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Use of short-pulse experiments to study bacteria transport through porous media

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ABSTRACT

Continuous-flow column experiments with short-pulse inputs of one hydrophobic and one hydrophilic bacterium were used to study the retention of bacteria on quartz (negatively charged), hematite-coated quartz (positively charged) and polymer-coated quartz (hydrophobic surface), at pH 7.3. Both bacteria were Gram-negative rods. All breakthrough peaks occurred about one pore volume after the input pulse, and were attenuated compared to a bromide-tracer peak. Maximum bacteria concentrations in the column outlet were 0.08–57% of the peak bromide concentration. A one-dimensional advection–dispersion transport model with first-order bacteria removal described by colloid-filtration theory was used to estimate attachment and detachment rate coefficients and the relative sticking efficiency (α) of bacteria in each experiment. Attachment was reversible, with rate coefficients for attachment on the order of 10^{-4}–10^{-3} s^{-1}, implying that the time scale for attachment was of the same order as the column detention time of 1.2 h. The time scale for detachment was on the order of days to weeks. This slow detachment could be important in deep subsurface environments where transport on geologic time scales is important, and in some shallow aquifer recharge situations where soils are used to eliminate pathogenic bacteria from sewage effluent. Values for α were 0.04–0.4. Slower attachment and detachment rates were observed for the hydrophilic vs. hydrophobic bacteria, suggesting that hydrophilic bacteria could move further before being removed by attachment to soil, but once attached, would be resuspended at a slower rate.

INTRODUCTION

Interest in movement of bacteria in groundwater has over the past decade gone beyond the traditional concern of pathogens in public water supplies to in situ biodegradation of contaminated soils, enhancement of crude-oil recovery, and facilitating transport of radionuclides and other dissolved contaminants. Bacteria have been shown to move through soil columns at pore velocities of 3–30 m day^{-1} in laboratory experiments (Wollum and Cassel,

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1978; Smith et al., 1985; Fontes et al., 1991) as well as field studies (Harvey et al., 1989; Harvey and Garabedian, 1991; Martin et al., 1991). Chemical and biochemical factors controlling transport and retardation of bacteria generally are neither known or controlled in natural field experiments. Laboratory column experiments have been used to examine the influence of hydrophobic effects, pH and ionic strength (Fontes et al., 1991; Kinoshita et al., 1993).

Steady-state filtration theory has been applied to interpret laboratory column studies of bacteria transport (Martin et al., 1991; Kinoshita et al., 1993) and field studies of bacteria transport (Harvey et al., 1989; Harvey and Garabedian, 1991; Bouwer and Rittmann, 1992). Fontes et al. (1991) applied a non-steady transport model to laboratory column results; but these data were too coarse to interpret rate coefficients using filtration theory. Bales et al. (1991) illustrated use of filtration theory to interpret virus transport and retardation under kinetically limited, non-steady conditions. They found similar results in steady-state experiments (Kinoshita et al., 1993). A non-steady transport model that gave estimates of bacteria retardation under kinetically limited conditions was used in this study because steady-state conditions were not achieved and bacteria removal was slow compared to advection.

The purpose of this work was to compare conditions promoting attachment and to determine the relative time scales for attachment and detachment of two bacteria — one with a hydrophobic and one with a hydrophilic surface — in granular porous media. Porous media with three different surfaces were used: a negatively charged quartz, a positively charged hematite-coated quartz and a hydrophobic surface (polymer-coated quartz).

MODEL

Governing equations for one-dimensional colloid transport in a porous medium with two types of sites for colloid attachment to and detachment from surfaces, one of which is kinetically limited, have been given by various investigators (e.g., Cameron and Klute, 1977; Rao et al., 1979):

$$\theta\frac{\partial C}{\partial t}+\rho_b\left[\frac{\partial S_1}{\partial t}+\frac{\partial S_2}{\partial t}\right]=\theta D\frac{\partial^2 C}{\partial z^2}-u\theta\frac{\partial C}{\partial z} \tag{1}$$

