Functional branch analysis as tool for fractal scaling above- and belowground trees for their additive and non-additive properties

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Abstract

Empirical allometric scaling equations ($Y = aD^b$) for tree biomass on the basis of stem diameter D are often used in forest inventories and for assessment of carbon and nutrient stocks in vegetation. When shifting from plantation forestry to mixed forestry or multi-species agroforestry systems, however, short-cuts to the empirical approach for establishing such equations are desirable. Fractal branching models provide a transparent scheme for deriving tree-specific scaling rules (especially, the b parameter) on the basis of easily observable, non-destructive methods. The relation between link (section of stem or branch between two branching points) length and link diameter has a direct influence on the b parameter of the allometric equation in the range 2–3.5, providing substantial variation around the claims of a universal value of 8/3. Apart from the total tree biomass, the models can provide rules for total leaf area; relative allocation of current growth to leaves, branches or stem. The power of the allometric scaling relation (b) necessarily has the same value, for a given tree, for all properties that are dominated by the endpoints of the branching process, and that are thus 'additive'. Below ground, similar descriptions hold for individual root axes, where the proximal root diameter can be used for predicting total length or biomass of all its branches. Sampling error was analyzed to derive rules for the number of branching points that should be observed for reliable estimates of the fractal branching parameters. For the inherent parameter variability that was chosen as default setting a minimum number of 50 branching points should be observed. A spreadsheet model (functional branch analysis, FBA) is made available through the WWW that allows users to derive results for new parameter combinations and/or seek new applications. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Trees cover a broader range of scale in their size than any other organism (Thomas, 2000) and the concept 'tree' needs a scalar before any meaningful statements about biomass, nutrient stocks or uptake, water use, carbon sequestration, pro-

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ductivity or any other functional ecological property can be made. Foresters have long term experience in scaling trees on the basis of stem diameter at a specified height above the ground (Brown, 1997), but their empirical rules need re-calibration for each tree species and stand density, and can not be easily applied in mixed species forests or in situations where trees grow in more open conditions rather than in a closed stand (Brown et al., 1995; Ketterings et al., 2001). When comparisons include several orders of magnitude, simple scaling rules may give the impression that all trees (West et al., 1999) or even all forests (Enquist and Niklas, 2001) of the world are behaving in the same way and can be captured by a single allometric scaling rule. If the target is an answer of the right order of magnitude, we may indeed use a generic scaling rule with a power of 8/3 or 2.67. If we care about errors of a factor 3, however, a method that predicts the power for scaling relations for each tree species (or even individual tree...) is relevant. Thus, the need remains for achieving a better understanding of the empirical scaling rules for trees and, ideally, a scheme that allows simple observations of tree shape to be translated into reasonable estimates of the scaling rules.

Trees can not have any form—there are clear constraints in 'designing' trees, as all parts must be connected to ensure transport, it must meet minimum mechanical stability and it should be able to grow, i.e. all steps between its current form and a start (usually from a seed) must have been possible as well. Beyond these minimum requirements, there are considerations of resource capture and resource use efficiency, which probably lead to differences in 'fitness' of different shapes (Niklas, 1994).

We can explore the apparent logic of real world trees and use non-destructively observable properties to reconstruct allometric equations—this is what we do in 'functional branch analysis' or FBA.

Aboveground trees, root systems, rivers and road networks share common properties, which have gradually been recognized on the basis of 'fractal' analysis (Mandelbrot, 1983), although some of the concepts date back to Leonardo da Vinci. Fractal properties can emerge if a relatively simple set of rules is applied consistently across a range of scales, e.g. stating that the diameters after a branching point are a certain proportion of the diameter before branching. If such rules are applied repeatedly, a form can be constructed with remarkable similarity to a tree or river system. Different reasons may be given for such a rule, for example a constant total transport requirement before and after the branching point, or the need for mechanical stability which requires each branch to be designed to carry its share of the total weight load (Niklas, 1992).

Fractal or self-repeating branching models are essentially based on assumptions of 'self-similarity' across scales: this means that a picture of a branching point looks the same, whether it is taken from the first or last branching point of a tree, relative to the diameter of the branches. This suggests a simple test: measure the diameter of branches before and after a branching point and test in regression analysis whether or not the derived parameters depend on current diameter.

The objectives of our research were to develop a procedure for deriving allometric equations for biomass and other properties of trees on the basis of parameters that can be measured non-destructively, and in future may be derived by visual estimation on individual trees in mixed stands. In developing this procedure we need to know, which parameters have major impact on the final result, and we need guidelines for the number of replicate observations needed to derive the input parameters for the model, for the type of variability to be expected in real trees.

