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Modelling vertical allocation of tree stem and branch volume for hardwoods

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Whole-tree volume equations are in great demand due to the need to quantify the distribution of wood volume within trees for estimating whole-tree utilization potential. While main stem volume has been extensively studied, related to computing the merchantable timber volume of trees, the relative volume of branches has received much less attention. It is particularly challenging to quantify branch volume in trees with deliquescent branching architecture (i.e. hardwoods) where branching is complex and not strongly controlled by a dominant stem. Here, new mixed-effects cumulative volume profiles are presented that allow for simultaneous volume estimation of the dominant stem and whole tree from ground to the top of the tree. Cumulative branch volume can be estimated at different relative heights from the whole-tree and dominant stem profiles by simple subtraction. The models were developed from destructive sampling of 32 trees from a temperate hardwood forest in Michigan, US. The species in the sample were primarily American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.). The results produce whole-tree cumulative volume models that include all branches in trees and demonstrates the value of studying the whole tree even when the dominant stem is the object of interest.

Introduction

Models for predicting components of tree volume have been a hallmark of forest measurement science since its inception, beginning with simple volume tables to estimate bole saw timber volume to a fixed merchantable top diameter (Gevorkiantz and Olsen, 1955), progressing to increasingly more sophisticated stem profile models, aka 'taper' models, which can predict the volume of the main stem to any height from base to tip (Jordan *et al*., 2005). Clearly, the next phase in tree volume modelling must be to describe the 'whole' tree, i.e. predicting at least tree branch volumes, if not the volume of the root systems, along with the volume of the main stem. Whole-tree volume models are needed to inform sustainable usage of whole trees (Flewelling, 2004; Zakrzewski, 2011), not just their merchantable boles. Tree volume estimation should also be made compatible with whole-tree biomass estimation and carbon accounting systems (MacFarlane, 2011; Van Deusen and Roesch, 2011).

Although whole-tree biomass models are widely available, whole-tree volume models are lacking. Only a few approaches have been developed specifically for estimating whole-tree, above-ground volume including a centroid-based method (MacFarlane, 2010), a volume expansion factor method (MacFarlane, 2011) and an estimation method based on importance sampling (Van Deusen and Roesch, 2011). Recently, MacFarlane (2010) and Zakrzewski (2011) published cumulative volume profiles compatible with taper modelling theory that included wood from both the main stem and large (merchantable) branches, but these works did not include smaller (non-merchantable) branches.

Here, new whole-tree volume profile models are presented, including volume from all branches in trees, with the goal of advancing the field of whole-tree modelling, while accommodating the continued need for accurate and flexible estimation of merchantable main stem volume. A segmented modelling approach is used for fitting of two separate models (for segments below and above crown height) into a whole-tree model similar to the segmented approach used by Max and Burkhart (1976). The crown height is fixed as the join point for the two models, similar to the switching model of Valentine and Gregoire (2001), respecting the onset of branching as a critical inflection point in tree stem form (Adu-Bredu *et al*., 2008; MacFarlane, 2010). A mixed-effects modelling approach is also employed to reflect the within-tree correlations (Valentine and Gregoire, 2001; Leites and Robinson, 2004; Westfall and Scott, 2010) and because mixed-effects modelling often performs better than a fixed-effects modelling approach (Valentine and Gregoire, 2001).

The manuscript is organized as follows. First, a whole-tree model is described along with associated whole-tree and dominant stem cumulative volume profile models. Then, the models

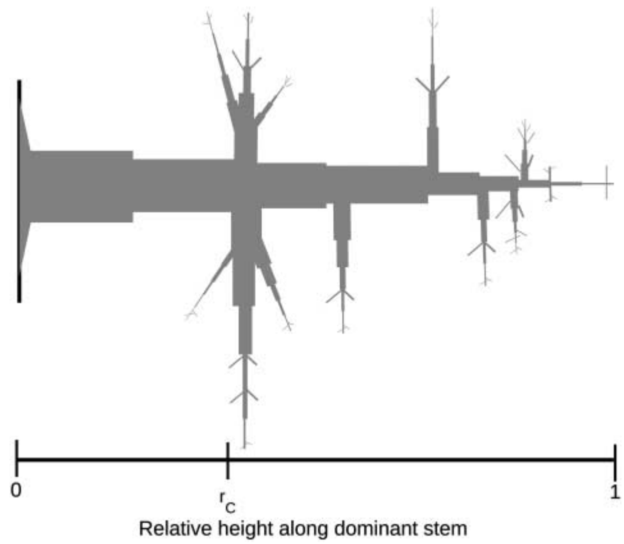

Figure 1 A simplified hardwood tree schematic showing the location of branch volume accumulation along the dominant stem as a function of relative height, ranging from zero at base to one at top of the tree. The first branches encountered are at relative crown height (r_C).

are fit to real trees and the profiles are examined to look at concurrent shifts in whole-tree *vs* dominant stem volume profiles, including shifts in the centroids of volume.

Methods

Whole-tree and dominant stem models

We began with a model of a whole tree that contains a 'dominant' stem to which a set of first-order branches are attached, to which a set of second-order branches are attached, etc. (Figure 1). Here, we use the term *dominant* stem instead of the more commonly used term 'main' stem (or 'bole'), because it is a more biologically meaningful term that reflects the relationship between a dominant stem and other stems in the crown, i.e. the branches.

Like traditional tree volume profile models (e.g. Van Deusen *et al.* 1982), tree volume accumulates in this model from tree base to tree top, assuming some shape of the tree's dominant stem. From the ground to the base of the tree's crown, where the first branch begins, the dominant stem is unambiguous, since there is only one continuous stem. Above the crown base; however, there are multiple stems at each node and one must be chosen to be the dominant one; the rest are called branches. For most conifers, which have a strong apical dominance that suppresses branch growth, the dominant stem is clearly recognizable and the branches subordinate. For some conifers and many hardwoods, apical control is weaker and a more deliquescent branching architecture is realized, making the dominant stem sometimes ambiguous (Oliver and Larson, 1996). To generalize the model and disambiguate main stems and branches, the dominant stem is defined for any tree as the largest and most vertical stem at each branch node, following a path through the tree, from the base to a terminal shoot at the top of the tree; all other parts are called branches.

