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Evaluating a non-destructive method for calibrating tree biomass equations derived from tree branching architecture

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Abstract

Key message **Functional branch analysis (FBA) is a promising non-destructive method that can produce accurate tree biomass equations when applied to trees which exhibit fractal branching architecture.**

Abstract Functional branch analysis (FBA) is a promising non-destructive alternative to the standard destructive method of tree biomass equation development. In FBA, a theoretical model of tree branching architecture is calibrated with measurements of tree stems and branches to estimate the coefficients of the biomass equation. In this study, species-specific and mixed-species tree biomass equations were derived from destructive sampling of trees in Western Kenya and compared to tree biomass equations derived non-destructively from FBA. The results indicated that the non-destructive FBA method can produce biomass equations that are similar to, but less accurate than, those derived from standard methods. FBA biomass prediction bias was attributed to the fact that real trees diverged from fractal branching architecture due to highly variable length–diameter relationships of stems and branches and inaccurate scaling relationships for the lengths of tree crowns and trunks assumed under the FBA model.

Keywords Tree biomass · Functional branch analysis · Fractal geometry · Allometry

Introduction

Allometric scaling equations, which relate different measureable properties of organisms to each other, have been widely applied to estimate the biomass and carbon content of trees during forest carbon stock inventories (Brown 1997; Gibbs et al. 2007). Typically, allometric biomass equations (hereafter, simply referred to as a biomass equations) relate stem diameter at breast height (DBH) to tree mass, because DBH can be easily and accurately measured and is highly correlated with tree mass (West 2009). Since forest inventories are generally conducted to survey standing trees and because standing trees cannot be weighed to determine their mass, biomass equations provide one of the only ways for estimating standing tree biomass or carbon stocks. However, the main method for developing these equations is to engage in destructive sampling, where trees are felled, measured and weighed and then a prediction equation is developed from the resultant data. Destructive sampling is costly and generally unacceptable in areas where conservation of trees, especially rare ones, is important.

Functional branch analysis (FBA) is a model-based method that allows coefficients of equations that relate tree

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DBH to tree mass to be derived from measurements of standing trees, without the need for destructive sampling (Santos-Martin et al. 2010). FBA can derive these latter coefficients, without having to know the actual mass of the trees, because it derives proxy estimates of whole tree volume from tree stem and branch measurements, using fractal branching rules, and combines these proxy volumes with inputs describing the wood density of tree volume components (e.g., stems and twigs) to calculate mass (Van Noordwijk and Mulia 2002). FBA draws on theories regarding the fractal geometry of tree branching architecture, especially "pipe model" theory (Shinozaki et al. 1964a; Mäkelä and Valentine 2006; Eloy 2011). Pipe model theory assumes that a tree consists of unit pipes that support a respective proportion of foliage by connecting each foliage element to the functional roots, centered on the hypothesis that the sum of squared diameters of branches is equal to the squared diameter of stem or branch before branching occurs (Shinozaki et al. 1964a; Mäkelä and Valentine 2006; Eloy 2011). Although some of the assumptions under pipe model theory deviate from reality (West et al. 1999; Enquist 2002; Eloy 2011), the theory has been successfully employed to model tree structure and dry matter allocation (Shinozaki et al. 1964b; Van Noordwijk et al. 1994; Van Noordwijk and Purnomosidhi 1995; Ozier-lafontaine et al. 1999; Mäkelä and Valentine 2006). FBA has been recently applied to estimate root length, root biomass and shoot biomass (Salas et al. 2004; Smith 2001) and to predict tree component biomass from standing tree measurements (Santos-Martin et al. 2010).

In this study, tree biomass equations derived from destructive sampling of trees in Western Kenya were directly compared to tree biomass equations derived from the non-destructive FBA method. Different methods were applied to the same trees to see how substitutable the FBA method might be for the standard allometry approach. It was hypothesized that the FBA would produce very similar equations to those derived from standard allometry.

Materials and methods

Study area and trees

Field measurements of trees and destructive biomass sampling were carried out in three 10 km × 10 km blocks in Western Kenya. The blocks were located in Lower Yala, Middle Yala and Upper Yala, along the Yala River basin. Altitudes in Yala range between 1,200 and 2,200 m above sea level. Mean annual rainfall in Lower, Middle and Upper Yala sites, respectively, are 1,479, 1,950 and 1,028 mm, indicating climatic conditions associated with 'tropical moist' forests (Chave et al. 2005). However, very little natural forest is left in this region. Instead, trees in Western Kenya are mostly part of a complex agricultural mosaic, ranging from groves of fruit crop trees, such as *Mangifera indica*, in Lower Yala (Kuyah et al. 2012), to small stands consisting of indigenous and exotic timber species (e.g., *Eucalyptus spp*.), which are interspersed around homesteads, along farm boundaries and among croplands and pastures (Henry et al. 2009).

Destructive sampling

Trees were destructively sampled in randomly selected 30 m × 30 m plots contained within each 100 km^2 block as part of a tree biomass study by Kuyah et al. (2012). Trees from the plots were stratified by size into six DBH classes: <10; 10.1–20; 20.1–30; 30.1–40; 40.1–60 and >60 cm and selected for destructively sampling by stratified random sampling. Forty trees from five species (*Acacia mearnsii*, *Eucalyptus camaldulensis*, *Eucalyptus grandis*, *Eucalyptus saligna* and *M. indica*) that had sufficient number and DBH range to fit species-specific biomass equations were selected from the larger dataset of Kuyah et al. (2012) for this study. *E. grandis and E. saligna* which are similar in form and natural range (Burgess 1988) were combined into a single group to increase sample size. The DBH of target trees was measured with a diameter tape, then trees were felled and separated into main stem and branches with a power saw and leaves were harvested. The fresh weight of each component was determined on site using a ±0.1 kg balance (Kuyah et al. 2012). Stem and branch samples weighing approximately 1 kg were collected in the field using a ±0.1 g balance, transferred to the laboratory and oven dried at 105 °C for 24 h. The dry biomass of each tree component was calculated as the product of the component fresh weight and the respective dry weight-to-fresh weight ratio.