The questions considered in this paper are:
- can we design a consistent and transparent system for describing trees in terms of branching properties and relate this to total size properties,
- can allometric equations for relating total tree size to initial stem diameter be predicted from properties of the branching system;
- which properties of the branching system have a major impact on the allometric equations and which a minor one (sensitivity analysis);
- how many observations will be required in practical applications to reduce uncertainty to an acceptable level?

- can we relate the fractal dimension of various properties of a tree (e.g. leaf area, biomass) to each other, for a given branching pattern? Can we identify scaling rules for different properties of the same set of trees from characteristics of these properties?

- can we relate a property such as 'specific root length' to the diameter of proximal roots?

2. Methods

2.1. Basic fractal branching rules

Fractal branching models repeatedly apply the same equations to derive subsequent orders of the branching process. For practical applications, a rule is added for stopping when a certain minimum size is reached. The rules can refer to the diameter, length and/or orientation of the next order of branches. Van Noordwijk et al. (1994) and Spek and Van Noordwijk (1994) applied rules that are primarily based on the diameter to simulate (tree) root systems. Five parameters (n, p, q, L_m and r) are needed in this approach (Fig. 1):

n = number of branches into which the current link (section of stem or branch between two branching points) splits at the following branching point; $n \geq 2$

$p = D_i^2/(\Sigma_j^n D_{i+1, j}^2)$, describes the change in diameter^2 from link order i to its n derivative links of order $i + 1$ and hence cross-sectional area (cssa) of the stem (this parameter was earlier referred to as α);

$q = D_{i+1, 1}^2/(D_{i+1, 1}^2 + D_{i+1, 2}^2)$, for $n = 2$ and $D_{i+1, 1} > D_{i+1, 2}$ ($0.5 < q \leq 1$) to describe the relative equity among the branches. With these definitions we obtain for $n = 2$:

$$D_{i+1, 1} = D_i \sqrt{\frac{q}{p}}$$

$$D_{i+1, 2} = D_i \sqrt{\frac{(1-q)}{p}} \qquad (1)$$

L_m is the length of a link of minimum diameter, and r is the relative increment in link length per unit relative increment in diameter, hence:

$$L(D) = L_m \left(1 + r \left(\frac{D}{D_{min}} \right) \right) \qquad (2)$$

For fractal (scale-independent) models to apply, the parameters p and q should be independent of current diameter D. Subsequent work on tree root systems, as well as, aboveground trees (Van Noordwijk and Purnomosidhi, 1995) has shown that this assumption of independence may be used as first approximation for a substantial range of diameters, but at small diameters the average p may increase, although the scatter in calculated values from observations is often large. If a (weak) dependence of p or q on diameter is found, the branching pattern can still be reconstructed by repeated applications of the same set of rules, but the program needs some modification.

2.2. Rules for end-structures

The basic model can be extended by providing rules for 'end structures' such as leaves or fine roots (of a diameter less than D_{min}), as a function of current diameter. In the simplest form we need two parameters:

I_{end} describes the number of endstructures per unit link length, and

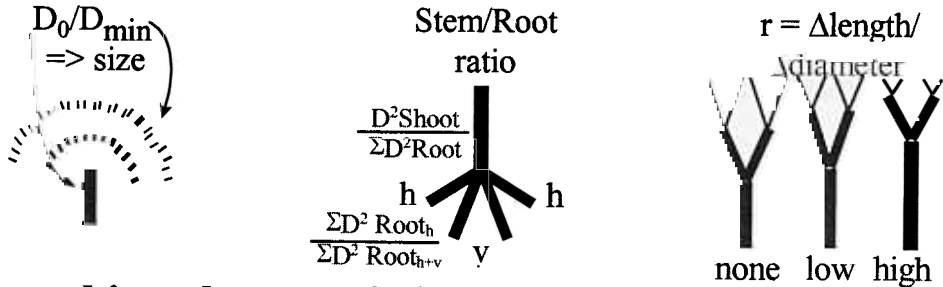$D_{endstr, max}$ indicates the maximum diameter that still carries endstructures.