The dominant stem has a total height, H, and an infinite number of height points from base to tip, denoted as h. Volume (v) can be summed to any relative height in the tree, reaching an asymptote fixed at the total volume of the dominant stem of the tree. The mixed-effects model selected for the cumulative volume of the dominant stem was based on a simple solid of revolution described by Van Deusen *et al.* (1982) and MacFarlane (2010)

$$v_{D_{ij}} = V_{D_j} * (1 - (1 - r_{ij})^{\alpha_1 + u_{1j}}) + \epsilon_{ij}, \tag{1}$$

where $v_{D_{ij}}$ is the dominant stem cumulative volume of position i for tree j in m^3, V_{D_j} is total dominant stem volume in m^3, r_{ij} is relative height of position i for tree j, α_1 is a fixed-effect parameter to be estimated, u_{1j} is a random-effect parameter to be estimated and ϵ_{ij} is a random error term.

Just as a taper model can be integrated to produce a cumulative volume profile, a taper model can be derived from a cumulative dominant stem volume profile (Broad and Wake, 1995). The first derivative of the cumulative volume profile of the dominant stem (equation (1)) divided by H_j gives a function describing the change in the cross-sectional area of the dominant stem over its length, i.e. a taper model:

$$\frac{v'_{D_{ij}}}{H_j} = \frac{V_{D_j}}{H_j} * (\alpha_1 + u_{1j}) * (1 - rh_{ij})^{\alpha_1 + u_{1j} - 1} + \epsilon_{ij}. \tag{2}$$

Unlike traditional tree volume profile models, the volume of the whole tree in this model accumulates both the volume of the dominant stem and the volume of each first-order branch attached to it, and all associated higher-order branches at the point of attachment to the dominant stem (Figure 1).

Below the crown (i.e. the first branch point), the cumulative volume profile is the same for both the dominant stem and the whole tree, but above the crown height (h_C) the profiles diverge (MacFarlane, 2010). Thus, a segmented modelling approach was used, with the join point being the relative height of the crown ($r_C = h_C/H$). The whole-tree cumulative volume model is the volume below crown height plus the cumulative volume above crown height, fixing the intercept to the volume at crown height:

$$v_{C_{ij}} = V_{r_{C_j}} + \beta_j * (1 - (1 - (r_{ij} - r_{C_j}))^{\alpha_2 + u_{2j}}) + \epsilon_{ij}, \tag{3}$$

where $v_{C_{ij}}$ is the whole-tree cumulative volume of stem position i in tree j in m^3, $V_{r_{C_j}}$ is total tree volume at relative crown height (r_C) in m^3, α_2 is a fixed-effect parameter to be estimated, u_{2j} is a random-effect parameter to be estimated, and ϵ_{ij} is a random error term. The term β_j is fixed for tree j as

$$\beta_j = \frac{V_{W_j} - V_{r_{C_j}}}{1 - r_{C_j}{}^{\alpha_2 + u_{2j}}}, \tag{4}$$

where V_{W_j} is the total whole-tree volume for tree j in m^3.

Table 1 Species, code, sample size (n), mean diameter at breast height (DBH), mean height (H) with standard deviation (SD), minimum (min), and maximum (max) values by species

Species	Code	n	Mean DBH (cm) [SD, min, max]	Mean H (m) [SD, min, max]
American beech (*Fagus grandifolia* Ehrh.)	FG	15	56.6 [19.5, 15.3, 91.1]	30.8 [4.9, 16.5, 36.1]
Sugar maple (*Acer saccharum* Marsh.)	AS	13	44.6 [12.4, 27.5, 63.2]	28.4 [3.3, 22.2, 34.0]
Pignut hickory (*Carya glabra* Mill.)	CG	1	62.6 [NA, NA, NA]	34.5 [NA, NA, NA]
Black cherry (*Prunus serotina* Ehrh.)	PS	1	23.0 [NA, NA, NA]	19.1 [NA, NA, NA]
American basswood (*Tilia americana* L.)	TA	1	41.0 [NA, NA, NA]	24.0 [NA, NA, NA]
Slippery elm (*Ulmus rubra* Muhl.)	UR	1	71.5 [NA, NA, NA]	33.3 [NA, NA, NA]
All	ALL	32	50.9 [17.6, 15.3, 91.1]	29.4 [4.7, 16.5, 36.1]

The mixed-effects whole-tree cumulative volume profile was specified as follows:

$$v_{W_{ij}} = I_1 v_{D_{ij}} + I_2 v_{C_{ij}}, \tag{5}$$

where $v_{W_{ij}}$ is the whole-tree cumulative volume of stem position i in tree j in m^3, I_1 is an indicator variable, with a value of 1 when relative height is at or below relative crown height, and a value of 0, when relative height is above relative crown height, and I_2 is an indicator variable with values of 0, when relative height is below relative crown height and 1 when relative height is above relative crown height.

Study site and data collection

Tree data were collected for model fitting within a 36-ha second-growth maple-beech stand at the Fred Russ Experimental Forest in southwestern Michigan, which is owned by Michigan State University. The Fred Russ Experimental Forest is located in Cass County, in Decatur, Michigan, with a total area of 381 ha that supports a diverse range of species and stand conditions. Kalamazoo, Ormas and Oshtemo are the three primary soil series found at the site. Average annual precipitation over 30 years is 1035 mm (NCDC, 2011). The Kalamazoo and Oshtemo soil series are fine-loamy and coarse-loamy, mixed, mesic typic hapludalfs, respectively. The Ormas soil series is a coarse-loamy, mixed, mesic arenic hapludalfs on an outwash plain landform with a level topography (Soil Survey Staff, 2011).

In the spring of 2010, a windstorm uprooted >200 trees in the 36 ha stand providing an opportunity for whole-tree measurements as part of a salvaging operation. A sample of 32 wind-thrown trees with intact crowns was selected from the population of uprooted trees for measurement. Tree selection sought to include as wide a range of tree sizes (stem diameters at breast height (DBH)) as possible, irrespective of species. Table 1 lists the size range and species of the sample trees. The sample trees had a size range from 15- to 91-cm DBH and a mean height of 29.4 m, with 87.5 per cent of the trees being either American beech (*Fagus grandifolia* Ehrh.) or sugar maple (*Acer saccharum* Marsh., Table 1). After salvaging the wind-thrown trees, the residual basal area of the stand was 22.13 m^2 ha^{-1}. No inventory data for this stand were available prior to the windstorm to compute the pre-storm basal area.