FBA model

FBA uses a model to generate fractal trees comprised of woody 'links' of different lengths and diameters, beginning with an initial link, which is the 'trunk' of the tree beneath the first branching point. The trunk splits at the first branching point into more than one link, forming the base of the tree's crown, and then each of these links split again into more branches, iteratively, until terminal links of a specified minimum size are generated. The FBA model allows links to be separated into different categories to allow for length–diameter scaling relationships to be analyzed separately for different types of links in the tree's crown. These categories of links are called "twigs", "branches", "wood" in the model, defined as links with diameter of <2 cm, 2–8 cm, and >8 cm, respectively.

Trunk length is specified by a separate input parameter and the pseudo-length of the crown is generated by adding links with lengths specified by length–diameter relationships to the top of the tree, until terminal links of the specified minimum size are finally added.

The total volume of the fractal tree is the sum of the volume of the initial (trunk) link plus that of all the links in the crown. The mass of the tree is the total volume multiplied by the density of the links. Terminal links may also have some number of leaves attached and, using leaf specific parameters (e.g., specific leaf area), the surface area and mass of leaves can also be generated. The model may also be applied to model root structures in an analogous fashion.

To generate allometric scaling relationships for trees of different sizes, fractal trees of different initial link diameters are generated based on input parameters, generating the pseudo-tree-mass data necessary for fitting tree trunk diameter–mass relationships. There was insufficient data to calibrate the leaf or root model, so parameters pertaining to roots and leaves were set to null values, so that the model would only generate biomass of above-ground woody parts of trees.

The main input parameters for modeling the above-ground woody parts of a tree are as follows:

- Average number of branches at each branching point.
- Minimum link diameter (the smallest twigs).
- Link wood density (mass per unit volume).
- Link length–diameter relationships.
- Link taper (change in diameter from base to top).
- Probability distributions for p and q, which are, respectively, the scaling factor for the change in total cross-sectional area at branching points and the allocation parameter describing the relative size of the largest link at a branching point:

$$p = D_{\mathrm{B}}^2 / \sum_{i=1}^{n} D_{\mathrm{A}}^2 \quad (1)$$

$$q = \mathrm{Max}\left(D_{\mathrm{A}}^2\right) \Bigg/ \sum_{i=1}^{n} D_{\mathrm{A}}^2 \quad (2)$$

where D_{B} and D_{A} are the stem diameters above and below a branching point, Max (D_{A}) is the diameter of the largest stem after a branch point and n is the number of branches at that point. Parameters p and q combine to determine, e.g., whether a tree yields links of similar size or a dominant link with branches that are much smaller in size (Van Noordwijk et al. 1994).

The necessary tree measurements for calibrating FBA can be collected on standing trees by professional tree climbers or using tools such as laser rangefinders and optical dendrometers (Clark et al. 2000). FBA link density can be estimated using either small tree cores extracted from a sample of trees (Wiemann and Williamson 2011) or from published species-specific values. Here, FBA-related measurements were collected after the trees were felled, because they were already being destructively sampled to generate standard biomass equations. Starting with the first link, the lower diameter (D_{proximal}), the diameter in the middle of the link (D_{middle}), the diameter at the distal end of the link (D_{distal}) and length of each link were measured with calipers and a tape measure, respectively. Diameters were measured in two perpendicular directions and averaged to account for non-circular branch shapes. At the first branch point, the continuing main stem was defined and then the largest 'branch' (usually the second largest link at a forking point) was selected and followed to a terminal (usually leaf bearing) shoot at the end of a path through the tree's branching network; measurements were repeated on each successive link in the path. Then, returning to the main stem link, it was measured and followed to the next branching point; this process was repeated, moving up the tree, following and measuring connected links to different terminal links. The successive, non-repetitive link number and its parent link number were noted and recorded. Link measurements were repeated to the tip of the tree for a minimum of 100 link measurements per tree. The diameters and lengths of links at each ramification that were not followed to a terminal twig were also measured to allow for computation of parameters p and q.

Estimation of biomass equation coefficients

The total biomass of above-ground woody parts (M_{w}) and the DBH of each tree were known from the destructive sampling and these data were used to fit regression models to a standard biomass equation:

$$M_{\mathrm{w}} = a\mathrm{DBH}^{b} \quad (3)$$

where a and b, respectively, are the proportionality and power coefficients of the equation.

For the standard method, model coefficients were estimated from log-transformed mass and DBH data using both linear least squares regression analysis (LS) and least trimmed squares (LTS) robust regression analysis (Rousseeuw 1984); the latter method to account for heteroscedascity and potential outliers in the data.

For the FBA method, coefficients a and b were an output of WanFBA (ver. 1.4 http://www.worldagroforestrycentre.org/af2/fba_download). WanFBA required specification of linear length–diameter relationships. Length–diameter relationships were fitted to the measurement data using least squares linear. Since WanFBA has stochastic components (such as allowing link lengths to vary around their mean trend), biomass equation coefficients a and b (Eq. 3) differ every time the model is run. It was determined that after about ten runs the model coefficients stabilized at a coefficient of variation for a and b of about 8 and 1 %, respectively. So, the average of ten runs was used to compute the mean coefficients for each model tested.

Since the FBA model does not use standard fitting techniques to estimate coefficients, standard fit statistics are not automatically generated by WanFBA. Thus, the standard and FBA-based biomass equations were compared based on the relative error of prediction (RE), computed as follows:

$$\mathrm{RE} = \left(\frac{M_{\mathrm{w\ predicted}} - M_{\mathrm{w\ measured}}}{M_{\mathrm{w\ measured}}}\right) \tag{4}$$

where $M_{\mathrm{w\ predicted}}$ is the mass value predicted from either regression modeling or FBA and $M_{\mathrm{w\ measured}}$ is the mass obtained from destructive sampling. The mean relative error (MRE) for each model was the average RE over all trees fitted to the model.