2.3. Fractal branching model

With these basic rules, a founding link of diameter D_0 can be split into links that can be put in a 'parental queue' and be subsequently split, as long as more than 1 of their offspring has a diameter exceeding the minimum diameter D_{min}. In the flowchart (Fig. 2), a central concept is that of a 'parental queue' if links that have yet to be 'split' to derive their offspring. Without a minimum diameter for links, this process would be infinite, as each branching event adds more links to the parental queue than it removed. But with a minimum diameter (D_{min}) rule, splits in roots with:
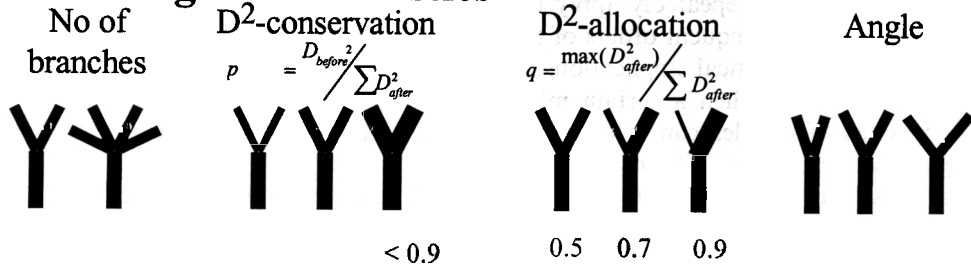
$$D < D_{min} \sqrt{\frac{p}{(1-q)}}$$
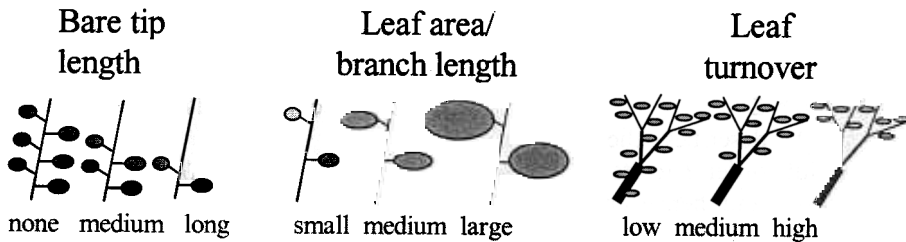
Functional Branch Analysis = FBA

