

axis. Finally, the proportion of the excess manganese associated with particles is variable.

By taking a conservative approach and grouping those plumes in which the maxima occur at the same depth, five sources can be identified, that is stations 2, 4 and 5; stations 6 and 7; station 8; station 9; and stations 10 and 11. This analysis predicts a frequency of one source per 340 km of ridge; of course the actual frequency may be much higher.

The position of venting in the rift appears to vary with latitude. Results from stations 8 and 9 are consistent with venting from the east wall, whereas results from station 10 indicate a west-wall source. Furthermore, these results are consistent with discharge from the valley walls, but they do not eliminate the possibility that venting occurs from the valley floor. Finally, hydrothermal manganese along this section appears to be confined

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to the median valley and does not spill over into the adjacent ocean basins, although it may leak out through fracture zones.

The anomalies reported here are smaller than those found near venting in the Pacific<sup>4-7</sup>. However, this difference is an artefact of the regional sampling strategy of this survey and is not a true indication of the relative impact of venting from the MAR on geochemical cycles and the heat budget. Such information can be acquired only by site-specific work.

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## Fractal dimension of vegetation and the distribution of arthropod body lengths

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Following Mandelbrot<sup>1</sup>, recent studies<sup>2-6</sup> demonstrate that some natural surfaces are fractal. Here we show that transects across vegetation are fractal, and consider one possible consequence of this observation for arthropods (mainly insects) living on plant surfaces. An important feature of a fractal curve or surface is that its length or area, respectively, becomes disproportionately large as the unit of measurement is decreased<sup>1</sup>. This suggests that if vegetation has a fractal structure, there is more usable space for smaller animals living on vegetation than for larger animals. Hence, there should be more individuals with a small body length than a large body length. We show that this is the case, and that relative numbers of small and large individual arthropods collected from vegetation are broadly consistent with theoretical predictions originating from the fractal nature of vegetation<sup>7</sup> and individual rates of resource utilization.

Mandelbrot<sup>1,4</sup> asks, how long is the coast of Britain? Measuring its length by stepping round with successively shorter divider step-lengths allows finer and finer resolution of the coastline; if the log of divider step-length is plotted against the log of total length measured, a straight line of negative slope is obtained<sup>1,4,8</sup>. Mandelbrot<sup>1,4</sup> interprets this as evidence that coastlines are fractal and that the slope of the graph is an estimate of  $1-D$ , where  $D$  is the fractal dimension of the coastline. The relationship between  $D$ , step-length  $r$  and the perceived length of the line  $l(r)$  measured with step  $r$  is given by

$$l(r) \propto r^{(1-D)} \quad (1)$$

By definition<sup>1</sup>, for a line (that is, a transect across a surface),  $D$  must lie in the range  $1 \leq D \leq 2$  and for a surface,  $2 \leq D \leq 3$ .

The fractal dimension of vegetation might also be measured by stepping along a transect over the surface with a pair of dividers set to a series of step-lengths and using equation (1). This was the method used to measure the fractal dimension of

transects across a coral reef<sup>6</sup>. An alternative widely used method (see ref. 1, p. 130), which has some practical advantages, is as follows.

Enclose the object (or a subsection of it) in a square of side  $S$  and divide the square into  $(S/\lambda)^2$  squares of side  $\lambda$ . Let  $N(\lambda)$  be the number of squares the edge of the object enters and plot  $\log N(\lambda)$  against  $\log 1/\lambda$ . Suppose that for small values of  $\lambda$ , the graph is almost linear with slope  $D$ . Then  $D$  can be interpreted as the fractal dimension, since