Results

Tree parameters

Basic tree parameters derived from 4,862 links measured on 40 trees are shown in Table 1. Basic differences between the species examined were that *Eucalyptus* species were taller with longer trunk lengths and longer links in the crown than either *A. mearnsii* or *M. indica*. There were also differences in mean values for p and q between species. With $p = 1$ and $q = 0.6$, *M. indica* was closest to a theoretical pipe model tree, but was more branchy than the other species, with about 2.5 branches at each node. The other species showed typically two branches at a node and average q values of around 0.8, indicating about 80 % of the total cross-sectional area at branch nodes was found in a dominant branch (Table 1). However, the distribution of q values, which are bounded between 0 and 1, was fairly wide with most values of $q > 0.5$, indicating that one branch was larger than the others (Fig. 1). For *A. mearnsii* and *M. indica* the distribution of q values was generally even, while both *E. grandis/saligna* and *E. camaldulensis* showed a skewness toward higher q values, particularly for larger links, which indicates a stronger apical dominance for the *Eucalyptus spp*. than for the other two species.

Looking at the distribution of p (Fig. 2), there was a wide range of values, but with modal values tightly centered around $p = 1$, especially for larger links which approached a fairly constant p value ≈ 1. However, the distributions were distinctly skewed toward higher p values (>1.25, Fig. 2), particularly for twigs and smaller branches. This much greater cross-sectional area below a fork relative to the sum of the cross-sectional areas of ramifications above a fork could be attributed to dieback of terminal twigs or epicormic branching, in cases where larger links have higher values for p. This pattern is conspicuous for *E. camaldulensis* (Fig. 2), a species known to produce epicormic branches (Souter et al. 2010).

Analyses of tree measurement data revealed that while mean link length increases with link diameter class for trees of different species (Table 1), length–diameter relationships (Table 2) are not typically linear (Fig. 3). Thus, average link lengths for different link categories (Table 1) were used to parameterize WanFBA instead of using linear models (shown in Table 2) to predict link lengths from link diameters. This was accomplished by setting the intercept of length–diameter relationships to the mean length of links and setting the slope to zero. A term based on the link length deviation was used to allow link length to vary around the mean parameter value during model runs.

Table 1 Mean (SD) tree attributes for the FBA model

Parameter	*A. mearnsii*	*E. camaldulensis*	*E. grandis/saligna*	*M. indica*
# trees	8	19	7	6
DBH (cm)	25.3 (10.4)	43.52 (16.6)	15.8 (8.2)	31.2 (16.1)
Height (m)	13.4 (4.8)	29.5 (7.9)	17.0 (6.3)	7.6 (3.1)
Number of branches	2.09 (0.31)	2.10 (0.48)	2.13 (0.38)	2.50 (0.73)
p	1.03 (0.25)	1.20 (0.42)	1.23 (0.48)	1.00 (0.31)
q	0.77 (0.15)	0.79 (0.42)	0.81 (0.14)	0.60 (0.16)
Twig length (cm)	22.5 (16.3)	32.5 (27.6)	29.7 (26.5)	18.7 (15.2)
Branch length (cm)	49.9 (31.9)	92.3 (81.1)	65.6 (70.3)	38.5 (29.7)
Wood length (cm)	82.5 (63.8)	159.0 (243.8)	80.4 (112.3)	62.7 (57.7)
Trunk length (cm)	229.6 (151.5)	1,065.2 (476.6)	470.0 (306.5)	181.7 (55.0)
Link taper (cm cm^{-1})	0.006 (0.011)	0.006 (0.008)	0.004 (0.009)	0.008 (0.008)
Wood density (g cm^{-3})	0.63 (0.09)	0.53 (0.08)	0.42 (0.02)	0.56 (0.05)

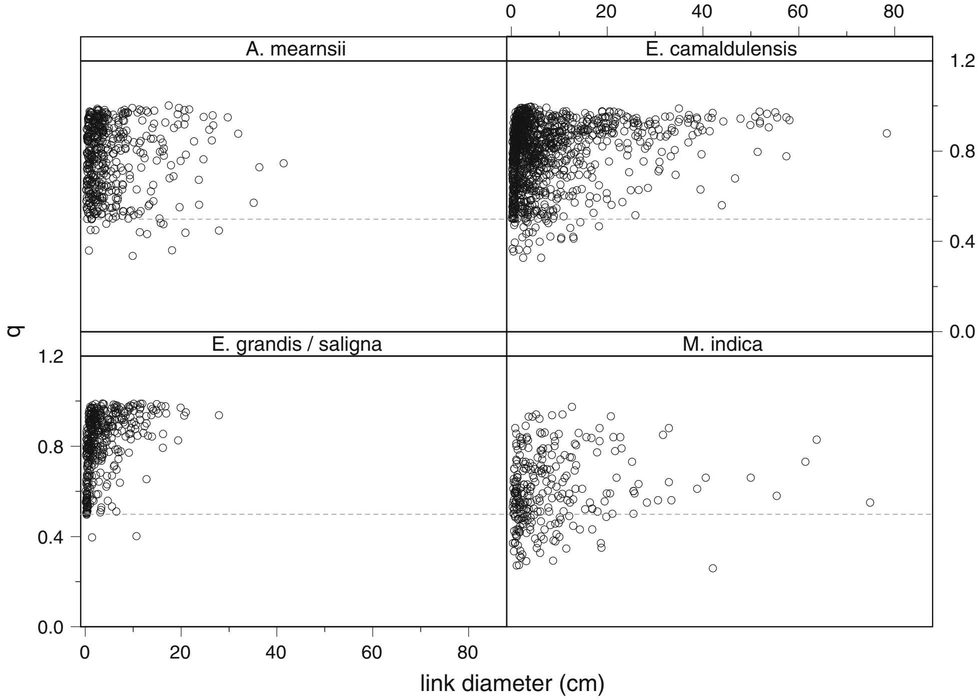


Fig. 1 Distribution of the branch allocation factor, *q*, as a function of link diameter for different species. The *horizontal line* represents a perfect fork ($q = 0.5$)

