Fractal analysis of foliage distribution in loblolly pine crowns

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Abstract: A new method for estimating fractal characteristics (fractal dimension and foliage density) of a single crown or its portions is developed. The proposed method operates with volume and mass of natural units of the crown, such as shoots and branches, rather than with numbers of regular cubes. Fractal dimension alone is not sufficient to describe foliage distribution in the crown because it says nothing about the density of foliage at a given point. The density is defined as the ratio of foliage mass to fractal volume it occupies. Fortunately, the intercept of the regression, which contains fractal dimension as the slope, provides a measure of foliage density. Thus the method makes it possible to separate purely spatial factors represented by fractal dimension from ecophysiological effects characterized by foliage density. Application of the method showed that neither fractal dimension nor foliage density of the studied loblolly pines (*Pinus taeda* L.) correlates with current diameter increment. At the same time, there is a pronounced negative correlation between fractal dimension and crown size. These results suggest that as crowns become larger, the amount of foliage located at the crown periphery increases in proportion to the foliage amount inside the crown. As a spin-off of this analysis, a method for estimating relative foliage density (defined as the ratio of actual to maximal foliage mass for a given branch) is developed.

Résumé : L'auteur a développé une nouvelle méthode pour évaluer les caractéristiques fractales (densité du feuillage et dimension fractale) d'une seule cime ou de ses portions. La méthode qui est proposée fonctionne avec l'ampleur du volume et de la masse des unités naturelles de la cime, telles que les pousses et les branches, plutôt qu'avec les nombres de cubes réguliers. La dimension fractale seule n'est pas suffisante pour décrire la distribution du feuillage dans la cime parce qu'elle ne dit rien de la densité du feuillage en un point donné. La densité est définie comme le ratio de la masse foliaire sur le volume fractal qu'elle occupe. Heureusement, le point d'intersection de la courbe de régression, dont la pente est la dimension fractale, fournit une mesure de la densité du feuillage. Par conséquent, la méthode permet de séparer les facteurs purement spatiaux, représentés par la dimension fractale, des effets écophysiologiques caractérisés par la densité du feuillage. L'application de la méthode montre que ni la dimension fractale, ni la densité du feuillage du pin à encens (*Pinus taeda* L.) qui a été étudié, ne sont corrélées à l'accroissement courant en diamètre. En même temps, il y a une forte corrélation négative entre la dimension fractale et la taille de la cime. Ces résultats suggèrent qu'à mesure que la cime grossit, la quantité de feuillage à la périphérie de la cime augmente proportionnellement à la quantité de feuillage à l'intérieur de la cime. Une retombée de cette analyse est le developpement d'une méthode pour évaluer la densité relative du feuillage qui est définie comme le ratio de la masse actuelle sur la masse maximale de feuillage pour une branche donnée.
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Fractal geometry and tree crowns

Length, area, and volume of many natural objects cannot be measured as easily as those of cubes, circles, and cylinders. The diameter of a solid, such as a tree stem, makes sense, but the width of a porous crown is much less so. There is something intrinsically vague about the width of a maze of protruding branches and the voids in between. Similarly, we cannot talk about crown volume, which encompasses mostly empty space, in the same sense as we talk about solid stem volume. These peculiarities of tree crowns call for a new approach for their measurement.

Calculation and modeling of tree productivity and many other ecophysiological variables require, first of all, the precise measurement of crown surface. This surface intercepts sunlight and produces the larger part of all organic matter on the earth. However, it is hard to be precise when one does not know what to measure. Should we measure the surface of a convex hull that would envelope the crown, or should we take into account cavities, cuts, and gaps in the crown? If so, what is the smallest cavity that should be considered? Should the foliage area be used as the crown surface? Should we pay attention to the "ups and downs" of foliage surface? Or should we, perhaps, go deeper and measure the surface of cells or pigment molecules?

The solution to these problems lies outside biology. Classical geometry with its rigid contrast between lines, surfaces, and volumes is not suitable for defining and measuring tree crowns and many other natural objects. Tree crown is neither a three-dimensional solid nor a two-dimensional photosynthetic surface. It can be viewed as a collection of holes that serves to conduct sunlight and gases or as a multilevel hierarchy of clustered dots (pigment molecules and chloroplasts). The crown is a hybrid of surface and volume. Fractal geometry (Mandelbrot 1983) provides concepts and tools needed to describe such objects common in nature. Mandelbrot's (1983) book is entitled *The Fractal Geometry of Nature* and contains many references to trees. Fractal geometry allows one to condense information on crown structure into a few meaningful numbers such as fractal dimension, which is a generalization of the integer spatial dimension of classical geometry.

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Menger's sponge

The best way to understand the concept of fractal dimension is to construct a classical three-dimensional fractal, Menger's sponge (Mandelbrot 1983). The process of construction can be presented in a series of repetitive steps. At the first step, we divide a cube with a side length equal to 1 into 27 smaller cubes with side lengths equal to 1/3. The faces (sides) of nine of these smaller cubes appear on each side of the original cube. If they are numbered in rows or columns, the middle face will be No. 5. Suppose we can push through and remove this middle cube and the two others behind it. Repeating the same procedure from the adjoining side and again from the top will remove an additional two cubes each because the central one is already removed. As a result, a total of seven cubes will be removed and 20 (out of 27) cubes will remain. The second and all subsequent steps are repetitions of the first on a smaller scale: we divide each of the 20 cubes into 27 smaller cubes with sides equal to $(1/3)^2$. Again, we remove the middle rows of cubes and proceed to the next step of division and removal. With each step, mass is disappearing while the overall volume of the resulting sponge remains the same.

