Correcting for finite spatial scales of self-similarity when calculating the fractal dimensions of real-world structures

G. M. BERNTSON[1]* AND P. STOLL[2]

[1]*Harvard University, Department of Organismic and Evolutionary Biology, Biological Laboratories, 16 Divinity Avenue, Cambridge, MA 02138, USA*
[2]*Royal Veterinary and Agriculture University (KVL), Deptartment of Agricultural Sciences, Agroecology Agrovej 10, DK-2630, Taastrup, Denmark*

SUMMARY

Fractal geometry is a potentially valuable tool for quantitatively characterizing complex structures. The fractal dimension (D) can be used as a simple, single index for summarizing properties of real and abstract structures in space and time. Applications in the fields of biology and ecology range from neurobiology to plant architecture, landscape structure, taxonomy and species diversity. However, methods to estimate the D have often been applied in an uncritical manner, violating assumptions about the nature of fractal structures. The most common error involves ignoring the fact that ideal, i.e. infinitely nested, fractal structures exhibit self-similarity over any range of scales. Unlike ideal fractals, real-world structures exhibit self-similarity only over a finite range of scales.

Here we present a new technique for quantitatively determining the scales over which real-world structures show statistical self-similarity. The new technique uses a combination of curve-fitting and tests of curvilinearity of residuals to identify the largest range of contiguous scales that exhibit statistical self-similarity. Consequently, we estimate D only over the statistically identified region of self-similarity and introduce the finite scale-corrected dimension (FSCD). We demonstrate the use of this method in two steps. First, using mathematical fractal curves with known but variable spatial scales of self-similarity (achieved by varying the iteration level used for creating the curves), we demonstrate that our method can reliably quantify the spatial scales of self-similarity. This technique therefore allows accurate empirical quantification of theoretical Ds. Secondly, we apply the technique to digital images of the rhizome systems of golden rod (*Solidago altissima*). The technique significantly reduced variations in estimated fractal dimensions arising from variations in the method of preparing digital images. Overall, the revised method has the potential to significantly improve repeatability and reliability for deriving fractal dimensions of real-world branching structures.

1. INTRODUCTION

The space-filling properties of branching biological structures result from a complex interplay of topology, morphology, and geometry (Lynch & Nielson 1996). Therefore, quantitatively describing these branching structures can be a difficult task. One approach that has been valuable in providing simple characterizations of how complex branching structures fill space is the fractal dimension (D). D is a measure of how apparent structure varies with the scale on which that structure is being examined. Typically, the fractal dimension of a real-world object is calculated using the box-counting method (and related techniques, reviewed in Hastings & Sugihara 1993; Sugihara & May 1990; Vicsek 1992). The technique has been applied to such varied structures as plant shoot systems (Corbit & Garbary 1995; Morse *et al.* 1985) and root systems (Berntson 1996), nerve ganglia (Morigiwa *et al.* 1989), and blood vessels (Masters 1994). The wide array of applications suggest that this method can provide a powerful tool for quantifying the space-filling properties of complex structures. For example, the D of plant root systems has proved useful as an integrated measure of space-filling properties, showing high correlation with many different architectural measures such as density and link-length (Berntson 1994; Fitter & Stickland 1992). In addition to the spatial domain, fractal measures have been applied in the time domain to quantify stability (Melzer & Hastings 1992) and for abstract structures such as taxonomic systems (Burlando 1990).

Recently, Panico & Sterling (1995) suggested that many biological branching structures that had been previously characterized as being fractal using the

---

* Author for correspondence (`berntson@oeb.harvard.edu`).

box-counting method and related techniques are not true fractals. They came to this conclusion by examining moving-window (see Isaacs & Srivastava 1989) estimates of D where the moving-window covered a finite range of spatial scales (box sizes). Using these moving-window plots of D, they asserted that in order for an object to be fractal it needed to exhibit invariance in estimates of D over the range of spatial scales examined. They judged invariance qualitatively for each object they examined. The neuronal branching structures that they examined did not show invariant estimates of D, and so they concluded that they were not fractal. This work is extremely valuable insofar as it demonstrates that non-integer values derived from the box-counting technique may not accurately describe true space-filling properties. It also suggests that any estimate of D depends critically on the spatial scales, especially the lower and upper cut-offs used for deriving estimates of D. However, their analysis is limited since the determination of whether a structure is fractal is a subjective judgement.