Dominant stem volume

For each tree, dominant stem circumference was measured at stump height, at 37-cm above ground level, and at breast height, 137-cm above ground level. Additional circumference measurements were taken at 2-m length intervals up to the first branch junction (h_C), and then continued along the dominant stem for all branch junctions until reaching the terminal shoot (Figure 2). Upon encountering the first branch node, circumference measurements were taken at the before fork (BF) location of the stem and then at the after fork (AF) location of dominant stem and each associated branch (Figure 2). The BF was defined as the location where included bark due to branching was no longer visible, as this is most likely the origin of branches off the dominant stem. The AF was the location immediately after the point at which the fork occurred above any swelling at the branch collar. The total dominant path length from base to tip along the dominant stem was measured to define H.

The volume of a section, f, of the dominant stem was determined by Smalian's formula for volume:

$$v_f = \frac{A_{1f} + A_{2f}}{2} * z, \tag{6}$$

where v_f is the volume of section f, in m^3, A_{1f} is the cross-sectional area, in m^2, of the lower end of section f, A_{2f} is the cross-sectional area, in m^2, of the upper end of section f, and z, in m, is the length of section f.

The cumulative dominant stem volume profile, $v_D(h)$, was found by iteratively summing all sections

$$v_D(h) = \sum_{f=1}^{n(h)} v_f, \tag{7}$$

where n is the number of segments to a measured height, h. The volume of the stump section was added to equation (7), which was approximated by a cylinder, ignoring the root flare near ground level. The total dominant stem volume was determined by summing n segments up to H and adding the stump volume.

Whole-tree volume: random branch sampling

Estimating the total volume of all of the branches for each tree would have been an enormous undertaking, so an estimate of V_W

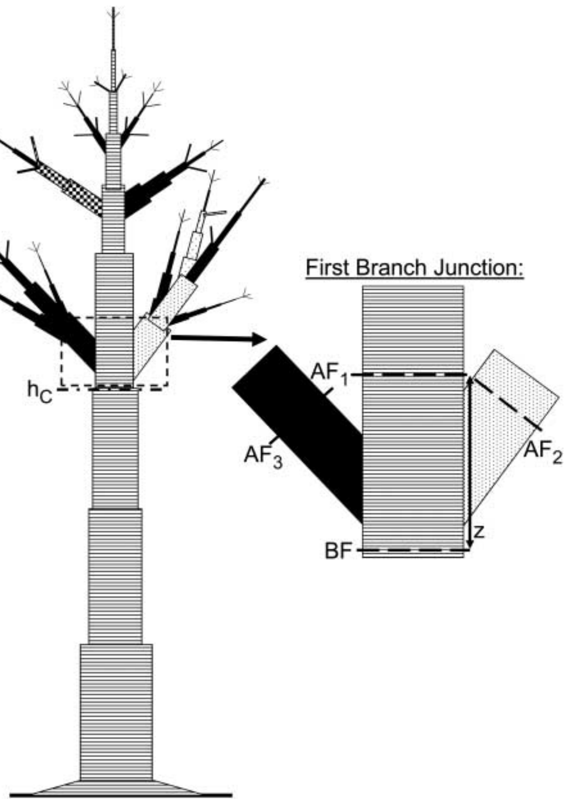

Figure 2 A simplified hardwood tree schematic where the dominant stem is indicated by horizontal lines, the first random branch path is indicated by a checkered pattern, the second random branch path is indicated by dots, and non-sampled branches are solid. The first branch junction at crown height (h_C) demonstrates the length (z) and circumference measurements taken at each branch junction for the BF and the AF locations.

(outside bark) was obtained using the method of random branch sampling (RBS, Gregoire *et al.*, 1995). The same measurement methods as described above for the dominant stem were used, but at each branch junction a segment was selected for measurement based on probability proportional to the cross-sectional area of the AF (the square of diameter), following a path through the tree until a point it diverged from the dominant stem and then along that branch to a terminal shoot. The probability, p_q, of selecting a particular AF was determined by

$$p_q = \frac{d_{\mathrm{AF}q}^2}{\sum_{q=1}^{m} d_{\mathrm{AF}q}^2}, \tag{8}$$

where $d_{\mathrm{AF}q}$ is the diameter of the qth AF, and m is the number of AF at that particular branch junction.

A random number between 0 and 1 were generated with a field computer to enable random selection. For example, suppose the first branch junction shown in Figure 2 had three AFs with probabilities of selection of 0.5, 0.3, and 0.2 for AF_1, AF_2 and AF_3, respectively. If the random number generated was ≤ 0.5 then AF_1 was selected, >0.5 and including 0.8 then AF_2 was selected and >0.8 then AF_3 was selected.

The sectional volume for the random path was used to compute the volume of the whole tree, using the inverse of the cumulative selection probability as expansion factors for a section in the random path to represent parts of the tree not selected (Valentine *et al.*, 1984; Gregoire *et al.*, 1995). A second random branch path was sampled on each tree to determine mean whole-tree volume and the variation of whole-tree volume estimates between the two different selected paths. The (mean) volume of all branches in the tree (V_B) was then calculated by subtracting the total dominant stem volume from the estimate of whole-tree volume.

To describe the distribution of branch volume in the tree, V_B was distributed back to each first-order branch, v_{Bl}, proportional to its basal diameter squared

$$v_{Bl} = V_B * \frac{d_{Bl}^2}{\sum_{l=1}^{k} d_{Bl}^2}, \tag{9}$$

where d_{Bl} is the diameter of the lth first order branch, and k is the total number of first-order branches in an individual tree. The volumes for each first-order branch and all attached higher-order branches were incorporated into the profile at the relative height of the associated AF of the dominant stem (Figure 1). The redistribution of branch volume ensured that the final observation of the cumulative whole-tree volume profile was equal to the mean total whole-tree volume outside bark from the two random branch paths.

Model fitting

Fixed-effects models were selected for each individual tree with parameters estimated using the nlsList function from the nlme package (Pinheiro *et al.*, 2011). The parameters from the fixed-effects model were used as starting values for the mixed-effects models using the nlme function in the nlme package. The models were fit to all species and individual species with multiple tree observations with the best-fit model being selected based on the lowest Aikaikes Information Criterion, AIC, value. Models were also selected to be compatible with the estimated total volumes. All statistical models were fit in the R statistical environment (R Development Core Team, 2010).

