Clearly the underlying mechanism of interaction is not always competition; disturbance and stress do alter the intensity of competition, sometimes preventing it occurring at all. Indeed it is so transparently obvious that '. . . disparities in the performance of neighbouring plants may arise from independent responses to the prevailing physical and biotic environment.' (Grime, 1979), that one is tempted to wonder how the disagreement between ourselves and Tilman has arisen. As pointed out by Thompson (1987), the problem is largely semantic. Tilman's (1987) definition of competition appears to coincide closely with Grime's (1979) definition of dominance. Dominant plants exert deleterious effects (e.g. shading) on their neightbours but an ability to deprive neighbours of light is not necessarily part of the mechanism by which such plants achieve dominance in the first place. Thus, we would entirely agree with Tilman (p.313) that trees are the true, long term dominants of ungrazed pasture but we would not agree that this automatically makes them good competitors.

As Milne (1961) pointed out: '. . . competition ought to have only one meaning – clear, precise and unambiguous. . .' and there is a sense in which the exact meaning is unimportant, as long as it is clear and widely acknowledged. Nevertheless, there are good reasons for preferring definitions which, within reason, are as narrow as can be arranged. One word should clearly apply to one process. In very many cases the plant which eventually comes to dominate a given habitat does so as a consequence of its ability to tolerate the deficiencies or excesses of soil and climate, resist the attentions of predators and pathogens, and capture resources at rates faster than those achieved by competitors. To lump all these processes together as 'competition' seems to us to squander the usefulness of a very valuable term.

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Fractal geometry and caterpillar dispersal: or how many inches can inchworms inch?

The irregularities and rough textures of natural substrates pose many problems for field biologists. Fortunately, fractal geometry (Mandelbrot, 1983) provides a quantitative approach that explicitly deals with irregularities and has started to find its way into ecological literature (see Burrough, 1981; Loehle, 1983; Bradbury & Reichelt, 1983; Bradbury, Reichelt & Green, 1984; Morse *et al.,* 1985; Lawton, 1986; Pennycuick & Kline, 1986; Krummel *et al.,* 1987). One of the primary characteristics of fractals is that surface distances and areas depend upon the scale at which measurements are taken. Thus, fractal geometry offers an important framework in which animal mobility may be studied.

Dispersal by caterpillars plays a primary role in population dynamics of many species of Lepidoptera. The period spent by larvae dispersing from dead or defoliated host plants in search of new food can be a major source of mortality (e.g. Dethier, 1959; Douwes, 1968; Jones, 1977; Cain, Eccleston & Karieva, 1985). Not suprisingly, larger larvae are more likely to find new host plants since they can move greater distances. Prediapause larvae of *Euphydryas editha bayensis* Sternitzky (Nymphalidae) may have to disperse when their host plants senesce or are defoliated (Singer, 1972). First instar larvae must be within 10 cm of edible food to survive dispersal, while second and third instar larvae can travel up to several meters. Given their limited mobility, 95–99% of prediapause larvae may starve to death.

Postdiapause caterpillars of *E. editha bayensis* often disperse many meters from cool slopes to warmer slopes in their grassland habitat and thus

grow faster (Weiss *et al.*, 1987). The earlier these postdiapause caterpillars transfer, the more they decrease their development time. Shortened development time results in earlier adult flight, which in turn enhances the chances that adult males will find mates (Iwasa *et al.*, 1983; Baughman, Murphy & Ehrlich, 1988) and that females will oviposit early enough for their offspring to reach diapause before their annual herbaceous host plants senesce.

Therefore, characteristics of natural surfaces which impede dispersal by caterpillars can have important consequences for survival and reproductive success. This short study analyses how the irregularities of rough-textured surfaces affect the dispersal capabilities of caterpillars of varying sizes, using a simple fractal model of topography (Mandelbrot, 1967, 1983).

We assume that caterpillars disperse over a surface between two reference points A and B, 1 m apart, keeping a constant compass heading. The path is modelled after Mandelbrot's (1967) coastline model where:

$$L(c) = L(1)c^{1-D.} \quad 1 < D < 2 \qquad \text{Equation 1}$$

$L(c)$ = length of path, c = step length, D = dimension,

$L(1)$ = length of linear distance travelled (1 meter in this example).

The exponent D is the fractal dimension of the path. For completely smooth surfaces, $D = 1$. Level paths in natural non-vegetated topography have D ranging from 1·02 to 1·25, with the lower value representing very smooth landscapes and the higher value relatively more rugged ones. For further explanation consult Mandelbrot (1967, 1983).