The method for deriving Ds of real-world structures has not been explored in detail. Preliminary analyses suggest that variations in the method of sampling and preparing images for analysis can have a non-trivial effect on the estimation and interpretation of fractal measures of natural features (Berntson 1994; Loehle & Li 1996; Panico & Sterling 1995). It is likely that this difficulty is largely driven by variations in D within real-world structures. For example, fracture and fault lines in the Earth's crustal plates (Hatton *et al*. 1994), spatial and temporal variability in zooplankton biomass (Pascual *et al*. 1995), borders between disturbed and non-disturbed habitats (Krummel *et al*. 1987), and the above- (Morse *et al*. 1985) and below-ground (Berntson 1997) branching structures of plants, can all exhibit either discrete or continuous scale-dependent variations in D. This scale-dependent variation in real-world structures has been acknowledged since the beginning of work with fractal geometry. Early work in soil science, for example, referred to this phenomenon as 'partial self-similarity' (Burrough 1981, 1983). As a result Mandelbrot (1983) suggested that strict scale invariance is likely to apply only between well-defined bounds wherein a particular process determines structure. This problem was discussed by Hilborn (1994), but systematic procedures to define these bounds in real-world structures have neither been offered nor applied.

Practically speaking, these scale-dependent variations in D imply that errors in estimates of D can be introduced while creating the digital images used for deriving estimates of D. In general, we suggest that there are two important classes of scale-dependent errors that are likely to be introduced given currently applied methodologies for deriving D. First, studies of plant and algal architecture have demonstrated that the thickness of the lines within digitized images can have a large and significant impact on estimated D (Berntson 1994; Corbit & Garbary 1995). This demonstrates that current methods of deriving D are sensitive to both the overall space-filling properties of a given structure, but also to smaller-scale morphological characteristics. Second, when digitizing real-world structures the resolution of acquired images needs to be carefully considered. This decision has the effect of truncating the minimum spatial scale that can be examined. Given that we expect *a priori* only a finite range of spatial scales to exhibit self-similarity, how do we choose the appropriate range and what is the effect of digitizing at different scales or resolution?

In this paper we present a new technique for quantitatively determining the spatial scales over which a complex structure shows statistical self-similarity. Once these scales have been identified, the finite scale-corrected dimension (FSCD) within this finite range of self-similar structure can be determined. We demonstrate the utility of this approach for identifying the spatial scales of true self-similarity using computer-generated images of fractal curves with finite levels of iteration. We then apply this technique to real-world branching patterns (rhizome systems of *Solidago altissima*) to see if FSCD represents an unbiased estimate of the space-filling properties. In particular, we compare FSCDs from a single set of rhizome systems which have been digitized (i) with all diameters present or as skeletonized (one-dimensional) lines, and (ii) at different resolutions. Because the proposed technique is conceptually simple, applications to estimate exponents in other power law relationships are straightforward.

2. MATERIALS AND METHODS

(*a*) *Calculating fractal dimensions using grid-intercept counts*

For all the images we analysed, box sizes and the resultant number of occupied boxes (box counts) were determined using image processing software developed by Berntson (1994). To remove effects of image orientation (Voss 1988) in deriving box-counting dimensions (D), four affine-transformed copies of each image were processed as an aggregate (four box-count estimates for each box size). Affine transformations involved rotating the image in 90° increments. The box-counts for each affine-transformed image and box size were saved and used for all moving-window plots, estimates of D (Tatsumi *et al*. 1989), and the FSCD.

(*b*) *Testing for self-similarity*

Rather than using estimates of local slopes from a moving-window to determine whether a given image deviated from self-similarity over the range of spatial scales (box sizes) examined (cf. Panico & Sterling 1995), we examined the residuals of the log-log plot of box size versus box-counts. Standard residual plots, i.e. residuals versus predicted values, were in some cases clearly curvilinear, and therefore the analysed images did not exhibit self-similarity over the range of examined box sizes. We therefore fitted second-order polynomials to the residual plots and took significant second-order polynomials (a test of curvilinearity; Sokal & Rohlf 1981) as evidence that a given image did not exhibit self-similarity over the examined range. An important *a priori* step in this process was the selection of an appropriate p-cut-off. Low p values would only identify strong deviations from linearity. To provide a more critical assessment of self-affinity (i.e. statistical self-similarity for real-world patterns) we chose a p-cut-off of 0.1. Any residual plot that displayed curvilinearity at a p value of less than 0.1 was taken as evidence that the image was not self-affine over the examined range. In developing this technique, we explored a range of p cut-off values (ranging from 0.001 to 0.25), and selected 0.1 because it resulted in a reasonable characterization of linearity for the majority of cases we examined. Use of smaller p cut-off values ($p<0.1$) led to a reduction in the number of cases classified as nonlinear, and larger p cut-off values ($p>0.1$) led to increases in the number of cases classified as nonlinear.

