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THE FRACTAL DIMENSION OF PLANTS

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Abstract

Measured fractal dimensions of roots and shoots provide a quantitative description of the self-similar features of plant architecture. A first-principles general model of biological distribution systems predicts these fractal-like properties. We use it to calculate the fractal dimension, d, of plants, as measured using "box-counting" methods. We show how empirical values of d are sensitive to the resolution and magnification of the image, and to the dimensionality, D, of the plant. For example, the model predicts $d = 3/2$ for plants grown in three dimensions ($D = 3$), and $d = 4/3$ when grown in two dimensions, in excellent agreement with observation.

Plants have obvious fractal-like properties. In recent years this has been quantified by measuring the fractal dimension, d, of branching architectures in both shoots [1] and roots [2–4]. Typically, these studies find $d \approx 1.5$ with some variation depending on the period of growth, size of the network, and the scale of resolution. Such measurements give an overall quantitative measure of the self-similar character of plant architecture. As yet, however, there has been no explanation for the observed value of the fractal dimension.

We have presented an integrated model for the structure and function of biological distribution systems [5]. Based on general biomechanic and hydrodynamic principles it gives a quantitative description of branching networks that is in excellent agreement with data. It predicts many scaling relationships both within and between organisms and, in particular, shows that these networks are expected to be self-similar fractal-like structures. For both plants and animals this is supported by the observation of power laws and the successful prediction of their scaling exponents. Additional support comes from the direct measurement of fractal dimensions of roots and shoots [1,2]. The connection between scaling exponents and empirically measured "fractal dimensions", however, is not entirely straightforward. Here we clarify this connection and show that the model accurately predicts the measured fractal dimensions of plants. It also reconciles an apparent discrepancy between two different fractal dimensions reported for roots.

The fractal dimension, d, has typically been measured by making a two-dimensional projection of the plant at different magnifications and resolutions, and measuring either the boundary enclosing, or the area filled by, the image of the network. This is frequently done using the "box-counting" method in which a sequence of square grids of varying size is placed over the image of the plant and the number of enclosed squares, $\mathcal{N}$, counted, (see Fig. 1). At a given resolution, the area enclosed, A, is given by

$$A = \mathcal{N}\epsilon^2 \tag{1}$$

where ϵ is the length of the side of the square box. Since $\mathcal{N}$ is dimensionless, it can be expressed as a function of the dimensionless ratio L/ϵ, where L is some arbitrary, non-fractal length scale characteristic of the system. A self-similar fractal [6] is then defined as one where

$$\mathcal{N}\left(\frac{L}{\epsilon}\right) = a\left(\frac{L}{\epsilon}\right)^{d} \tag{2}$$

where a is some number. Thus, combining Eqs. (1) and (2), $A = aL^d\epsilon^{2-d}$. In the limit when $\epsilon \to 0$. A therefore does not go to a finite, non-zero number except in the special case when $d = 2$. This case defines a non-fractal object with simple geometric scaling for which $A = aL^2$, independent of the resolution, with a representing the total area in units of L^2. In an idealized mathematical fractal where $d \neq 2$, self-similarity as described by Eq. (2), continues *ad infinitum*. However, in real plants this is valid only over a limited range determined by the arbitrary values of ϵ and L, since there is a minimum value of the length, l_N, and radius, r_N, of the smallest branches, namely the petioles and terminal rootlets. Thus, when the resolution increases such that the box-size becomes smaller than the terminal branches ($\epsilon < r_N$ and $< l_N$), the overall image of the plant remains essentially unchanged.

In our model [5], we treat the resource distribution network as a tree which branches continuously from the trunk or primary root, (level 0), to the petioles or terminal rootlets, (level N, say). For ease of presentation we use the terminology of the above-ground network, namely trunk, branch, and petiole; correspondence with the root system is straightforward. An arbitrary level, or generation, is denoted by k. The length, l_k, and radius, r_k, change in a regular way between successive branching levels, k and $(k+1)$:

$$\beta \equiv \frac{r_{k+1}}{r_k} = n^{-1/2} \tag{3}$$

$$\gamma \equiv \frac{l_{k+1}}{l_k} = n^{-1/3} \tag{4}$$

Here n, the branching ratio, is the number of daughter branches derived from a parent branch, and is assumed to be independent of k. Eq. (3) reflects area-preserving branching, i.e., $\pi r_k^2 = n\pi r_{k+1}^2$. For the above-ground network this follows from the assumption that mechanical constraints are uniform throughout the tree (elastic similarity, $l_k^3 \propto r_k^2$ [7]). Below-ground networks are not subject to the same biomechanical constraints. To a good approximation, however, roots are composed of many parallel tightly-bundled conducting vessels as in an electrical cable, so for them area-preserving follows automatically [5]. Eq. (4) follows from the assumption that the network is volume-filling, as shown below. In addition to this assumption, our general model also assumes that terminal branches, such as petioles, or terminal rootlets, are invariant units. These constraints are sufficient to define a self-similar fractal-like network with a fixed minimal size of the terminal branches. Thus, r_N and l_N are taken to be the same both within a single plant and among plants of varying size. These general assumptions, together with a minimization of energy principle applied to the fluid flow, are sufficient to derive scaling laws for many parameters of plant structure and function.