This result, a volume with little mass, is similar to the crown: the filled cubes of the sponge can be associated with spaces that contain foliage, while empty spans left by the removed cubes may represent gaps between branches. Along with this conceptual similarity, the crown differs from Menger's sponge in the way the solid content is "removed" and the form of the resulting voids. The method to be developed should be able to account for all of these differences and similarities.

Fractal dimension

Any spatial dimension, D, be it Euclidean integer dimension or fractal dimension, is represented by the power of the relationship between the number of units, N (such as smaller cubes), and the linear size of the unit, r, which is the length of its side (Mandelbrot 1983):

$$[1] \quad N = \frac{1}{r^D}$$

When the original cube is split on $N = 27$ smaller cubes (each with $r = 1/3$) and none of them is removed, we are dealing with a regular Euclidean object. Its dimension is

$$[2] \quad D = -\frac{\ln(N)}{\ln(r)} = -\frac{\ln(27)}{\ln(1/3)} = 3$$

In this case the dimension coincides with the number of coordinates. The power, however, need not be restricted to this number. Even when the power is not an integer, it does represent a spatial dimension. The power is a more general representation of spatial dimension than that of Euclidean geometry. When, as in the case of Menger's sponge, the number of remaining cubes is 20 and the process of subdivision goes on, the spatial dimension is no longer an integer. It is fractional or, using another Mandelbrot (1983) neologism, fractal. Fractal dimension is individual for each object. For Menger's sponge, it is equal to

$$[3] \quad D = -\frac{\ln(20)}{\ln(1/3)} = 2.727...$$

Mathematically, fractal dimension is defined (Pfeifer and Avnir 1983) as the limit

$$[4] \quad D = -\lim_{r \to 0} \frac{\ln(N(r))}{\ln(r)}$$

Mass of the object disappears in the process; it tends to zero. Physical objects are less perfect fractals than mathematical constructs. Self-similarity breaks at certain finite unit sizes, called inner and outer cutoffs (Mandelbrot 1983). For tree crowns, the inner cutoff may be the side length of the volume occupied by foliage of a single shoot (Zeide 1993).

Existing approaches to measuring fractal dimension

Many studies report fractal dimensions of two-dimensional projections of crowns (Morse et al. 1985; Strand 1990; Gunnarsson 1992; Mizoue and Masutani 1993). These dimensions, aptly named by Mandelbrot (1983) "sieve dimensions", are different from fractal dimensions of actual crowns occupying three-dimensional space (called "sponge dimension"). While sponge dimensions are always greater than 2, sieve dimensions never exceed this value. The chief attraction of sieve dimensions is that, unlike sponge dimension, they can be easily calculated using photographs or videotapes. Sieve dimension, however, tells us little about real three-dimensional crowns. The same sieve dimension can correspond to objects with different sponge dimensions and vice versa. Sponge and sieve dimensions are related only by an inequality: their difference is less than 1 (Pfeifer and Avnir 1983).

At present, a method for determining fractal dimension of a single three-dimensional crown does not exist. The two-surface method provides such a dimension for a group of trees (Zeide and Pfeifer 1991; Corona 1991; Osawa 1995). The standard method for determining fractal dimension, the box-counting method, is not practical. It would require slicing the crown into many layers without distortion of its structure, subdividing them into cubic boxes, and counting the number of nonempty boxes. This procedure is repeated many times using various box sizes. The fractal dimension of the studied object is one of the parameters of the relationship between the number of boxes and their size.

Technical difficulties make this procedure all but impossible. While it can be easily applied to obtain a sieve dimension of a photographed image, dissecting the crown into regular boxes would destroy the structure we are trying to capture. Besides technical problems, the box-counting method instills two mental blocks that hamper analysis of three-dimensional crown geometry. The method makes us think about crown measurements in terms of (*i*) regular cubes and (*ii*) consecutive sequences of their sizes and counting.

Method of natural units

Division of the crown into regular cubes and complete enumeration of them is not the only way to obtain fractal dimension. As its name indicates, the proposed method uses natural units of the crown such as shoots and branches of various orders. Besides technical convenience, these irregular bodies are closer to the spirit of fractal geometry than unnatural cubes and straight lines.

Table 1. Development of a mass fractal (Menger's sponge) with decreasing unit size.

