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Nematode movement along a chemical gradient in a structurally heterogeneous environment. 2. Theory

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Summary – The effects of structural heterogeneity on both chemical diffusion and nematode movement are examined with the development of a theoretical model. The model considers three factors affecting nematode movement : soil structure, nematode foraging strategy and chemotaxis. Using a continuous model, we develop a discrete system which allows nematode trails to be simulated in any of the four experimental conditions given by Anderson *et al.* (1997). We show that structural heterogeneity causes mixed levels of attractant concentration over small areas as well as " fingering " of the attractant. Soil structural heterogeneity also restricts the foraging strategy of the nematode which then becomes a strategy to avoid structural " traps ". The effect of localised increases in structural density is shown to increase significantly " fingering " of the attractant.

Résumé – ***Déplacement des nématodes en fonction d'un gradient chimique dans un milieu à structure hétérogène. 2. La théorie –*** L'influence de l'hétérogénéité sur la diffusion chimique et le déplacement des nématodes est étudiée par le biais d'un modèle théorique. Ce modèle prend en compte trois facteurs influant sur le déplacement des nématodes : la structure du sol, la stratégie de recherche de nourriture et la chémotaxie. Utilisant un modèle continu, nous avons mis au point un système discret permettant de simuler les traces des nématodes dans chacune des quatre situations définies par Anderson *et al.* (1997). Nous avons montré que l'hétérogénéité structurale provoque aussi bien des taux variables de concentrations du composé attractif dans des aires réduites que la reconnaissance de ce composé. L'hétérogénéité structurale du sol limite également la stratégie de recherche de nourriture du nématode lequel adopte alors une stratégie permettant d'éviter les pièges structuraux. Il est démontré que des augmentations localisées de la densité structurale accroissent significativement la reconnaissance du composé attractif.

Key-words : cellular automata, chemotaxis, diffusion, foraging strategy, heterogeneous structure, nematode movement, theoretical model.

Models of nematode movement and chemotaxis are virtually unknown in the literature. This is particularly true in consideration of the effects of environmental heterogeneity. Croll and Sukhdeo (1981) treat the nematode as a random walker and Ward (1978) has developed a theoretical model of gradient detection for *Caenorhabditis elegans* which, however, did not consider movement. Chemotaxis models have been investigated in more detail for bacterial populations, using linear diffusion (Murray, 1990; Lauffenburger, 1991; Tranquillo, 1992). In the wider context of modelling insect movements, random walk models have been considered (Marsh & Jones, 1988) and the related diffusion approximations (Alt, 1980; Okubo, 1980, 1986). Nonlinear diffusion models have been examined (Gurtin & MacCamy, 1977), including modelling of the dispersal of ants (Shigesada, 1980). Correlated random walks, which take into account biased movement, have also been used to model insect movement, in particular butterfly movement (Bovet & Benhamou, 1988; Kareiva & Shigesada, 1989; McCulloch & Cain, 1989; Johnson *et al.*, 1992).

This paper develops a theoretical model which will aid in the quantification of the effect of structural heterogeneity on nematode movement, chemical gradients and any resulting interactions. Work presented in the first paper of this series (Anderson *et al.*, 1997) has shown that nematodes do indeed alter their direction towards chemical gradients within structure, and other workers have obtained similar results without structure (Dusenbery, 1985; Grewal & Wright, 1985; Bargmann *et al.*, 1993). In the following work we make no assumption as to the phase in which the gradient exists as the model is able to account for water-soluble or gaseous attractants.

Materials and methods

MATHEMATICAL MODEL

The development of the mathematical model accounts for the general movement patterns observed by Anderson *et al.* (1997). The model considers three main factors affecting nematode movement : soil structure, nematode foraging strategy and chemotaxis. The latter is influenced by the level of attractant diffusing from a

bacterial food source, which depends on the concentration of bacteria and which, in turn, is mediated by the level of substrate available to the bacteria. Soil structure and nematode foraging are interdependent, that is without structure the nematode forages freely, within structure foraging behaviour is restricted and more random movements dominate (Anderson *et al.*, 1997). A plausible scenario covering the above interactions is the movement of a free-living nematode towards a root in response to a diffusing chemical emanating from rhizosphere bacteria; the bacteria population growing in response to root exudate and nutrients.