$$S_1=K_{p1}C \tag{2}$$

$$\rho_b\frac{\partial S_2}{\partial t}=\theta k_1 C-\rho_b k_2 S_2 \tag{3}$$

where C is the bacteria concentration in aqueous phase; S_1 and S_2 are the concentrations bound to the surface for fast and kinetically limited sites, respectively; θ is porosity; ρ_b is the dry bulk density of the solid material; D

is the longitudinal dispersion coefficient; u is the average interstitial velocity; k_1 is the pseudo-first-order rate coefficient (s^{-1}) for attachment, which depends on the bacteria's molecular diffusion coefficient and the sticking efficiency (i.e. net energy of interaction between bacteria and porous medium); and k_2 is a pseudo-first-order detachment rate coefficient, which also depends on the energy of bacteria–surface interaction.

It is often useful to express the model parameters in dimensionless terms. The total partition coefficient is related to the retardation factor:

$$R = 1 + \frac{\rho_b(K_{p1} + K_{p2})}{\theta} = 1 + \frac{\rho_b K_{p1}}{\theta} + \frac{k_1}{k_2} \tag{4}$$

The Péclet number:

$$P = \frac{Lu}{D} \tag{5}$$

indicates the time scale for dispersion divided by the residence time in the system. The dimensionless mass-transfer coefficient is a Damköhler number or ratio of physical to chemical time scale (Valocchi, 1985; Bahr and Rubin, 1987):

$$\omega = \frac{L/u}{1/k_1} = \frac{k_1 L}{u} \tag{6}$$

where L is the length of the column. When $\omega > 100$, local equilibrium applies, and as ω drops below ~ 0.1–0.5, adsorption is too slow to observe and the solute appears to be conservative. A fourth parameter, β, related to the ratio of equilibrium to total adsorption, can be defined by:

$$\beta = \frac{\theta + \rho_b K_{p1}}{\theta + \rho_b K_{p1} + \theta k_1/k_2} = 1 - \frac{k_1}{k_2 R} = 1 - \frac{\omega u}{k_2 L R} \tag{7}$$

For the condition with no type-*1* (equilibrium) sites, a three- parameter ($K_{p1} = 0$; $\beta = 1/R$) model (first-order model) can be used. For no type-*2* (kinetically limited) sites ($\beta = 1/R$ and $\omega > 100$), a two-parameter equilibrium model can be used.

Physical and chemical factors influencing the magnitude of k_1 can be described using the single-collector removal efficiency, η, and the sticking efficiency, α (O'Melia, 1980).

$$\eta\alpha = \frac{2}{3}\frac{k_1 d}{u}\frac{1}{1-\theta} \tag{8}$$

If close-approach effects are neglected, single-collector removal efficiency can be estimated by the following (O'Melia, 1985):

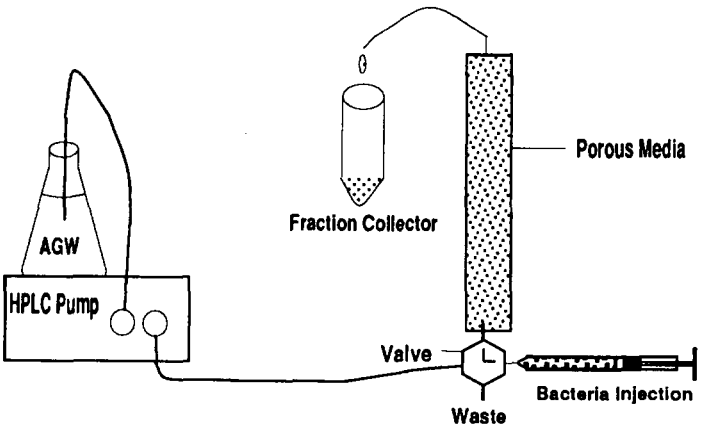

Fig. 1. Illustration of column experiment set up. AGW is artificial groundwater.

