-porous trees. McCulloh et al. (2010) noted that scaling between stem hydraulic conductivity and stem size, which they defined as network conductance, was more dependent on stem size for conifers compared to diffuse-porous trees. Regardless of the mechanism responsible for these differences, the finding is consistent with our results from the examination of within-crown scaling of the pipe model ratio, which also showed size dependence in spruce but not aspen. Consequently, the modifications to the pipe model theory would be needed to account for these size-related changes if within-crown estimation of foliage mass from sapwood area (or vice versa) is desired.

Conclusion

The results presented here show that the assumption of constant allometric scaling between whole crown foliage mass and crown length generally holds for both spruce and aspen. The assumption of a linear relationship between whole crown foliage mass and $A_{s_{cb}}$ also appears to hold on average for spruce. However, there are concerns over the precision in the estimates of foliage mass given the model's poor performance for any single diameter class. For aspen, tests of the pipe model were not convincing. Thus, we conclude that if the Crobas model is to be used within larger area represented by our study sites, consideration must first be given as to how

sapwood is measured as well as how adjustments to the pipe model could improve predictions across all tree sizes. With respect to the latter, this may include the use of additional tree- or stand-level covariates as suggested by Schneider et al. (2008) or a modification to accommodate the gradual transition of sapwood to heartwood as proposed by Mäkelä (2002). Finally, for the relationships that we examined, inconsistencies between the trends seen at the whole-crown level and those seen at the within-crown level were noted. Specifically, those at the whole-crown level appeared far more regular than those at the within-crown level. This feature has been also noted by Mäkelä and Vanninen (2001) and Schneider et al. (2008; 2011). Testing the adjustments that have been suggested to reconcile these differences would be the next logical step.

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539 *Tables*

Table 1. Means (with standard deviation in parentheses) by diameter class (Diam class) of select variables for the sampled spruce and aspen trees.

Diameter class	DBH (cm)	Height (m)	CI (m)	W _f (Kg)	A _{cb} (cm ²)	R _p	n	Age
Spruce								
Diam class1 (<16cm)	15.07 (0.86)	13.97 (1.87)	10.72 (1.94)	9.92 (3.49)	99.78 (29.23)	0.0998 (0.015)	11	125 (
Diam class2 (16.0-22.5cm)	20.56 (1.72)	18.01 (2.45)	11.73 (2.04)	16.12 (6.35)	145.38 (74.75)	0.1171 (0.027)	14	115 (
Diam class3 (22.5-30.0cm)	25.72 (2.21)	20.92 (3.94)	13.22 (3.11)	20.09 (5.93)	152.95 (55.51)	0.1461 (0.045)	15	68 (
Diam class4 (30.0-36.5cm)	32.12 (2.16)	26.64 (2.75)	16.09 (4.04)	29.69 (12.39)	190.23 (87.22)	0.1635 (0.034)	10	64 (
Diam class5 (36.5-45.5cm)	41.28 (2.23)	31.64 (1.67)	19.71 (4.56)	39.64 (12.46)	241.88 (94.46)	0.1729 (0.041)	15	45 (
Aspen								
Diam class1 (<16cm)	14.54 (1.09)	18.89 (2.31)	6.81 (1.46)	1.26 (0.43)	42.74 (13.31)	0.0296 (0.004)	15	65 (
Diam class2 (16.0-22.0cm)	18.83 (1.54)	20.52 (1.87)	7.62 (1.58)	2.01 (0.43)	69.16 (22.56)	0.0303 (0.011)	11	61 (
Diam class3 (22.0-28.0cm)	25.37 (1.82)	24.72 (2.42)	9.68 (1.31)	3.34 (1.10)	131.18 (45.17)	0.0269 (0.008)	14	39 (
Diam class4 (28.0-35.0cm)	31.38 (1.89)	26.06 (2.64)	8.00 (2.27)	3.87 (1.19)	136.76 (56.71)	0.0312 (0.013)	6	30 (

Note: Variable symbols are DBH (diameter at breast height; 1.3m); Height (total tree height); CI (live crown length); W_f (foliage mass); A_{cb} (sapwood area at crown base); R_p (pipe model ratio at crown base); n (sample size). Age is the cambial age at breast height.

Table 2. Symbols and associated description of variables used for the analyses.