Results

Total volume estimates

Table 2 shows V_D and V_W computed for each tree in the dataset. V_D was measured directly, but V_W was estimated from two random branch samples, so it has additional uncertainty associated with it. The results show that RBS performed well, overall, as the average coefficient of variation of V_W for trees was 0.11, with 20 of the 32 trees having a coefficient of variation of ≤ 0.10. The smallest coefficient of variation (CV) was 0.01 and the largest ($CV = 0.49$) for the massive-crowned 91-cm *Fagus grandifolia* which had a total estimated $V_W = 33.2\,\mathrm{m}^3$. Presumably, larger

Table 2 Diameter at breast height (DBH), species code (spp), total dominant stem volume (V_D), total volume estimate from the first random branch sample (V_{W_1}), total volume estimate from the second random branch sample (V_{W_2}), mean total volume (V_W), standard deviation of total volume (SD), and coefficient of variation of total volume (CV) summary statistics for each individual tree

DBH	spp	V_D	V_{W_1}	V_{W_2}	V_W	SD of V_W	CV of V_W
15.3	FG	0.14	0.24	0.23	0.23	0.01	0.03
23.0	PS	0.36	0.51	0.49	0.50	0.01	0.03
27.5	AS	0.74	1.11	1.01	1.06	0.07	0.07
31.7	AS	0.82	1.71	1.21	1.46	0.35	0.24
33.1	AS	1.13	1.56	1.91	1.73	0.25	0.14
33.9	AS	0.95	1.73	2.21	1.97	0.34	0.17
35.6	AS	1.29	2.03	2.24	2.13	0.14	0.07
36.7	FG	1.25	1.98	2.64	2.31	0.47	0.20
38.8	AS	1.54	2.19	2.05	2.12	0.10	0.05
41.0	TA	1.47	2.01	1.99	2.00	0.01	0.01
42.8	AS	2.39	2.89	2.92	2.90	0.02	0.01
42.9	FG	1.86	3.25	3.52	3.38	0.19	0.06
45.1	FG	2.73	3.71	5.40	4.55	1.20	0.26
46.0	FG	2.51	3.46	4.38	3.92	0.65	0.17
47.1	FG	2.42	3.95	4.46	4.21	0.36	0.09
48.1	AS	2.26	4.41	3.82	4.11	0.42	0.10
48.5	AS	2.79	4.64	4.12	4.38	0.37	0.08
50.1	FG	2.10	4.68	6.13	5.41	1.03	0.19
54.6	AS	2.85	5.32	4.66	4.99	0.47	0.09
55.1	FG	3.32	4.87	5.87	5.37	0.71	0.13
56.3	FG	3.77	6.81	7.04	6.92	0.16	0.02
60.4	AS	3.49	7.05	6.82	6.94	0.17	0.02
61.9	AS	4.86	7.53	7.28	7.40	0.17	0.02
62.6	CG	5.16	8.77	8.44	8.60	0.24	0.03
63.2	AS	4.35	8.47	9.21	8.84	0.52	0.06
63.6	FG	4.34	6.63	7.42	7.03	0.56	0.08
67.5	FG	3.91	6.46	8.63	7.55	1.54	0.20
71.5	UR	6.39	13.66	14.04	13.85	0.27	0.02
75.4	FG	4.47	8.86	11.74	10.30	2.04	0.20
78.2	FG	7.04	12.31	16.83	14.57	3.20	0.22
78.5	FG	7.61	11.45	11.83	11.64	0.27	0.02
91.1	FG	8.06	21.75	44.58	33.17	16.14	0.49

trees might have needed more branch paths sampled to produce better whole-tree volume estimates; however, DBH was not a good predictor of the need for more branch samples as indicated by a low correlation between the CV of V_W and DBH (Pearsons r $= 0.29$). The per cent branch volume (V_B/V_W) was a better indicator ($r = 0.65$) of the CV of V_W, but that could not be known a priori, because it was computed from V_D and V_W. On average, ~41% of the volume of these hardwoods was estimated to be in the branches, with a range of 18–75% of the V_W in branches. In general, the larger DBH trees had larger proportions of branch volume, but the overall correlation was not strong ($r = 0.55$). Because of the high uncertainty associated with the volume of the massive-crowned 91-cm *Fagus grandifolia*, it was eliminated from further analyses.

Regression analysis (excluding the very large *Fagus*) revealed that V_W was strongly non-linearly correlated with DBH ($V_W = 0.0003(\mathrm{DBH})^{2.4823}$, $r^2 = 0.98$) and that V_D was strongly non-linearly correlated with V_W ($V_D = 0.649(V_W)^{0.9178}$, $r^2 = 0.97$), the latter indicating a general shift of whole-tree volume from the dominant stem to branches as these trees became more massive.

Table 3 Parameter estimates of model (1) for the cumulative volume of the dominant stem for the all-species (ALL), American beech (FG), and sugar maple (AS) mixed-effects models. For the fixed parameters, the standard error of estimates is given in parantheses

Parameter	ALL estimate	FG estimate	AS estimate
α_1	2.769 (0.048)	2.807 (0.068)	2.782 (0.076)
var(u_{1j})	0.064	0.058	0.072
ϵ_{ij}	0.044	0.048	0.030
AIC	−6342.906	−3054.503	−2955.086

Table 4 Parameter estimates of model (3) for the cumulative whole-tree volume above relative crown height for the all-species (ALL), American beech (FG), and sugar maple (AS) mixed-effects models. For the fixed parameters, the standard error of estimates is given in parantheses

Parameter	ALL estimate	FG estimate	AS estimate
α_2	4.453 (0.281)	4.500 (0.447)	4.446 (0.383)
var(u_{2j})	2.226	2.569	1.784
ϵ_{ij}	0.139	0.158	0.096
AIC	−1736.471	−665.477	−1115.896

Cumulative volume profiles

Table 3 gives the parameter estimates of model (1). The dominant stem form coefficient α_1 was not very different between the all-species model or the separately fit models for American beech and sugar maple trees, and the AIC value for the all-species model was lower than that of either the American beech or sugar maple models, indicating a fairly similar dominant stem form for the trees in this stand regardless of their species. The α_1 values were estimated with a relatively low error and the overall estimated error in the models was generally low. Additionally, the random effects term indicated that relatively small adjustments needed to be made to fit the model to individual trees (roughly a 2% adjustment to the mean form coefficient).