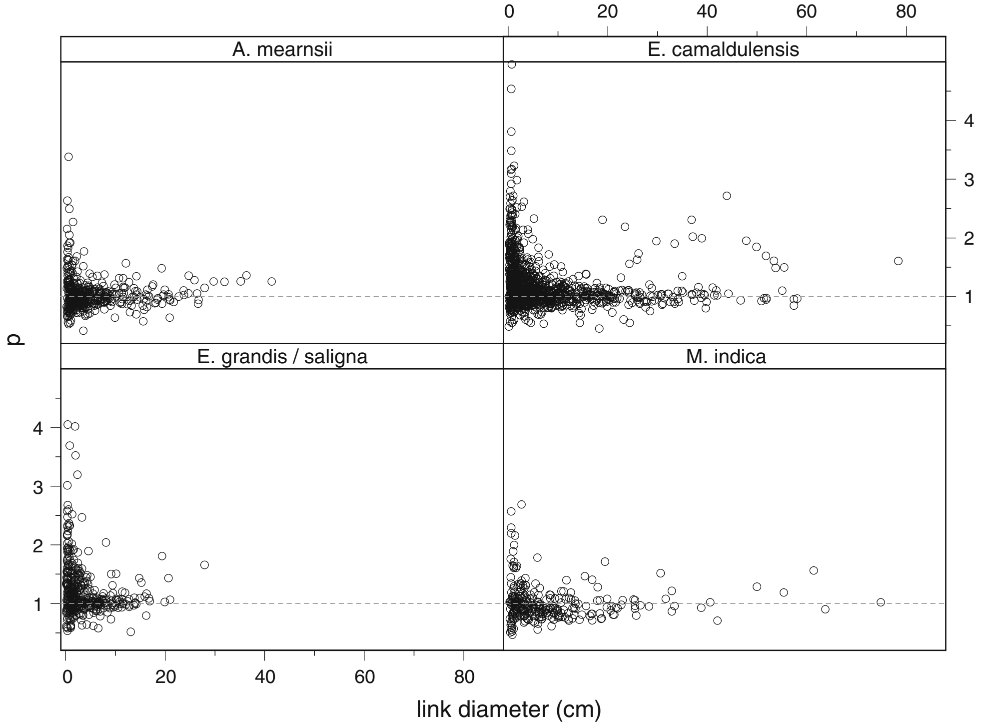


Fig. 2 Distribution of the branch transfer coefficient, *p*, as a function of link diameter for different species. The *horizontal line* represents a conservation of cross-sectional area across a branch point ($p = 1$)

Standard versus FBA-derived biomass equations

When Eq. 3 was fitted to the destructive sample data, coefficients estimating using LS regression provided a lower MRE then LTS regression for individual species equations, except for *E. grandis/saligna*, where the LTS performed slightly better (Table 3). Because *A. mearnsii* and *M. indica* appeared to have a similar branching architecture that was quite different from the two *Eucalyptus* species, two more equations were fitted to see how grouping similar-formed species would affect the results. In these latter cases, LS provided superior results and there was a small loss in predictive power by grouping four different species together. There was a negligible improvement from grouping similar-formed species

Table 2 Linear regression models relating link length (cm) to link diameter (cm) for trees of different species of different sizes

	A. mearnsii	*E. camaldulensis*	*E. grandis/ saligna*	*M. indica*
Twigs				
Intercept	6.263	31.305	28.813	6.207
Slope	16.61	1.426	1.063	12.656
R^2	0.247	0.001	0.001	0.158
p	<0.0001	0.3151	0.5929	<0.0001
Branches				
Intercept	25.471	43.862	87.694	20.567
Slope	5.524	11.623	−5.78	4.111
R^2	0.088	0.053	0.016	0.056
p	<0.0001	<0.0001	0.0546	<0.0001
Wood				
Intercept	50.662	26.664	15.792	40.119
Slope	1.83	7.53	5.333	1.315
Range length	0.617	0.768	0.949	0.699
R^2	0.110	0.119	0.025	0.067
p	<0.0001	<0.0001	0.236	0.002
Trunk				
Intercept	14.3625	882.701	−117.167	176.090
Slope	8.504	4.264	31.911	0.162
R^2	0.338	0.039	0.759	0.003
p	0.135	0.390	0.054	0.915
All Links				
Intercept	28.84	39.319	31.848	22.87
Slope	2.86	7.442	4.7387	2.145
R^2	0.298	0.214	0.073	0.212
p	<0.0001	<0.0001	<0.0001	<0.0001

together (Table 3). Overall, the difference between the two fitting methods was slight, indicating little sensitivity of the data to assumptions of LS fitting methods. All of the regression models fit the data well (Table 3).

Coefficients generated for Eq. 3 from the FBA model for each species and mixed-species groups are shown in Table 3. The FBA method had slightly more bias than the standard method, when used for *A. mearnsii* and *M. indica* and the mixed-model fit to both these species. Looking at the scatter of predictions of the standard regression method around a 1:1 line, where predicted is exactly equal to measured, we can see that biomass predicted by the FBA method for these two species is very similar to that predicted by the standard method, except for the large individual of *M. indica* (Fig. 4). On the other hand, biomass estimates using the FBA-derived coefficients were highly biased for *Eucalyptus spp.*, especially *E. camaldulensis*, where FBA overestimated mass across a wide range of tree sizes (Fig. 4). FBA-derived *E. grandis/ saligna* equations overestimated the mass of smaller trees and underestimated the mass of larger trees. Consequently, both the *Eucalyptus* mixed-species model and the all-species mixed-species equations derived from FBA were also highly biased (Table 3). The bias for FBA-derived mixed-species and all-species equations were predictable from the individual species equations, as the input parameters were essentially weighted average values of the individual species equations. Clearly, mixing species with quite different branching architectures did not improve the FBA results.