(*c*) *Spatial scales of self-similarity*

If an image deviated from self-similarity as judged by the residuals from a standard estimate of D, extreme box sizes were sequentially removed, one box size at a time, until either too few points remained to perform a regression or the image showed self-similarity (via the residual test) over the remaining spatial scales. This erosion was performed in three ways: (1) starting with the smallest box size, boxes of increasing size were removed (leaving the largest spatial scales); (2) starting with the largest box size, boxes of decreasing size were removed (leaving the smallest spatial scales); and (3) the largest and smallest box sizes were removed, leaving the intermediate box sizes. The erosion technique which yielded the largest absolute range of box sizes was used. We refer to this revised estimate of D as the finite scale-corrected dimension (FSCD).

(*d*) *Curves with known dimensions: fractal and Euclidean*

To test this technique, we examined six fractal curves based on the Koch (Mandelbrot 1983, p. 43) and Dragon curves (Mandelbrot 1983, p. 67) with actual values of D ranging from 1.12 to 1.65. We varied D for these curves by varying the relative length of each line segment within the iterators. Curves were created using a range of iteration levels (between 3 and 9; see figure 1*a*) (Becker & Dörfler 1989; Mandelbrot 1983). Each fractal curve, regardless of the iteration level, was created using a starting line of 1080 pixels (a single pixel wide). By generating curves with varying iteration levels, different images contained different spatial scales within which the fractal curves filled space in their predicted fractional manner (e.g. $1.0<D<2.0$). The software and actual generators used to create these curves are available on the World Wide Web (see § 2*f* below). With these images, we tested our method for identifying the spatial scales of self-similarity. If our method allows us to accurately estimate the theoretical dimension of space-filling curves with only a few iterations, then the FSCD is a reliable estimate of actual D within images where only a finite range of spatial scales actually show self-affinity. In addition to processing fractal curves with varying iteration levels, we also used our method to derive the box-counting dimension for standard Euclidean objects with integer dimensions: a line and a square. We used these structures as benchmarks for extreme values for D (and FSCD).

(*e*) *Real-world branching structures: rhizome systems*

Rhizomes are perennial below-ground, branched storage organs of clonal plants. In this study, we examined rhizome systems of the goldenrod (*Solidago altissima* L.) from an old field population in Basel, Switzerland (Stoll 1995). The rhizomes branch and form two-dimensional growing systems that perform transport processes between root and shoot populations of individual plants (genets). Rhizome systems were measured in early spring for five consecutive years. They were measured by removing litter and topsoil (without severing any roots), and mapping the exposed rhizomes on transparent sheets. Afterwards they were covered again with soil so that they could resume growth during the following growing season. The maps of the rhizome systems were digitized using a digitizer tablet. From this digital information, we created four images for each rhizome system. Each of these images consisted of a combination of two different resolutions (10 pixels cm^{-1} and 20 pixels cm^{-1}), and where the rhizomes were drawn to scale with their actual thicknesses (*ca.* 5 mm) or with as small a diameter as could be represented in the digitized image resolution (this is what we refer to as 'skeletonized', which typically refers to binary images that