$$\eta = \eta_D + \eta_I + \eta_G \tag{9}$$

$$\eta = 0.9A_s^{1/3}\left[\frac{\bar{k}T}{\mu d_p du}\right]^{2/3} + \frac{3}{2}As\left[\frac{d_p}{d}\right]^2 + \frac{(\rho_p - \rho)gd_p^2}{18\mu u}$$

where η_D is for collection by Brownian diffusion, η_I collection by interception and η_G collection by settling; A_s is a parameter that accounts for the effects of adjacent medium grains on the flow about a collector; $\bar{k}$ the Boltzmann constant; T the solute temperature; μ the water viscosity; u the approach velocity; d_p the bacterial diameter; ρ the water density; ρ_p the bacterial density (specific gravity of bacterial biomass); and g the gravitational constant. Equivalent expressions derived for non-spherical particles differ only slightly (Bales, 1984). For a spherical collector, A_s has been given as:

$$A_s = \frac{1 - \epsilon^5}{1 - 1.5\epsilon + 1.5\epsilon^5 - \epsilon^6} \tag{10}$$

where $\epsilon = (1 - \theta)^{1/3}$ (O'Melia, 1985). Using Eq. 9 to estimate removal efficiency, η is substituted into Eq. 8 with the parameter k_1 from experimental data to estimate the sticking coefficient.

MATERIALS AND METHODS

Column experiments

Porous media were wet-packed into 21 × 1 cm glass chromatography columns (Rainin Corp.), with Teflon® fittings and tubing (Fig. 1). For all experiments, a milli-molar ionic strength artificial groundwater (AGW) (1 L

deionized water, 35 mg $MgSO_4 \cdot 7H_2O$, 12 mg $CaSO_4 \cdot 2H_2O$, 12 mg $NaHCO_3$, 6 mg NaCl and 2 mg KNO_3) was filter-sterilized (0.2 μm) following Scholl et al. (1990). The flow rate of AGW in each column experiment was held at a constant 0.1 mL min^{-1} by an high-performance liquid chromatography (HPLC) pump (Isco®). The average pore velocity of each experiment was $\sim 4.0 \pm 0.1$ m day^{-1}. A 0.5-mL pulse of bacteria in the AGW suspension was injected by a syringe pump at ~ 0.1 mL min^{-1}, with bacteria concentrations ranging from $5.0 \cdot 10^8$ to $3.6 \cdot 10^9$ CFU mL^{-1}. It was assumed that a single bacterium grows into a single colony on agar plate and is counted as a colony forming unit (CFU). The start of each experiment ($t = 0$) was designated by the start of the syringe pump. Prior to each experiment, the HPLC pump, tubing and glass column were sterilized with 5% NaClO and rinsed with sterile AGW. Columns were packed with sterile porous medium and 2 PV (pore volumes) of AGW were pumped through prior to bacteria injection. Column effluent was collected in 0.3-mL fractions using sterile microtubes. In all column experiments, AGW effluent had a total organic carbon of 0.28–0.30 mg L^{-1}, a pH of 7.2–7.4 and a temperature of 22–24°C.

The procedures of this study were modeled after Scholl et al. (1990). They demonstrated the reproducibility of the methods; thus we ran single column breakthrough experiments on each medium with each bacterium.

Bromide tracer experiments, which consisted of measuring the time and bromide concentration passing through the column at a known flow rate, were run on the two quartz columns to evaluate the void volume and dispersion in the packed column.

Bacteria

Two bacterium strains isolated from a shallow groundwater aquifer were acquired from A. Mills (University of Virginia, Department of Environmental Sciences). S*5* was a non-motile Gram-negative rod, 1.25 μm × 1.0 μm in size; it had a contact angle of 10°, indicating a hydrophilic surface. S*139*, was a non-motile Gram-negative rod, 2.0 μm × 0.75 μm in size; it had a contact angle of 65°, indicating a hydrophobic surface. Contact angle measurements were made on bacteria cultures 24 h after the bacteria had been washed and suspended in AGW. Although washing may have altered the original bacteria surface, the contact angle measurements do represent the relative hydrophobicity of the bacteria that moved through the columns.

Bacteria were cultured in the same manner for each experiment. Cultures were grown to stationary phase in a 50% concentration peptone and yeast-extract broth (PYE) for 24–36 h at 30°C. Cultures were centrifuged (1 h each) and washed three times with AGW, suspended in AGW at concentrations of

10^8–10^9 cells mL^{-1}, and were allowed to reach a resting state in the AGW suspension by resting 18–24 h at 23°C prior to the transport experiments. Samples of suspended cultures were counted at 12-h intervals for 3 days and found that there was no measurable growth or death for 72 h after resuspension in AGW.