Analyses of residual error of estimation of the FBA equations revealed that RE in *Eucalyptus* species was significantly ($p < 0.0001$) negatively correlated with crown length ($R^2 = 0.57, 0.56$) and total tree height ($R^2 = 0.75, 0.71$) for both *E. camaldulensis* and *E. grandis/saligna*, but not the other two species (results for crown length are shown in Fig. 5). This resulted in short/shorter-crowned *E. grandis/ saligna* trees being predicted to have crowns that were too massive and taller/longer-crowned ones to have crowns that were proportionally too small. The residual bias for *E. camaldulensis* was similar to that of *E. grandis/saligna*, but the overestimation for shorter-crowned trees was so dramatic that the longer-crowned trees were still overestimated (Fig. 5). For a real tree, tree height is the sum of the crown length and the trunk length. However, tree height is ambiguous in fractal trees, because the trunk has no fractal dimension and the crown has a pseudo-length proportional to average “pipe” length (Mäkelä and Valentine 2006). This suggests that the very different results for the *Eucalyptus* species, as compared to *A. mearnsii* and *M. indica*, arose from determinants of crown length (which is computed as total height minus trunk length). Average trunk length, a major determinant of crown length, was much higher for the Eucalypts than the other species (Table 1), indicating specification of the trunk length parameter as a possible source of bias.

A simple simulation was conducted with *E. camaldulensis* to determine the sensitivity of the WanFBA model to changes in specification of average trunk length. The average trunk length parameter was varied within reasonable bounds to define fractal trees with different crown ratios, while all of the other input parameters were fixed. The results of this sensitivity analysis showed that doubling average trunk length leads to a proportional increase in coefficient a (Fig. 6a), while at the same time causing a negative exponential decline in the power coefficient b, which asymptotically approaches a value of $b = 2$ (Fig. 6b). Average trunk length was also set to zero, simulating a multi-stemmed (shrub-like) growth form, where the trunk is essentially a zero thickness disk at ground level. As average trunk length approached zero, there was a proportional decrease in the value of a, and a concomitant exponential increase in b (Fig. 6b), until the latter reached the diameter–mass allometric scaling dimension of the tree’s crown depicted by the model. For this group

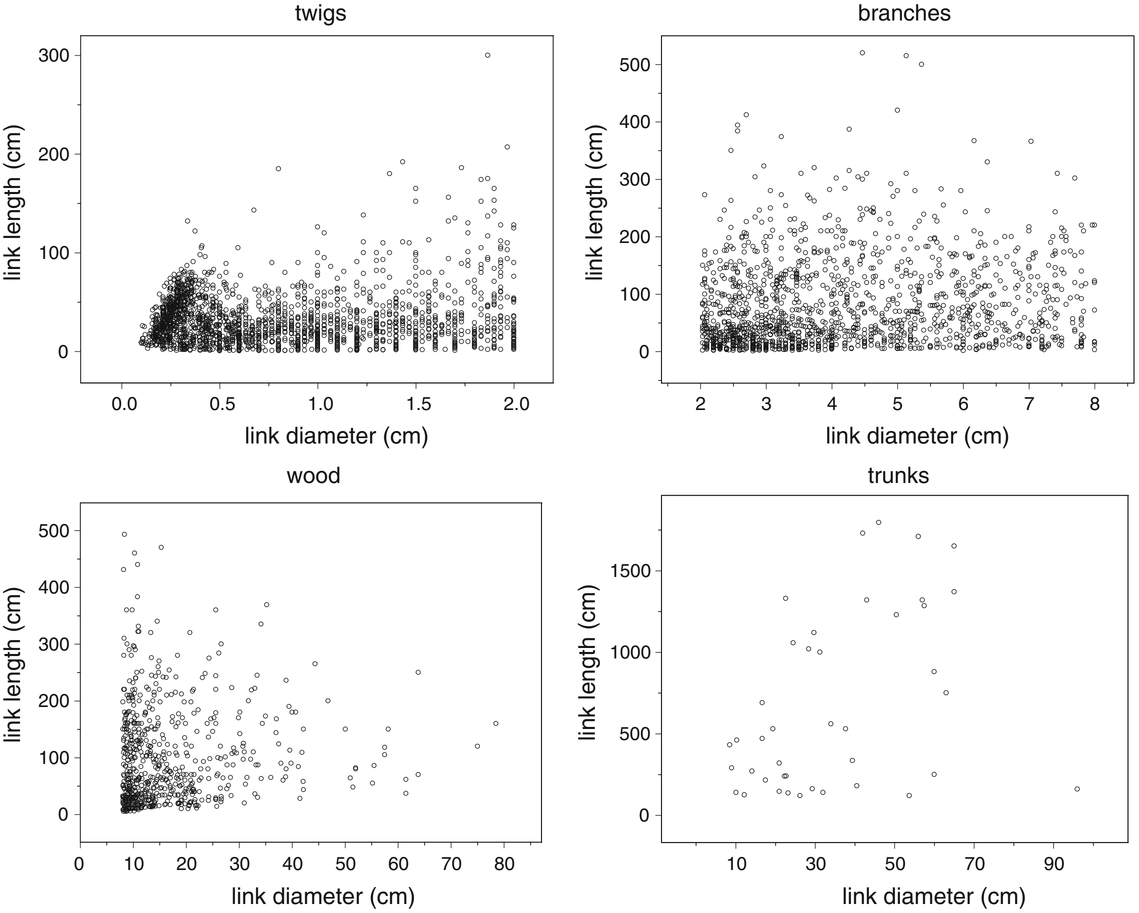


Fig. 3 General link length–diameter relationships for different categories of links used in the FBA model

