



A generalized tree component biomass model derived from principles of variable allometry



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ARTICLE INFO

Article history:

Received 16 April 2015

Received in revised form 11 June 2015

Accepted 14 June 2015

Available online 9 July 2015

Keywords:

Tree biomass

Allometry

Hardwoods

Mass components

ABSTRACT

Accurate estimates of forest biomass stocks are critical for scientists, policymakers and forest managers trying to address an increasing array of demands on forests, to sustain human well-being and a broader diversity of life forms on Earth. Thus, it is important that forest biomass estimates are translatable into both biologically and economically meaningful components. Here, a new variable-form, variable-density tree mass component model is presented. The model decomposes a tree into a system of tree component-specific equations that: (a) reflect variation in scaling relationships between major portions of the tree body that define variation in whole-tree growth form and (b) relate to commercially relevant portions of the tree. When tested using data collected from felled and dissected hardwood trees of different size and species, growing over a range of stand conditions, the variable-form, variable-density models gave superior predictions for all components of tree mass, when compared to standard fixed-form, fixed-density models that predict tree mass components only from stem diameter at breast height (DBH). The results demonstrated why the standard approach of estimating mass components from DBH with a power function is fairly limited, because base-, trunk-, crown- and main stem-DBH relationships are all variable within and between tree species. Species-specific models were generally superior, but a mixed-species model gave equivalent and sometimes better results than equations fitted to each species individually. The results provide a theoretical basis for biologically-meaningful, robust estimation of tree biomass components over a range of species and forest conditions and may offer new flexibility in producing ecologically and economically relevant biomass inventories.

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1. Introduction

Accurate estimates of forest biomass stocks are critical for scientists, policymakers and forest managers trying to address an increasing array of demands on forests, to sustain human well-being and a broader diversity of life forms on Earth. With broad concern about global climate change, it is recognized that forests are important global sinks for CO₂ (Domke et al., 2012a; Chave et al., 2014), as well as sources of biologically renewable products and fuels (Domke et al., 2012b). The Food and Agricultural Organization of the United Nations (FAO, 2010) recently estimated that thirty percent of the world's forests are primarily used for production of wood and non-wood forest products. In the USA, forest fluxes (including that from harvested wood) accounted for 88% of total 2012 net CO₂ flux (USEPA, 2014). Therefore, it is important that forest biomass estimates are translatable into both biologically and economically meaningful components.

Since standing trees cannot be weighed, estimates of forest biomass come principally from tree biomass equations, which are applied to measurements of trees during forest inventories. So, improving tree biomass equations is fundamental to improving forest stock estimates (Chave et al., 2014; Sileshi, 2014; Weiskittel et al., 2015). The standard tree mass equation predicts total tree mass as a power function of stem diameter at breast height (DBH):

$$M_W = \alpha D^\beta \quad (1)$$

where M_W (kg) is the above-ground dry mass of a tree, D (cm) is its DBH (measured 1.3 m above ground) and α and β are coefficients to be estimated for a population of trees. This equation has biologically meaningful coefficients relating to the theory of "allometric" scaling relationships, which are relationships between the sizes of different parts of an organism relative to the whole (Huxley and Tessier, 1936). For example, a metabolic scaling theory predicts a universal relationship of $M = \alpha D^{8/3}$ (e.g., West et al., 1999; Enquist, 2002). Allometric relationships often take the form of a power equation

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(Stevens, 2009), as in Eq. (1), but need not be confined to any particular mathematical form.

Though biologically interesting, the generality of simple allometric models has been called into question because allometric scaling relationships are apparently non-stationary within species, across the large spatial domains over which tree biomass equations are typically applied (Ducey, 2012). Niklas (1995) demonstrated that allometric relationships change, even within the lifetime of individuals of a single species, growing under homogenized conditions, and cited this “size-dependent” allometry as evidence that no universal allometric scaling coefficients could be estimated for trees. Further, Chave et al. (2009) demonstrated a high degree of variability in relationships between tree size and wood density, reinforcing findings that simple dimensional measurements may be insufficient for accurate estimation of tree mass, in the face of varying wood density (Chave et al., 2005).

Ketterings et al. (2001) showed how Eq. (1) could be generalized to explicitly reference tree height (H) and density (ρ), with the assumption that $H \propto D^\gamma$ making β in Eq. (1) equal to $2 + \gamma$, and $\alpha \propto \rho$. This work provides a theoretical linkage from Eq. (1) to a more generalized and biologically meaningful “form-factor” model for tree biomass (modified here from Cannell, 1984):

$$M_W = F \rho \frac{\pi}{4} D^2 H \quad (2)$$

where H (m) is total tree height above ground, ρ is its density (kg m^{-3} , measured 1.3 m above ground) and F is a ‘whole-tree’ form factor (Gray, 1966; Cannell, 1984) for indexing the mass of a tree, relative to a proxy mass which is a proxy tree volume ($\frac{\pi}{4} D^2 H$) multiplied by tree density (i.e., $\rho \frac{\pi}{4} D^2 H$).