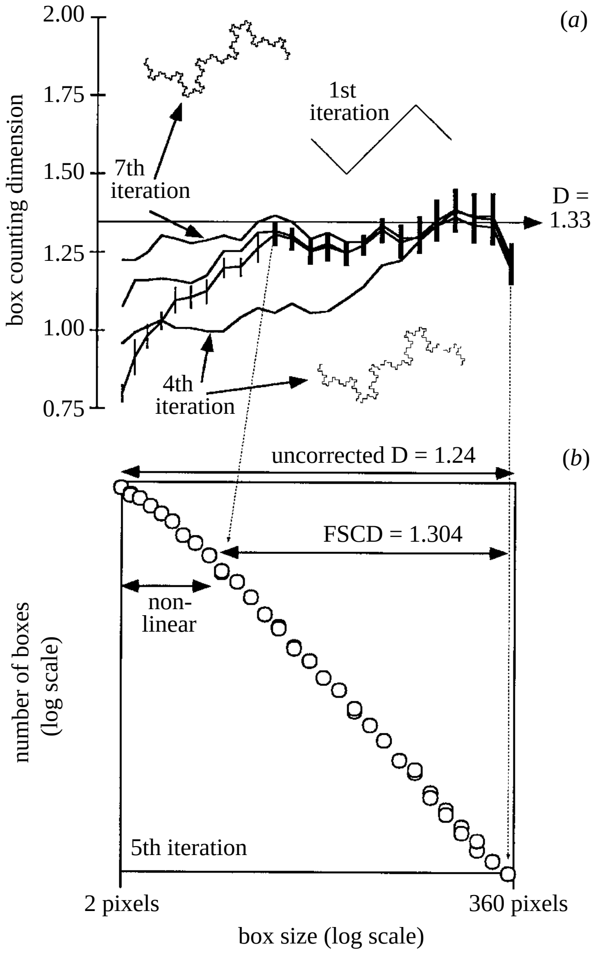


Figure 1. Illustration of scale-dependent variations in box-counting estimates of D for the DragonSkin Curve. The upper panels are moving-window plots illustrating scale dependence of derived box-counting dimensions (*sensu* Panico & Sterling 1995). Confidence limits (99%) of individual moving-window estimates of D over six box sizes (with four replicate affine box count estimates per box size for a total of 24 points per local-slope estimate) are included for the fifth iteration (derived from the standard error of the slope used to calculate D). Error bars are shown only for those spatial scales (range of box sizes) that exibited statistical self-similarity. The lower panels contain scatterplots of actual counts of boxes versus box size (on a log-log scale) for the iteration which has the error bars. The spatial scale that exhibited self-similarity (linear scaling in the lower plot) is indicated by dashed lines connecting the upper and lower panels.

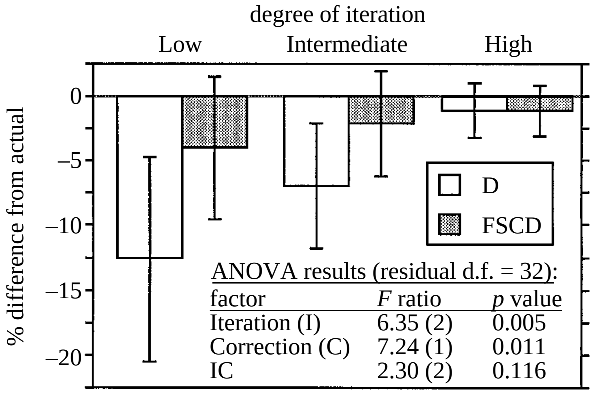


Figure 2. Summary of how variations in the degree of iteration and use of FSCD affect estimates of actual D for the six different fractal curves we examined. Each bar represents the per cent difference from actual D. Error bars are 95% confidence limits. Included in the frame of the figure are the results of a two-way ANOVA comparing the effects of the degree of iteration and the method of estimating D. The degrees of freedom for each factor in the ANOVA table are included in parentheses next to each *F* ratio.

have had all pixels eroded away leaving a single pixel-wide image).

(*f*) *Software*

All of the image processing software described in this manuscript was written in Pascal for the Macintosh computer and is available free on the World Wide Web. Separate programs are available for (i) performing initial calculations of box size versus box-count and uncorrected estimates of D ('Root Length +'); (ii) performing sequential residual versus predicted tests of statistical self-affinity (and creating local slope plots) on output raw counts and box sizes from Root Length + ('DResidAnal'); and (iii) creating fractal curves using standard and modified fractal curve generators ('Fractal Curve Generator'). This software is available at the following URL: `http://plantecohost.harvard.edu/gmbwww/rootappl.html`.

3. RESULTS

Using Panico & Sterling's moving-window approach for identifying deviations from invariant self-similarity, we observed that increases in the degree of iteration (from a low of 3–4 to a high of 7–9) altered the spatial scales of apparent self-similarity in the fractal curves (e.g. figure 1*a*). Increasing the degrees of iteration led to increases in the range of spatial scales (box sizes) over which local slopes did not vary from one another and were approximately equal to the theoretical value of D. As the level of iteration decreased, local slopes were significantly reduced at small box sizes (approaching a value of 1.0), while local slopes at large box sizes remained unchanged.