Table 4 gives the parameter estimates and fit statistics for equation (3). As with the dominant stem form, the overall trend showed a similar mean whole-tree form coefficient α_2 for the all-species model and the species-specific models fit to American beech and sugar maple; however, the variation around the coefficients (relative standard error of α_2) was relatively large. Further, the random-effect parameter indicated that relatively large shifts in α_2 were needed to have the model conform to individual trees. Thus, individual tree variation in whole-tree form was much greater than that of the dominant stem. Nonetheless, the models generally fit the data quite well (Figure 3).

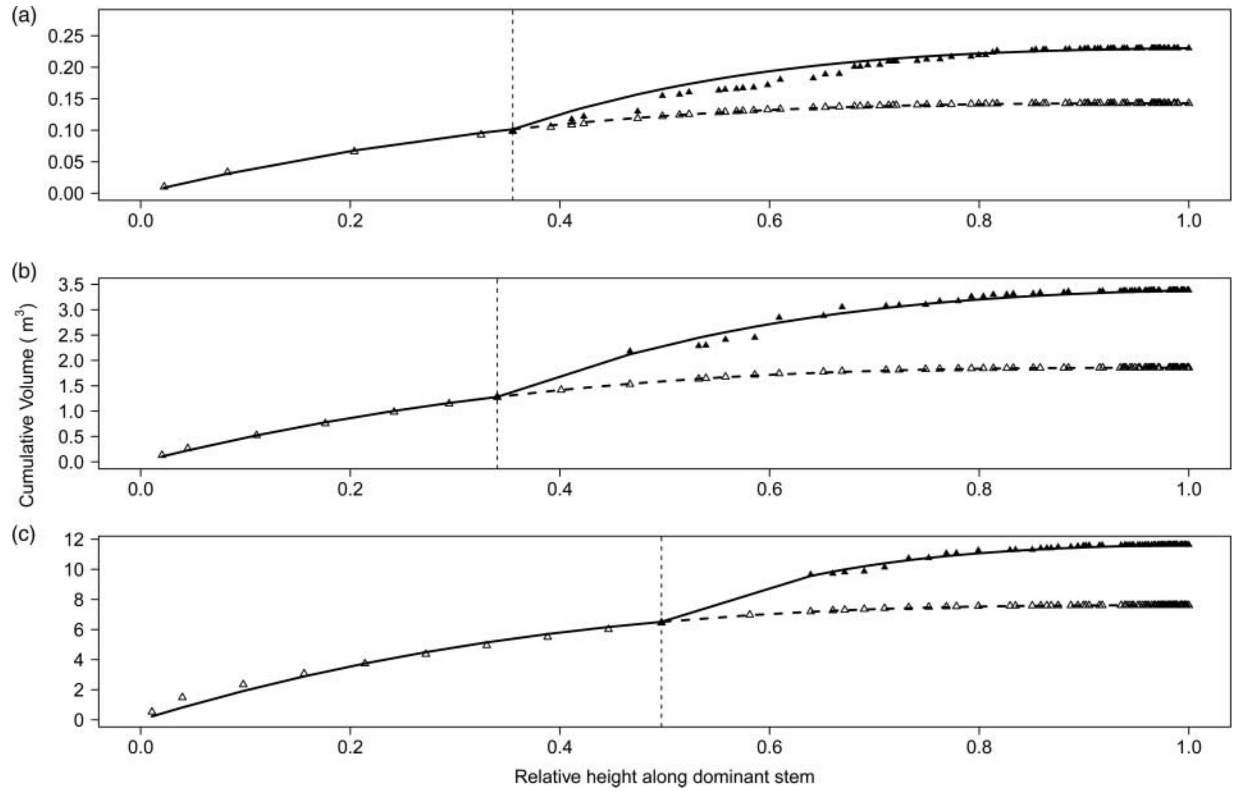

Figure 3 Cumulative volume, m^3, profiles for the dominant stem (model (1)), represented by a dashed line above relative crown height, and whole tree (model (5)), represented as the solid line, as a function of relative height along the dominant stem for the (a) minimum, (b) median, and (c) second largest DBH American beech (FG) trees. The vertical dashed line represents relative crown height.

Figure 3 shows examples of the whole-tree and dominant stem cumulative volume profile for American beech trees of three different sizes. First, it can be observed that whole-tree volume increases by ∼1.5 orders of magnitude over the size range of trees examined, but the cumulative volume profiles look similar in form. The branch volume is the difference between the two curves above relative crown height (Figure 3) and it is clear that significant volume is accumulating in branches for trees of very different sizes. In some cases, the model form was too simple to capture the irregularity of branch volume accumulation, which tends to occur in 'jumps', where large branches are encountered after a series of smaller ones nearer to the base of the crown (e.g. the tree in Figure 3a); the model essentially smooths out these jumps in the profile. It is also clear that the higher the crown height the more the whole-tree volume profile is dominated by the dominant stem.

Derived taper models

The derived taper model (equation (2)) generally fit the dominant stem data well (Figure 4), although it did not capture the flare of the stem near the base of the tree well, nor some of the subtle inflection points along the rest of the profile, as the cumulative volume profile chosen was a simple one. A dominant stem taper model that better describes inflection points in a tree's stem might fit the dominant stem better, but would also make fitting the crown-segmented cumulative volume profile more complicated (e.g. Valentine and Gregoire, 2001). A whole-tree taper model could be similarly derived from the cumulative whole-tree volume profile, but its meaning would be ambiguous because in the tree model the branch orientation in the vertical vector of the dominant stem was unknown and assumed horizontal (Figure 1).

Centroids of dominant stem and whole-tree volume

The centroid of volume is defined as the location aboveground in a tree where half of the total volume is above and half of the total volume is below. It has a theoretical value for understanding dominant stem-whole-tree volume relationships (Forslund, 1982; MacFarlane, 2010). Cumulative volume profiles enable the estimation of the centroid of volume for trees which enables exploration of these relationships.

The centroid of dominant stem volume was found by expressing the cumulative dominant stem volume in terms of relative volume, setting relative volume equal to a half and solving for relative height

$$x_{D_j} = 1 - 0.5^{1/(\alpha_1 + u_{1j})}, \tag{10}$$

where x_{D_j} is the centroid of dominant stem volume for the jth tree, and α_1 and u_{1j} are given in Table 3.

The centroid of whole-tree volume for every tree j has two possible solutions, due to the segmented model (equation (5)).