Table 3 Allometric scaling coefficients for standard biomass equations, fitted with least squares and least trimmed robust regression methods, and mean output coefficients from the WanFBA model

	A. mearnsii	*E. camaldulensis*	*E. grandis/saligna*	*M. indica*	*E. spp. mix*	*Am-Mi spp. mix*	*All spp. mix*
Least squares (LS)							
a	0.105	0.069	0.035	0.047	0.053	0.084	0.064
b	2.488	2.518	2.739	2.649	2.590	2.520	2.554
R^2	0.98	0.99	0.99	0.99	0.99	0.97	0.99
p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
MRE (%)	0.75	0.74	0.59	0.67	0.78	0.61	0.93
Least trimmed squares (LTS)							
a	0.103	0.067	0.031	0.048	0.057	0.117	0.054
b	2.501	2.525	2.784	2.635	2.567	2.419	2.591
R^2	0.94	0.99	0.99	0.99	0.99	0.97	0.99
p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
MRE (%)	3.38	0.81	0.48	−3.06	1.69	1.73	−3.14
FBA							
a	0.111	0.407	0.152	0.079	0.327	0.094	0.261
b	2.476	2.214	2.246	2.486	2.216	2.488	2.270
MRE (%)	3.1	92.2	20.7	−2.9	78.5	2.1	59.8

MRE is the mean relative error of prediction

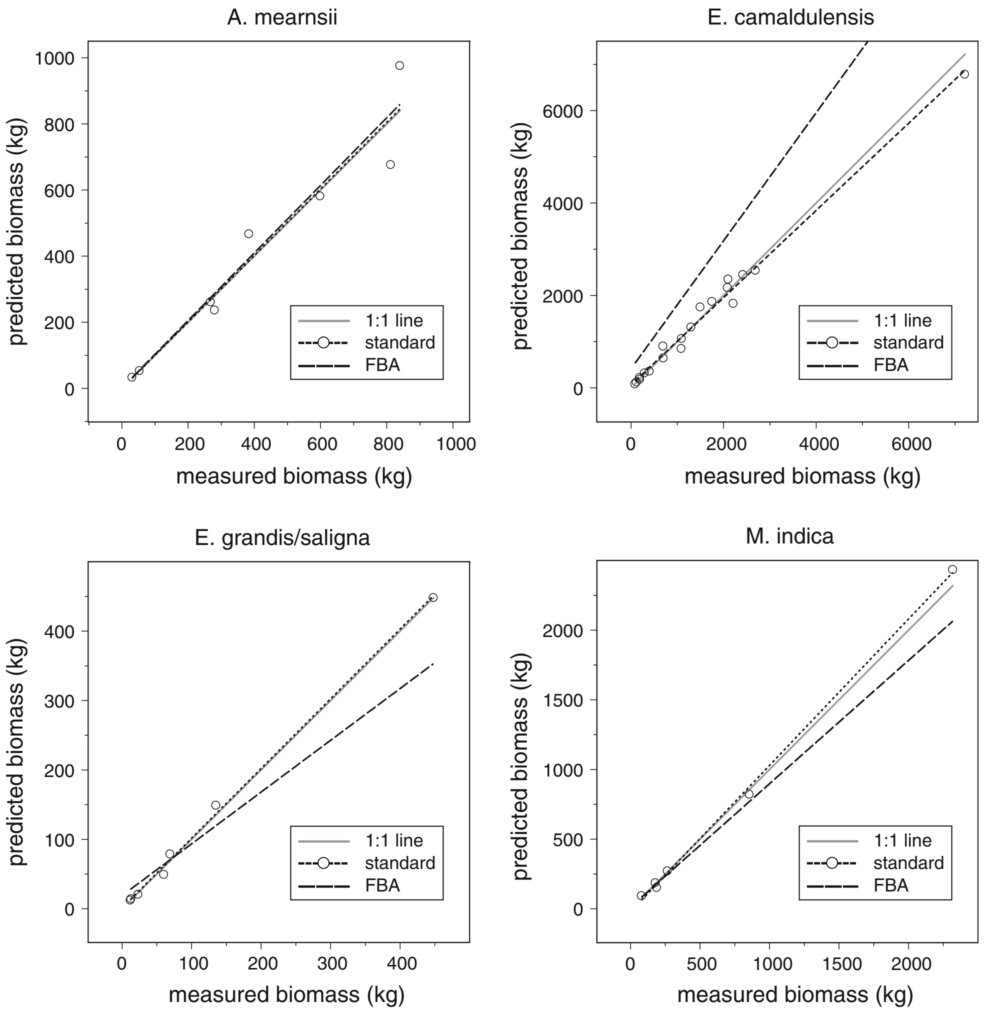


Fig. 4 Predicted versus measured biomass estimates for *A. mearnsii* and *M. indica*, *E. camaldulensis* and *E. grandis/saligna*). The *short-dashed* and *long-dashed lines* are regression lines of the predicted–measured relationship for the standard and FBA-derived approaches, respectively, and *hollow circle* symbols are the values for standard approach. The *solid gray line* is the 1:1 line representing complete agreement between predicted and measured

of *E. camaldulensis* trees, WanFBA predicted that woody crown mass scales as a power $b \approx 2.7$ of DBH with a proportionally constant of a ≈ 0.04 (Fig. 6) and total wood mass (including the trunk) scaled as a power $b \approx 2.2$ with a proportionally constant of a ≈ 0.4 (Table 3). In reality (as depicted by the standard regression models, Table 3), total wood mass scaled as an approximate power $b \approx 2.5$ of DBH with a proportionally constant of a ≈ 0.07.