In order to interpret the empirical measurements of plant fractal dimensions in terms of our model, it is necessary to distinguish the volume of space "filled" by the branching network from the actual physical volume of the branches. The volume of space in the canopy associated with a terminal branch, v_N, can be approximated by the volume of a sphere whose diameter is the petiole length, l_N: thus, $v_N = (4/3)\pi(l_N/2)^3$. This is to be distinguished from the actual volume of the petiole $V_N = \pi r_N^2 l_N$. Since there are n^N terminal branches, the total canopy volume filled by the network is the sum of n^N such spheres:

$$V_{NET} = n^N v_N = (1/6)\pi n^N l_N^3 \tag{5}$$

This volume, V_{NET}, is preserved throughout the network in the sense that it can be equally well approximated using branches at *any* arbitrary level k [5]: thus, $V_{NET} = (1/6)\pi n^k l_k^3$. This invariance leads to the result quoted in Eq. (4) that $\gamma = n^{-1/3}$. It can be straightforwardly generalized to a D-dimensional space-filling network, giving:

$$\gamma = n^{-1/D} \tag{6}$$

In contrast to the volume filled by the network, the actual physical volume of the plant

is

$$V_B = \pi \sum_{k=0}^{N} n^k r_k^2 l_k \approx \frac{(\gamma\beta^2)^{-N} V_N}{(1 - n\gamma\beta^2)} \propto n^{4/3N} r_N^2 l_N \tag{7}$$

where N is assumed to be large and the sum is evaluated using Eqs. (3) and (4). Since V_B is directly proportional to the total mass of the plant and, as such, is non-fractal, it must be expressible as $V_B = vL^3$, where v is the plant volume in units of L^3. On simple geometric grounds, a two-dimensional projection of an image taken perpendicular to the principal axis of the network has an area $A \approx V_{NET}^{2/3}$. From Eq. (5) this can be expressed as $A \propto n^{2/3N} l_N^2$ so, using Eq. (7) to eliminate n^N, gives

$$A \propto \frac{V_B^{1/2} l_N^{3/2}}{r_N} \propto \frac{L^{3/2} l_N^{3/2}}{r_N} \tag{8}$$

From Eq. (1), the number of boxes of area ϵ^2 enclosed by the projection is therefore

$$\mathcal{N} = \frac{A}{\epsilon^2} \propto \left(\frac{L}{\epsilon}\right)^{3/2} \left(\frac{l_N}{\epsilon}\right)^{3/2} \left(\frac{\epsilon}{r_N}\right) \tag{9}$$

As emphasized above, at high resolution where $\epsilon < r_N$ and $< l_N$, the size of the petiole sets a fundamental scale for the network. Eq. (9) then gives $\mathcal{N} \propto \epsilon^{-2}$ and A does not change as the resolution becomes finer. So, as $\epsilon \to 0$, $d \to 2$ and the fractal nature of the network is effectively lost. On the other hand, when $\epsilon > l_N$ and $> r_N$, it is ϵ that sets the scale for the size of the smallest branch that can be resolved; in this case, the *apparent* size of the petiole increases, so that both l_N and $r_N \approx \epsilon$. Eq. (9) now gives $\mathcal{N} \propto \epsilon^{-3/2}$, and therefore $d = 3/2$. Note that as the resolution decreases (ϵ increases) there is a concomitant logarithmic decrease in the number of branching generations, N, that can be resolved.

Care must be taken when comparing predicted with empirical measurements of d. Published values have often been obtained by counting the number of boxes, $\mathcal{N}'$, *intersecting the boundary* of the projected two-dimensional figure [1,2]. When a many-branched volume-filling network is observed at a relatively coarse resolution, $\epsilon > l_N$ and $> r_N$, this procedure is equivalent to counting the number of boxes *enclosed within the projected figure.* As an example, see the illustration of a complete root system in Figs. 1A-C. The two procedures (counting boxes intersecting the boundary versus counting those enclosed by it), start to give divergent values when the resolution is fine enough to resolve the detailed architectural pattern and size of individual branches. At fine resolution it is only the linear boundary of the image, C, that is approximated by counting the number of intersected boxes. This is illustrated in Fig. 1D where a sparse network with just three major branches is shown. By analogy with Eqs. (1) and (2), C can be expressed in terms of a fractal dimension, d', as

$$C = \mathcal{N}'\epsilon \quad ; \quad \mathcal{N}'\left(\frac{L}{\epsilon}\right) = c\left(\frac{L}{\epsilon}\right)^{d'} \tag{10}$$