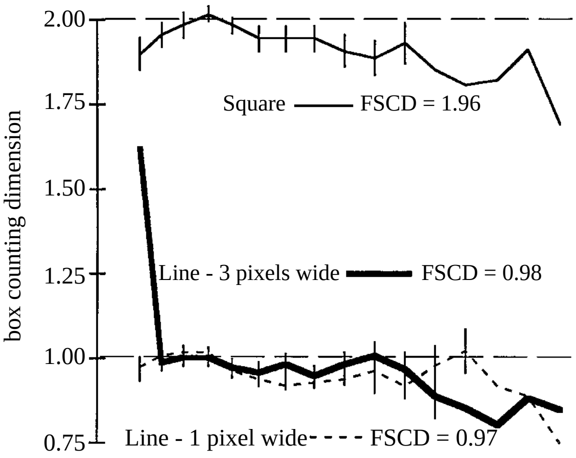


Figure 3. Local-slope plots for Euclidean geometric benchmarks. Confidence limits (99%) of individual moving-window estimates of D (over six box sizes with four affine replicate counts per box size) are included (derived from the standard error of the slope used to calculate D). Error bars are shown for those spatial scales (range of box sizes) that exibited statistical self-similarity. Dashed horizontal lines at dimensions of 1.0 and 2.0 represent the theoretical dimensions of the square and lines, respectively. Estimates of D′ for each object are included in the figure.

Both FSCD and uncorrected estimates of D tended to underestimate actual space-filling dimensions, but uncorrected estimates of D led to a significantly greater underestimation than did the FSCD estimates (figure 1*b* and figure 2). For all of the fractal curves we examined, uncorrected estimates of D underestimated actual D by 6–25% for the lowest levels of iteration. FSCD estimates of D led to significant improvements in the estimate of D, especially at these low levels of iteration (figure 2). At any degree of iteration, FSCD did not differ significantly from actual D. At the low and intermediate levels of iteration, uncorrected estimates of D significantly underestimated actual D.

In addition to the six fractal curves, we calculated FSCD for lines and a square to see how reliable our estimates are for non-fractal objects. In general, we found that FSCD was reliably estimated (within 2–4% of actual values) for standard Euclidean objects (figure 3). Our estimates of FSCD for a single-pixel wide line and a three-pixel wide line were nearly identical. When calculating FSCD, the smallest boxes, which had inflated estimates of D due to the thickness of the line, were ignored. This filtering resulted in improved reliability of estimated dimensions. Overall, FSCD was a fairly reliable estimator of actual dimensions for both fractal and non-fractal objects. A linear regression between actual D and FSCD (with no intercept, as it was non-significant) had a slope of 0.984 and an r^2 of 0.995.

For the rhizome systems, we observed a non-significant effect of image resolution on either local slope patterns within moving-window plots or overall estimates of uncorrected D or FSCD (figures 4 and 5). In contrast, skeletonizing the images as opposed to keeping the actual thickness of the rhizomes had a large effect on local slope patterns within moving-window plots and uncorrected estimates of D. The moving-window plots illustrate that the skeletonized and non-skeletonized images converge on a common value of D at the large box sizes (figure 4). At the smaller box sizes, the skeletonized images underestimated the common estimate of D. In contrast, non-skeletonized images overestimated D at small box

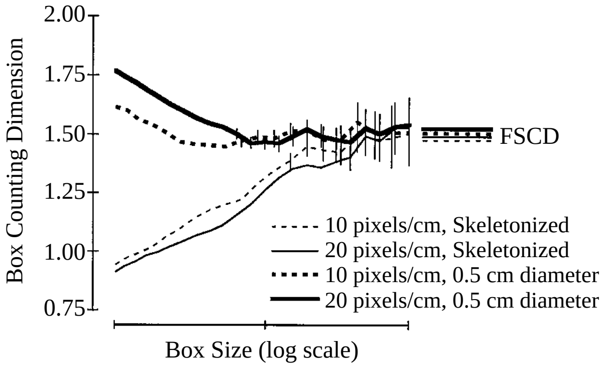


Figure 4. Local-slope plots for a sample of *Solidago* rhizome systems. Confidence limits (99%) of individual moving-window estimates of D are included (derived from the standard error of the slope used to calculate D). Error bars are shown only for those spatial scales (range of box sizes) that exibited statistical self-similarity. The lines to the right of the local-slope plots labelled FSCD represent the FSCD estimates for each of the different methods of image preparation. For this sample rhizome system, FSCD did not differ by method of image treatment. The *x* axis represents different actual box sizes for the two different spatial resolutions. Images were processed with box sizes ranging from two pixels to 33% of the total size of the image. See § 2 for details on image preparation.

