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## Scaling behaviour of an extended Eden model

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Abstract. Computer simulations of cluster growth have been performed using an extended version of the Eden model. The scaling exponents for the surface width depend on the value of a parameter q which determines the extent of cluster relaxation. This model has a particular relevance to the growth of bacterial colonies in nutrient-rich environments.

The Eden model (Eden 1961) is a simple sequential model for the stochastic growth of compact clusters. In this model each new element of a cluster is added at a growth site that is chosen, with equal probability, from a list of all the possible growth sites. The possible growth sites are defined, at each time, by a microscopic rule for cluster expansion which, in general, identifies sites that are on the cluster edge. The list of possible growth sites reflects the instantaneous shape of the cluster.

Eden clusters are compact in all space dimensions (Richardson 1973) but their surfaces have a self-affine fractal geometry (e.g. see Mandelbrot 1982, Sander 1992). Interest has focused on the non-trivial scaling properties of the cluster surfaces and computer simulation methods have been used extensively to examine the interfacial properties of lattice-based Eden clusters (Plischke and Racz 1984, Jullien and Botet 1985a, b). Jullien and Botet (1985a) clearly identify three microscopically distinct versions of the Eden growth process, labelled A, B and C, and show that they all have similar scaling behaviours with a finite size (or roughening) exponent  $\alpha = 0.50 \pm 0.02$ and a dynamic exponent  $\beta = 0.30 \pm 0.03$  (see below for definitions). Further versions of the model, which differ only by small modifications of the microscopic rules, are expected to have identical scaling. In this sense the Eden model is representative of a large class of irreversible, interfacial growth processes which includes processes described by continuum equations such as the one proposed by Kardar *et al* (1986).

Applications of Eden-like models are extensive and varied. They include crystal growth (Langer 1980), the build up of granular deposits (Jullien *et al* 1992), and the proliferation of cancer cells (Williams and Bjerknes 1972). However, the original Eden model was proposed as a lattice-based representation for the development of bacterial colonies. Unfortunately, in this context, the Eden model is of limited validity since, in a bacterial colony, cell division may take place within the colony, away from the surface, and it may be accompanied by structural relaxations. However, the form of many bacterial colonies does suggest the action of a non-equilibrium, Eden-like growth process (Ben-Jacob *et al* 1992). (An exception occurs in nutrient-limited regimes when growth is controlled by a diffusion process and colonies have fractal structures (Ohgiwari *et al* 1992).)

Recently, Vicsek et al (1990) have examined, using digitized photographs, the surface of a quasi-(1+1)-dimensional colony of *Escherichia coli* grown on a nutrient-rich agar substrate. They found that the leading edge of the colony had a self-affine geometry but the scaling behaviour was not Eden-like and had a finite size exponent  $\alpha > \frac{1}{2}$ . This observation has prompted an examination of an Eden-like lattice model of cluster growth that contains additional features to mimic, more closely, the growth of real bacterial colonies. This model incorporates, in a simple way, both the division of cells at locations, in a finite-sized zone, beneath the cluster surface and the instantaneous relaxation of the cluster structure surrounding a site of cell division. Both direct and indirect experimental evidence supports the existence of a finite-sized zone of actively dividing cells beneath the surface of bacterial colonies. First, photographic observations of immobilized colonies (Parker 1993, Shapiro 1987) often show concentric regions within the colony, which advance with the colony surface, that contain cells with different levels of metabolic activity. Second, examinations of surface colonies using microelectrodes (Wimpenny and Coombs 1983, Fraleigh and Bungay 1986, Robinson et al 1991) show that the local concentrations of oxygen, nutrient and organic acids, which control the cell growth rate, are strong functions of position inside the colony. The relaxation processes, which occur concurrently with the growth and division of one cell in a group of cells, are substantially unquantified. For very small groups of E. coli cells Shapiro and Hsu (1989) have shown that rod-like cells favour side-by-side alignments following divisions, but these observations cannot easily be extrapolated to describe the correlations which must exist in large collections of cells which have polydisperse shapes. In the extended Eden model, described below, relaxations are restricted to the synchronous motion of a train of neighbouring cells.