Thus, $C = cL^{d'}\epsilon^{1-d'}$. A non-fractal length has $d' = 1$; in the cases considered here this arises when $\epsilon \rightarrow 0$, because of the finite size of the smallest branch. The difference between the two measured fractal dimensions, d and d', expressed in Eqs. (1) and (2), and Eq. (10), respectively, depends on the magnification and resolution used to make the image. For a given image size, high magnification produces an image of only a small local part of the network, so the number of boxes intersected by the boundary of the projected figure is less than the number enclosed within the boundary, so $\mathcal{N} \neq \mathcal{N}'$ and $d \neq d'$. Low magnification, on the other hand, tends to produce an image of a large, more complete network, but at low resolution such that $\epsilon > l_N$ and $> r_N$. In this case, the number of boxes intersected tends to be the same as the number enclosed by the boundary, so $\mathcal{N} = \mathcal{N}'$ and $d = d'$. It should be emphasized that these complications are largely due to the fact that plants cannot be true mathematical fractals over an arbitrary range of the parameters, because of a lower limit on the size of branches.

We now compare our predictions with empirical values. Our model predicts that measurements made at low magnification should give $d \approx 3/2$, whereas data taken at high magnification should give a lower value, eventually approaching 1.0. Measurements of above-ground branches show good agreement with this prediction: $d \approx 1.5$ at low magnification and lower values at high magnification [1,8]. Data for roots appear to give two conflicting values even though both were measured at low magnification. Earlier measurements of whole-root systems [2] gave $d \approx 1.5$, whereas a more recent measurement gave $d \approx 1.3$ [3]. The major difference was that, in the first case, the roots were grown in a three-dimensional medium but the measurements were taken from a two-dimensional projection of the network; in the second case, the roots were forced to grow in two dimensions, between glass plates only 3mm apart, and measurements were taken *in situ*. Thus, the two measurements reflect different functional dimensionality, which we now show to be the origin of the apparent discrepancy.

When grown between minimally separated glass plates, the root system fills a functional area rather than a volume. So, in this case, from Eq. (6), $\gamma = n^{-1/2}$ and, consequently, from Eq. (7), $V_B \propto n^{3/2N} r_N^2 l_N$. In the direction transverse to the plates, length scales are constrained by the negligibly small fixed distance, t, between the plates. Scaling is therefore only relevant in the plane of the plates, so, instead of $V_B = vL^3$, we must write $V_B = v' L^2 t$. Similarly, the area filled by the network must now be estimated by adding up circles, instead of spheres, of diameter l_N associated with terminal branches. Thus, $A \approx n^N \pi l_N^2$. Using the above equation for V_B appropriate to two dimensions then leads to

$$A \propto \frac{V_B^{2/3} l_N^{4/3}}{r_N^{4/3}} \propto \frac{L^{4/3} l_N^{4/3}}{r_N^{4/3}} \tag{11}$$

in place of Eq. (8). Since the number of boxes counted is A/ϵ^2, provided $\epsilon > l_N$ and $> r_N$ this straightforwardly leads to $d = 4/3$, which is essentially identical to the observed value of 1.3 [3]. It is likely that the same argument explains the value for $d(\approx 1.3)$ reported for above-ground branches measured under high-magnification [1]. Since, as illustrated in Fig. 1D, these terminal twigs were less than 10cm long and typically consisted of only $2-3$ branchings, they are effectively two-dimensional objects. From the above argument our model predicts $d \approx 4/3$, as observed.

As measured by the box technique, the fractal dimensions, (either d or d'), provide only an indirect measure of the quantitative scaling of the network. For the same network, this technique can give different values depending on the measurement scale, ϵ, and the degree of magnification. Furthermore, an empirical determination of d or d' gives a single value representing averages of the branching pattern over the whole network. Care must therefore be taken in comparing measurements by the box technique with theoretical predictions. When defined properly, however, the fractal dimension can provide evidence for the self-similarity of plants and other fractal-like networks.

Our general model [5] is one of the few treatments that provides a theoretical framework for determining fractal and self-similar features of nature. The plant version of the model accurately predicts empirical measurements of scaling for both shoots and roots. In particular, it explains observed variation in values of the fractal dimension obtained by measuring plants at differing degrees of magnification and resolution. Most critically, it predicts differences in the values obtained when roots are forced to grow and extract resources in spaces of contrasting dimensionality. This is strong evidence that the fractal-like properties of plant architecture reflect structural and functional constraints on the processes of resource distribution embodied in our model.