Variable Symbol	Description
W_f	Foliage mass (Kg)
A_{cb}	Sapwood area at crown base (cm ²)
Ra_k	Ratio of cumulative W_f to CPA at the base of crown quarter section k
Rp_k	Ratio of cumulative W_f to As at the base of crown quarter section k
Cl	Length of live crown (m)
$Rdinc$	Relative crown depth from tree apex (0=crown apex, 1=crown base)
H_k	Distance from ground to base of crown section k (m)
$Crdpth$	Crown depth from tree apex (m)
SLA	Specific leaf area (cm ² /g)
Diam class	Diameter class (1 to 5 for spruce; 1 to 4 for aspen) ¹
Bal	Basal area of larger trees (m ² ha ⁻¹)

¹ See Table 1 for diameter class ranges used for each species.

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Table 3. Estimated parameters (standard error, SE, in parentheses) and fit statistics from the constant and variable allometric models (CAR and VAR; Equation 1 and 2 in text) fitted to spruce and aspen data. For each species, the CAR and VAR models were fitted as a function of crown length (Cl ; m).

	Parameters (SE)			Adj.- R^2	Likelihood ratio test ¹	p-value	RMSE
	δ_0	δ_1	δ_2				
Spruce							
CAR	0.47 (0.18)	1.45 (0.14)	-	61%	-	-	8.41
VAR	0.09 (0.15)	2.41 (0.95)	-0.06 (0.06)	61%	1.101	0.2939	8.36
Aspen							
CAR	0.15 (0.09)	1.29 (0.28)	-	31%	-	-	1.02
VAR	0.19 (0.48)	1.07 (2.21)	0.02 (0.27)	30%	0.01	0.917	1.03

¹ Likelihood ratio tests and associated p-value were the result of comparing the CAR to the VAR model.

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Table 4. Parameter estimates (standard error, SE, in parentheses) for Equations 3a to 3d, describing the relationship between foliage mass and crown length for the four crown sections (k = section 1, 2, 3, 4). The asterisk (*) denotes a significant difference between δ_0 (from Equation 1) and φ_k (from Equations 3a to 3d).

	φ_k (SE)	p-value	Adj.- R^2
Spruce			
Top - 25% ($k=1$)	0.89* (0.05)	<0.05	63%
25 - 50% ($k=2$)	0.68* (0.04)	<0.05	56%
50 - 75% ($k=3$)	0.44 (0.02)	<0.05	11%
75% - Crown base ($k=4$)	0.24* (0.02)	<0.05	9%
	φ_k (SE)	p-value	Adj.- R^2
Aspen			
Top - 25% ($k=1$)	0.11* (0.07)	<0.05	16%
25 - 50% ($k=2$)	0.18 (0.01)	<0.05	50%
50 - 75% ($k=3$)	0.21* (0.02)	<0.05	23%
75% - Crown base ($k=4$)	0.14 (0.02)	<0.05	5%

Table 5. Results of equivalence tests on prediction of from the fitted pipe model (Equation 4) and from published DBH and Height-based equations [Spruce = Manning (1984); Aspen = Alemdag (1984)]. Equivalence tests of predictions from the fitted pipe model are for the full dataset (all DBH classes) and by individual DBH classes (diam class 1 to 5 for spruce and diam class 1 to 4 for aspen).

Spruce		Equivalence tests				
Data Grouping	CI (Intercept)	Region of Similarity	Min. Region of Equivalence for Intercept	CI (Slope)	Region of Similarity	Min. Region of Equivalence for Slope
Full dataset	21.77-25.46	21.30-26.03	10%	0.76-1.14	0.75-1.25	25%
diam class 1	35.33-44.46	22.07-45.85	35%	0.24-1.07	0.2-1.8	80%
diam class 2	25.94-34.12	17.36-36.05	35%	0.59-1.36	0.55-1.45	45%
diam class 3	18.50-22.97	18.25-24.69	15%	0.06-0.75	0.04-1.9	90%
diam class 4	14.77-17.14	14.28-26.53	30%	0.44-0.72	0.45-1.55	55%
diam class 5	8.82-10.89	8.40-19.61	40%	0.36-1.01	0.35-1.65	65%
Manning (1984)	21.40-25.78	19.08-89.96	65%	0.16-0.27	0.15-1.85	85%
Aspen		Equivalence tests				
Data Grouping	CI (Intercept)	Region of Similarity	Min. Region of Equivalence for Intercept	CI (Slope)	Region of Similarity	Min. Region of Equivalence for Slope
Full dataset	2.15-2.68	2.06-3.10	20%	0.38-0.92	0.35-1.65	65%
diam class 1	1.16-1.38	1.06-1.43	15%	0.78-1.27	0.7-1.3	30%
diam class 2	1.68-2.18	1.41-2.63	30%	-0.33-0.56	-0.35-2.35	135%
diam class 3	2.84-4.31	2.68-4.99	30%	-0.21-1.60	-0.35-2.35	120%
diam class 4	3.05-4.00	2.91-4.86	25%	-0.13-0.76	-0.2-2.2	120%
Alemdag (1984)	2.17-2.60	1.41-55.34	90%	0.04-0.06	0.03-1.95	100%