Computer simulations have been performed, on a square lattice, in a (1+1)-dimensional strip geometry with size L. Planes at y=0 and y=L are periodic boundaries and the strip is infinite in the x-direction. Initially all the lattice sites with  $x \leq 0$  are occupied and all those with x > 0 are empty. At each time step an occupied lattice site r is chosen randomly. Then, if there are any unoccupied sites, r', such that r-r'=sk, where k is a lattice vector and  $s \leq q$ , the site r becomes, momentarily, doubly occupied. This double occupancy is then relaxed by the occupation of a site chosen at random from the set of unoccupied sites r' for which |r-r'| is a minimum. In most cases this set has only one member. This growth process may be pictured in terms of the doubling of the cell at r combined with the relaxation of surrounding cells onto a point of structural inefficiency inside the cluster. The relaxation is constructed from the simultaneous motions of a train of neighbouring cells, in the direction of least resistance, with a maximum train length q. Note that for q=1 this growth process maps onto the model C Eden process defined by Jullien and Botet (1985a).

The growth process leads to a compact cluster with an irregular, rough surface. The edge of a typical cluster with q=4 and L=96 is shown in figure 1. At any time the surface of the cluster may be defined by a set of heights,  $h(y_i)$ ,  $1 \le i \le L$ . The heights  $h(y_i)$  represent the extension of the cluster in the x-direction at a lateral point  $y_i$ . For a cluster with constant density, the mean height

$$h_0 = L^{-1} \sum_{(i=1,L)} h(y_i)$$
 (1)

is proportional to the number of cell divisions. For a particular value of  $h_0$ , the standard deviation of the heights

$$\sigma(L, h_0) = \sqrt{\left[L^{-1} \sum_{(i=1,L)} (h(y_i) - h_0(L))^2\right]}$$
(2)



Figure 1. The edge of a typical cluster, obtained from the extended Eden model with q=4, in a strip with L=96.

is a representation of the surface roughness, and this has a scaling form

$$\sigma(L, h_0) = L^a f(h_0 L^{-z})$$
  
$$\sim h_0^\beta \qquad h_0 \ll L^z \qquad (3a)$$

$$\sim L^{\alpha} \qquad h_0 \gg L^z$$
 (3b)

where f(x) is a scaling function and  $z = \alpha/\beta$ . This picture describes a surface with a width that initially increases and then, after a time which depends on the strip width L, reaches a saturated value. In figure 2 we have plotted the logarithm of the steady-



Figure 2. A double logarithmic plot of the squared, steady-state surface width against the strip size, L, for extended Eden growth with  $q=2, 4, 8 (\times, \bigcirc, \bullet)$ . Straight lines are best fits in the scaling regimes. The data sets have been shifted to the left by  $\log(q)$ .

state surface widths (squared) against the logarithm of the strip widths for simulations with q=2, 4 and 8. The data correspond to strip widths  $16 \le L \le 512$  and, in each case, the points represent mean results from an ensemble between 10 and 1000 independent realizations. Error bars are indicated for selected points and, for clarity, the data sets have been shifted to the left by  $\log(q)$ . For the largest strip widths the final clusters each contain in excess of  $8 \times 10^6$  particles. In figure 2 the straight lines indicate a scaling regime with  $\alpha = 0.49 \pm 0.03$ ,  $0.45 \pm 0.03$  and  $0.42 \pm 0.03$  for q=2, 4 and 8, respectively. These results show that the extended Eden model has a scaling behaviour that is clearly distinct from that of the traditional lattice Eden model. This deviation is also apparent for the dynamic exponent  $\beta$ . Simulations with size L=384 show that, for small  $h_0$ , the surface width has a well defined power-law dependence on  $h_0$  with  $\beta = 0.27 \pm 0.03$ ,  $0.22 \pm 0.02$  and  $0.22 \pm 0.02$  for q=2, 4 and 8, respectively.