Eq. (2) has been advocated as a generalized tree biomass model, useful over a range of species and forest ecosystems across the globe (Cannell, 1984; Chave et al., 2014), with an alternative form that allows for non-proportional scaling relationships between M_W and proxy tree mass:

$$M_W = F \left(\rho \frac{\pi}{4} D^2 H \right)^B \quad (2a)$$

When $B \neq 1$, the relationship is not proportional, indicating that form changes as the tree changes in mass.

While allometric scaling relationships have been fundamental to understanding the eco-physiology of tree species and forest ecosystems worldwide (Enquist, 2002), they also have economic meaning relevant to forest management. For example, greater allocation of tree biomass to main stem versus branch components has important implications for forest utilization (Adu-Bredu et al., 2008; MacFarlane, 2011), because the most valuable parts of trees are in straight, sound parts of the main stem and the less valuable portions are in branches. While branches are much more likely to be utilized for biomass fuel or remain as slash on the forest floor, they also contain disproportionate fractions of nitrogen and other nutrients critical for sustaining forest productivity (Egnell and Valinger, 2003). Thus, improved estimation of tree biomass components is of value to forests managers as well as tree biologists.

Simple allometric models (like Eq. (1)) have been widely used to predict components of tree biomass (e.g., branches, bole, stump) from DBH (e.g., Bi et al., 2004; Brandeis et al., 2006), but there is substantial evidence that DBH is a generally poor predictor of component fractions of whole-tree biomass (Jenkins et al., 2003; Weiskittel et al., 2015). This likely relates to important differences in the scaling of tree parts, relative to the whole, i.e. allometry. For example, trees with disproportionately large crowns can have different total mass-DBH relationships than those with more proportional crowns (Goodman et al., 2014). This suggests that

improved estimation of biomass components could also help improve estimation of whole-tree mass.

Here, a new tree mass component model, derived from Eq. (2), is presented. The model was developed with three major goals in mind: (1) the model should incorporate prevailing scientific theories of tree allometry; (2) total tree biomass would be estimated as the sum of major biologically- and economically-important components of the tree; (3) the model would be robust across multiple species, growing under different forest conditions, based on an underlying hypothesis that species differences could be captured by general relationships describing variability in tree form and wood density. In the sections that follow, the model is described and then tested using data collected from felled and dissected hardwood trees of different size and species, growing over a range of stand conditions. The model is then compared with an alternative model that uses only DBH to predict each major tree mass component and three prevailing models for predicting whole-tree mass (Eqs. (1), (2) and (2a)).

2. A variable-form, variable-density tree mass component model

2.1. Theoretical background for model derivation

Derivation of a new tree mass component model from the form-factor model (Eq. (2)) was based on the idea that different parts of the tree change in shape as trees increase in size and should have allometric scaling coefficients that differ from that of the whole tree (i.e., allometric scaling is not isometric). Most scientific studies of tree form have been focused on the main stem of the tree, producing large numbers of stem profile (a.k.a. “taper”) models to describe changes in the shape of the main stem from tree base to top (Kozak, 2004). By contrast, the prevailing theories of allometric scaling in trees are directly or indirectly based on tree branching architecture; these are: (1) pipe model theory, which is based on Da Vinci’s model of a constant cross-sectional area of stems as they split into branches (Van Noordwijk and Mulia, 2002), (2) metabolic scaling theory (West et al., 1999), which suggests universal allometric scaling based on fractal-like branching networks, and (3) several variants of models based on mechanical stress principles, where the form of the tree is a response to wind and gravitational loading of the crown on the trunk of the tree (Eloy, 2011). An important paper by Mäkelä and Valentine (2006) united key elements of these theories by highlighting that (a) fractal branching geometry only pertains to the crown of the tree and (b) tapering of the trunk below the crown is a direct reflection of past branching events and branch losses. Recent empirical studies of tree fractal branching by MacFarlane et al. (2014) confirmed that divergence of real trees from theoretical fractal trees was due to variation in the size and tapering of the trunk relative to the crown, along with constraints on crown spread due to constrained growing space. So, both theoretical and empirical studies suggest that separating out the crown and trunk components and recognizing both internal and external constraints on tree crown expansion are critical to explaining more of the variation in tree mass allometry.

2.2. Vertical segmentation of tree form

The currently-accepted paradigm for modeling stem form suggests that the main stem can be divided into three vertical segments: the base, middle and top of the tree, which are approximately neolodial, paraboloidal and conical in shape, respectively (Zakrzewski and MacFarlane, 2006). In reality, stem geometry is more complex than that and a number of studies have

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