Initially we will examine the case of nematode movement without soil structure. The model could be classed as a variation of linear diffusion models and takes the form,

$$\begin{aligned}
\frac{\partial n}{\partial t} &= \textit{random movement of nematode} - \textit{chemotactic term} - \textit{foraging terms} \\
\frac{\partial a}{\partial t} &= \textit{diffusion of attractant} + \textit{bacterial term} \\
\frac{db}{dt} &= \textit{bacterial growth - bacterial decay} \\
\frac{dc}{dt} &= - \textit{nutrient decay}
\end{aligned} \tag{1}$$

where *n, a, b* and *c* represent the nematode, attractant, bacteria and nutrient concentrations at time *t,* respectively.

The nematode concentration is to be interpreted as the density distribution of nematode trails. This distribution is formed by experimentally tracking a nematode from a given origin for some time, repeatedly from the same origin. Thus, after many different trails, we see that the area they cover grows with time. Given the existence of some preferred direction, towards the bacteria for example, we expect the trail density to be denser in that direction, *i.e.,* more nematodes will have moved in the preferred direction.

The chemotactic term (Murray, 1990) represents the influence that the attractant has over the nematodes. The actual system of differential equations has the form,

$$\begin{aligned}
\frac{\partial n(x,y,t)}{\partial t} &= D_1\left(\frac{\partial^2 n}{\partial x^2}+\frac{\partial^2 n}{\partial y^2}\right)-\frac{\partial}{\partial x}\left(n\frac{\partial a}{\partial x}\right)- \\
&\quad \frac{\partial}{\partial y}\left(n\frac{\partial a}{\partial y}\right)-\varepsilon_1\frac{\partial n}{\partial x}\sin(\rho t)-\varepsilon_2\frac{\partial n}{\partial y}\cos(\rho t) \\
\frac{\partial a(x,y,t)}{\partial t} &= D_2\left(\frac{\partial^2 a}{\partial x^2}+\frac{\partial^2 a}{\partial y^2}\right)+\alpha b \\
\frac{db(t)}{dt} &= \lambda b(1-b)-\frac{\beta b}{c+c_0} \\
\frac{dc(t)}{dt} &= -\gamma b
\end{aligned} \tag{2}$$

where D_1 and D_2 are diffusion coefficients and ε_1, ε_2, ρ, α, λ, β, c_0 and γ are all positive parameters.

The last two terms of the nematode equation are perturbation terms representing the foraging behaviour of the nematode, assumed for simplicity to be a looping type of movement, which was observed previously (Anderson *et al.*, 1997). Small values for ε_1, ε_2 (*i.e.,* perturbations) are used, since data from experiments clearly showed that the foraging behaviour was only relevant under conditions where the nematode did not sense the attractant gradient, or where no attractant gradient was present. In the presence of an adequate attractant gradient, however, the nematode is expected, after a certain time, to sense the attractant and move directly towards the bacteria, without further foraging (Anderson *et al.*, 1997).

The attractant *(a)* increases in direct proportion *(α),* to the concentration of bacteria *(b),* and diffuses randomly with diffusion constant D_2. Bacterial growth is assumed to be logistic with a carrying capacity λ, and decays proportionally *(β)* to the amount of nutrient *(c)* available. The nutrient concentration decays inversely proportional *(γ)* to the concentration of bacteria.

The nematode and attractant equations are functions of both space and time. The bacteria and nutrient do not move, which is reasonable when compared to the scale of nematode movement.

Discretised model

Our objective is to model nematode trails, rather than nematode density. To this end we consider a discrete system derived from (2). This is done using Euler finite difference approximations (Wait & Mitchell, 1985), which involves approximating the two dimensional *(x, y)* space of the nematode as a grid of points (mesh size *h*) and time *(t)* by discrete increments (magnitude *k*).