Overall characteristics

D_0/D_{min}
=> size

Stem/Root ratio

$$\frac{D^2 Shoot}{\Sigma D^2 Root}$$

$$h \qquad h$$

$$\frac{\Sigma D^2 Root_h}{\Sigma D^2 Root_{h+v}} \qquad v$$

$r = \Delta length/ \Delta diameter$

none   low   high

Branching characteristics

No of branches

D²-conservation

$$p = \frac{D_{before}^2}{\Sigma D_{after}^2}$$

< 0.9

D²-allocation

$$q = \frac{max(D_{after}^2)}{\Sigma D_{after}^2}$$

0.5   0.7   0.9

Angle

Final structures: leaves

Bare tip length

none medium long

Leaf area/ branch length

small medium large

Leaf turnover

low medium high

Final structures: fine roots

Bare tip length

none medium long

Fine root branch length

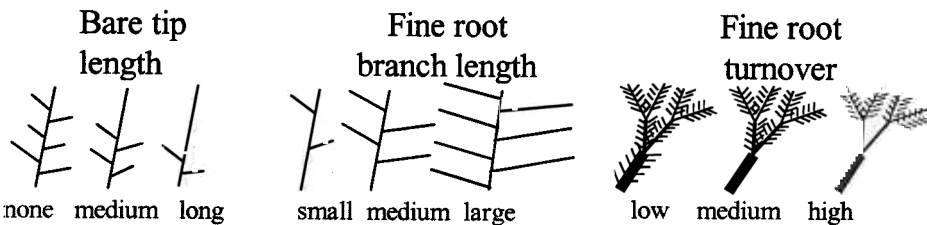small medium large

Fine root turnover

low medium high

Fig. 1. Elements of a 'functional branching analysis' (FBA) scheme, which can be applied for above- as well as belowground parts of trees; combinations of the various parameters—either visually assessed or measured—can be used to predict total size (weight, surface area, length, height, lateral extent) and the allometric scaling equations between these.
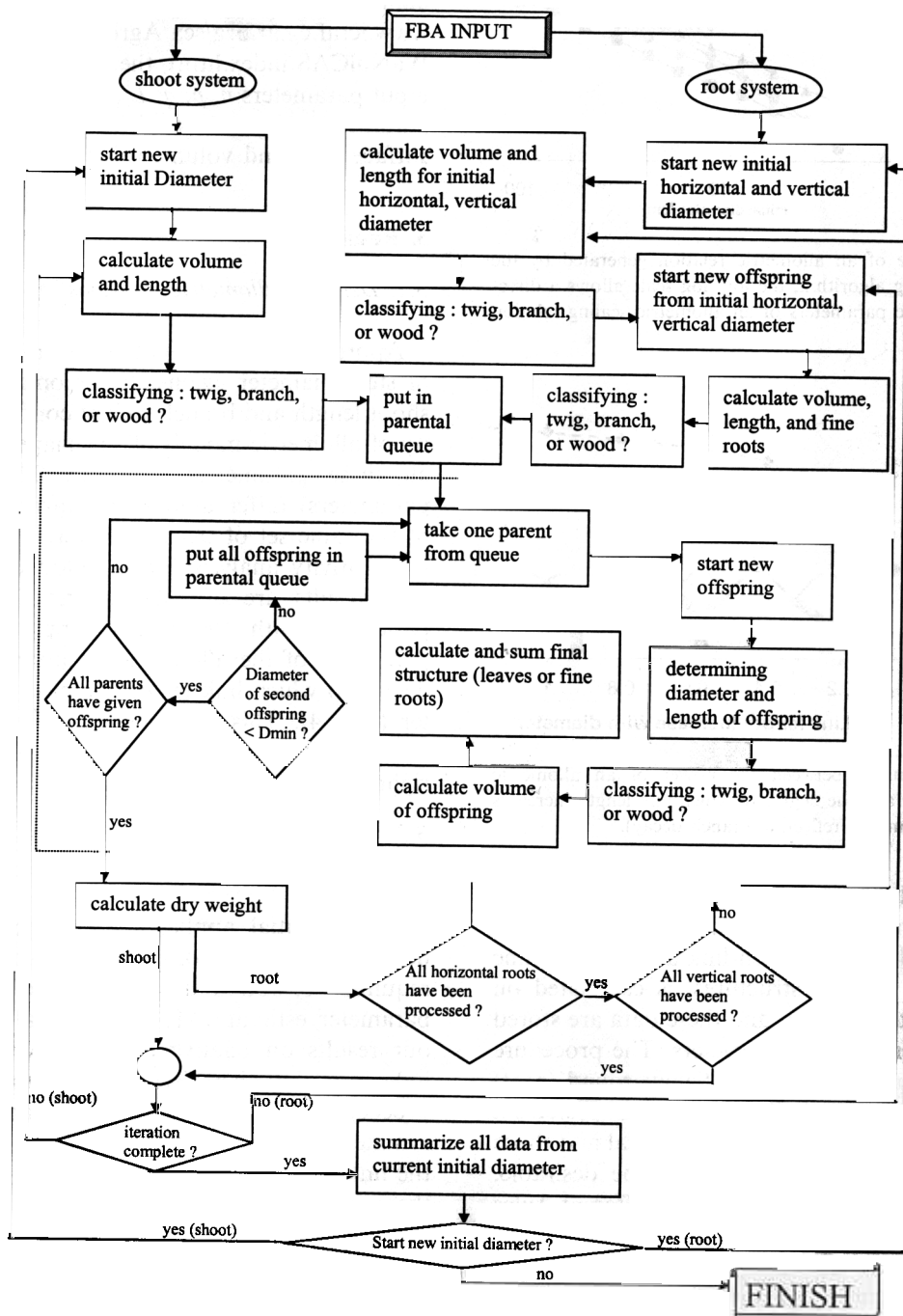
Fig. 2. Flowchart of the FBA module, implemented in a spreadsheet model available on ICRAF's web site.
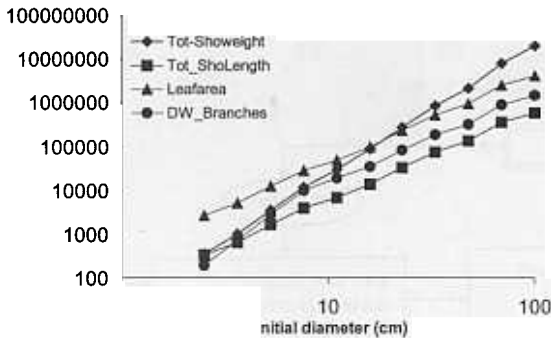
Fig. 3. Example of an allometric relation generated by the fractal branching algorithm; the log–log scale allows a direct derivation of the parameters of an allometric scaling relation $Y = aX^b$.
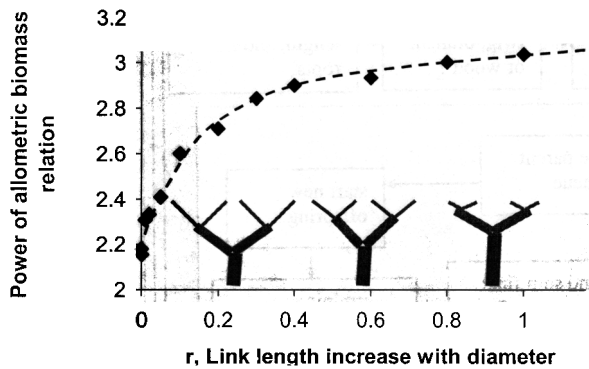

Fig. 4. Relationship between the power of an allometric biomass relation and the degree to which link length increases with branch diameter (reflecting branch decay).

will not produce offspring, so the parental queue does not continue to grow and the calculations can be completed. For each link a length, volume and number of 'end structures' is calculated on the basis of its diameter, and these data are stored in various summation parameters. The procedure for aboveground (shoot) and belowground (root) systems of trees are similar, but in root systems a distinction between roots with a vertical and those with a horizontal orientation may be desirable, and the initial split may follow different rules (leading to a large number of root axes for a single stemmed tree).