$$\log N(\lambda) \approx D \log 1/\lambda + \log K \quad (2)$$

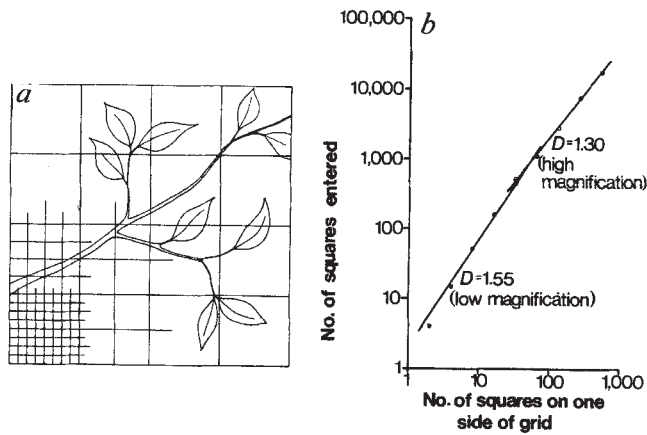
where  $K$  is a constant, whence

$$N(\lambda)\lambda^D \approx K \quad (3)$$

The method is explained in greater detail in Fig. 1 legend, together with an example.

Photographs were taken of a variety of plants during early spring. The plants were either leafless, just coming into leaf or evergreen. By careful choice of plant-parts and camera focal length, the resulting photographs were approximately two-dimensional, greatly simplifying their interpretation under the grid (Fig. 1a). Two different arbitrarily sized grids (128 mm or 256 mm along one edge) were partitioned into  $2^n$  squares along each edge. Depending on the grid size,  $n$  varied from 2 to 6 or 7, down to a square size of 2 mm. The grid was randomly repositioned several times to give semi-independent estimates of the fractal dimension of the same piece of vegetation. The slope of the resulting line (for example, Fig. 1b) was estimated by regression analysis.

There are several points to note in the interpretation of such graphs. One is that when the number of divisions is small, it is probable that all the squares will be entered, hence the slope of the graph will be  $D=2$ . This is an artefact of the method; consequently, in the present study all points that fell on the line  $y=2x$  (on a log/log plot) were omitted when estimating the slope of the line. At the other extreme of resolution, when a very large number of squares is used, the slope of the graph will in general fall to 1. This could be due to a lack of resolution in the photograph or because irregularities in the outline of the plant no longer occur at that scale. Taking a photograph at a much larger scale (higher magnification) resolves this problem. The graph may be convex<sup>9,10</sup> between the extremes of  $D=2$  and  $D=1$ , or it could have two straight subregions characterized by different slopes (Fig. 1b). Similar changes in fractal



**Fig. 1** *a*, Photographs of plants at various magnifications were placed under a grid. The number of squares entered by the outline of the plant were counted, starting with a coarse grid of two large squares on one side, then  $2^n$  squares, with  $n$  varying from 2 to 6 or 7, depending on the grid size. For ease of representation, the plant's leaves in this figure are drawn flat; in reality they are orientated at all angles with respect to the grid. Also for clarity, the progressively finer divisions are only illustrated in one corner of the figure. The logarithm of the number of squares entered by the outline of the plant was then plotted against the logarithm of the number of squares along one side of the grid, as in *b*. The slope of the line equals the fractal dimension,  $D$ . *b*, Data gathered in this way for Virginia creeper, photographed without leaves in early spring. The twigs were photographed at one scale, then parts of the same twigs were rephotographed at a higher magnification, permitting  $D$  to be estimated at two levels of resolution.

dimension at different scales have been found in other natural objects<sup>1,3,11</sup>.

Table 1 presents data on the fractal dimension of a selection of plants. Estimates of  $D$  range from 1.28, for a close-up photograph of Virginia creeper, to 1.79 for cotoneaster. Those plants which one might, *a priori*, consider to have a more complex growth form have a higher fractal dimension. In those plants which were photographed at two scales, estimates of the fractal dimension are lower at the higher magnification, as would be expected from the above argument.