The full discretised system is derived in the appendix. For simplicity we consider only the equation governing nematode movement, that is,

$$n_{l,m}^{q+1} = n_{l,m}^{q} P_0 + n_{l+1,m}^{q} P_1 + n_{l-1,m}^{q} P_2 + n_{l,m+1}^{q} P_3 + n_{l,m-1}^{q} P_4 \tag{3}$$

where subscripts specify the location on the grid and the superscripts the time steps. That is $x = lh$, $y = mh$ and $t = qk$ where *l, m, h, k* and *q* are positive parameters. The purpose of equation (3) is essentially to determine the nematode concentration at position *(l, m),* time $q + 1$ by averaging the concentrations of the four surrounding neighbours at the previous time step *q*.

The advantage of using a discrete model is the manner in which it splits equation (3) into the five coefficients P_0 to P_4, which are factors of the nematode concentration at various positions. It is these coefficients that are the driving force behind the model, for they can be thought of as being proportional to the probabilities of the nematode being stationary *(P_0)* or moving left

(P_1), right *(P_2)*, up *(P_3)* or down *(P_4)*. This is reasonable, as a higher density of nematode trails towards a preferred direction will cause the weight of the coefficient, corresponding to that direction, to be larger and subsequently the probability of movement in that direction will be greater.

The coefficients P_1 to P_4 have the general form,

$$P_n = \textit{random movement} - \textit{chemotaxis} - \textit{looping term}, \quad (4)$$

thus showing how the discrete nematode equation is linked to the continuous nematode equation of system (1). P_0 has a similar form to the above but without the looping term. The exact forms of P_0 to P_4 involve functions of the attractant concentration near the nematode (see appendix). Therefore when there is no, or insufficient, attractant the values of P_1 to P_4 are equal with P_0 smaller, *i.e.*, there is no bias in any one direction and the nematode is less likely to be stationary. This is in agreement with observation. However, if there is an attractant gradient (strong enough for the nematode to react to), chemotaxis dominates and the coefficients P_0 to P_4 will become biased (larger or smaller) depending on the gradient of the attractant.

Having derived the discrete model, it is used to numerically simulate nematode trails in a homogeneous environment.

Numerical simulation

Numerical simulations are used to approximately solve systems of partial differential equations which would otherwise be intractable. They can also be used as the basis for cellular automata, with the discrete equations controlling the nearest neighbour interactions. This type of cellular automata may be considered as quantitative, since its rules are dependent on the discrete form of the reaction – diffusion equations which model nematode movement.

Each time step of the simulation involves solving the attractant, bacteria and nutrient equations numerically which then gives the five coefficients P_0 to P_4 (see appendix). Probability ranges are then computed by summing the coefficients to produce five ranges, $R_0 = 0$ to P_0 and $R_j = \sum_{i=0}^{j-1} P_i$ *to* $\sum_{i=0}^{j} P_i$, where $j = 1$ to 4. We then produce a random number between 0 and 1, and depending on which range this number falls into the nematode will be stationary *(R_0)* or move, left *(R_1)*, right *(R_2)*, up *(R_3)* or down *(R_4)*. The larger the coefficient the more probable it will be selected. The nematode therefore is restricted to move to one of its four orthogonal neighbouring grid points or remain stationary with each time step.

An important feature of the discrete model (3) is the stochastic element, used when choosing the direction of movement from the probability ranges R_0 to R_4, as this will cause the simulation to produce a different trail every time it is run. However, the trails produced in each simulation will all share the same behaviour : looping initially then moving linearly in the presence of the attractant gradient. Because of the random aspect of the simulations the time taken to enter the bacterial source is computed from an average of 50 different simulations (all with the same initial conditions).

Boundary conditions : the numerical simulations were carried out on a 200 × 200 grid, which is a discretisation of a 10 × 10 cm square approximating the homogeneous agar plate, used in the experiments (Anderson *et al.*, 1997), with a space step of $h = 0.05$ cm. No flux boundary conditions were imposed on the square grid, restricting both the nematodes and the attractant (the only variables which diffuse) to within the grid. Any diffusion on to the boundary region is reflected back. This is analogous to the experimental conditions of Anderson *et al.* (1997).

For the initial conditions, the bacteria takes up a tenth of the region and the nematode is placed just right of centre (Fig. 1). Initially, it is assumed that the nutrient for the bacteria covers the whole region uniformly and that there is no attractant.