If such an algorithm for constructing branching patterns is applied many times to trees (or root systems) of different initial diameter, D_0, a range

of properties of the tree (or root system) as a whole can be related to D_0, for example by fitting an allometric equation of the type $Y = aD^b$ to the data. In a spreadsheet model (available via www.icraf.cgiar.org/sea/AgroModels/ WaNulCAS/index.htm), the relations between the input parameters n, p, q, L_m and r and the output parameters a and b can be explored, for length, surface area and volume (or weight) of the tree.

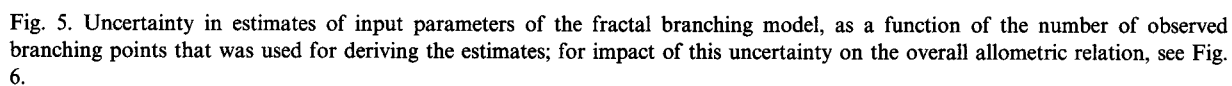## 3. Results

3.1. Deriving allometric relations

Approximately, straight lines on log–log plot of stem diameter against tree biomass, leaf area, shoot length and branch weight confirm the validity of allometric models of the shape $Y = aX^b$ for all these parameters (Fig. 3). The slopes (b parameters) differ among the various properties of the same set of trees, however.

Sensitivity analysis for the individual parameters (results are not shown) revealed that the parameter with the largest impact on the b parameter of the allometric equation is r, or the degree to which link length increases with diameter (Fig. 4). This parameter can be visually assessed in its more extreme values (Fig. 1, upper right).

3.2. Uncertainty in input parameters as function of number of observations

For potential applications we need to know how many observations on branching points are required to obtain a specified accuracy in the parameter estimates (Fig. 5). For all parameters our results on relative errors converge to zero, indicating that there is no bias in the estimation procedure. The error structure is approximately symmetric for the average p and q, and for L_m, the link length at minimum branch diameter. For the range of p, q and L, the errors are clearly asymmetric and small data sets will lead to an underestimation of the real value.

The impact of this uncertainty in parameter value for the overall allometric biomass equation was investigated by calculating the a and b

Fig. 5. Uncertainty in estimates of input parameters of the fractal branching model, as a function of the number of observed branching points that was used for deriving the estimates; for impact of this uncertainty on the overall allometric relation, see Fig. 6.
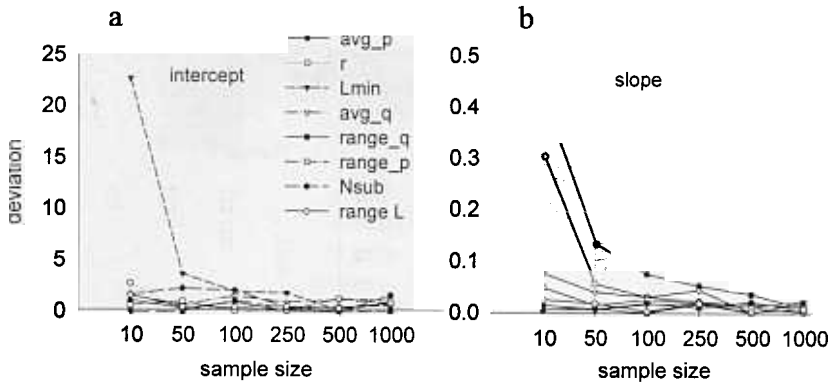
Fig. 6. Range in the two parameters of the allometric biomass equation (a and b) that result from the uncertainty in the value of the various input parameters, as a function of the number of observations from which the input parameters were derived.

parameter of that equation for the lowest (L) and highest (H) parameter estimates obtained for different number of observation (Fig. 6). The results here integrate over the uncertainty on the parameter as such and its impact on the overall scaling relationship. For the intercept of the allometric scaling relation, that equals the biomass for $D = 1$, the absolute range of uncertainty is less than 5 kg per tree as soon as the parameters were derived from at least 50 observations. The strongest impact on this uncertainty stems from the uncertainty on the L_m parameter. For the slope the uncertainty on the power of the scaling relation is less than 0.2 when the parameters were obtained from a data set of at least 50 branching points, or less than 0.1 for a data set of size 100. The strongest impact derives from uncertainty in the p parameter and in the r parameter, that is based on the relation between link length and link diameter.