	Unit		Number of units		
Step (s)	Length ($l_s = r^s$)	Volume ($v_s = r^{3s}$)	Total ($N_s = r^{-3s}$)	Filled ($n_s = r^{-Ds}$)	Mass of a unit ($m_s = \rho(n_k v_k)/n_s$)
0	1	1	1	1	$\rho(n_k v_k)/1$
1	1/3	$(1/3)^3$	$3^3 = 27$	$3^D = 20$	$\rho(n_k v_k)/3^D$
2	$(1/3)^2$	$(1/3)^6$	27^2	3^{2D}	$\rho(n_k v_k)/3^{2D}$
3	$(1/3)^3$	$(1/3)^9$	27^3	3^{3D}	$\rho(n_k v_k)/3^{3D}$
4	$(1/3)^4$	$(1/3)^{12}$	27^4	3^{4D}	$\rho(n_k v_k)/3^{4D}$
⋮	⋮	⋮	⋮	⋮	⋮
k	$(1/3)^k$	$(1/3)^{3k}$	27^k	3^{kD}	$\rho(n_k v_k)/3^{kD}$

Fractal dimension from mass and volume of branches

Unlike the boxes which can be filled or empty, branches are filled with foliage by definition. They are "nonempty boxes". Therefore, mere counting of branches is not sufficient to produce fractal dimension. The proposed method obtains fractal dimension from the relationship between foliage mass of a branch and volume occupied by its foliage. The imperfectness of physical objects, expressed in finite cutoffs, saves their mass from the disappearance exhibited by mathematical fractals. As a result, we can relate mass and volume of branches. Mass is proportional to the compressed volume of all leaves (or needles) of a branch or a crown. In other words, when the unit length is equal to the inner cutoff, mass is proportional to the product of the size and number of the units. The coefficient of proportionality is specific gravity of foliage in a shoot, which is the smallest crown unit.

To derive a relationship between mass and volume, consider their values at consecutive steps. In the context of crown structure, steps may be visualized as size of a branch. At the first step, we deal with the entire crown, at the second with large branches of first order, and then with smaller and smaller branches. At the last step k, we have a shoot, which was identified as the inner cutoff (smallest unit) of the crown. Mass of the units (branches) at each step is calculated assuming that at this last step the total mass of the crown is proportional to the filled volume. This filled volume is equal to the product of unit volume at this step, v_k, and the number of these filled units, n_k. At each step, s, the total mass is divided by the number of current units to produce the mass of the unit (Table 1).

For Menger's sponge and other mass fractals (like tree crowns), the volume of a unit, such as a branch, can be expressed in terms of r, that is, the length of the smallest unit reached at the k-step (Table 1):

$$[5] \quad v_s = r^{3s}$$

The mass of the same unit can be expressed as the ratio of the total mass of the object, $r^{3k}n_k$, and the number of units, n_s:

$$[6] \quad m_s = \frac{\rho r^{3k} n_k}{n_s}$$

where ρ is the specific gravity of foliage in the smallest crown unit (shoot).

In terms of r, the numbers of units are

$$[7] \quad n_k = r^{-kD} \text{ and } n_s = r^{-sD}$$

Therefore, the mass is

$$[8] \quad m_s = \rho r^{3k-kD+sD}$$

Both expressions for volume (eq. 5) and mass (eq. 8) contain parameter s. In addition to helping the explanation, steps are valuable algebraically: by excluding parameter s, we can at last relate mass and volume of a branch. From the equation for volume, it follows that

$$[9] \quad s = \frac{\ln(v_s)}{3\ln(r)}$$

In terms of mass, this parameter is

$$[10] \quad s = \frac{\ln(m_s) - (3-D)k\ln(r) - \ln(\rho)}{D\ln(r)}$$

Because in both cases s is the same, we can equate

$$[11] \quad \frac{\ln(v_s)}{3\ln(r)} = \frac{\ln(m_s) - (3-D)k\ln(r) - \ln(\rho)}{D\ln(r)}$$

Hence, on the log–log scale the mass contained in a unit of Menger's sponge is a linear function of unit's volume:

$$[12] \quad \ln(m_s) = a + b\ln(v_s)$$

where

$$[13] \quad a = (3-D)k\ln(r) + \ln(\rho) \text{ and } b = \frac{D}{3}$$

Parameters of the mass–volume relationship

When eq. 12 is fitted to mass and volume of branches, parameter b provides information on fractal dimension of the crown or its parts. Fractal dimension is equal to the slope of this linear regression multiplied by 3 (eq. 13). In addition to D, parameter a depends on the inner cutoff, r, and the number of steps, k, required to reach it (eq. 13).

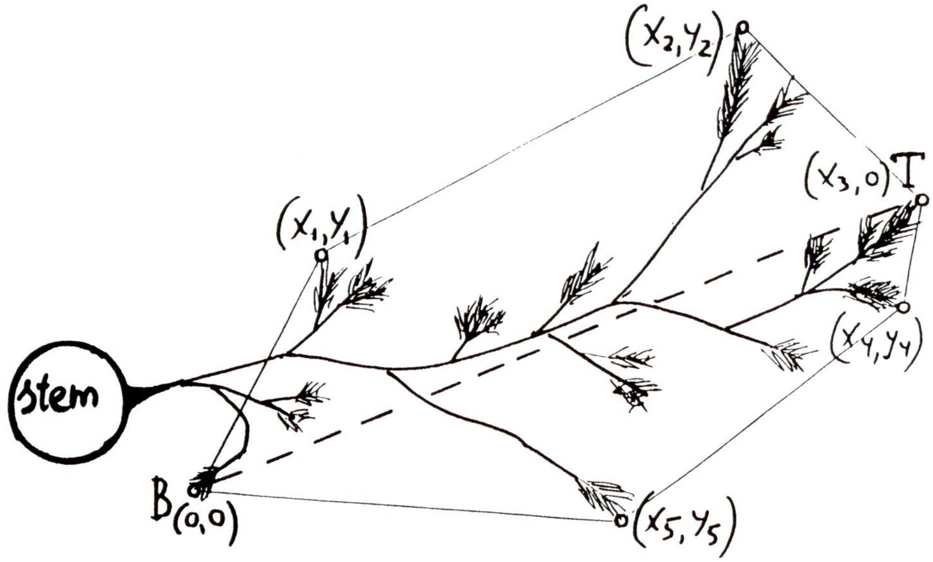
Parameter a can be viewed as a measure of foliage density. All filled cubes of fractal objects are assumed to be filled evenly. But the volume occupied by branches is filled to a varying degree. The density of foliage in branches exposed to sunlight at the crown top is much higher than that of shaded branches inside the crown. Besides location, density is affected by qualitative differences in foliage reflected in the terms "sun leaves" and "shade leaves." The resulting difference in foliage density is the major problem in applying fractal geometry to trees.