Theoretical results and discussion

Simulation of nematode movement in a homogeneous environment

Fig. 2 shows both the attractant gradient and the nematode trail after 60 000 (arbitrary) time steps. The colours here represent the different concentrations of attractant, darkest being the highest. The trail displays random looping behaviour before the nematode reacts to the attractant and subsequently becomes straighter and more directed as the nematode moves up the attractant gradient and finally reaches the bacteria.

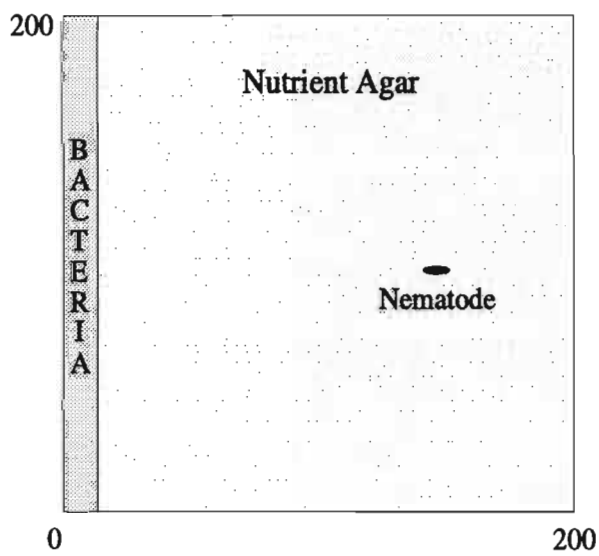

Fig. 1. *Initial conditions for numerical simulations (see text for details).*

For this simulation the diffusion coefficients are $D_1 = 0.5$ and $D_2 = 0.05625$, the space and time steps were $h = 0.05$, $k = 0.0011$ and the remaining constants have the values $\lambda = 0.4$, $\alpha = 0.9$, $\beta = 0.01$, $c_0 = 0.01$, $\varepsilon_1 = \varepsilon_2 = 0.3$ and $\rho = 1.4142136$. These parameters were chosen to qualitatively match behaviour observed by Anderson *et al.* (1996).

Simulation of nematode movement in a heterogeneous environment

Heterogeneous structure was included by means of digitised two dimensional soil sections or as digitised replicas of the experimental conditions used by Anderson *et al.* (1997). Every sand grain was considered to be an impregnable region deflecting the attractant and nematodes. In this way the nematodes and attractant are constrained to move through the pore network. The " deflective property " of the sand grains, means that pockets of high attractant concentration may form.

Simulations were carried out on the two dimensional digitised structure given in Fig. 1 of Anderson *et al.* (1997), which is a replica of the structure used for the nematode trail given in Fig. 1 D of Anderson *et al.* (1997). The initial and boundary conditions, diffusion coefficients and parameters are as before.

Fig. 3 A-D are snapshots in time of the attractant diffusing through the digitised structure from its bacterial source on the left. For clarity the structure is only revealed (as areas of zero attractant) as the attractant diffuses through it. Fig. 3 A indicates that the structure has affected the attractant after only 1 000 time steps.

It should be noted that the smooth linear concentration gradient that was produced in Fig. 2 has been transformed into a very complex mixture of high and low attractant concentration levels. The nematode trail produced from this simulation is given in each of the figures in white. In Fig. 3 B we see the emergence of " fingering " of the diffusing attractant from the bacteria, that is the protrusion of more concentrated attractant from the diffusion front. This is due to the attractant being deflected off the pore walls to a much larger degree in that area – purely because of the heterogeneity of the sand structure. This " fingering " effect becomes more pronounced as structural density increases. After 30 000 time steps (Fig. 3 C), the gradient has diffused through half of the structure. The nematode trail at this time remains localised due to the structure being very dense in this area and the still random nature of the nematode movement. It is also interesting to note that the concentration of attractant has reached the same peak level of 95 that the homogeneous simulation reached after 60 000 time steps. This is probably due to the manner in which the structure restricts the diffusion of the attractant and in so doing increases the concentration.