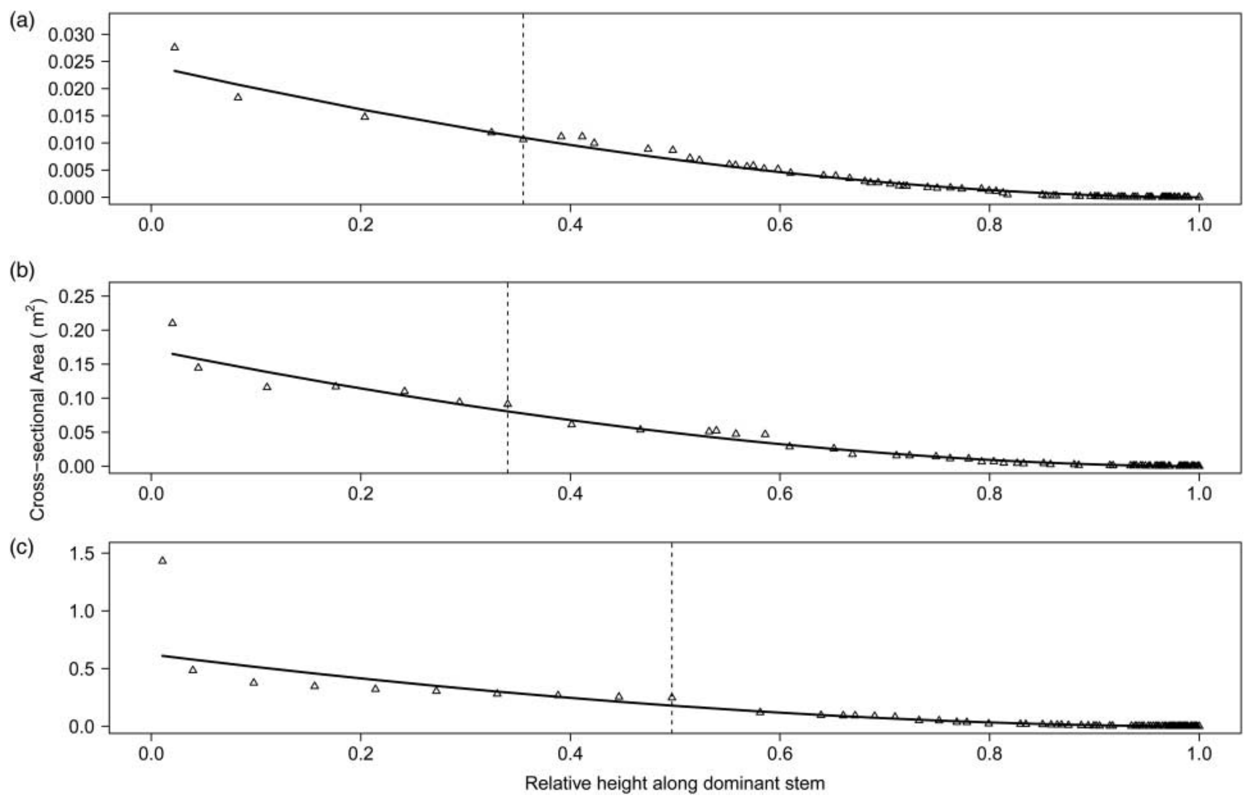

Figure 4 Cross-sectional area, m^2, (taper functions) of the dominant stem (equation (2)), represented by solid lines, as a function of relative height along the dominant stem for the (a) minimum, (b) median and (c) second largest DBH American beech (FG) trees. The vertical dashed line represents relative crown height.

The first solution occurs when the centroid of whole-tree volume occurs at or below relative crown height

$$x_{W_j} = 1 - \left(1 - \frac{V_{W_j}}{2V_{D_j}}\right)^{1/(\alpha_1 + u_{1j})}, \tag{11}$$

where x_{W_j} is the centroid of whole-tree volume for the jth tree and α_1 and u_{1j} are given in Table 3. The second solution occurs when the centroid of whole-tree volume occurs above relative crown height:

$$x_{W_j} = 1 + r_{C_j} - \left(1 - \frac{V_{W_j}}{2\beta_j} + \frac{V_{r_{C_j}}}{\beta_j}\right)^{1/(\alpha_2 + u_{2j})}, \tag{12}$$

where α_2 and u_{2j} are given in Table 4.

Applying equations (10)–(12) to these study trees, the mean centroid of dominant stem volume for all species was found to be 0.222, with a range from 0.185 to 0.251. For reference, a centroid of 0.20 indicates a neiloid-shaped stem, 0.25 a cone-shaped, and 0.5 a cylindrical (non-tapering) one (Forslund, 1982). The mean whole-tree centroid of volume was 0.391, ranging from 0.303 to 0.500. So, the average centroid of whole-tree volume was ~76% higher than that of the dominant stem, because the whole-tree tapers more gradually than the dominant stem and branch volume partially counterbalances vertical volume decline in the dominant stem due to tapering. Visualizing relative cumulative volume profiles helps to understand this pattern (Figure 5).

The same three trees shown in Figure 3 are shown in Figure 5, except that their relative cumulative volume profiles are plotted, which asymptotically approach 100% of their respective volumes. Note that the relative volume of the whole tree accumulates more gradually below relative crown height (Figure 5), because the volume below the crown is the same for both the dominant stem and the whole tree, but V_W is always larger than V_D. Above crown height, the additional volume from branches causes an abrupt rise in relative volume because all volume associated with that branch or branches is assigned to its origin off the dominant stem (see Figure 1). Then volume tapers again approaching the top of the tree. The difference between the two centroids reflects both the relative size of the crown and the relative height, where branching begins (Figure 5). The mean difference was 0.168, with a range of 0.072–0.280.