3.3. Allometric relations for additive properties

The observed similarity in exponents of the allometric relations for different properties gave rise to a further exploration of the underlying theory. For a number of properties in a branched system we can expect that the sum of the results after a branching event equal that before. Examples of properties for which this should hold true are the number of end-points of the branched system or the number (weight or area) of struc-

tures associated with the finer branches, such as leaves or fine roots. Such properties meet the requirement:

$$f(D_i) = f(D_{i+1,1}) + f(D_{i+1,2}) \tag{3}$$

where $D_{i+1,1}$ and $D_{i+1,2}$ originate from D_i.

If the function f is of the (allometric) form $Y = aD^b$ and applies across a substantial range of D values, we obtain:

$$Y_1 = Y_2 + Y_3 = aD_i^b = aD_{i+1,1}^b + aD_{i+1,2}^b \tag{4}$$

If scale-independent branching rules (Eq. (1)) are followed, p and q are independent of diameter D. If so, Eq. (4) for additive properties can only hold true for a single value of parameter b, for which:

$$p^{b/2} = q^{b/2} + (1 - q)^{b/2} \tag{5}$$

If $p = 1$, the solution is $b = 2$, irrespective of q. For the special case of $q = 0.5$, Eq. (5) leads to:

$$b = \frac{2 \log 2}{\log 2 + \log p} \tag{6}$$

(which also leads to $b = 2$ for $p = 1$).

For most values of p and q, Eq. (5) has to be solved iteratively. Results (Fig. 7A) show a strong (and interactive) impact of p and q on the b value of additive properties. For $q > 0.8$ the resulting b value responds very strongly to $p < 1$. Thus, for a given set of p and q, all response parameters that are additive will have the same power b of their allometric equations.

3.4. Allometric relations for non-additive properties

For many other tree properties Eq. (4) has to be modified, to account for the response variate between the points where D_i, and $D_{i+1,1}$ and $D_{i+1,2}$ are measured.

$$f(D_i) = f(D_{i+1,1}) + f(D_{i+1,2}) + g(D_i) \qquad (7)$$

For example, if the response variate is total tree biomass, $g(D_i)$ should reflect the weight of link i (or to be more precise, half the weight of link i plus half the weights of links $i+1$, 1 and $i+1$, 2, respectively). This means that Eq. (5) will be modified into:

$$p^{b/2}\left(1 - \frac{g(D_0)}{aD_0^b}\right) = q^{b/2} + (1-q)^{b/2} \qquad (8)$$

Again, iteratively we can find solutions for b (Fig. 7B), for a range of values of p, q and the term $g(D_0)/(aD_0^b)$.

We note that when the term $g(D_0)/(aD_0^b)$ is positive, the resulting power of the overall allometric equation will increase above the value for a truly additive property. The solutions for additive property thus reflect the lowest value of allometric equations for tree properties (as long as these properties are non-negative for the current link...).

If the function g uses a power of D_0 other than the b value calculated for additive properties, the term $g(D_0)/(aD_0^b)$ will introduce a dependence on D_0 of the resulting solution for b, and the scale-independent allometric equation will only be valid as approximation.

3.5. Specific root length

Specific root length for a root system can be derived under the following assumptions:
(A) an allometric equation for the dry weight of a (branched) root based on its proximal diameter D, $W(D) = a_1 D^{b_1}$
(B) a similar allometric equation for the length of a (branched) root $L(D) = a_2 D^{b_2}$
(C) a population of roots, with a frequency distribution of root diameters that can be described by:

$$\text{CumFreq} = \left(\frac{D}{D_{max}}\right)^n$$

where n is a parameter (equivalent to a Gini coefficient), and hence:

$$\text{Freq}(D) = \frac{d\text{Cumfreq}}{dD} = nD_{max}^{-n}D^{(n-1)}.$$
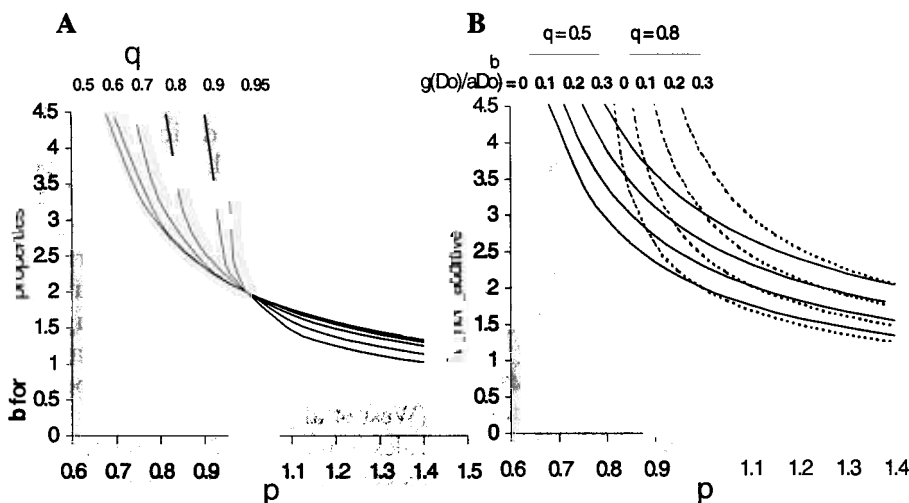
From these assumptions we derive that:

Fig. 7. (A) Power of the allometric equation b that is compatible with additivity, as a function of p and q; (B) influence of the term $g(D_0)/(aD_0^b)$ on the power b of the allometric equation, for $q = 0.5$ or 0.8 and a range of p values.

$$W_t = \int_0^{D_{max}} \mathrm{Freq}\, W \mathrm{d}D$$

$$= a_1 n D_{max}^{-n} \int_0^{D_{max}} D^{b_1+n-1}\mathrm{d}D = \frac{a_1 n D_{max}^{b_1}}{(b_1+n)} \quad (9)$$

Similarly, the sum of root diameter squares:

$$\mathrm{Sum}D_r^2 = \frac{n D_{max}^2}{(2+n)} \quad (10)$$

Eqs. (9) and (10) lead to:

$$D_{max} = \left\{ W_t \frac{(b_1+n)}{(a_1 n)} \right\}^{1/b_1} = \left(\mathrm{Sum}D_r^2 \frac{(2+n)}{n} \right)^{0.5} \quad (11)$$

Relations between W_t and $\mathrm{Sum}D_r^2$ can now be obtained as:

$$W_t = \frac{(a_1 n)}{(b_1+n)} \left\{ \mathrm{Sum}D_r^2 \frac{(2+n)}{n} \right\}^{b_1/2} \quad (12)$$

and

$$\mathrm{Sum}D_r^2 = \frac{n}{(2+n)} \left\{ W_t \frac{(b_1+n)}{(a_1 n)} \right\}^{2/b_1} \quad (13)$$

Similarly, from assumptions B and C we obtain:

$$L_t = \frac{(a_2 n)}{(b_2+n)} \left\{ \mathrm{Sum}D_r^2 \frac{(n+2)}{n} \right\}^{b_2/2} \quad (14)$$

and

$$L_t = \frac{(a_2 n)}{(b_2+n)} \left\{ W_t \frac{(b_1+n)}{(a_1 n)} \right\}^{b_2/b_1} \quad (15)$$

Finally, the specific root length SRL is obtained as function of W_t:

$$\mathrm{SRL}(W_t) = \frac{L_t}{W_t} = \frac{(a_2 n)}{(b_2+n)} \left\{ \frac{(b_1+n)}{(a_1 n)} \right\}^{b_2/b_1} W_t^{b_2/b_1 - 1}$$

4. Discussion

The results of our analysis show that a consistent and transparent system can indeed be designed for describing trees in terms of branching properties and relate this to total size properties by allometric equations. The parameter of the branching system with the single largest effect on overall allometrics for biomass, appeared to be

the relation between link length and link diameter. Fractal dimensions of various properties of a tree (e.g. leaf area, biomass) appear to follow specific patterns, depending on the degree to which the property in question follows rules for 'additivity'. The fractal branching procedure can also be used to estimate specific root length as a function of tree stem diameter. Other applications are in the estimation of 'green' versus 'brown' light interception in savannah trees and the implications this has for modifying temperature with or without competition for water with other parts of the vegetation (Van Noordwijk and Ong, 1999). Applicability of these equations depend on whether or not the assumptions underlying the fractal (scale-independent) process are met in the real world. A procedure for testing this on individual trees is available (Van Noordwijk and Purnomosidhi, 1995; Van Noordwijk et al., 1996). The basic assumptions underlying fractal branching have been tested and found to be applicable as acceptable first approximation for a wide range of tropical trees, above, as well as belowground, although a number of extensions of the theory have been suggested for various situations (Pages et al., 2000; Ozier-Lafontaine et al., 1999; Rowe, 1999; Smith, 2001).

If the basic assumptions do indeed apply, uncertainty on parameter values becomes the next issue. Results presented here suggest that a minimum of 50 but preferably 100 branching points should be used for deriving the main parameters of the fractal branching process; from the graphs and table presented here one can derive more specific recommendations once the required precision in the overall outcome is specified.