The mean fractal dimension of the samples in Table 1 is 1.44. For ease of calculation, assume that, typically,  $D \approx 1.5$ . It follows from equation (1) that for an order-of-magnitude decrease in

ruler length, the expected distance between two points on a linear transect (of dimension  $D = 1.5$ ) across a fractal surface increases by a factor of  $\sqrt{10} = 3.16$ . The difficulties of measuring the fractal dimension of a surface are considerable and no data are yet available. However, squaring the increase in linear distance (that is, adding the fractal dimensions of the orthogonal transects; ref. 1, p. 365) gives a heuristic upper bound estimate for the expected increase in surface area. Therefore, the maximum expected increase in surface area is  $3.16^2 = 10.0$  for an order-of-magnitude decrease in ruler length. Bearing in mind the disconnected character of the surface of vegetation, an estimate for the lower bound of the fractal dimension is obtained by adding 1 to the linear fractal dimension (for example,  $1.5 + 1$ ; see ref. 1, p. 365). This holds exactly under some circumstances, and in particular when the surface is flat in a direction transverse to the cross-section (which is clearly not the case for vegetation). This lower bound predicts a 3.16-fold increase in surface area for an order-of-magnitude decrease in ruler length, when  $D = 1.5$ .

Now consider the implications of the fractal nature of plant surfaces for the animals living on them. As a first approximation, substitute animal body length ( $L$ ) for step-length ( $\lambda$ ) in equation (1). If the way in which animals perceive and use their environment is proportional to their body length<sup>12</sup>, then for a homogeneous fractal surface having transects with  $D = 1.5$ , the area perceived by animals 3 mm long may be up to an order of magnitude greater than the area perceived by animals 30 mm long, for the same reference area. This increase in available space for animals of smaller body length may be combined with a consideration of the way in which metabolic rate scales with body length<sup>13,14</sup> to make predictions about the distribution of body lengths of animals living on vegetation.