Electrophoretic mobility of the bacteria was measured by the Coulter Delsa® *400* version *1.1*. The mean electrophoretic mobilities of S*5* and S*139* at pH 7.3 were −0.9 and −2.8 $\mu m\ s^{-1}$ cm V^{-1}, respectively. The net negative electrophoretic mobility of the hydrophobic S*139* bacteria was more than double the negative electrophoretic mobility of the hydrophilic S*5*, which is consistent with previously reported correlation that many hydrophobic bacteria have a higher surface potential than hydrophilic bacteria (van Loosdrecht et al., 1987). Electrophoretic-mobility measurements were made 24 h after bacteria had been suspended in AGW, which is approximately the same age as the bacteria cultures used in the column experiments. Bacteria particle-size measurements were provided by A. Mills.

Bacteria counts were done by serial dilution and spiral plating on 50% PYE agar plates. S*5* plates were allowed to incubate 18 h at 30°C, with 30-h incubation for S*139*. A Spiral Systems Instrument® Bacteria Colony Counter (Model *500*A) was used to plate 10-cm plates and count the number of CFU. Three dilutions were plated twice for each sample. Therefore, each data point reported in the breakthrough curves represents an average of up to six separate plate counts.

Porous media

The three types of porous media were: (1) negatively charged quartz at pH 7.3; (2) hematite-coated quartz, giving the surface a net positive charge at pH 7.3; and (3) hematite- and polyethyleneoxide-coated quartz (hydrophobic coating). The polymer coating was chosen to simulate the effects of organic carbon in a natural porous medium. Iota® quartz, standard grade, sieved to uniform sizes with an average diameter of 162 μm, baked at 700°C for 4 h and washed in 1 *M* HNO_3 for 24 h, was used for all experiments. Hematite (Fe_3O_2) -coated quartz was prepared by mixing sieved and washed quartz with 0.5 *M* $FeCl_2$ and 0.1 *M* HCl in a rotating water bath flask at 100°C for 24 h. Both the quartz and hematite-coated quartz were sterilized by baking at 200°C for 1 h prior to mixing with sterile AGW and wet packing the column. The polymer-coated quartz was made with the hematite-coated quartz in a saturated solution of polyethyleneoxide for 24 h. The polymer-coated quartz was soaked in $3 \cdot 10^{-3}$ *M* sodium azide for 24 h and rinsed with sterile AGW 10 times prior to wet packing a column.

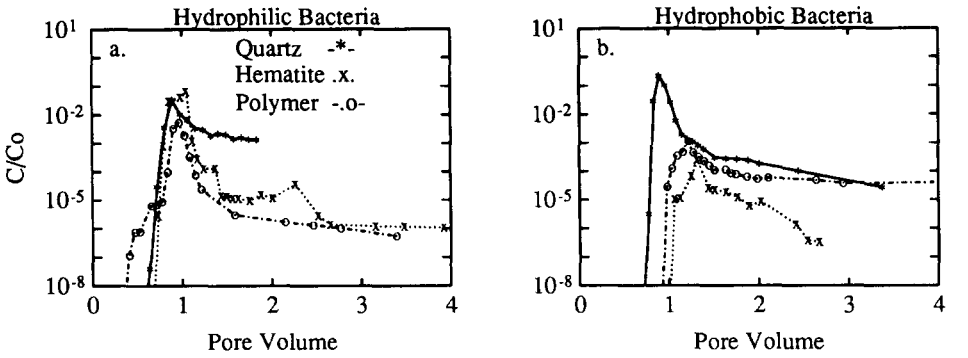

Fig. 2. Breakthrough curves of: (a) experiments *1* (quartz), *2* (hematite) and *3* (polymer), with hydrophilic bacteria S*5*; and (b) experiments *4* (quartz), *5* (hematite) and *6* (polymer), with hydrophobic bacteria S*139*.

RESULTS

Results of the six bacteria transport experiments are shown in Fig. 2; the bromide-tracer breakthrough curve is shown, along with model results, in Fig. 3.