Thus, growth from beneath the surface of an expanding cluster leads to an interface that roughens slowly compared to one that is driven by a simple surface addition process. For the extended model  $z\approx 2$  and the temporal spread of height fluctuations is diffusive. This is in contrast to the superdiffusive behaviour of pure Eden and ballistic deposition models where z < 2. In addition, in the steady state of the extended Eden model, the fluctuations of the heights are less correlated along the surface than in the case of pure 'deposition', i.e. in the extended model the surface is less 'rough'. The results are currently insufficient to establish the precise dependence of the exponents on the parameter q but they clearly establish a qualitative change, in an observable property of the cluster morphology, that arises as a result of the subsurface growth.

The average Green's function, g(r-r'), for the steady-state growth in the extended Eden model has also been measured. This function is largely independent of the system size and geometry, and it represents, quite generally, the probability that an unoccupied site at r' becomes occupied at the same time as a new particle is introduced at site r. Figure 3 shows a representation of g(r-r') for extended Eden growth with q=8. The dark bars give the probability histogram for relaxation in the lateral direction. This is a steadily decreasing function of the distance r. Light bars show the corresponding histogram for relaxation in the direction of the growth. This function has a well defined minimum, at a separation of two lattice units, and rises steadily for  $3 \le r \le 8$ . There is



Figure 3. The average Green's function for extended Eden growth with q=8. The dark bars correspond to relaxations in the lateral direction and light bars correspond to relaxations in the growth direction. r is the separation between the growth site and the occupied site.

also a finite probability ( $\sim 0.002$ ), not represented in figure 3, that relaxation occurs in the opposite direction to the growth.

Figure 3 shows clearly that the relaxation mechanism effectively promotes growth from sites that are not surface sites. The probability of growth increases with the distance beneath the surface because the number, m, of equally weighted, growth sites increases with the depth through the surface profile. Simulations with  $q > \sigma(L, \infty)$ confirm that  $g(r) \rightarrow$  constant for  $r > \sigma(L, \infty)$ . The average Green's function may thus be used in a numerical scheme to construct, directly, clusters in different geometries. Direct comparisons, between lattice-based simulation results for g(r) and real colony shapes, are, at this stage, unprofitable. However, there is some evidence (Shapiro and Hsu 1989) that colony morphologies may be indicative of the underlying characteristic relaxation processes.

The observations above do not account for the large value of  $\alpha$  measured by Vicsek *et al.* However, note that the image analysis made by Vicsek *et al.* quantifies the scaling behaviour for the leading edge of a three-dimensional surface colony. The growth of colonies of *E. coli* includes a component of front propagation that is normal to the planar substrate. Preliminary investigations indicate that  $\alpha$  does not increase above 0.5 as a result of including this element of the growth process. Parallels with more general stochastic growth modelling suggest several microscopic mechanisms which may lead to enhanced roughening, and hence larger values of  $\alpha$ , but these do not yet have clear interpretations in terms of bacterial colony development. First the introduction of power law noise or quenched disorder into the growth process may lead to isolated surface abnormalities, such as large steps, and hence to larger values for the roughening exponent (Csahok *et al.* 1993). Secondly, and more likely, other relaxation processes such as the surface diffusion of cells, leads to rougher interfaces. It is hoped to include some of these elements into future simulations.

The development of a colony is one expression of the growth of a bacterial population and, in general, the form of a colony reflects a, more fundamental, underlying growth process for the bacteria. The complexity of multicellular structures and the adaptability of living microorganisms makes the correlation between form and growth non-trivial. However, the model introduced above highlights a particular feature of colony development, an active growth zone, and establishes its consequences in terms of an observable property of the dynamics, namely the scaling behaviour of the interfacial structure. This correlation is a constraint on the range of biological activity that may lead to observed colony morphologies and it establishes fundamental, transferable details of the processes which constitute colony growth. In practical applications, such as the contamination of food by pathogenic microorganisms, the details of the population growth in complex environments are paramount. These details also depend on the fundamental processes which underlie the growth. At this stage our analysis is only semiquantitative but our results are sufficiently complete to encourage closer examinations of the surfaces of bacterial colonies.

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