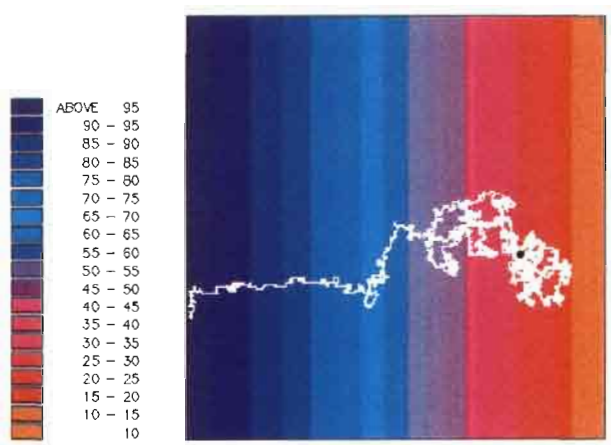

Fig. 2. *Homogeneous simulation after 60 000 time steps, with attractant (arbitrary scaling) concentration displayed on the left (nematode trail is given in white and ● denotes starting position).*

Fig. 3 D displays the state of the attractant gradient at 120 000 time steps, by which stage the nematode trail has made its way through the pore network and into the bacterial source. An interesting feature that occurs is the appearance of small regions of attractant that have a gradient in a different direction to the one emanating from the bacterial source. This would be due to the build up of attractant in enclosed or restricted pore space, and would result in guiding the nematode out of blocked pore pathways. The concentration of the attractant has increased by, at most, 10 % from Fig. 3 C to Fig. 3 D, implying that the bacteria have started to decay and are therefore producing less attractant. The trail shows that the circling behaviour of the nematode has been restricted due to the limited pore space, although it does appear to be very tortuous at times. This is due to the nematode being trapped occasionally in smaller pores, as can be seen roughly halfway through the structure. Again, the trail becomes straighter and more directed as the gradient becomes stronger, however, even at this stage the nematode may get trapped within constricting areas.

There are two main differences between the trails of Fig. 2 and Fig. 3; initially the time taken for the nematode trail to enter the bacteria is approximately twice as long in the case of the heterogeneous nematode. This is in agreement with the experimental work (Anderson *et al.*, 1997). Secondly, the characteristic foraging (looping) behaviour observed without structure has been constrained by the structure. However, there is a caveat to this, and that is where the nematode becomes blocked from moving in the direction of the bacteria by structure. At this point the foraging behaviour becomes important, allowing the nematode to randomly " search " for a way around the obstacle. This foraging strategy therefore becomes an avoidance strategy, in the presence of structural heterogeneity, which allows the nematode to escape structural " traps ". Having escaped, the nematode then returns to its biased-walk, via chemotaxis, towards the bacterial source.