Overall, the fractal branching analysis offers promise for a better understanding of why, when and how to modify allometric scaling relations from the generic 'default' values recommended in the forestry literature. Although the 8/3 rule for allometric scaling of trees has a biomechanical interpretation that may appear to be generic (West et al., 1999), our results suggest that scaling rules in the range 2–3.5 are consistent with shapes as can be observed in real trees (Fig. 4).

We are currently testing the degree to which the parameters of the fractal branching process are characteristic of tree species, and thus can be

meaningfully entered in databases, or whether they essentially depend on site and management conditions and thus require location specific tuning. The fact that the major parameters, at least in their more extreme values, can be visually recognized should lead to more confidence in the use of the method. The allometric scaling relations as derived with the FBA module can be directly used in the WaNuLCAS model of tree–soil–crop interactions (Van Noordwijk and Lusiana, 1999, 2000).

Acknowledgements

References

Brown, S., 1997. Estimating biomass and biomass change of tropical forests, a primer. FAO Forestry paper 134, FAO, Rome.

Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Ferreira, C.A.C., Victoria, R.A., 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. Forest Ecology and Management 75, 175–189.

Enquist, B.J., Niklas, K.J., 2001. Invariant scaling relations across tree-dominated communities. Nature 410, 655–660.

Ketterings, Q.M., Coe, R., Van Noordwijk, M., Ambagau', Y., Palm, C.A., 2001. Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forest. Forest Ecology and Management 146, 201–211.

Mandelbrot, B.B., 1983. The Fractal Geometry of Nature. Freeman, New York.

Niklas, K.J., 1992. Plant Biomechanics: an Engineering Approach to Plant Form and Function. University of Chicago Press, Chicago, London, p. 607.

Niklas, K.J., 1994. Plant Allometry, the Scaling of Form and Process. University of Chicago Press, Chicago, London, p. 365.

Ozier-Lafontaine, H., Lecompte, F., Sillon, J.F., 1999. Fractal analysis of the root architecture of *Gliricidia sepium* for the spatial prediction of root branching, size and mass: model development and evaluation in agroforestry. Plant Soil 209, 167–180.

Pages, L., Asseng, S., Pellerin, S., Diggle, A., 2000. Modelling root system growth and architecture. In: Smit, A.L., Bengough, A.G., Engels, C., van Noordwijk, M., Pellerin, S., van de Geijn, S.C. (Eds.), Root Methods, A Handbook. Springer, Berlin, pp. 113–146.

Rowe, E.C., 1999. The safety-net role of tree roots in hedgerow intercropping systems. PhD. Thesis, Wye College, University of London, UK, pp. 288

Spek, L.Y., Van Noordwijk, M., 1994. Proximal root diameters as predictors of total root system size for fractal branching models. II. Numerical model. Plant and Soil 164, 119–128.

Smith, D.M., 2001. Estimation of tree root lengths using fractal branching rules: a comparison with soil coring for *Grevillea robusta*. Plant Soil 229, 295–304.

Thomas, P., 2000. Trees: Their Natural History. Cambridge University Press, Cambridge, UK, p. 286.

Van Noordwijk, M., Purnomosidhi, P., 1995. Root architecture in relation to tree-soil-crop interactions and shoot pruning in agroforestry. Agroforestry Systems 30, 161–173.

Van Noordwijk, M., Lusiana, B., 1999. WaNuLCAS, a model of water, nutrient and light capture in agroforestry systems. Agroforestry Systems 43, 217–242.

Van Noordwijk, M., Ong, C.K., 1999. Can the ecosystem mimic hypotheses be applied to farms in African savannahs? Agroforestry Systems 45, 131–158.

Van Noordwijk, M. and Lusiana, B. 2000, WaNuLCAS 2.0, Background on a model of water nutrient and light capture in agroforestry systems. International Centre for Research in Agroforestry (ICRAF), Bogor, Indonesia, pp. 186.

Van Noordwijk, M., Spek, L.Y., De Willigen, P., 1994. Proximal root diameters as predictors of total root system size for fractal branching models. I. Theory. Plant and Soil 164, 107–118.

Van Noordwijk, M., Lawson, G., Groot, J.J.R., Hairiah, K., 1996. Root distribution in relation to nutrients and competition. In: Ong, C.K., Huxley, P.A. (Eds.), Tree–Crop Interactions—a Physiological Approach. CAB International, Wallingford, pp. 319–364.

West, G.B., Brown, J.H., Enquist, B.J., 1999. A general method for the structure and allometry of plant vascular systems. Nature 400, 664–667.