The peak concentration in the conservative-tracer breakthrough curve only reached 40% of the input concentration due to the short duration of the input pulse.

TABLE 1

Experimental conditions and fitted model parameters with 95% confidence intervals

Experiment[a]	Timing of peak (PV)	Maximum C/C_0	%[b] Retained	η	Fitted parameters			
					R	P	β ($\times 10^{-3}$)	ω
S*5 bacteria*:								
1-Q	0.89	0.040	80.8	0.033	18 ± 0.27	500 ± 165	48 ± 0.7	2.35 ± 0.15
2-H	1.05	0.060	77.6	0.034	2,000 ± 32	600 ± 84	0.47 ± 0.05	1.50 ± 0.28
3-P	0.96	0.006	98.4	0.033	2,000 ± 20	500 ± 123	0.47 ± 0.05	4.20 ± 0.07
S*139 bacteria*:								
4-Q	0.89	0.230	46.3	0.035	18 ± 0.1	600 ± 167	50 ± 0.4	0.70 ± 0.13
5-H	1.32	0.0003	99.9	0.036	400 ± 6	500 ± 258	3.3 ± 0.07	7.20 ± 0.19
6-P	1.22	0.001	99.2	0.034	86 ± 1	500 ± 47	13.7 ± 0.2	5.75 ± 0.15

PV = pore volume.

[a] Media indicated by Q (quartz), H (hematite) or P (polymer).

[b] Percent of injected bacteria retained in the column (not recovered) after passing four pore volumes of AGW.