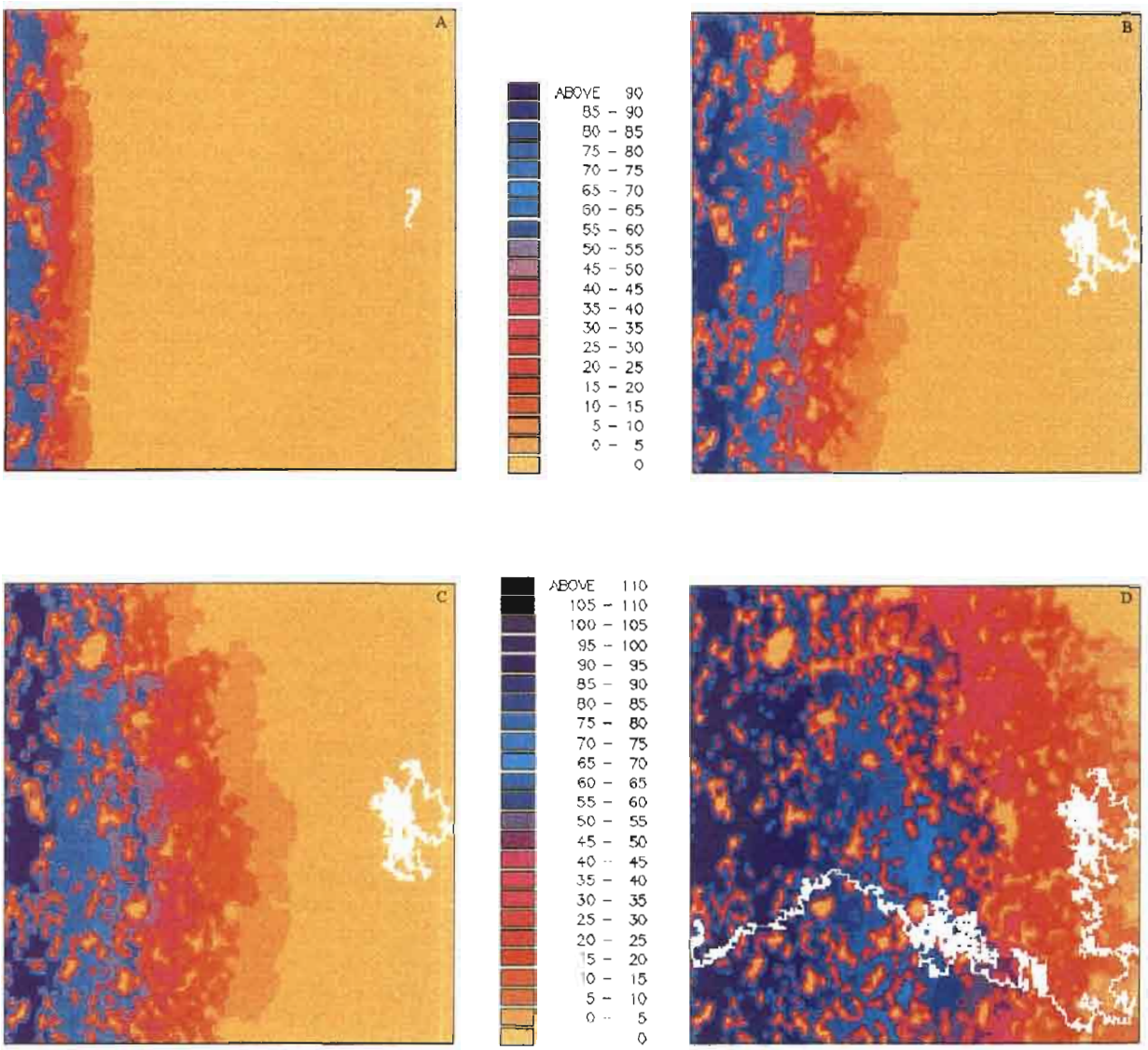

Fig. 3. *Heterogeneous simulation. A : 1000 time steps; B : 15 000 time steps; C : 30 000 time steps; D : 120 000 time steps (concentrations displayed as in Fig. 2).*

Simulation of nematode movement in a heterogeneous gradient

To analyse the effect of structural density on both nematode movement and attractant diffusion a structure was digitised which had increased structural density near the bacterial source. This situation is analogous to the increased soil bulk densities observed around roots (Guidi *et al.,* 1985) and emerging coleoptiles (Liddell, 1992) and has been observed in the field (Cooke, 1993).

Fig. 4 A-D show the results of the simulation on this structure, with the same initial and boundary conditions, diffusion coefficients and parameters as before. Comparing Fig. 4 A and Fig. 3 A we can see that after 1000 time steps there is a slight difference in the attractant gradient. However comparing Fig. 4 B with Fig. 3 B, there is a dramatic difference in the diffusion of the attractant, in particular the increase of " fingering " due to the increased structural density.

After 100 000 time steps (Fig. 4 C) the attractant gradient has become more evenly spread, this is because the density is only greater in the vicinity of the bacteria. The nematode trail has remained localised due to the structure and because the nematode has not yet detected the attractant gradient. In fact it takes 190 000 steps before the nematode reaches the bacteria (Fig. 4 D), which is over 50 % longer than the time taken for the nematode in

