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Role of chemotaxis in the transport of bacteria through saturated porous media

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Abstract

Populations of chemotactic bacteria are able to sense and respond to chemical gradients in their surroundings and direct their migration toward increasing concentrations of chemicals that they perceive to be beneficial to their survival. It has been suggested that this phenomenon may facilitate bioremediation processes by bringing bacteria into closer proximity to the chemical contaminants that they degrade. To determine the significance of chemotaxis in these processes it is necessary to quantify the magnitude of the response and compare it to other groundwater processes that affect the fate and transport of bacteria. We present a systematic approach toward quantifying the chemotactic response of bacteria in laboratory scale experiments by starting with simple, well-defined systems and gradually increasing their complexity. Swimming properties of individual cells were assessed from trajectories recorded by a tracking microscope. These properties were used to calculate motility and chemotaxis coefficients of bacterial populations in bulk aqueous media which were compared to experimental results of diffusion studies. Then effective values of motility and chemotaxis coefficients in single pores, pore networks and packed columns were analyzed. These were used to estimate the magnitude of the chemotactic response in porous media and to compare with dispersion coefficients reported in the field. This represents a compilation of many studies over a number of years. While there are certainly limitations with this approach for ultimately quantifying motility and chemotaxis in granular aquifer media, it does provide insight into what order of magnitude responses are possible and which characteristics of the bacteria and media are expected to be important.

Keywords: Bacteria; Chemotaxis; Motility; Diffusion; Dispersion; Groundwater; Bioremediation; Transport; Migration; Porous media; Pore-scale

1. Introduction

Many soil-inhabiting bacteria that degrade chemical contaminants are motile and chemotactic, suggesting that chemotaxis has provided competitive advantage in contaminated soil environments [48]. *Pseudomonas putida* respond to chlorinated hydrocarbons that they perceive as potential carbon sources [49,31]. Chemotaxis to naphthalene has been observed in naphthalene-degrading species [42]. Deep subsurface bacteria have been shown to exhibit strong chemotactic responses to a variety of contaminants, including trichloroethylene [32,39]. Researchers have suggested that chemotaxis is important in guiding subsurface microbial populations toward chemical contaminants [60,9,28]. A chemotactic response to an electron acceptor has been observed for *Pseudomonas stutzeri* KC, a natural aquifer isolate that transforms carbon tetrachloride under denitrifying conditions without the production of chloroform [17]. Dybas et al. reported migration of KC downstream of a conservative tracer in laboratory columns packed with aquifer material. They attributed this to a chemotactic response to nitrate gradients generated by metabolism [61]. After employing bioaugmentation to accelerate TCE degradation for a pilot study at Dover Air Force Base (Dover, DE) it was reported that bacteria injected into the center inoculation well were found in the outside

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Nomenclature

a	chemoattractant concentration [moles/L^3]
b	bacterial concentration [1/L^3]
c	parameter characteristic of geologic media [L^{1-m}]
d_{pore}	pore diameter [L]
D	diffusivity [L^2/T]
D_{eff}	effective diffusion coefficient in porous medium [L^2/T]
D_{K}	Knudsen diffusion coefficient [L^2/T]
E	dispersion coefficient [L^2/T]
K_d	chemotaxis receptor constant [moles/L^3]
L	longitudinal distance [L]
m	scaling exponent [–]
N_{b}	flux of bacteria [1/L^2 T]
t	time [T]
u	average linear fluid velocity [L/T]
v	individual cell swimming speed [L/T]
v_{c}	chemotactic velocity [L/T]
$v_{\text{c,pore}}$	chemotactic velocity in a pore [L/T]
x	distance [L]
α	turn angle between successive runs [deg]
α_{L}	longitudinal dispersivity [L]
α_{p}	turn angle between successive runs restricted in a pore [deg]
χ_0	chemotactic sensitivity coefficient [L^2/T]
λ	length of the run between tumbles [L]
μ	random motility coefficient [L^2/T]
μ_{eff}	effective (or apparent) motility coefficient [L^2/T]
μ_{K}	random motility coefficient restricted in a pore [L^2/T]
μ_{pore}	random motility coefficient in a pore [L^2/T]
μ_0	random motility coefficient in the absence of a chemical gradient [L^2/T]
τ	tortuosity parameter [–]

monitoring wells (about 20 ft on either side) that were intended to be negative controls [19]. Chemotaxis was suggested as a possible mechanism for the observed migration. Although the studies described above clearly implicate chemotaxis as a potentially important process in bioremediation, the complexity of field-scale studies has not allowed the magnitude of the chemotactic effect to be distinguished.

In this paper, a selection of laboratory-scale studies, from swimming behavior of individual cells to packed columns, that focus on transport via motility and chemotaxis is highlighted. It is organized in the following manner. Transport properties in bulk aqueous solution are analyzed first, then how these properties are altered by the presence of a granular (porous) medium, initially for stagnant systems and then for homogeneous steady flow. A summary of measured motility and chemotaxis properties is also included in tabular format.

2. Molecular basis of motility and chemotaxis

Bacteria are able to sense and respond to chemical gradients through receptor molecules embedded in the cell membrane. Although individual *Escherichia coli* bacteria sense temporal changes in the number of occupied receptors [41], they also respond to spatial gradients because they actively swim through them, thus exposing the receptors to a temporal variation in chemical concentration. This distinguishes bacteria from larger cells (e.g., flagellated protozoa) which are able to instantaneously sense spatial gradients along the length of their cell body. *E. coli* bacteria sense chemoattractants such as aspartate in their surroundings when molecules of aspartate bind to the methyl-accepting chemotaxis proteins *tar* that span the cell membrane. These binding events external to the cell membrane trigger a conformational change of the *tar* proteins on the cytoplasmic side of the cell membrane that initiates an internal cascade of phosphorylation reactions. Phosphate is passed from intracellular signaling molecules cheA to cheY and the increase in phosphorylated cheY suppresses flagellar motor reversal associated with a tumble event. Less frequent tumbling results in greater run lengths in the direction of the chemoattractant source and biases the overall migration in a direction that is perceived to be favorable for survival. In the absence of a chemical concentration gradient, phosphorylation of cheY is not augmented and tumbling occurs at regular intervals, about once every second. The chemosensory pathway and its regulation are well documented [57].

3. Swimming properties

The trajectories of swimming bacteria like *E. coli* are described as a series of runs and tumbles. Bacteria are propelled through surrounding media by rotation of helically-shaped flagella. When rotary motors that turn the flagella rotate counterclockwise, the 6–8 flagella on *E. coli* tend to form a coordinated bundle behind the cell body and the cell swims smoothly forward. When one or more of the motors reverse direction, the bundle unravels and the cell tumbles chaotically, reorienting itself prior to the start of another run [59]. By this alternating series of runs and tumbles, bacteria trace out a 3D random walk somewhat analogous to diffusion of molecules in a gas. A mathematical relationship between the run-and-tumble swimming behavior of individual cells and the observed spreading or diffusion of a population of bacteria, described by the