The proposed method addresses this problem by introducing the concept of foliage density and identifying it with parameter a. Mass of uniform nonfractal objects is proportional to volume, and density is defined as the ratio of these variables. Due to this proportionality, density is independent of volume. In fractals, mass is proportional to volume raised to the power of $D/3$. As a result, the ratio of mass to volume (that is, density) changes with volume. This irrelevant, for our purposes, link between density and volume can be eliminated, if density is defined as the ratio of foliage mass, M, to volume it occupies, V, raised to the power of $D/3$.

Since the mass–volume relationship is described in terms of logarithms, it is convenient to define foliage density, FD, in the log-transformed form

$$[14] \quad \text{FD} = a = \ln(M) - \frac{D}{3}\ln(V)$$

Fig. 1. Measurement of the area of foliage space. B, needle closest to the tree stem; T, tip of the needle farthest from the stem. The broken line depicts the horizontal axis.



This definition of foliage density differs in two respects from the ordinary concept of density exemplified by density of wood or water. First, to make density independent of volume, the volume has to be raised to the power of $D/3$. Density of Euclidean objects with $D = 3$ is a particular case of this definition of density because the power becomes 1. The second difference is in using the logarithmically transformed ratio of mass and volume. When compared with eq. 12, it becomes evident that foliage density is identical to parameter a. Depending on the degree of exposure to sunlight, foliage density and, accordingly, parameter a vary within the crown. This variation allows the crown fractal dimension to remain invariant. The same fractal dimension can characterize exposed and shaded branches, as well as the entire crown.

Volume occupied by foliage

Volume occupied by natural objects such as branches with shoots haphazardly sticking out cannot be estimated as easily as volume of cones or spheres. It is tempting to follow individual shoots and present volume of a branch with various dents and bulges. The danger is that for fractal objects, there is no objective way to stop the process of indenting. As soon as we start excising empty parts from the branch volume, one can go after smaller and smaller voids between secondary branches, shoots, fascicles, needles, cells, molecules, and so on. After all, even objects that look solid, such as metals, are mostly holes among tiny electrons and nuclei.

A solution is to define branch volume as the smallest convex hull that envelops all of the space with foliage growing on a given branch. Convex hull refers to a solid without any indentations. In more exact terms, convex hull is a solid in which a segment, joining any two points in its interior, lies wholly within the hull. This definition leads to including the space that is not occupied by foliage.

In this study the volume occupied by foliage of a given branch was estimated as the product of the area of the convex polygon that circumscribes the foliage and the foliage depth in the direction perpendicular to the polygon. To obtain the area, imagine a line BT (Fig. 1) connecting the leaf or needle closest to the tree stem with the tip of the needle farthest from the stem. Assuming that this line is the x-axis with the origin at the closest leaf, record the x,y- coordinates for the points located at the outer limits of the foliage area (Fig. 1). These points are the corners of the convex polygon that circumscribes the projection of the foliage space. Convex polygon refers to a closed plane figure bounded by straight lines without any indentations.

The second factor of the volume is foliage depth. Measurements of depth should be done with the branch attached to the tree stem. If this is too difficult, measure the angle between the branch and the stem, cut the branch, and hold it at that angle. Take several (5–10) measurements of the distance between the tips of extreme needles in the direction perpendicular to the polygon. These measurements should be distributed evenly throughout the space occupied by foliage.

Summary of the proposed method

The method of natural units estimates fractal dimension and foliage density using the relationship (eq. 12) between foliage mass of branches and the volume they occupy. The method can be applied to a group of branches and provide the parameters for several trees, a single crown, or any crown portion such as top or bottom.

There are three differences between the proposed method and the box-counting method. First, the natural units method is selective as opposed to the box-counting method, which requires visiting each unit of a studied object. Using the proposed method, we may sample a filled volume here and there in the crown. There is no ambiguity in selecting these volumes. Each of them is a separate branch. It is not necessary to measure all branches or count them in a certain order. The method of natural units relies on sampling rather than complete enumeration. A related feature is that we are entitled to disregard voids between filled spaces (branches).