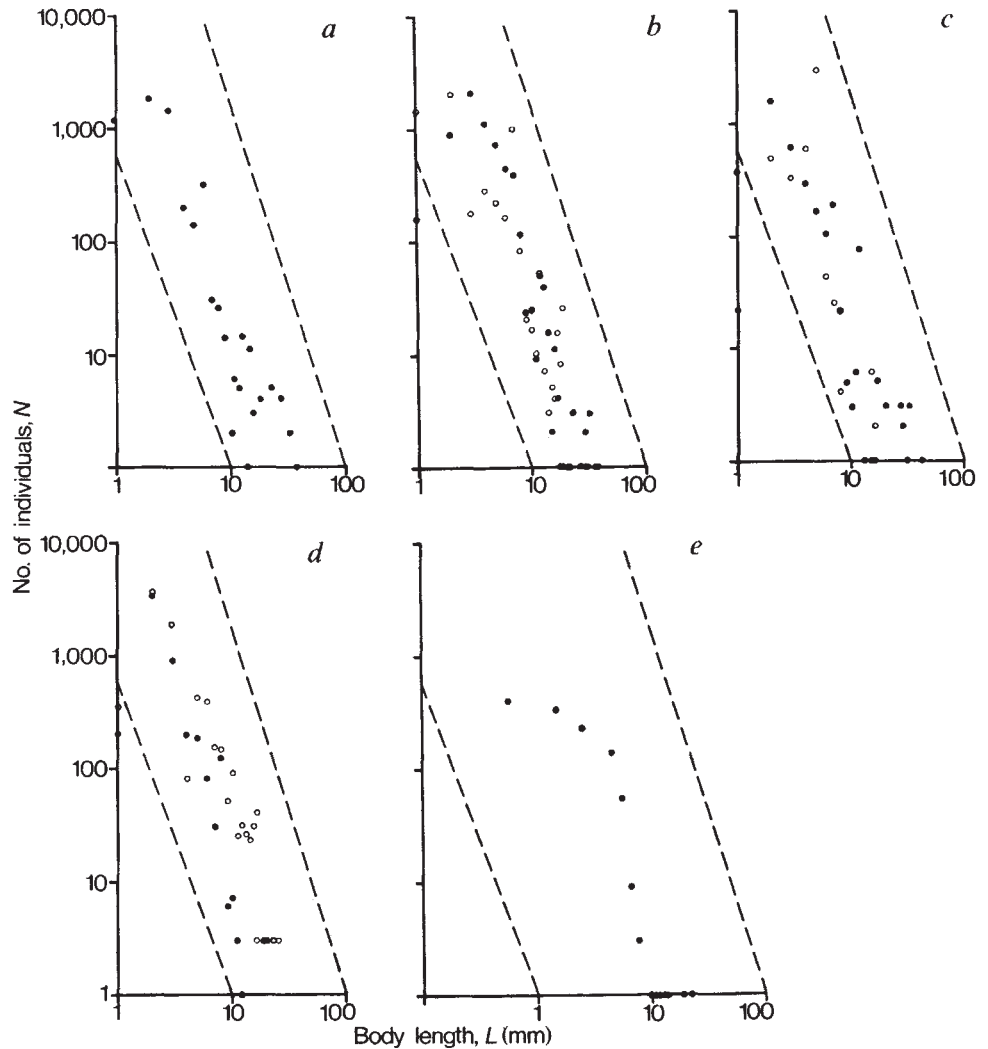
The metabolic rate of individual animals<sup>13,14</sup> scales approximately as the 0.75 power of body weight,  $W$ , that is, as  $(L^3)^{0.75}$ . Next, suppose that population densities are approximately proportional to the reciprocal of individual rates of resource utilization (that is, to metabolic rate<sup>-1</sup>; see, for example, ref. 13). Then, if use of resources per individual is proportional to  $W^{0.75}$ , it follows that population density,  $N$ , scales as  $(L^3)^{-0.75}$ . Hence, all other things being equal (especially the rate of appearance of new resources), a 10-fold decrease in body length results in a  $(10^3)^{0.75} = 178$ -fold increase in the density of individuals. This increase in density may be combined with the expected increase in the available surface area, outlined above, for a given decrease in body length, to predict relative numbers of individual animals of different body lengths living on the surface of vegetation. For an order-of-magnitude decrease in body length, such calcula-

**Table 1** Estimate of the fractal dimension,  $D$ , of woody plants for arbitrarily positioned transects across their surfaces

Species	Magnification	No. of estimates	Mean $D$	s.d.
Barberry, <i>Berberis vulgaris</i> L. (evergreen)	High	3	1.46	0.018
	Low	3	1.43	0.042
Virginia creeper, <i>Parthenocissus tricuspidata</i> (Sieb. and Zucc.) Planch. (twigs and buds)	High	6	1.28	0.078
	Low	3	1.55	0.009
Weeping elm, <i>Ulmus glabra</i> forma <i>pendula</i> (Loud.) Rehd. (twigs and buds)	Low	6	1.41	0.111
Cotoneaster, <i>Cotoneaster horizontalis</i> Decaisne (twigs and leaves)	High	3	1.35	0.019
	Low	6	1.79	0.093
Ivy, <i>Hedera helix</i> L. (evergreen)	Low	18	1.39	0.050
Yew, <i>Taxus baccata</i> L. (evergreen)	High	3	1.47	0.042
	Low	3	1.68	0.099
Silver birch, <i>Betula pendula</i> Roth (twigs and leaves)	Medium	3	1.40	0.040
Downy birch, <i>Betula pubescens</i> Ehrh. (twigs and leaves)	Medium	3	1.40	0.035
Ash, <i>Fraxinus excelsior</i> L. (twigs and leaves)	Medium	3	1.42	0.083
Sycamore, <i>Acer pseudoplatanus</i> L. (twigs and leaves)	Medium	3	1.31	0.023

Photographs of branches and twigs of a selection of woody plants, with or without leaves, were taken from the University of York campus or Skipwith Common, North Yorkshire. High-magnification estimates were derived from close-up photographs of twigs ~10 cm long; low-magnification estimates were from photographs of twigs >50 cm long. Single medium estimates were made from specimens >25 cm long. The state of each plant when photographed and the plant part photographed is indicated in parentheses after the species name. (Note that sample transects inevitably tended to follow twigs and other 'principal axes' in the natural structure of the vegetation. This could introduce some bias into the estimates of their fractal dimension.)