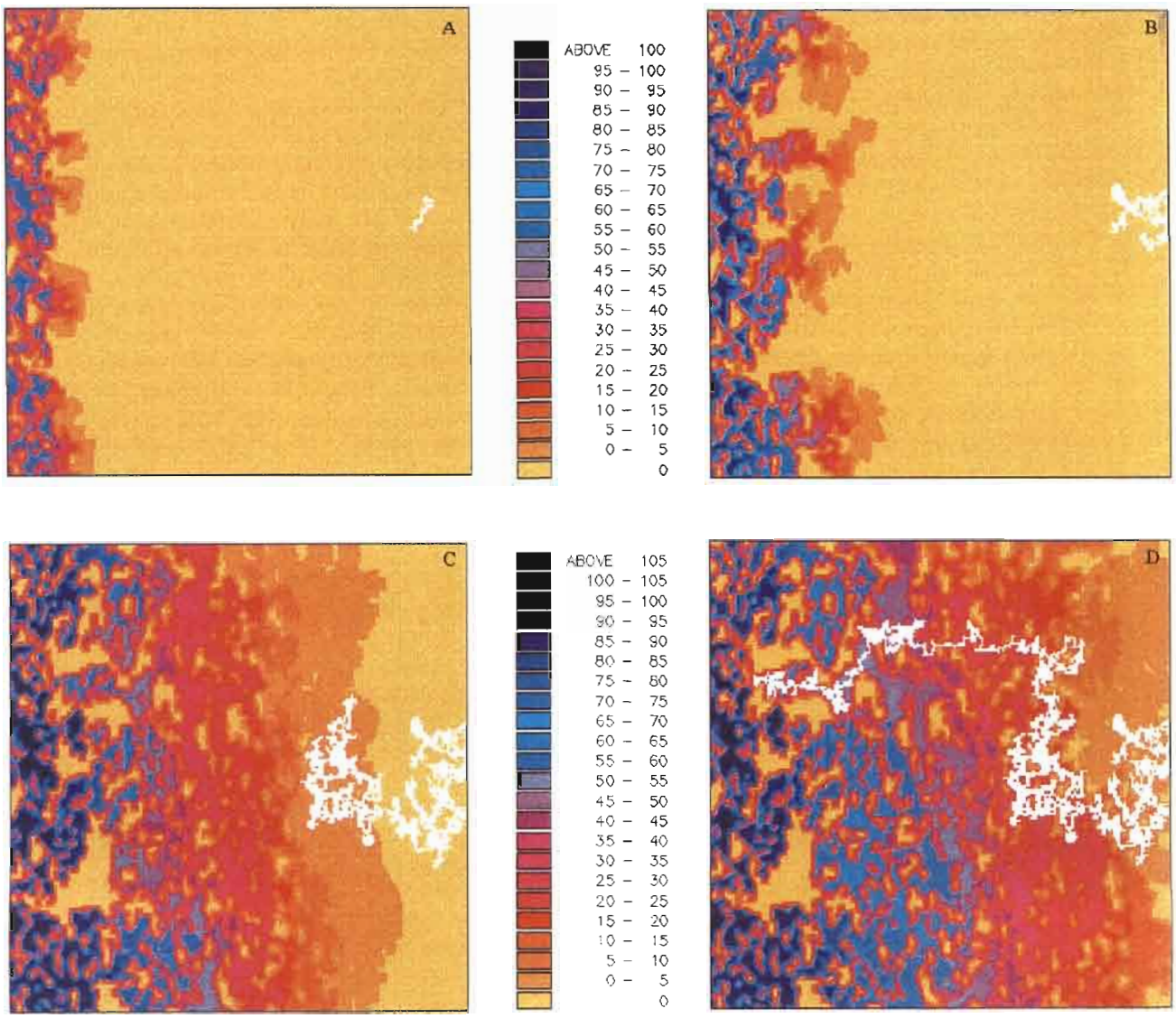

Fig. 4. *Heterogeneous simulation with varied sand density (higher towards the left hand side); concentrations displayed as before. A : 1000 time steps; B : 15 000 time steps; C : 100 000 time steps; D : 190 000 time steps.*

Fig. 3. In this case however, the increased structural density within and around the bacteria physically stops the nematode proceeding further into the bacterial source. This is primarily due to a decrease in pore connectivity associated with decreased porosity.

Conclusion

In this paper we have for the first time developed a theoretical model which aids in our understanding of the effects of structural heterogeneity on both gaseous diffusion and nematode movement. The theoretical model used a novel cellular automata type technique to generate a discrete trail from a system of continuous differential equations. There is a large degree of consistency between nematode movement patterns in the simulations and the experiments reported in Anderson *et al.* (1997), especially in the presence of structural heterogeneity. The simulations also gave an understanding of how structure may affect gaseous gradients, particularly the formation of " fingers " and mixed levels of concentration over very small areas.

