Abstract.—New models were presented to understand the relationship between the dominant stem and a whole tree using cumulative, whole-tree mass/volume profiles which are compatible with the current bole taper modeling paradigm. New models were developed from intensive, destructive sampling of 32 trees from a temperate hardwood forest in Michigan. The species in the sample were primarily American beech (Fagus grandifolia Ehrh.) and sugar maple (Acer saccharum Marsh.). The new profile models allowed for both mass and volume of both the dominant stem and branches to be estimated from ground level to the top of the tree. Nonlinear mixed effects models were used in the model development to account for the correlations among multiple measurements of an individual tree. Allometric scaling relationships between the dominant stem and branches can be directly derived from the new models and can be used to define sampling approaches to localize predictions of generalized whole-tree models via measurements of simple branch parameters.

INTRODUCTION

Integrated whole-tree biomass and volume equations are in great demand due to the simultaneous need to improve estimation of forest carbon stocks and to quantify the distribution of wood volume within trees for estimating whole-tree utilization potential. While the volume of the dominant stem in a tree, generally referred to as the bole, has been extensively studied, the relative mass and volume of branches has received much less attention. It is particularly challenging to quantify the branch volume and branch mass in trees with a deliquescent branching architecture (i.e., hardwoods), and it is even more difficult to model the bole for such trees because the lack of apical dominance makes definition of the bole more obscure. Here, a dominant path through a tree’s branch network is defined as the cumulative bole profile and other nondominant branches contribute to cumulative volume and mass along the dominant path.

METHODS

Study Site and Tree Selection

The study site included 20.8 ha of a 36-ha second-growth maple-beech stand at the Fred Russ Experimental Forest in southwestern Michigan owned by Michigan State University. The Fred Russ Experimental Forest is located in Cass County, in Decatur, MI, 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. 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 (USDA NRCS 2011). The 30-year average annual precipitation is 1035 mm (NOAA 2011). The residual basal area of the stand is 22.1 m²/ha.
In the spring of 2010, wind-thrown trees with intact crowns were sampled following a windstorm that uprooted more than 200 trees. Sampling began in late spring of 2010 and included as wide a range of diameter at breast height (d.b.h.) as possible, irrespective of species, with at least one individual in each 10 cm size class ranging from 10-95 cm. Selected trees were relatively isolated from other fallen trees so that the branches were easily measurable. The 32 sample trees had a mean d.b.h. of 50.9 cm and mean height of 29.4 m with 87.5 percent of the trees being American beech (*Fagus grandifolia* Ehrh.) or sugar maple (*Acer saccharum* Marsh.).

**Volume Profiles**

The dominant stem in this study was defined by following the largest and most vertical branch at each fork to an apical control point. For each tree, circumference was measured at stump height, 37 cm above ground level, followed by d.b.h. Additional circumference measurements were taken at 2-m length intervals up to the first branch junction. Upon encountering the first branch, circumference measurements were taken at the before fork (BF) location of the stem and then at the after fork (AF) location of each branch based upon functional branch analysis protocols (van Noordwijk and Mulia 2002). The BF was defined as the location where bark due to branching was no longer visible, as this is most likely the origin of the branches off the dominant stem. The AF was the location immediately after the point at which the fork occurred. The length from the BF to the AF was also recorded. The process of length and circumference measurements continued by following the dominant stem until the terminal bud was reached. The volume of each section was determined by Smalian’s formula for volume (Avery and Burkhart 2002). The cumulative dominant stem volume profile is the accumulation of consecutive sections as a function of height.

An estimate of the total aboveground volume outside bark of an entire tree was obtained by random branch sampling (Gregoire and Valentine 2008). The same measurement methods as for the dominant stem were used, but a segment was selected based on probability proportional to size at each branch junction. 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 (Gregoire and Valentine 2008). The volume of branches was found by subtracting the total dominant stem volume from the whole tree volume. 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 total branch volume determined from the two random paths was then distributed back to each first order branch immediately off the dominant stem. The volume for each first order branch and all higher order branches were incorporated into the profile at the height at which the first order branch connected to the dominant stem. The redistribution of the branch volume ensured that the final observation of the cumulative whole tree volume profile was the same as the mean total whole tree volume outside bark from the two random branch paths.

**Density Profiles**

To obtain a dominant stem mass profile, a profile of density for each tree was developed by harvesting tree discs. Discs were harvested at every circumference measurement location below crown height. Above crown height, discs were collected at every AF along the dominant stem path. Approximately 5- and 10-cm-thick discs were harvested for smaller and larger circumferences, respectively. Each disc was measured for green mass and green volume immediately after transportation to the laboratory. Mean disc thickness was calculated by averaging the thickness of eight locations at 45° angles. Green volume was calculated as the product of mean disc thickness and cross-sectional area of the disc. After being oven-dried at 105 °C until constant mass was reached, each disc was reweighed to calculate moisture content, dry mass, and basic specific gravity (Williamson and Wiemann...
The basic specific gravity of each disc was assumed to be constant in the radial direction of the disc. The basic density, in units of kg/m³, of each disc is the basic specific gravity of the disc multiplied by 10³.

Whole tree cumulative mass profiles were developed by harvesting tree discs. To reduce costs, discs were collected at every AF for only the second random branch path, and the density along the path length was assumed to vary equally along the first random branch path and the second random branch path.

The statistical analysis was performed using the R statistical environment (R Development Core Team 2010). The nlme package was used to fit the linear and nonlinear mixed effects models of the volume and density profiles (Pinheiro et al. 2011).

RESULTS

Figure 1a shows an example of a cumulative volume profile for a sugar maple using nonlinear mixed effects modeling for the dominant stem and whole tree. For this particular tree, most of the whole-tree volume is in the dominant stem, but a significant amount of additional volume accumulates in branches above relative crown height (RCH), although slowly at first, as the first branch encountered is not of large size compared to branches encountered later in the vertical profile. The difference between the dominant stem and whole-tree profiles gives the volume of branches in the tree.

Figure 1b shows the basic density profile for the same sugar maple which oscillates around the average wood density of sugar maple as determined by the Forest Products Laboratory (USDA FS 2010). Stem wood is dense at the base of the tree then density declines to a point about half-way to the base of the crown, increases into the middle of the crown and then decreases again toward the tip. The model for the basic density shows that after the relative path length at which the random path diverges from the dominant stem (RHD), the branches are denser at higher relative heights of the dominant stem. By combining the cumulative volume and basic density profiles, a cumulative mass profile can be attained. For this example tree (Fig. 1a and b), the branch mass fraction of whole-tree mass would be somewhat higher than the branch volume fraction of whole-tree volume.

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LITERATURE CITED


Figure 1.—(A) The cumulative volume profile for the dominant (DOM) stem and whole-tree (WHT) of a sugar maple with d.b.h. = 42.8 cm, total height = 34.0 m, and relative crown height (RCH, vertical line) of 0.500. The measured DOM locations are represented by filled circles, and WHT locations are represented by open circles. (B) The mixed-effects vertical stem density (wood plus bark) profile for the DOM stem and the random branch path (RBP) of the same sugar maple tree with relative path length at which the random path diverged from the dominant stem (RHD, vertical line) of 0.714. The average wood density of 560 kg/m$^3$ for sugar maple trees (USDA FS 2010) is shown as a horizontal dashed line.


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