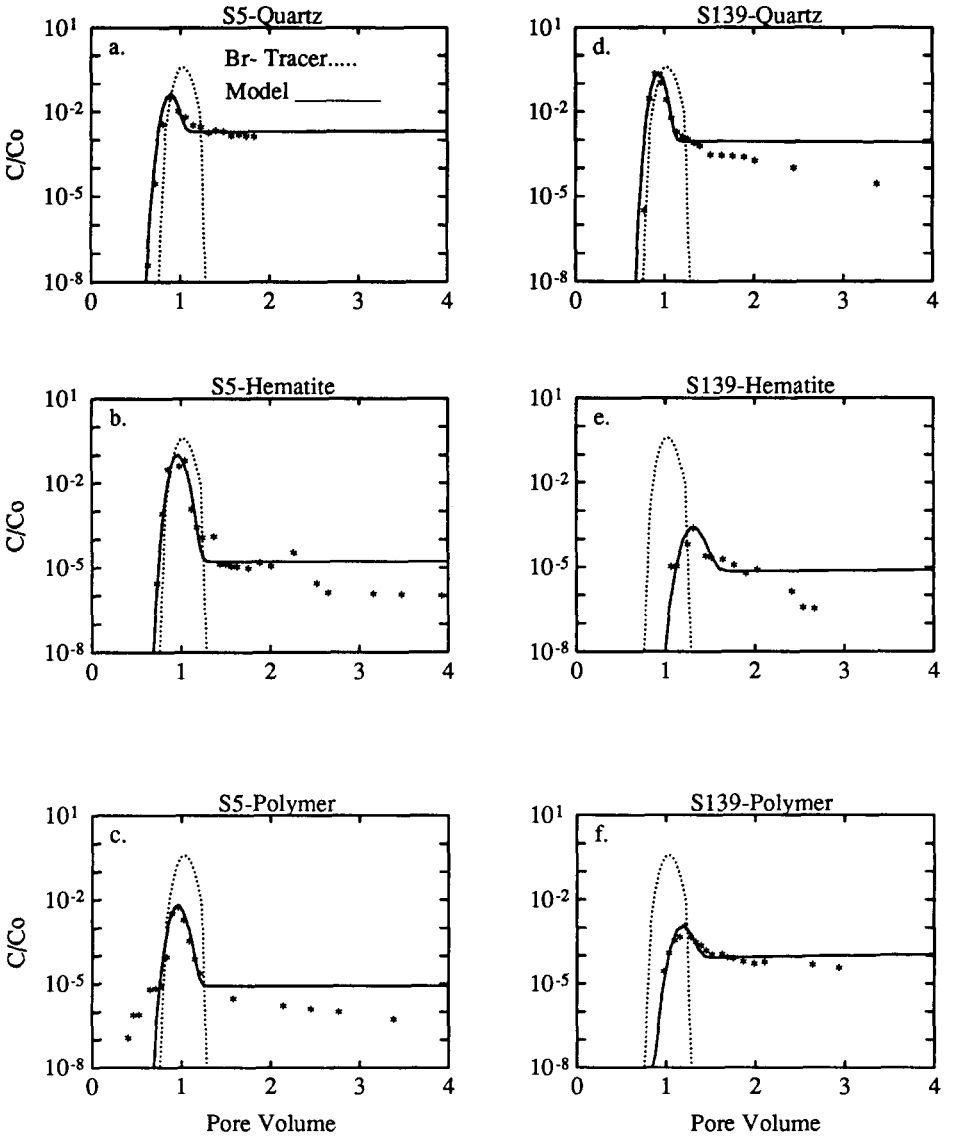

Fig. 3. Observed bacteria breakthrough data with best-fit first-order non-steady transport model and bromide tracer breakthrough.

The breakthrough peaks of the hydrophilic S*5* bacteria in quartz and polymer-coated porous media moved through the columns in < 1 PV and were slightly retarded in the hematite-coated medium (Table 1). The breakthrough peak for the hydrophobic S*139* bacteria in quartz media moved through the column in the same time as the S*5* bacteria. However, the S*139*

TABLE 2

Transport parameters with 95% confidence intervals

Experiment[a]	D (10^{-4} cm^2 s^{-1})	k_1 (10^{-3} s^{-1})	k_2 (10^{-6} s^{-1})	α
S*5 bacteria*:				
1-Q	1.92 ± 0.48	0.50 ± 0.03	25.0 ± 1.38	0.15 ± 0.009
2-H	1.67 ± 0.21	0.33 ± 0.06	0.16 ± 0.03	0.09 ± 0.017
3-P	1.92 ± 0.38	0.90 ± 0.01	0.42 ± 0.003	0.26 ± 0.004
S*139 bacteria*:				
4-Q	1.65 ± 0.36	0.15 ± 0.03	7.90 ± 1.58	0.04 ± 0.008
5-H	2.05 ± 0.70	1.61 ± 0.04	5.40 ± 0.05	0.41 ± 0.011
6-P	1.92 ± 0.17	1.23 ± 0.03	17.0 ± 0.21	0.35 ± 0.009

[a] Media indicated by Q (quartz), H (hematite) or P (polymer).

bacteria breakthrough peaks were retarded in both the hematite-coated and polymer-coated quartz.

In all experiments except the hydrophobic S*139* bacteria with quartz, breakthrough peaks were attenuated by an order of magnitude or more when compared with the bromide tracer. Each breakthrough curve had significant tailing for 3 PV after the peak. We fitted the bromide data with the equilibrium model. Retardation was equal to one by definition, and the best-fit Péclet number was 500.

All of the bacteria breakthrough curves were fit to the two-site model (Fig. 3a–f). The best model fit was determined by visual inspection of plotted model solutions and the observed data. We did not use non-linear least-squares curve fitting as we have done previously (Bales et al., 1991). In our experiments, accurate data span multiple log units and least-squares fitting sums squared errors, which would essentially ignore low C/C_0 points in favor of the higher C/C_0 points. We tried using a non-linear least-squares algorithm with similar data, but it yielded good visual fits only when initial guesses for at least some of the model parameters were set to near-optimum values.

Table 1 shows the experimental conditions and fitted model parameters with 95% confidence intervals. Péclet numbers of 500–600 were needed to fit the slope of the breakthrough curves, slight variations in velocity and porosity between experiments resulted in small differences in dispersion coefficients. Comparing retardation values (18–2000) indicates the differences in the attachment vs. detachment time scales between experiments. Retardation values of both bacteria on quartz were the same (18). Retardation factors for the hydrophilic bacteria (2000, 2000) were much larger than the hydrophobic