Second, the natural units method requires more information about each unit than that involved in the qualitative filled–empty dichotomy. We have to estimate two quantities: volume of the unit and mass represented in our case by foliage. Third, the intercept of eq. 12 provides information about foliage density, which complements fractal dimension.

Although the method of natural units was derived using Menger's sponge as an example, the resulting relationship between mass and volume is general and holds true for any mass fractal.

Data analysis: applying the natural units method to trees

The method of natural units was derived for an abstract mathematical object. This object is symmetrical from top to bottom, while the crown is not. In addition to purely spatial considerations, various ecophysiological processes influence foliage distribution. The analogy between the crown and mass fractals such as Menger's sponge cannot explain shading of branches, vigorous growth of needles in the exposed parts of the crown and their disappearance in areas where light intensity drops below the compensation point, and differences in structure, chemistry, and productivity between sun and shade leaves. Parameter a (eq. 12) accounts for these ecophysiological processes. As a result, fractal analysis allows one to separate geometrical and ecophysiological factors determining crown structure. This separation may facilitate the investigation of each of the involved factors and unraveling patterns of foliage distribution.

To apply the natural units method, accurate measurements of such uncommon variables as volume of space occupied by foliage are needed. For this purpose, 34 loblolly pine trees (*Pinus taeda* L.) from the plantations east of the Appalachian mountains were thoroughly measured. These measurements were collected with the cooperation of Harold Burkhart and Ralph Amateis of the Virginia Polytechnic Institute and State University, Blacksburg, Va. The trees, mostly dominant and codominant, were measured when they were in "full leaf" (July and August). Tree ages ranged from 9 to 30 years.

After measuring total height, diameter at breast height, crown class, and height to the crown base on standing trees, they were felled and diameters of all branches of the first order were measured above the base swell. Six of these branches (two from the top, middle, and bottom portions) from each crown were selected for detailed measurements. Their length, diameter, angle, and distance from the ground were recorded. Mass of first- and second-year needles was determined. The coordinates of the convex polygon that circumscribed the foliage and the foliage depth in the direction perpendicular to the polygon were measured using the procedure described above. In a similar manner, branches of higher orders were measured. The total number of measured branches was 536.

Mass and volume of branches varied a great deal. (The term "branch" mass or volume indicates the mass of foliage supported by a given branch or the volume occupied by this foliage.) The range of branch mass covered six orders of magnitude: from 0.01 to 882 g with a mean of 65 g. Volume changed from 0.00002 to 1.96 m^3 with a mean of 0.14 m^3. Mass of the entire crowns, estimated from regressions of foliage mass on branch diameter, reached 20 752 g (mean 5640 g). Maximum crown volume was 174 m^3 (mean 57 m^3).

The central relationship of this study between mass and volume occupied by foliage of branches is described by a power function, known in biology as an allometric relationship. Although mass is not a linear function of volume, this relationship can be easily linearized by taking logarithms of both variables. The slope of the linearized allometric equations does not require any correction. However, to assure that the sum of the calculated masses is equal to the sum of actual masses, the scale factor (the exponent of intercept) should be corrected using the untransformed mass.

Results

Relationship between foliage mass and volume

If the crown is a fractal, then the regression of the logarithm of foliage mass of branches on the logarithm of volume occupied by foliage should be linear in the simplest meaning of this word: being plotted, it appears as a straight line. One way to test this prediction is to include in the regression a variable reflecting curvature. Since the studied relationship is monotonic and not inflected, the squared logarithm of volume would do the job. If the regression parameter of this term differs significantly from zero, then the relationship is not linear. In this case the relationship is almost perfectly linear: the parameters of the quadratic terms do not differ from zero (Table 2, regressions 2 and 4).

Slope of the mass–volume regression and fractal dimension

As was shown above, the slope of the regression of the logarithm of foliage mass on the logarithm of volume is equal to $D/3$ where D is fractal dimension. It is expected that D is confined between 2 and 3 for any branch order as well as for the entire crowns. The slopes computed using the ordinary least squares regression (OLS) do not support this prediction: every one of them is less than 2/3 (Table 2, regressions 5–9). The problem here is with the statistical technique rather than with the proposed method. OLS produces unbiased estimates of the dependent variable when the predictor contains no errors. This study is concerned with the value of the parameters, rather than with predicting the dependent variable (foliage mass). Another difference is that as a result of natural variability and measurement inaccuracies the predictor (volume) does contain errors.

There are other methods to relate variables subject to errors (Bartlett 1949; Sprent and Dolby 1980; Ricker 1984; Leduc 1987). One of the most popular is the reduced major axis method (RMA). While OLS minimizes the sum of the vertical deviations along the y-axis, RMA estimates regression parameters by minimizing the sum of the products of the horizontal (along the x-axis) and vertical deviations. The RMA slope is the geometric mean of the slope obtained by regressing y on x and the slope obtained by regressing x on y. An equivalent method to calculate the RMA slope is to divide the OLS slope by the correlation coefficient (square root of R^2). Using this method and statistics given on regression 3 (Table 2), the RMA slope for all 536 branches, b_r, is

$$[15] \quad b_r = \frac{0.6653}{0.7449^{1/2}} = 0.771$$

Unlike OLS, RMA is designed to estimate parameters when

Table 2. Analysis of spatial and linear variables of branches.