Note: Confidence intervals (CI) for the intercept (test of bias) and slope (test of accuracy) were obtained using a non-parametric bootstrap based on 5000 replicates. Regions of similarity, which fall within the CIs, were obtained after determining the minimum region of equivalence at which the null hypothesis of dissimilarity could be rejected. All tests were evaluated at alpha=0.05.

Table 6. Estimated parameters (with standard errors, SE, in parentheses) for the relationship of the pipe model ratio (Rp_k = foliage mass/sapwood area at crown quarter section k) as a function of relative depth from crown apex ($Rdinc$) and as a function of distance from ground (H_k) (see Equation 6).

Spruce	Model: $Rp_k = f(Rdinc)$			Model: $Rp_k = f(H_k)$		
	Parameters (SE)			Parameters (SE)		
	λ_0^1	λ_1^1	Adj.- R^2	λ_0^1	λ_1^1	Adj.- R^2
diam class 1	974.08 (78.45)	31.09 (97.95)	1%	999.98 (56.32)	-1.05 (8.10)	1%
diam class 2	1422.27 (110.65)	-250.26 (123.14)	4%	932.31 (57.33)	30.38* (7.71)	19%
diam class 3	1535.32 (141.64)	-57.72 (176.41)	1%	1149.96 (93.69)	27.30* (8.91)	16%
diam class 4	2048.51 (248.21)	-300.09 (335.97)	1%	1488.18 (170.72)	22.09* (14.45)	5%
diam class 5	2117.28 (158.99)	-368.84 (186.46)	3%	1551.73 (189.43)	17.24* (8.72)	6%
Aspen	Model $Rp_k = f(Rdinc)$			Model $Rp_k = f(H_k)$		
	Parameters (SE)			Parameters (SE)		
	λ_0^1	λ_1^1	Adj.- R^2	λ_0^1	λ_1^1	Adj.- R^2
diam class 1	434.55 (29.53)	-134.61* (34.80)	6%	287.03 (54.18)	3.83 (3.58)	1%
diam class 2	459.97 (57.42)	-150.65* (69.63)	9%	80.77 (63.61)	18.62* (5.42)	1%
diam class 3	357.51 (43.34)	-66.48 (57.66)	1%	129.58 (99.69)	10.00* (5.17)	8%
diam class 4	352.75 (75.05)	-35.12 (98.97)	1%	9.78 (135.70)	15.44* (6.33)	18%

* Denotes parameters that are significantly different from the zero at alpha = 0.05.

Table 7. Parameters estimates (standard errors, SE, in parentheses) for the relationship describing specific leaf area (SLA; cm²/g) as a function of crown depth (*Crdpth*) (Equation 7).

	Parameters (SE)		p-value	Adj.-R ²
	η_0	η_1		
Spruce				
diam class 1	56.32 (4.91)	0.31 (0.77)	0.68	<0.05%
diam class 2	43.23 (2.80)	0.37 (0.37)	0.32	<0.05%
diam class 3	39.54 (2.89)	0.31 (0.36)	0.39	<0.05%
diam class 4	37.68 (2.57)	0.23 (0.27)	0.40	<0.05%
diam class 5	41.93 (3.25)	0.42 (0.25)	0.10	2%
	Parameters (SE)		p-value	Adj.-R ²
	η_0	η_1		
Aspen				
diam class 1	93.33 (5.41)	3.88 (1.09)	<0.05	10%
diam class 2	94.23 (6.67)	3.56 (1.50)	0.02	10%
diam class 3	81.48 (4.93)	3.73 (0.91)	<0.05	25%
diam class 4	79.93 (7.66)	5.66 (1.16)	<0.05	32%

543 **Figure captions**

Figure 1. Whole-crown allometry between foliage mass (Kg) and crown length (m) for white spruce (panel a) and aspen (panel b). Lines are predictions from the fitted constant (black lines) and variable (grey lines) allometric equations (Equation 1 and 2, respectively).