bacteria (400, 44) on the hematite and polymer, indicating that the hydrophilic bacteria spent more time attached than moving in solution. Lower relative retardation values suggest that the hydrophobic bacteria moved farther and faster through porous media. The range of ω, 0.7–7.2, implies that nonequilibrium conditions existed in our experiments. In all experiments, except S*139* in quartz, the majority of the injected bacteria remained in the columns after 4 PV of bacteria-free AGW was passed through. Although 99% of the injected bacteria was retained in the column in some experiments, the estimated coverage of the porous medium was much less than 1% (based on the average grain diameter). The sloping tail of the breakthrough curves could not be fitted with this model, resulting in a near-horizontal line. β-Values were very close to $1/R$, so the fit was very close to that of a first-order model. For the first-order model, K_{p1} would be zero. Small changes in β, from $1/R$, were necessary to get the best fits. However, this was only a minor perturbation to the model, as β is only a second-order effect (Hornberger et al., 1992). Almost all of the attachment sites were kinetically controlled, as indicated by the low β-values required for good fits.

Values for k_1, k_2 and α were calculated from the fitted model parameters (Table 2). Attachment coefficients, k_1, ranged from 10^{-4} to 10^{-3} s^{-1}, suggesting that attachment rates of bacteria were within an order of magnitude on different surfaces. Detachment coefficients, k_2, had a much larger range 10^{-7} to 10^{-5} s^{-1}, suggesting that bacteria had different detachment capabilities with different surfaces.

The calculated sticking efficiencies, α (0.04–0.41), are calculated from and thus related to attachment rates and inversely related to C/C_0 peaks; the higher the α, the faster the attachment rate and lower the C/C_0 peak. Values of constants used in the calculations were: $T = 296$ K, $\mu = 0.014$ g cm^{-1} s^{-1}, $\bar{k} = 1.4 \cdot 10^{-16}$ g cm^{-1} s^{-1} K^{-1}, $d = 162.5$ μm, $d_p = 1.25$ μm for S5, $d_p = 2.0$ μm for S*139*, $g = 980$ cm s^{-2}. Bacteria cell densities have been reported to range from 1.01 to 1.13 g cm^{-3} with an average of 1.10 g cm^{-3} (Bouwer and Rittmann, 1992). We used the average cell density in our calculations. The largest dimension of the bacteria was used in calculating η, which assumes that rotational diffusion should be fast relative to advection in our experiments.

DISCUSSION

The model fits were quite sensitive to small changes in ω and R. Fig. 4a and b shows the effects of small changes in ω and R, respectively, on the fits to experiment-*1* data. A higher ω resulted in a lower peak concentration, and a higher R moved the breakthrough curve to the right. These plots illustrate that the fitted model parameters best represent the data.

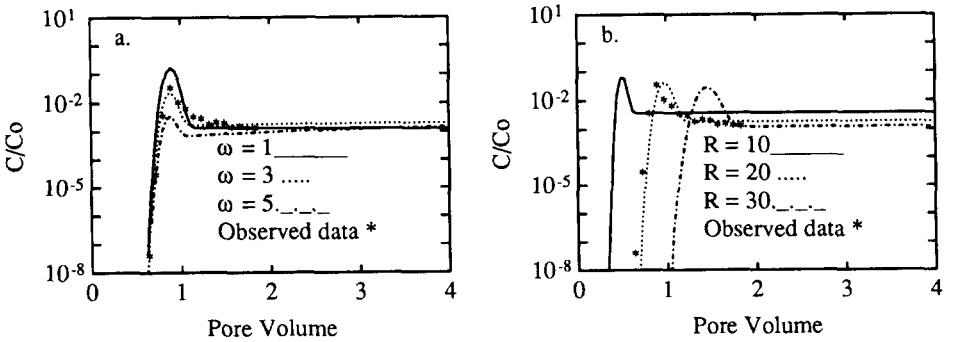

Fig. 4. Variation in model fits with small changes in ω and R indicates that visually fitting the model to the experiment-*1* data was the best method. Note that: (a) ω affects the peak height; and (b) R affects the horizontal position of the peak and the vertical position of the tail of the breakthrough curve.

Experiments *1* and *4* showed that the two bacteria may have experienced a small amount of size exclusion because the breakthrough peak occurred after only 0.89 PV, ahead of the Br^- peak. The large bacteria could have moved preferentially through the larger pores where the velocities were higher than the average pore velocity and reached the end of the column before a conservative bromide tracer; but this effect may be of limited significance as it was not observed in the other experiments.