sizes, especially with higher image resolution. For the skeletonized images, FSCD was always significantly greater than the uncorrected estimates of D. For the non-skeletonized images, FSCD was not significantly different from D at low image resolutions due to the relatively small inflation of D at small box sizes. At higher image resolutions, FSCD led to a significant reduction relative to uncorrected D. Overall, the reductions and increases in estimates of D using FSCD led to a more consistent estimation of D regardless of the method of image preparation.

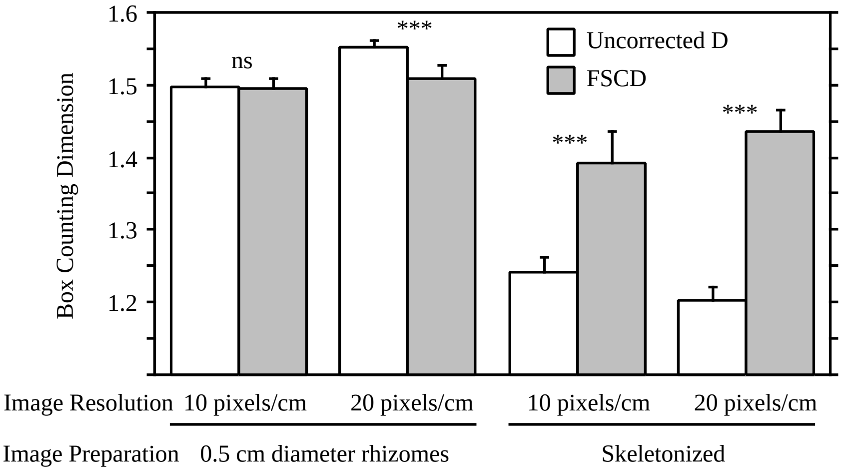
4. DISCUSSION

In this paper we have introduced a new, objective method for deriving corrected estimates of space-filling properties as estimated by the box-counting dimension (D). This method is important because it derives D using only those spatial scales within an object which exhibit statistical self-similarity. We have demonstrated that this method leads to a significant improvement in the reliability of estimates of D when a given object exhibits statistical self-similarity over a finite range of scales, as is expected for real-world structures. In addition, this method can remove artefacts within images that can significantly bias estimates of D. This is illustrated in figure 3, where the line with a thickness of three pixels shows a greatly inflated estimate of D at the smallest box size. Our method of deriving D only over those spatial scales that exhibit statistical self-similarity removes this anomaly and correctly estimates D as approximately 1.0.

We have also demonstrated that use of our method for deriving corrected estimates of D (FSCD) are useful for minimizing artefacts that can be inadvertently introduced during image preparation (see Berntson 1994; Corbit & Garbary 1995). Using digitized maps of the rhizome systems of *Solidago altissima*, we found that uncorrected estimates of D varied significantly depending on the method of image preparation (figures 4 and 5). In contrast, FSCD showed significantly less variation in response to differences in the method of image preparation. This demonstrates that our method for calculating FSCD successfully removes the non-self-similar structure of objects introduced during image preparation, and thus characterizes the space-filling structure of the object which was indeed invariant.

Panico & Sterling (1995) suggested that any object which exhibits scale-dependent variation in D, judged qualitatively by local-slope plots, does not have self-similar structure and therefore is not fractal. We agree with Panico and Sterling's general assertion, insofar as this is qualitative evidence that a given object is not a fractal exhibiting scale-invariant self-similarity. However, we suggest that Panico and Sterling's approach is not appropriate for the study of space-filling properties of real-world objects, as it is reasonable to *a priori* expect that most real-world branching structures will exhibit fractal properties only over a finite range of scales. These scales will vary depending on the composition and processes of development of a given structure. Take the example of plant root and rhizome systems. These structures grow by the iterative growth of modules (a branching event and the elongation of a meristem). These modules define the absolute minimum spatial scale over which the whole root systems structure would exhibit self-similarity (Berntson 1996). The overall size or extent of the root system represents the maximum spatial scale. This example could easily be extended to other biological structures that exhibit modular iterative growth, such as nerve ganglia, blood vessels, or fungal hyphae.