**Fig. 2** Data on the number of individual arthropods (mainly insects) of different body lengths collected from vegetation. *a*, Understorey foliage in primary forest, Finca Tabogo, Costa Rica<sup>15</sup>; *b*, Osa secondary vegetation (●) and Kansas secondary vegetation (○); *c*, Tabogo primary riparian vegetation (●) and Icacos vegetation (○)<sup>16</sup>; *d*, understorey foliage in cacao plantations in Dominica (●) and at Finca La Lola, Costa Rica (○)<sup>17</sup>; *e*, Birch (*Betula pubescens*) trees at Skipwith Common, North Yorkshire. In *a-d*, arthropods were collected by sweep net, in *e* by pyrethrum knock-down of the tree canopy. The lower bound prediction that, for an order-of-magnitude decrease in body length, there should be a 560-fold increase in the number of individuals, is indicated by the lower dashed line on each graph; the upper bound prediction—a 1,780-fold increase for an order-of-magnitude decrease in body length—is shown by the upper dashed line. Regression lines were fitted through the log-transformed data, the anti-logarithm of the slopes of the lines were taken and are as follows: *a*, 390; *b*, 1,040 (●) and 700 (○); *c*, 360 (●) and 980 (○); *d*, 21,800 (●) and 530 (○); *e*, 1,440. The decline in the numbers of individuals of <1 mm body length may be due to a variety of factors<sup>12</sup>, not least of which is the difficulty in sampling very small arthropods. Consequently, when fitting regression lines to the data, in *a-d* the 1 mm body length data point and in *e* the first three data points were omitted.



tions predict an increase of between  $178 \times 3.16 = 560$ -fold and  $178 \times 10 = 1,780$ -fold in the number of individual animals<sup>7</sup>.

Data on the number of individual animals of different body lengths collected from the surface of vegetation are scarce. Figure 2 shows such data for sweep-net samples of terrestrial arthropods<sup>15-17</sup> and original data collected by pyrethrum knock-down of a tree (*Betula pubescens*) canopy. All the data show a steep increase in the number of individuals for an order-of-magnitude decrease in body length, in general agreement with our predictions (Fig. 2).

The above heuristic calculations may be reversed, allowing prediction of the expected fractal dimension of the surface of vegetation, given the mean of the fitted slopes for the distribution of individuals' body lengths shown in Fig. 2. This calculation results in a prediction of the fractal dimension of the surface of vegetation of  $D = 2.78$ .

Clearly, approximate agreement between data and our predictions does not prove that the fractal nature of vegetation contributes to a steep increase in number of individuals as arthropods get smaller. Moreover, different values for  $D$  (1.28-1.79; Table 1) and the metabolic rate exponent (0.62-0.86; refs 13,14) lead to different predicted slopes in Fig. 2, as will the precise form of the relationship between the fractal dimension of a surface and transects across that surface. It remains to be seen whether detailed differences in the fitted slopes apparent in Fig. 2 can be explained by differences in the fractal dimension of particular plant surfaces, and by the biology of associated arthropods.

We know of no other attempts to explain patterns in the body size distributions of arthropods living on plant surfaces, although previous studies have examined species/frequency distributions for animals of different sizes<sup>12,18</sup>. Theoretical and empirical links between patterns in the number of species and number of individuals of different body lengths constitute an important unsolved problem.

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