The position of the crown base (i.e. relative height) relative to the centroids of volume serves to further illustrate how branching effects the relative allocation of volume within trees (Figures 5 and 6). For about three-quarters of the trees (23 of 31),

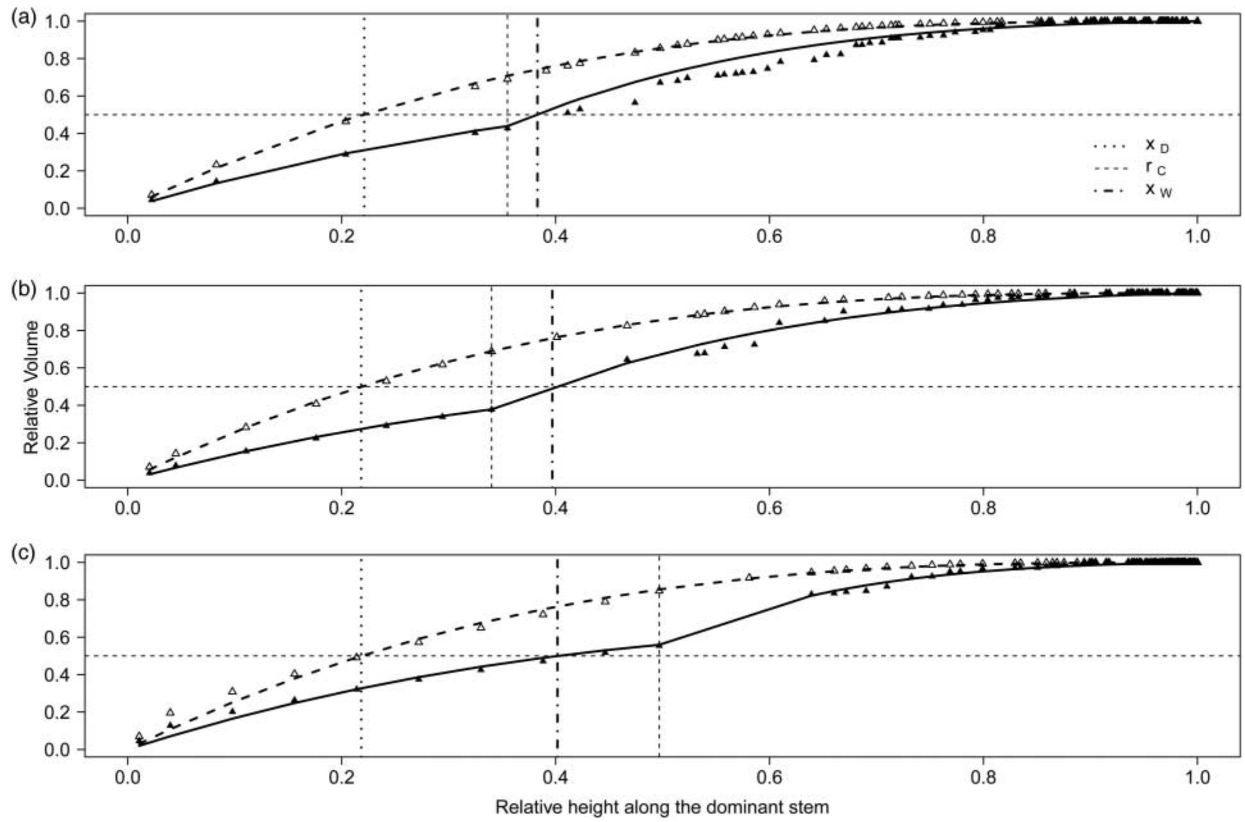

Figure 5 Relative volume profiles of the dominant stem (model (1)), represented by a dashed line, and whole tree (model (5)), represented as the solid line, as a function of relative height along the dominant stem for the (a) minimum, (b) median, and (c) second largest DBH American beech (FG) trees. The horizontal dashed line indicates a relative volume of 0.5, the centroid of volume. The dotted vertical line indicates the relative height of the centroid of volume for the dominant stem (x_D), the vertical dashed line represents relative crown height (r_C) and the dash and dot vertical line indicates the relative height of the centroid of volume for the whole tree (x_W).

the relative crown height fell between the centroids of dominant (x_D) and whole-tree volume (x_W); the other eight had centroids below relative crown height (Figure 6). In general, when branches are attached lower on the dominant stem x_W is shifted downward (Figure 6). There was a fairly strong linear correlation between x_W and relative crown height (Table 5), with the notable exception of an outlying sugar maple tree, which had a relatively small per cent branch volume (18%) compared with other trees branching at the same relative height (circled in Figure 6). The cumulative volume profile of this tree was mostly defined by the dominant stem profile. For all but two of the trees, x_D was below the crown base (Figure 6). x_D was much less sensitive to the relative crown height than x_W although x_D was still significantly positively correlated with it (Table 5). A model for Michigan hardwoods developed by MacFarlane (2010) accurately predicted this pattern (Figure 6), but systematically underestimated x_D for the trees in this study (Table 5), because MacFarlane's model included only volume from large branches. Since smaller branches tend to be higher up in the tree and towards the periphery of the crown, it makes sense that including them would result in an upward shift in the centroid of volume for the whole tree.

Discussion

New whole-tree models

The new model system presented here builds on a traditional approach to modelling tree volume to any height (e.g. Van Deusen *et al*., 1982), but extends it by adding additional volume from all branches at their attachment points to the dominant stem. This approach preserves the dominant stem model as an object of interest, but places it in a larger model framework that contains the whole (aboveground) tree.

While there are scarcely any models to contrast results from this study with, the closest is that of Zakrzewski (2011), who recently offered a cumulative tree volume model conforming to a contemporary stem taper modelling approach, but which also accumulates volume from both the main stem and tree branches. A major difference is the underlying tree model. Zakrzewski's underlying tree model virtually folds branches upward, parallel with the dominant stem, so that the cross-sectional area of all tree parts are oriented in a vertical plane, as opposed to here where they were 'folded out' (Figure 1). 'Folding up' allowed Zakrzewski to create a fully integrable/differentiable tree volume profile, whereas folding out only allowed that property for the

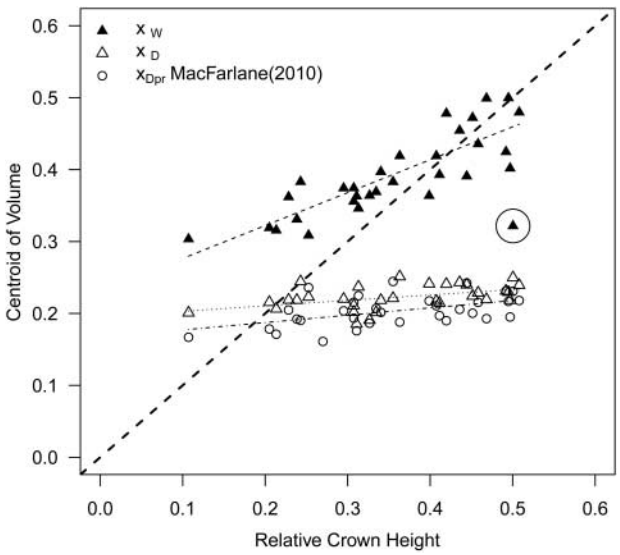

Figure 6 Scatter plot for the centroid of dominant stem volume (x_D), shown as open triangles, and the centroid of whole-tree volume (x_W), shown as filled triangles, against relative crown height. The open circles show the predicted centroid of dominant stem volume (x_{Dpr}) for the best prediction model from MacFarlane (2010). Linear regression lines are also shown for each set of data points. The outlying point (circled) for x_W was excluded from the linear regression for x_W. The 1:1 line represents the location where the centroid of volume is located at relative crown height.