Regression	Branch order	Equation	RMA slope	N	R^2	SEE
Regressions including branches and the entire crowns						
1		$lm = 5.74 + 0.68(\pm0.01)lv$		570	0.83	0.95
2		$lm = 5.73 + 0.69(\pm0.02)lv + 0.003(\pm0.003)lv^2$		570	0.83	0.95
Regressions including only branches						
3		$lm = 5.68 + 0.67(\pm0.02)lv$		536	0.74	0.98
4		$lm = 5.68 + 0.66(\pm0.06)lv - 0.0005(\pm0.006)lv^2$		536	0.74	0.98
Regressions by branch order						
5	0	$lm = 5.99 + 0.64(\pm0.09)lv$	0.81(±0.09)	34	0.63	0.34
6	1	$lm = 5.58 + 0.43(\pm0.02)lv$	0.56(±0.02)	204	0.59	0.71
7	2	$lm = 3.94 + 0.37(\pm0.04)lv$	0.69(±0.04)	168	0.29	0.87
8	3	$lm = 4.09 + 0.47(\pm0.06)lv$	0.83(±0.06)	129	0.32	0.92
9	4	$lm = 3.86 + 0.51(\pm0.10)lv$	0.77(±0.10)	35	0.44	0.85
Regressions on branch diameter and length						
10		$lm = 3.16 + 0.33(\pm0.09)ll + 1.72(\pm0.14)ld$		536	0.81	0.83
11		$lv = -3.66 + 0.74(\pm0.11)ll + 1.73(\pm0.19)ld$		536	0.81	1.09
Mass–volume regressions for branches with different foliage density						
Branches with the highest foliage density						
12		$lm = 6.44 + 0.64(\pm0.04)lv$	0.69(±0.04)	200	0.86	0.55
13		$lm = 6.82 + 0.64(\pm0.03)lv$	0.70(±0.03)	100	0.83	0.51
14		$lm = 7.36 + 0.68(\pm0.05)lv$	0.76(±0.05)	50	0.80	0.52
15		$lm = 7.88 + 0.70(\pm0.08)lv$	0.80(±0.08)	25	0.77	0.52
Branches with the lowest foliage density						
16		$lm = 5.09 + 0.75(\pm0.02)lv$	0.79(±0.02)	200	0.89	0.68
17		$lm = 4.51 + 0.73(\pm0.02)lv$	0.77(±0.02)	100	0.90	0.64
18		$lm = 3.95 + 0.70(\pm0.03)lv$	0.74(±0.03)	50	0.90	0.60
19		$lm = 3.50 + 0.69(\pm0.04)lv$	0.72(±0.04)	25	0.91	0.61
Regressions of mass on branch length and diameter, separately						
20		$lm = 3.86 + 1.33(\pm0.03)ll$		536	0.76	0.95
21		$lm = 2.93 + 2.22(\pm0.05)ld$		536	0.81	0.83
Regressions of mass on length and diameter of branches of extreme foliage density						
Branches with the highest foliage density						
22		$lm = 4.01 + 0.87(\pm0.09)ll + 0.85(\pm0.14)ld$		200	0.90	0.47
23		$lm = 4.17 + 1.03(\pm0.14)ll + 0.51(\pm0.25)ld$		100	0.80	0.56
24		$lm = 4.44 + 1.34(\pm0.19)ll - 0.08(\pm0.33)ld$		50	0.76	0.57
25		$lm = 4.54 + 1.34(\pm0.51)ll + 0.01(\pm0.68)ld$		25	0.59	0.71
Branches with the lowest foliage density						
26		$lm = 2.47 + 0.16(\pm0.14)ll + 1.88(\pm0.23)ld$		200	0.80	0.94
27		$lm = 1.94 + 0.02(\pm0.20)ll + 1.94(\pm0.33)ld$		100	0.90	1.00
28		$lm = 1.74 + 0.09(\pm0.29)ll + 1.62(\pm0.52)ld$		50	0.90	1.13
29		$lm = 1.36 + 0.08(\pm0.44)ll + 1.73(\pm0.84)ld$		25	0.56	1.40
Regression of mass on length of 25 branches with the highest foliage density						
30		$lm = 4.54 + 1.35(\pm0.24)ll$		25	0.59	0.69

Note: *lm*, *lv*, *ll*, and *ld* are the natural logarithms of foliage mass, volume, length, and diameter, respectively, N is the number of observations, R^2 is the coefficient of determination (proportion of explained variance), and SEE is the standard error of the estimate. Standard errors of slopes are given in parentheses.

predictors contain errors. For this reason and also because this study is concerned with the value of the parameters, rather than with predicting the dependent variable, RMA is more suitable for this investigation than OLS. The RMA slopes (Table 2, regressions 5–9) also make more sense because most of them are greater than 2/3.

RMA is the maximum-likelihood or least biased estimator of the functional relationship when theoretical errors of the variables are unknown. Without this knowledge, "there must be uncertainty about the slope of any line reasonably compatible with the data" (Sprent and Dolby 1980, p. 548). These authors indicated that the minimum additional information about the error variances needed to remove this uncertainty is a knowledge of their ratio. To be sure about our estimates, the RMA slope for all branches (0.771) was compared with that produced by Sprent and Dolby's (1980) estimator.