Caterpillar length is used as the step length. The caterpillars in this example hatch at 1 mm and grow to 3 cm. Fig. 1 shows the distances travelled by different sized caterpillars for $D = 1·1$ to 1·5. Even slight surface roughness, $D = 1·1$, results in disparate distances travelled for larvae of different sizes. Caterpillars of 1 mm length, travel 2·00 m to cover a linear meter; 5 mm caterpillars travel 1·70 m; and 3 cm caterpillars travel 1·42 m. As D increases, distance travelled from A to B increases for all size classes.

Surfaces with low D are reasonable approximations of bare soil surfaces. The range of D for grassland surfaces is not known but is certainly greater than D of bare soil. In the range $D = 1·3-1·5$, distances expand dramatically. At $D = 1·4$, 1 mm caterpillars travel 15·8 meters to cover 1 linear meter; 5 mm caterpillars travel 8·32 meters;
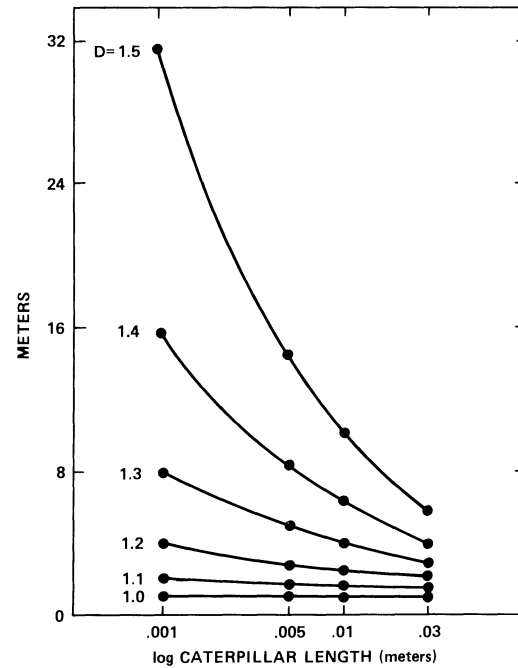

Fig. 1. Distance actually travelled for every meter of straight-line distance. D is defined in text equation 1.

and 3 cm caterpillars travel 4·08 meters. If D of a grassland surface is greater (see Burrough, 1981 and Morse *et al.*, 1985) then distances are magnified even further.

To calculate dispersal distances in terms of body length, $N(c)$, we divide the distance travelled by the length of the caterpillar (c), leaving:

$$N(c) = L(1)c^{-D} \qquad \text{Equation 2}$$

Results from Equation 2 are presented in Table 1. At $D = 1·2$, 5 mm caterpillars must travel 2·89 m to cover 1 meter, or 577 body lengths; for 1 cm caterpillars every meter travelled requires 2·51 m, or 251 body lengths, a 2·30:1 ratio for distances travelled in terms of body lengths. On a smooth surface $(D = 1)$, the ratio of body lengths travelled is only 2:1. Therefore, the fractal surface contributes another 15% beyond the ratio of body

Table 1. Distance travelled in body lengths.

D	Caterpillar length (m)			
	0·03	0·01	0·005	0·001
1	33	100	200	1000
1·1	47	158	340	1995
1·2	67	251	577	3981
1·3	95	398	980	7943
1·4	136	631	1665	15849
1·5	192	1000	2828	31623

lengths. At $D = 1\cdot4$, 5 mm caterpillars travel 1665 body lengths per meter, while 1 cm caterpillars travel only 631 body lengths, a ratio of $2\cdot64{:}1$, i.e. a 32% contribution from the fractal component. Again, as D increases, the contribution from the fractal surface becomes proportionately greater.

Thus, fractal properties of a surface can contribute significantly to caterpillar dispersal distances. This phenomenon affects two growth stages in the life cycle of *E. editha bayensis*, as mentioned above; i.e. when prediapause larvae search for food and when postdiapause larvae disperse between thermal micro-environments. Travel between thermal micro-environments 5–50 m apart, which can significantly affect larval growth rates, is virtually impossible for 2 mm larvae just out of diapause. Such dispersal must wait until the final two postdiapause instars when larvae reach 1 cm or greater in length. Therefore, thermal micro-environments in the grassland might be viewed as coarse-grained (*sensu* Levins, 1968) for small postdiapause larvae and become more fine grained for more mature larvae. Environmental grain size depends greatly on the size of the life stage considered and has a significant fractal component.

The point to be made from this brief analysis is that distances travelled between reference points depend upon both animal size and substrate texture. Morse *et al.*, (1985) and Lawton (1986) make this point with respect to the distribution of arthropod body lengths and biomass on plant surfaces. All natural substrates have fractal features (Burrough, 1981; Mandelbrot, 1983), which have conseqeunces for numerous ecological situations beyond the simple example discussed here.

Acknowledgments

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