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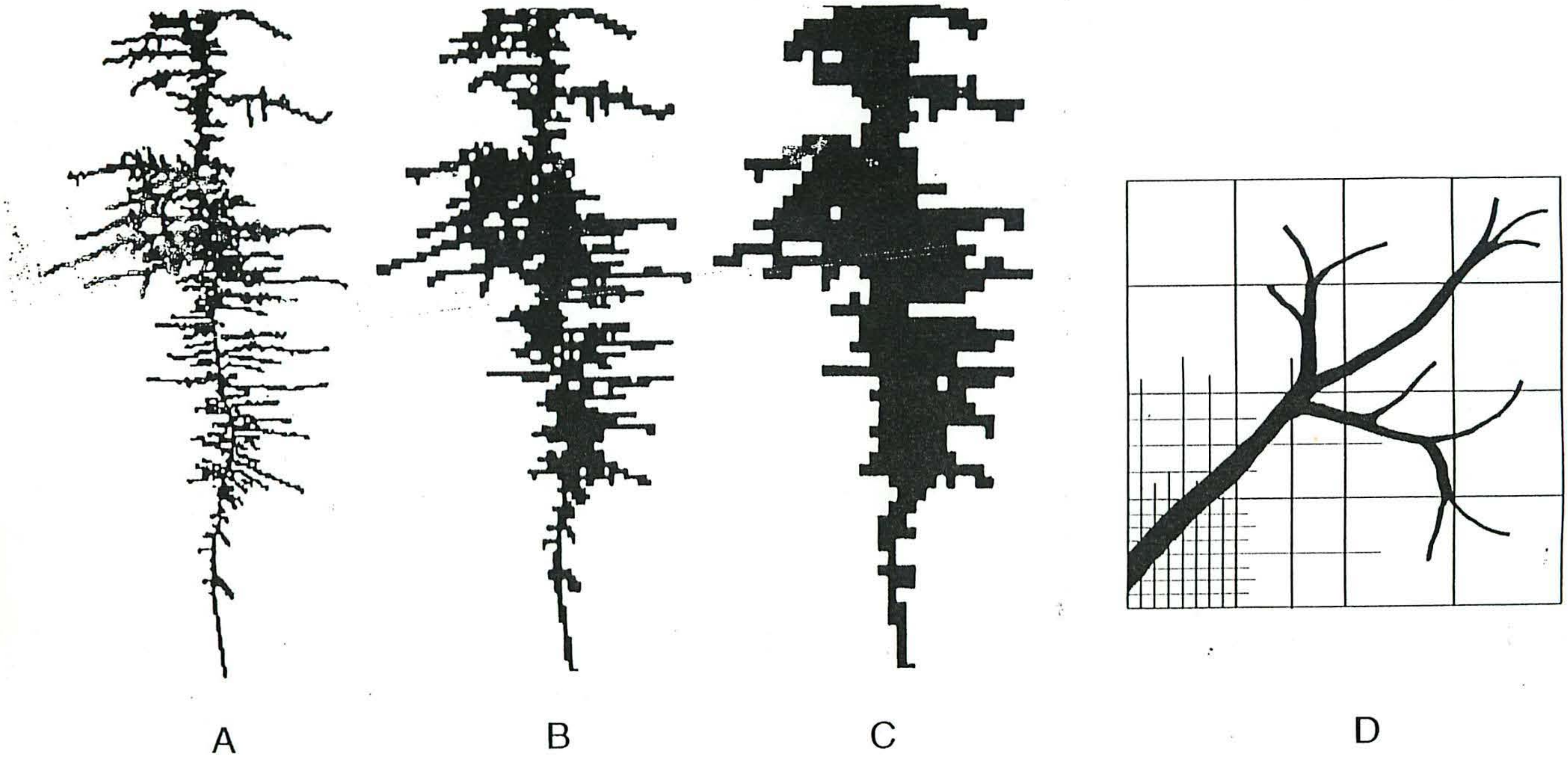
FIGURES

FIG. 1.

Illustration of the "box-counting" method showing images of two-dimensional projections of a complete root system taken at different resolutions (A-C), and of a terminal shoot system (D). In A-C the resolution is defined by the varying size, ϵ, of the pixels used to create the image, and in D by the analogous varying size of the grid squares. The fractal dimension, d', is determined from the total number of pixels, or boxes, $\mathcal{N}'$, intersecting the boundary of the image. It is clear that, especially in B and C, where the resolution is relatively coarse, $\mathcal{N}'$ is identical to the number of pixels, $\mathcal{N}$, filling the area of the projection. Notice that the apparent size of the terminal branch is determined by ϵ and that the apparent number of branching generations decreases as ϵ increases. In contrast, when viewed at fine resolution, where ϵ is smaller than branch dimensions, the number of boxes intersecting the boundary differs from the number filling the enclosed area. This is especially true at high magnification as in D, where only a small part of the network is captured. A-C are adapted from ref. [2] and D from ref. [1].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