The difficulty in applying Sprent and Dolby's (1980) estimator is that instead of required variance, only its estimates are known. These estimates contain their own errors and as far as the Sprent and Dolby's (1980) estimator is concerned cannot substitute for the variance. In this study, Sprent and Dolby's (1980) estimator was applied using the conditional variances calculated from regressing each of these variables on length, *ll*, and diameter, *ld*, of the corresponding branches (Table 2, regressions 10 and 11). By regressing mass and volume on easily measured length and diameter, some of the random errors present in the sample variance are expected to be filtered out. The ratio of the conditional variances, λ, was estimated as the squared ratio of the standard errors of estimates of the equations (Table 2, regressions 10 and 11):

$$[16] \quad \lambda = \left(\frac{0.83}{1.09}\right)^2 = 0.58$$

Using this value, one can apply Sprent and Dolby's (1980) formula for the slope, b_s:

$$[17] \quad b_s = \frac{s_{yy} - \lambda s_{xx} + ((s_{yy} - \lambda s_{xx})^2 + 4\lambda s_{xy}^2)^{1/2}}{2 s_{xy}}$$

where s_{xx} and s_{yy} are the sums of corrected squares of the variables and s_{xy} is the sum of cross products. The result is $b_s = 0.772$, which is not too far from the RMA slope of 0.771.

Another check of the value of fractal dimension was done using Bartlett's (1949) three-group method. As the title of Bartlett's (1949) paper "Fitting a straight line when both variables are subject to error" indicates, this method was introduced precisely for the purpose that concerns us now. Bartlett (1949) proposed that the data be divided into three even groups. The slope should then be estimated using the line connecting the means of the two extreme groups. The inner group is not used in the slope calculation. Bartlett (1949) proved that using two out of three groups (and thus disregarding one third of the information) results in a more accurate estimate. Regression of foliage mass of 536 branches on the logarithm of their volume produced the slope of 0.674. When the variables were reversed, the slope was 0.905. The geometric mean of these two values is 0.781.

Since the differences between the calculated slopes, 0.771 (RMA), 0.772 (Sprent and Dolby), and 0.781 (Bartlett), are smaller than their standard errors (0.016–0.020), all three methods produced statistically indistinguishable results. These values indicate that fractal dimension of the studied loblolly pines is about 2.3–2.4. The described experience supports the conclusion at which Leduc (1987, p. 654) arrived after comparing methods most commonly used to relate two variables, both of which are subject to error: "It is found that reduced major axis is often the most applicable because of its desirable properties and ease of estimation."

Fractal dimension and foliage density

The main advantage of introducing a volume-invariant measure of foliage density (eq. 14) is the separation of purely geometric factors of foliage distribution from ecophysiological factors. As a result, fractal dimension should not vary with the degree of exposure to light. To test this inference that exposed and shaded branches have the same fractal dimension, all branches were sorted by foliage density and fractal dimensions were calculated for 25, 50, 100, and 200 branches with the highest values of foliage density and for equal numbers of branches with the lowest values of foliage density.

These results (Table 2, regressions 12–19) show that there is no difference between fractal dimensions of branches differing with respect to density. The range of fractal dimension of exposed branches with the highest foliage density (2.07–2.40) includes the range of shaded branches (2.16–2.37). The fractal dimension of all branches and crowns ($3(0.68/(0.83)^{1/2}) = 2.24$) is in the middle of either range.

Unlike one-dimensional (linear) length and diameter, mass and volume exist in space with dimension greater than 2 and can be referred to as spatial variables. In general, the linear variables are well correlated with both mass and volume of branches. Thus, the linear variables explain 81% of the variation in both mass and volume of all 536 branches (Table 2, regressions 10 and 11). Branch diameter, which alone accounts for 81% of the variation in mass, appears to be a slightly better predictor than length, which explains 76% of the variation (Table 2, regressions 20 and 21).

These results are expected. It is known that spatial variables, for example, stem volume, are functions of their linear dimensions, such as height and diameter. Something unexpected has been found for the branches of extreme foliage density. Length alone was sufficient to predict mass of branches with the highest foliage density (Table 2, regressions 24 and 25). The contribution of diameter was not significant. The opposite was true for branches with the lowest foliage density. Only branch diameter was a relevant predictor of mass (Table 2, regressions 28 and 29).

Calculation of the maximum foliage mass

To assess the effect of competition, it is interesting to know the foliage mass of a given branch if it was fully exposed to the sunlight. Usually the amount of foliage increases with the degree of exposure. The preceding results allow one to estimate the maximum foliage mass possible on a given branch. Calculation of the maximum foliage mass requires an assumption about the proportion of branches deemed to be fully exposed to the sunlight. Lacking any objective criteria, it was assumed that for dominant and codominant loblolly pine trees, this proportion is 5% of all branches, mostly on the basis of the custom in biology to regard the extreme 5% as exceptional.

Since branch diameter does not help much to predict mass of branches with the highest foliage density, mass of

Table 3. Correlation between fractal dimensions of the crowns of 34 trees and other variables.