Figure 2. Within-crown scaling between foliage mass (Kg) and crown length (m) for quarter sections of the crown (Equation 3). Top panel is for spruce, bottom panel is for aspen.

Figure 3. Pearson residuals from the relationship between foliage mass and crown length in white spruce by crown quarter section (Equation 3) plotted against basal area of larger trees (m^2ha^{-1} ; Bal).

Figure 4. Pearson residuals from the relationship between foliage mass and crown length in aspen by crown quarter section (Equation 3) plotted against basal area of larger trees (m^2ha^{-1} ; Bal).

Figure 5. Plots describing the relationship for the pipe model ratio (Rp_k) versus: 1) the relative distance from crown apex (Rd_{inc}) (left panel) and 2) the distance from ground (H_k ; m) (right panel) within the crowns of white spruce. Numbers at the top of each graph correspond to the diameter class (see text). Solid lines are the fitted linear regression (Equation 6).

Figure 6. Plots describing the relationship for the pipe model ratio (Rp_k) versus: 1) the relative distance from crown apex (Rd_{inc}) (left panel) and 2) the distance from ground (H_k ; m) (right panel) within the crowns of aspen. Numbers at the top of each graph correspond to the diameter class (see text). Solid lines are the fitted linear regression (Equation 6).

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Appendix 1

Scaling up from branch to tree

For both white spruce and aspen, the nonlinear mixed effects model used to obtain estimates of foliage mass at the branch level was:

[A1]
$$\hat{W}_{f,jkl} = \beta_1 \times A_{b,jkl}^{(\beta_2 + b_{2,j} + b_{2,jk})} \times Rdinc_{jkl}^{(\beta_3 + b_{3,j} + b_{3,jk})} + \varepsilon_{jkl}$$

where A_b is branch basal area (cm^2) and $Rdinc$ is the relative distance into the crown from tree apex and $\hat{W}_f$ is foliage mass (in Kg) for branch l in tree k , nested within plot j . The $\beta_1, \beta_2, \beta_3$ are fixed effect parameters, while $b_{2,j}, b_{2,jk}, b_{3,j}$ and $b_{3,jk}$ are the random effects for tree k , nested within plot j . Independent variables tested in the models were limited to those that were measured on all live branches. A power variance weight structure that was a function of branch basal area was used to account for heteroskedasticity, while autocorrelation was addressed through a continuous autoregressive structure. For spruce, the fixed + random effects explained 68% (only fixed effects = 57%) of the variability in branch-level $\hat{W}_f$ (RMSE = 0.08 Kg; $\beta_1=50.41, \beta_2=1.07, \beta_3=-0.63$). For aspen, fixed + random effects accounted for 86% (only fixed effects = 51%) of the variability in branch-level $\hat{W}_f$ (RMSE=0.03 Kg; $\beta_1=21.53, \beta_2=1.07, \beta_3=-1.67$).

Whole-crown allometry between foliage mass (Kg) and crown length (m) for white spruce (panel a) and aspen (panel b). Lines are predictions from the fitted constant (black lines) and variable (grey lines) allometric equations (Equation 1 and 2, respectively).

203x152mm (300 x 300 DPI)

Within-crown scaling between foliage mass (Kg) and crown length (m) for quarter sections of the crown (Equation 3). Top panel is for spruce, bottom panel is for aspen.
198x127mm (300 x 300 DPI)

Pearson residuals from the relationship between foliage mass and crown length in white spruce by crown quarter section (Equation 3) plotted against basal area of larger trees (m^2ha^{-1} ; Bal).
198x127mm (300 x 300 DPI)

Pearson residuals from the relationship between foliage mass and crown length in aspen by crown quarter section (Equation 3) plotted against basal area of larger trees (m^2ha^{-1} ; Bal).
198x127mm (300 x 300 DPI)

Plots describing the relationship for the pipe model ratio (Rp_k) versus: 1) the relative distance from crown apex ($Rdinc$) (left panel) and 2) the distance from ground (H_k ; m) (right panel) within the crowns of white spruce. Numbers at the top of each graph correspond to the diameter class (see text). Solid lines are the fitted linear regression (Equation 6).
254x120mm (300 x 300 DPI)

Plots describing the relationship for the pipe model ratio (Rp_k) versus: 1) the relative distance from crown apex ($Rdinc$) (left panel) and 2) the distance from ground (H_k ; m) (right panel) within the crowns of aspen. Numbers at the top of each graph correspond to the diameter class (see text). Solid lines are the fitted linear regression (Equation 6).
254x120mm (300 x 300 DPI)