The main conclusions to be drawn are : structural heterogeneity is both restrictive for the nematode and attractant diffusion, however the structure aids in the build-up of attractant as well as restricting the foraging behaviour and in certain situations, aids the nematode in

finding the bacterial source. These results neatly show how one structure can act on two processes, at two scales, in significantly different ways. We also showed that localised increases in structural density can have dramatic effects on the diffusion of the attractant, however, for this conclusion to be sustained we would require more than just local increases in density.

The conclusions are derived from a two dimensional structure that only imitates soil. In order to enhance this we are considering including the hydraulic conductivity properties of soil into the model.

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Appendix

To discretise the continuous system (2) we use Euler finite difference approximations (Wait & Mitchell, 1985), which leads to the system,

$$n_{l,m}^{q+1} = n_{l,m}^{q} P_0 + n_{l+1,m}^{q} P_1 + n_{l-1,m}^{q} P_2 + n_{l,m+1}^{q} P_3 + n_{l,m-1}^{q} P_4$$

$$a_{l,m}^{q+1} = a_{l,m}^{q}\left[k - \frac{4kD_2}{h^2}\right] + \frac{kD_2}{h_2}\left[a_{l+1,m}^{q} + a_{l-1,m}^{q} + a_{l,m+1}^{q} + a_{l,m-1}^{q}\right] + k\alpha\, b_{l,m}^{q}$$

$$b_{l,m}^{q+1} = b_{l,m}^{q}\left[1 + k\lambda(1 - b_{l,m}^{q}) - \frac{\beta k}{c_{l,m}^{q} + c_0}\right]$$

$$c_{l,m}^{q+1} = c_{l,m}^{q} - k\gamma\, b_{l,m}^{q}$$

with $x = lh$, $y = mh$ and $t = qk$.

The coefficient P_0, which is proportional to the probability of no movement, has the following form,

$$P_0 = 1 - \frac{4kD_1}{h^2} - \frac{k}{h^2}\left(a_{l+1,m}^{q} + a_{l-1,m}^{q} - 4\,a_{l,m}^{q} + a_{l,m+1}^{q} + a_{l,m-1}^{q}\right)$$

and the coefficients P_1, P_2, P_3 and P_4 which are proportional to the probabilities of moving left, right, up and down respectively and have the forms,

$$P_1 = \frac{kD_1}{h^2} - \frac{k}{4h^2}\left(a_{l+1,m}^{q} - a_{l-1,m}^{q}\right) - k\frac{\varepsilon_1 \sin(\rho t)}{h}$$

$$P_2 = \frac{kD_1}{h^2} + \frac{k}{4h^2}\left(a_{l+1,m}^{q} - a_{l-1,m}^{q}\right) + k\frac{\varepsilon_1 \sin(\rho t)}{h}$$

$$P_3 = \frac{kD_1}{h^2} - \frac{k}{4h^2}\left(a_{l,m+1}^{q} - a_{l,m-1}^{q}\right) - k\frac{\varepsilon_2 \cos(\rho t)}{h}$$

$$P_4 = \frac{kD_1}{h^2} + \frac{k}{4h^2}\left(a_{l,m+1}^{q} - a_{l,m-1}^{q}\right) + k\frac{\varepsilon_2 \cos(\rho t)}{h}$$

When there is no attractant in the same region as the nematode P_1 to P_4 are equal, except for the looping terms, since the value of a at any position is *0*. Also when there is an equal amount of attractant on either side of the nematode (the saturation effect or habituation) the values $a_{l,m-1}$ and $a_{l,m+1}$ cancel each other out as do $a_{l-1,m}$ and $a_{l+1,m}$ and therefore P_1 to P_4 are equal, except for the looping terms. Therefore, in both these circumstances the looping terms will dominate and cause the required foraging behaviour. However, if there is more attractant on one side of the nematode than the other, the probabilities will no longer be dominated by the looping terms and hence more directed movement will result.

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