Variable	Correlation coefficient	$P > 0$
Crown class	0.449	0.008
Age	–0.103	0.562
Tree height	–0.208	0.237
Crown length	–0.358	0.038
Crown radius	–0.190	0.281
Crown mass	–0.333	0.055
Crown volume	–0.373	0.030
W5B	–0.046	0.795
W5C	0.092	0.604

Note: $P > 0$ indicates the probabilities of the coefficients to be greater than zero. W5B and W5C are widths of the last five rings at stem base and crown base.

25 branches was regressed on length alone (Table 2, regression 30). Using parameters of this regression and the logarithm of branch length, *ll*, one can compute for each of 536 branches the logarithm of "full" mass, *lmf*, as follows:

[18] $lmf = 4.54 + 1.35ll$

A method for estimation of relative foliage density

This ability to calculate maximum foliage mass suggests a method to estimate relative foliage density without measurements of foliage mass and volume. Linear measurements of length and diameter of a branch are sufficient. Relative foliage density is defined as the ratio of actual to maximal foliage mass for a given branch. The problem is to express both masses in terms of branch length and diameter.

As was shown, maximal foliage mass depends only on branch length (eq. 18). The expression for the actual foliage mass was determined earlier (Table 2, regression 10). Using this regression and eq. 18, relative foliage density (the ratio of actual to maximal foliage mass), RFD, can be estimated as follows:

[19] $$\mathrm{RFD} = \frac{\exp(3.16 + 0.33ll + 1.72ld)}{\exp(4.54 + 1.35ll)} = 0.25l^{-1.02}d^{1.72}$$

where l is branch length in metres and d is diameter in centimetres. This estimate of relative foliage density is based on the assumption that 5% (=25/536) of all branches are exposed fully to sunlight and, consequently, have the highest relative foliage density (equal to 1). This relationship indicates that the shorter a branch and the larger its diameter, the greater its foliage density. The frequency distribution of relative foliage density for all 536 branches was fairly symmetrical with a mean of 0.53 and a minimum of 0.14. This mean indicates that, on the average, branches are "half-full" (or "half-empty") as compared with the densest branches.

Fractal dimension and foliage density in relation to other tree variables

The data at hand can be used to relate fractal dimension to crown class, crown size, and tree growth. To do this, fractal dimension was calculated for each of 34 trees. $D/3$ ranged from 0.65 to 0.93 with a mean of 0.77 and a standard deviation of 0.08. Pearson correlation coefficients were computed between fractal dimension and crown class, tree age, tree size (height, crown length, crown radius, logarithms of mass and volume of the entire crown), and tree growth (widths of the last five rings at stem base and crown base) (Table 3).

Table 4. Fractal dimension by crown class.

Crown class	N	Minimum	Maximum	Mean	SD
Dominant	12	1.94	2.48	2.16	0.17
Codominant	19	1.96	2.80	2.36	0.23
Intermediate	3	2.10	2.72	2.46	0.33
All	34	1.94	2.80	2.30	0.24

Note: N is number of trees.

These coefficients show that the correlation of fractal dimension with crown class is statistically significant. Although the differences in fractal dimensions among crown classes are not significant, they are consistent: fractal dimensions increase from dominant to intermediate trees (Table 4).

There is a consistent tendency of fractal dimension to decrease with increasing tree size. The negative correlation with age is probably a reflection of this tendency. Because crown mass and volume summarize and accentuate linear changes of size, the correlation with these spatial variables is stronger than that with linear variables (Table 3). The lack of correlation with widths of the last five rings at stem base and crown base indicates that fractal dimension is not related to rate of tree growth (Table 3).

Foliage density is related to fractal dimension (eq. 14), which explains a strong correlation between these variables (0.65). As is fractal dimension, foliage density is correlated negatively with tree size and dominance. There is no correlation with diameter increments.

Discussion

Tree crowns differ from solid objects of classical geometry. Their understanding requires new ideas about spatial relationships. Fractal geometry offers such ideas, concepts, and methods. The central concept of this geometry is fractal dimension. This study proposes a method to estimate fractal dimension of a single tree crown or its portions.

Branches of trees vary greatly in foliage density. Exposed branches at the treetop have denser foliage than branches inside the crown. To characterize spatial distribution of foliage, in addition to fractal dimension, we need a measure of foliage density. The intercept of the same regression that produces fractal dimension appears to be a suitable measure of foliage density. Foliage density complements fractal dimension both algebraically (because it is a part of the same equation) and ecologically (because foliage density expresses another aspect of the same phenomenon, foliage distribution). The relationship that connects mass and volume of branches (eq. 12) separates purely spatial factors from ecophysiological effects. Fractal dimension and foliage density quantify these facets of foliage distribution. The concept of foliage density was instrumental in selecting exposed branches and calculating relative foliage density.

Neither fractal dimension nor foliage density correlates with current diameter increment. Low correlation was found between fractal dimension and variables indirectly related to the crown, age, and tree height (Table 3). At the same time, there is a more pronounced negative correlation between fractal dimension and crown size. Fractal dimension also decreases from intermediate to larger, dominant trees (Table 4). These results suggest that as crowns become larger, the amount of foliage located at the crown periphery increases in proportion to the foliage amount inside the crown. The peripheral branches do not spread to provide light to the crown interior. Foliage tends to occupy the outer space while creating a leafless core inside. It seems that not only individual trees but branches of the same tree compete with each other.

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