Although widely used and applied across many disciplines, estimates of fractal dimensions have not regularly or systematically been checked against critical assuptions of the underlying theory, e.g. scale-invariance of the estimate over the examined range of spatial scales. This is somewhat surprising for several reasons. First, observations of scale dependence are not new (Burrough 1981, 1983) are found in almost all of the many applications (Morse *et al.* (1985) and references therein), and Sugihara & May (1990) suggest using this information to detect hierarchies in ecological systems. For example, Meltzer & Hastings (1992) noted a strong first-order autocorrelation among residuals from a linear regression of a log-log plot representing a hyperbolic distribution of the cumulative probability that grass patches have a certain size versus the area of the patches. By generating moving-window estimates of D on subsets of their data, they determine a break-point that separates small from large patches of vegetation such that the r^2 of two regressions are maximized and the autocorrelation of the residuals were minimized. They argue that below and above the break-point there are 'more than two size-related dynamic systems within a given ecology' because the residuals from regressions on the subsets were still autocorrelated. The right question in our



ANOVA results (residual d.f. = 72)

factor	*F* ratio	*p* value
Correction (C)	27.9	< 0.001
Skeletonized (S)	15.0	< 0.001
Resolution (R)	1.1	0.289
CS	45.4	< 0.001
CR	0.4	0.534
SR	1.0	0.310
CSR	3.8	0.056

Figure 5. Summary of effect of image preparation and FSCD on estimates of D in *Solidago* rhizome systems. ***indicates $p > 0.001$ from Bonferroni-corrected least squares means comparisons. See § 2 for details on image preparation. Included in the frame of the figure are the results of a three-way ANOVA comparing the effects of image preparation (diameter and resolution) and the method of estimating D. The degree of freedom for each factor in the ANOVA table is 1.

view would be over what scale (in this case area of vegetation patches) do we have linearity in the corresponding log-log plot? Secondly, there is actually a rich body of literature dealing with break-points in linear regression or deviations from linearity. Residual diagnostics, routinely applied in exploratory data analysis (Tukey 1977), offer a way to approach the question of relevant (spatial) scales over which scale-independent behaviour is observed. Finally, the notion of multi-fractals and their applications (Hatton *et al.* 1994; Pascual *et al.* 1995; Scheuring & Riedi 1994) essentially demonstrate that simple universal scaling laws might be an exception rather than the rule. In the systems dealt with here we do not expect multifractal behaviour, because unlike geological processes the branching patterns we studied do not extend over orders of magnitude. However, within their characteristic size range there may still be scale-dependent behaviour as shown by our analysis, but also by the observations and interpretations of others.

Differences in estimates can be very sensitive to the spatial scale examined (cf. figure 4). Thus, it is possible that many of the seemingly exciting results from a fractal analysis could be artefacts due to the demonstrated effects of variable scaling. Although there might be other alternatives to the proposed method to quantitatively determine the (spatial) scale of self-similarity, we believe that the proposed method is a pragmatic, objective, approach and will prove to be useful in standardizing future applications. This could also increase the potential of comparisons across studies.

In conclusion, we should like to emphasize that the proposed method is not restricted to the examples we used. We anticipate that it will be useful also in the time domain and the many other applications where exponents of hypothesized power law relations have to be estimated from empirical data.

Financial support for this work was provided by a post-doctoral fellowship from the United States National Oceanic and Atmospheric Administration to G.M.B., and from the Swiss National Science Foundation to P.S. while he was a visiting scientist at Harvard University.

REFERENCES

Becker, K.-H. & Dörfler, M. 1989 *Dynamical systems and fractals: computer graphics experiments in Pascal*. Cambridge University Press.

Berntson, G. M. 1994 Fractal analysis of plant root systems: how reliable are calculations of fractal dimensions? *Ann. Bot.* **73**, 281–284.

Berntson, G. M. 1996 Fractal geometry, scaling and plant root architecture. In *Plant roots*: *the hidden half*, 2nd edn (revised and expanded) (ed. Y. Waisel, A. Eshel & U. Kafkafi), pp. 259–272. New York: Marcel Dekker.

Berntson, G. M. 1997 Topological scaling and plant root system architecture: developmental and functional hierarchies. *New Phytol.* **135**, 621–634.