Electrostatic attraction and repulsion appeared to be important factors controlling the attachment of bacteria to collector surfaces. The S*139* bacteria had a electrophoretic mobility double that of S*5*, giving it a higher repulsive force with the negatively charged quartz and resulting in lower sticking efficiency (α). S*139* exhibited a much higher sticking efficiency with hematite than did the S*5* hydrophilic bacteria, suggesting that increased electrophoretic mobility of the bacteria will increase the sticking efficiency on hematite.

Results suggest that hydrophobic interactions were involved in attachments, but the relationship appeared weaker and less dominant than electrostatic interactions in milli-molar ionic strength water. The hydrophobic bacteria exhibited a much higher affinity for the polymer-coated media than for hydrophilic quartz surfaces. There was a slightly faster attachment rate of the hydrophilic bacteria with the polymer surface over the quartz surface. Sticking efficiencies on the hydrophobic polymer surfaces were slightly higher for the hydrophobic bacteria than for the hydrophilic bacteria.

Attachment rates (k_1) were similar for all combinations of bacteria and surfaces except for the order of magnitude faster attachment of the electronegative/hydrophobic S*139* bacteria to the positive hematite surfaces. Greater variability was observed in the detachment rates (k_2). All were within a factor of 5 except for the interactions of S*5* with hematite- and polymer-coated

surfaces (both an order of magnitude lower than any other k_2). The nature of, and reasons for, this relationship are unclear, but may be related to the nature of the attachment of S5 to iron, since it is possible that the polymer did not entirely mask the hematite. The S5 bacteria seemed to attach to all of the surfaces at approximately the same rate, but once attached, the S5 bacterium stayed attached longest on the hematite. These findings that bacteria strongly adhere to hematite are consistent with other investigators (Scholl et al., 1990).

Kinoshita et al. (1993) reported α's of 0.2–2.3 for bacteria transport in their silica column experiments; Bales et al. (1991), using glass-bead columns and bacteriophage, reported smaller α's, 0.001–0.01. The calculated α's in this study range between 0.04 and 0.4, showing that short-pulse column experiments can be used to estimate sticking coefficients in the same range as continuous feed experiments.

Attachment was shown to be reversible, however the time scales for detachment ($1/k_2$), 0.5–75 days, were much longer than the time scales for attachment ($1/k_1$), 0.2–2 hr. A bacterium that attaches in a few hours may take weeks to completely detach and move with the groundwater. If two bacteria had the same attachment rate, the bacterium with a larger k_2 would move farther and in greater numbers than bacteria with a small k_2. If a bacterium can survive in low nutrient conditions, as do deep subsurface bacteria (Balkwill et al., 1989), advective transport could be significant when considering geologic time scales.

CONCLUSIONS

Short-pulse experiments and non-steady models can be used to estimate time scales for attachment and detachment that are consistent with the sticking efficiencies found with steady-state filtration theory. Short-pulse experiments also can be used with colloid-filtration theory to estimate similar sticking coefficients found with continuous feed column experiments.

At the milli-molar ionic strength of AGW and a pH of 7.3, electrostatic interactions apparently controlled the rate of attachment and thus the transport of bacteria. Detachment rates were also important. Electrostatic and hydrophobic interactions affected the transport of both bacteria, but surface charge of the collector was the most important characteristic in influencing retardation. Slower attachment and detachment rates of hydrophilic bacteria suggest that although hydrophilic bacteria were able to travel further before attaching, the attachment was less reversible. Since all experiments had similar attachment rates, transport retardation was dependent on the rate of detachment.

This study shows that bacterial adsorption was reversible and that detachment would be important in estimating transport for long-term systems.

Given that time scales for detachment are on the order of weeks, bacterial growth may be more important than detachment in near-surface soil systems where doubling times are high. Chemotaxis and motility of bacteria may be the most important transport process in near-surface environments. In deeper, oligotrophic environments, detachment time scales may be large relative to doubling times, suggesting that the rate of detachment may be the most important transport process.

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