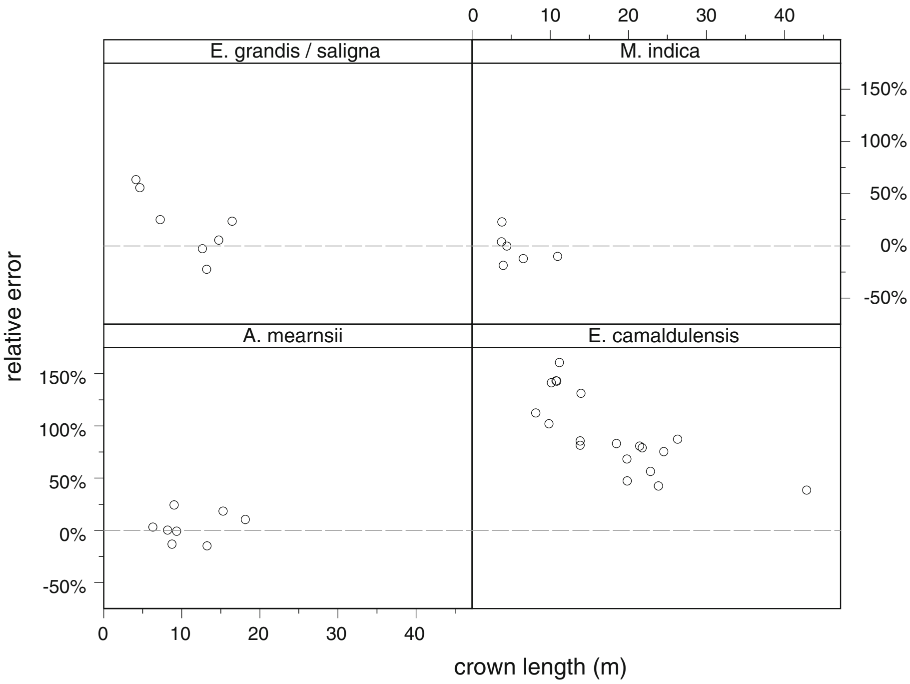
Discussion

Biomass estimation based on fractal branching principles

The results of this study suggest that the FBA method is capable of producing both good and poor estimates of tree biomass from the equations it generates, depending on how well the model was able to construct fractal-like trees with similar allometric scaling dimensions to the real ones it was trying to approximate. Given that none of the input parameters needed to run WanFBA (except the possible need to core some of the trees to estimate wood density) would require trees of interest to be felled or weighed, there is clear promise for this methodology. On the other hand, biomass equations coefficients estimated with FBA for the two *Eucalyptus* species examined were highly biased. This large discrepancy in outcomes for different species suggested both theoretical and practical limitations of the WanFBA model. Two simple questions arise: How much do real trees diverge from hypothetical fractal trees and how well can WanFBA account for these differences?

Universal fractal scaling rules give rise to realistic-looking tree structures and can be used for hypothesis testing regarding

Fig. 5 Relative biomass estimation errors (% diversion from the 1:1 lines in Fig. 4) plotted against crown length



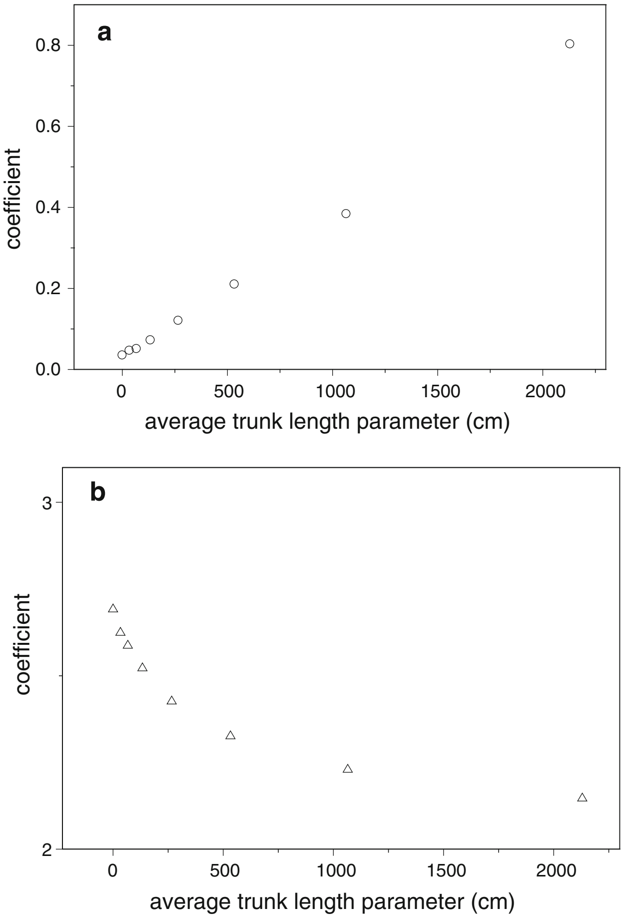


Fig. 6 Changes in biomass scaling coefficients **a** and **b** for the Eucalyptus model with changes in average trunk length