Burlando, B. 1990 The fractal dimension of taxonomic systems. *J. Theor. Biol.* **146**, 99–114.

Burrough, P. A. 1981 Fractal dimensions of landscapes and other environmental data. *Nature* **294**, 240–242.

Burrough, P. A. 1983 Multiscale sources of spatial variation in soil. I. The application of fractal concepts to nested levels of soil variation. *J. Soil Sci.* **34**, 577–597.

Corbit, J. D. & Garbary, D. J. 1995 Fractal dimension as a quantitative measure of complexity in plant development. *Proc. R. Soc. Lond.* B **262**, 16.

Fitter, A. H. & Stickland, T. R. 1992 Fractal characterization of root system architecture. *Funct. Ecol.* **6**, 632–635.

Hastings, H. M. & Sugihara, G. 1993 *Fractals. A user's guide for the natural sciences*. Oxford University Press.

Hatton, C. G., Main, I. G. & Meredith, P. G. 1994 Non-universal scaling of fracture length and opening displacment. *Nature* **367**, 160–162.

Hilborn, R. C. 1994 *Chaos and nonlinear dynamics*. Oxford University Press.

Isaacs, E. H. & Srivastava, R. M. 1989 *An introduction to applied geostatistics*. New York: Oxford University Press.

Krummel, J. R., Gardner, R. H., Sugihara, G., O'Neill, R. V. & Coleman, P. R. 1987 Landscape patterns in a disturbed environment. *Oikos* **48**, 321–324.

Loehle, C. & Li, B.-L. 1996 Statistical properties of ecological and geological fractals. *Ecol. Model.* **85**, 271–284.

Lynch, J. & Nielsen, K. L. 1996 Simulation of root system architecture. In *Plant roots: the hidden half*, 2nd edn (revised and expanded) (ed. Y. Waisel, A. Eshel & U. Kafkafi), pp. 247–258. New York: Marcel Dekker.

Mandelbrot, B. B. 1983 *The fractal geometry of nature*. New York: W. H. Freeman.

Masters, B. R. 1994 Fractal analysis of normal human retinal blood vessels. *Fractals* **2**, 103–110.

Melzer, M. I. & Hastings, H. M. 1992 The use of fractals to assess the ecological impact of increased cattle population: case study from the Runde Communal Land, Zimbabwe. *J. Appl. Ecol*. **29**, 635–646.

Morigiwa, K., Tauchi, M. & Fukuda, Y. 1989 Fractal analysis of ganlion cell dendritic branching patterns of the rat and cat retinae. *Neurosci. Res*. Suppl. 10, 131–140.

Morse, D. R., Lawton, J. H., Dodson, M. M. & Williamson, M. H. 1985 Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* **314**, 731–733.

Panico, J. & Sterling, P. 1995 Retinal neurons and vessels are not fractal but space-filling. *J. Comp. Neurol*. **361**, 479–490.

Pascual, M. F. A., Ascioti, A. & Caswell, H. 1995 Intermittency in the plankton: a multifractal analysis of zooplankton biomass variability. *J. Plankton Res*. **17**, 1209–1232.

Scheuring, I. & Riedi, R. H. 1994 Application of multifractals to the analysis of vegetation pattern. *J. Vegetation Sci*. **5**, 489–496.

Sokal, R. R. & Rohlf, F. J. 1981 *Biometry*, 2nd edn. New York: W. H. Freeman.

Stoll, P. 1995 Modular growth and foraging strategies in rhizome systems of *Solidago altissima* L. and branches of *Pinus sylvestris* L. Ph.D. thesis, University of Zürich, Switzerland.

Sugihara, G. & May, R. M. 1990 Applications of fractals in ecology. *Trends Ecol. Evol*. **5**, 79–86.

Tatsumi, J., Yamauchi, A. & Kono, Y. 1989 Fractal analysis of plant root systems. *Ann. Bot*. **64**, 499–503.

Tukey, J. W. 1977 *Exploratory data analysis*. Reading, MA: Addison-Wesley.

Vicsek, T. 1992 *Fractal growth phenomena*, 2nd edn. Singapore: World Scientific.

Voss, R. F. 1988 Fractals in nature: from characterization to simulation. In *The science of fractal images* (ed. H.-O. Peitgen & D. Saupe), pp. 21–70. Berlin: Springer.

Received 14 April 1997; accepted 16 June 1997