dominant stem. However, Zakrzewski's model does not allow for separation of branch *vs* dominant stem volume components as our model does; in his model they are confounded. Folding up allows for smoothing of the volume profile, but creates an artefact that the projected ends of branches may be higher than the height of the tree (see also Van Deusen and Roesch, 2011). Folding out generates discontinuities ('jumps') in the tree profile, but these can be handled by model segmentation and have heuristic value in that the magnitude of jumps at different crown positions relate to the relative allocation of wood to the dominant stem *vs* branches (discussed in the next section). Both folding up and folding out models of branch distribution differ from the exact vertical distribution of volume of the tree above ground, because a true branch volume distribution model would be incredibly difficult to fit to data from real trees, as it would require slicing the tree from top to bottom in discrete vertical planes and computing the volume in each subplane.

One challenge for application of the new volume models presented here is that they require estimates of total volume (V_W and V_D) as inputs. A variety of standard measurement techniques are available for estimating V_D and many different volume models have been developed across different regions of the US (Woodall *et al.*, 2011) and compiled in a volume equations library. DBH and total tree height (H) are the two most common predictor variables for total dominant stem volume (Hahn and Hansen, 1991). Fortunately, whole-tree volume is also highly correlated with DBH, H, and V_D is highly correlated with V_W, as our results showed here. Since DBH, H and r_C are all standard tree measurements, calibration of these models should not pose a significant burden and compatibility in model calibration of the dominant

Table 5 Parameter estimates for linear models of the centroid of whole-tree volume (x_W), the centroid of dominant stem volume (x_D), and the predicted centroid of dominant stem volume (x_{Dpr}) from MacFarlane (2010) for all trees

Parameter	x_W[1]	x_D	x_{Dpr}
b_0	0.2307 (0.0200)	0.1955 (0.0100)	0.1669 (0.0119)
b_1	0.4576 (0.0543)	0.0756 (0.0268)	0.1021 (0.0322)
R^2	0.7172	0.2149	0.2512

The standard error of estimates is given in parantheses.
[1]Excludes the outlying tree from the linear regression.

stem and whole-tree profiles can be assured through simultaneous estimation procedures for model parameters, such as seemingly unrelated regression (LeMay, 1990; Parresol and Thomas, 1996). If model building is associated with local destructive sampling, the measurements described here are relatively easy to obtain.

Dominant stem–whole-tree relationships

The cumulative models presented here allowed us to explore relationships between the dominant stem and the whole trees they are part of. The models parameterize this relationship explicitly through the magnitude of difference between V_W and V_D and the position of the join point r_C. The data support the theoretical model and observations of MacFarlane (2010), who found a very similar mean centroid of dominant stem volume for 11 common hardwood tree species in Michigan with large branches (10-cm diameter minimum), with a similar magnitude of shift in the centroid of the dominant stem for trees with and without large branches. Both of these values for trees with merchantable branches are lower than the 0.3 value for the centroid identified by Forslund (1982) for dominant stems of aspen (*Populus tremuloides*, Michx.) trees, and typically used for the centroid method of tree volume estimation (Wood *et al.*, 1990; Wiant, Jr. *et al.*, 1991), indicating a shift in the dominant stem volume profile due to branching. One possible difference between this study and other studies is that other studies typically seek to exclude forked trees or trees of poor form (e.g. Forslund, 1982), which might exclude a lot of trees with large branches. On the other hand, the relatively small magnitude of the shift of the centroid of dominant stem volume with changes in crown size indicates a homogenizing effect of stand conditions on dominant stem form (Figure 6). Also, the relatively high variation about the mean trend in x_D (Figure 6) may help to explain why it has been such a challenge to find consistent improvements in dominant stem profile models by introducing predictor variables relating to crown size (Valentine and Gregoire, 2001; Leites and Robinson, 2004).

Another interesting finding of this study was that a species-composite model was shown to be sufficient for the cumulative dominant stem volume profile for hardwood trees of mixed species. This means that the form of the dominant stem was not very different between the species, likely because they were growing under the same stand conditions. The same was true for the mean whole-tree form, except that the between-tree variation was much higher. This supports the rationale for using species-composite models in cases where within-species variation may exceed between-species variation (Gevorkiantz and Olsen, 1955), which might be common in mixed hardwood stands where a tree's personal growth history has much more to do with its volume allocation to a dominant stem *vs* branches. Obviously, a tree's species and shade tolerance has much to do with its allocation to branches (Sumida and Komiyama, 1997), but the tree's growing environment modifies these inherent tendencies. In particular, shading of branches from the sides generally increases the dominance of a 'main' stem, whereas top-shading of the terminal leader tends to decrease dominance (Oliver and Larson, 1996). Considering that hardwood species typically have weak apical control (Oliver and Larson, 1996), the architecture of the crown and dominance of a single main stem is likely highly plastic.

Ultimately, this new modelling system captures the relationship between changes in dominant stem form and a shifting allocation to branches in a new way. While some previous work with taper models focused on how branching (Adu-Bredu *et al.*, 2008) or crown size (Larson, 1963; Valentine and Gregoire, 2001; Leites and Robinson, 2004) can effect 'dominant' stem taper, such taper models do not consider or describe the accumulated branch volume associated with the rest of the tree, because the rest of the tree is essentially outside of the model framework. Adu-Bredu *et al.* (2008), for example, studied the stem profile of teak (*Tectona grandis*, L.f.) in West Africa, using a model that computed reductions in the dominant stem profile at forks, but did not account for the associated volume shifted into branches and away from the dominant stem. So, new whole-tree volume models should focus on how branches influence dominant stem form and vice versa in a common modelling framework.

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