tree structure and functions (e.g., Eloy 2011). These rules include an expected proportional relationship between link length (l_k) and link diameter (d_k) within any branch order within a fractal tree, i.e., $l_k \propto d_k^{\alpha}$ (Enquist 2002; Mäkelä and Valentine 2006). The parameter α has a theoretical value of 2/3 based on biomechanical principles (Enquist 2002; Eloy 2011) and the hypothetical fractal dimension of a tree's crown (Zeide 1998; Mäkelä and Valentine 2006). The analyses presented here showed a very wide variation between trees in the relationship between l_k and d_k, (Fig. 3), which appeared neither linear ($\alpha = 1$) nor anything like the theoretical value ($\alpha = 2/3$). That is not to say individual trees cannot show this latter relationship, but it appears that this is far from universal in populations of real trees. This result is not surprising, because real trees lose or shed twigs and branches due to factors such as shading of the crown or branch death or breakage, reducing the fractal dimension of the crown (Mäkelä and Valentine 2006). As such, trees could be thought of as 'disrupted fractals' where the lengths of links of different diameters are somewhat randomized due to historical branch losses that affect link lengths. This may explain why using average values for links of different link sizes (Table 1) instead of linear-proportional relationships did not seem to cause a major problem for estimating the mass of *A. mearnsii* or *M. indica*, though neither tree may have actually conformed exactly to a fractal crown. Clearly, branch losses might explain why fractal scaling appeared to over-predict the crown mass of the *Eucalyptus* species, which, growing in plantations, may have had lost considerably more branches than the fractal model generated.

A second major issue of relating fractal trees to real ones is highlighted by Mäkelä and Valentine (2006) who stated: "For the whole tree, the fractal approach is not directly applicable, because the trunk does not scale with crown dimensions". WanFBA attempts to deal with this problem by separately calculating the trunk mass and adding it to the fractal crown generated to get the total mass of the tree. Mäkelä and Valentine (2006) showed that allometric scaling coefficients are dependent on the relative size of tree crowns, which prohibits universal allometric mass scaling coefficients to be defined for trees based on fractal scaling rules (as suggested, e.g., by Enquist 2002). This natural variation around the theoretical, universal power coefficient of $b = 2.67$ suggested by West et al. (1999) is evident in the varying power coefficients found in this study using empirical data fitting procedures (Table 3). While WanFBA clearly allows total mass scaling coefficients to vary with both trunk and crown size, it allows them to do so independently, which can allow for the generation of extremely unrealistic crown or trunk masses not constrained to be realistic for whole trees. As the simulation for *E. camaldulensis* showed (Fig. 6), for any given crown size generated, a longer average trunk length will bring about over-scaling of shorter-crowned trees and under scaling larger-crowned ones (Fig. 5).

Future applications

The results of this study suggest that under the right conditions, the FBA method can generate equations that produce reasonably accurate estimates of whole-tree aboveground mass without the need to destructively sample trees from the population of interest. A previous study by Santos-Martin et al. (2010) also suggested that FBA-derived biomass equations could produce estimates close to observed biomass for some tree species, but the latter study did not compare FBA-derived predictions to prediction equations developed using the standard, destructive approach, nor did it investigate or attempt to explain any bias associated with the FBA method. Clearly, the accuracy of FBA-derived equations is highly conditionally dependent, so it is critical to have some sense of where and when to apply the model effectively.

In addition to defining some kind of variable for indexing relative crown size and constraining total tree height, two other trunk-related limitations to the WanFBA model should be overcome to improve it: (1) the outputs of the model lump trunk mass together with mass in the wood category, which prevents separate analysis of the crown versus trunk "wood"; and (2) WanFBA only allows specification of a tapering coefficient (Table 1) for links in the crown section and not the trunk. The latter may turn out to be the most critical improvement to the model, as tapering has been shown to be an integral part of the universal scaling laws based on fractal geometry (Enquist 2002). In fact, Mäkelä and Valentine's (2006) solution to the trunk scaling issue rests on the fact that the scaling of the crown to whole tree mass is directly proportional to the square of the live crown ratio which is proportional to the tapering of the trunk due to crown rise. This is relevant to the FBA method because the initial link diameter (i.e., the diameter of the trunk) is assumed analogous to the DBH of a tree. Since DBH is measured at 130 cm above ground, it is at about the midpoint of a trunk of length 260 cm. For the average *E. camaldulensis* tree in this study, the trunk length was about 1,065 cm, so the diameters at the base of the crowns of these trees are likely considerably less than DBH.

The two species the FBA method was successful for, *A. mearnsii*, and *M. indica*, were relatively short-trunked, mostly open-grown trees dotted among agricultural fields in Western Kenya. These trees were generally allowed to express their inherent branching architecture and thus more closely conformed to an idealized fractal tree. The *Eucalyptus* trees, on the other hand, were generally growing in rows or plantations and so had considerably more internal and external shading of their crowns, which likely caused shedding of branches in the crown, crown rise due to shedding of lower branches, which led to longer barer trunks, thus, significantly disrupting any inherent fractal architecture they might otherwise achieve. Based on these population attributes and the analyses presented above, it is likely that the FBA method would be most robust for developing biomass equations for open-grown or widely spaced trees; indeed agroforestry systems are where the model has shown success prior to this study (e.g., Santos-Martin et al. 2010). Trees growing in natural forests or intensive plantations likely exhibit the greatest disruption to their fractal branching architecture, so, without the necessary adjustments to the model, the FBA method should be used with caution under these conditions.

Given that the FBA method does not require destructive sampling it is useful to consider how it compares another non-destructive alternative: using another biomass equation already available. In a study related to this one, Kuyah et al. (2012) showed that regional tree biomass equations for Western Kenya (Henry et al. 2009), global equation for tropical moist forests (Chave et al. 2005) and a two different pantropical biomass equations (Brown et al. 1989; Chave et al. 2001) yielded MREs of -11, 22, 15 and 25 %, respectively, when applied to estimate biomass for trees in Yala Province; these are in a similar range to the relative errors for the FBA-derived *Eucalyptus grandis/saligna* equation ($\approx$21 %), much greater than errors for *A. mearnsii* and *M. indica*, and much better than the error generated for *E. camaldulensis*. Thus, under the right conditions, a locally valid model can be generated from FBA that is superior to a regional model, while under less desirable conditions for applying FBA, the regional model would likely be more desirable.

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Conflict of interest The authors declare that they have no conflict of interest to report regarding this submission.

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