Modeling Microorganism Transport and Survival in the Subsurface

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An understanding of microbial transport and survival in the subsurface is needed for public health, environmental applications, and industrial processes. Much research has therefore been directed to quantify mechanisms influencing microbial fate, and the results demonstrate a complex coupling among many physical, chemical, and biological factors. Mathematical models can be used to help understand and predict the complexities of microbial transport and survival in the subsurface under given assumptions and conditions. This review highlights existing model formulations that can be used for this purpose. In particular, we discuss models based on the advection–dispersion equation, with terms for kinetic retention to solid–water and/or air–water interfaces; blocking and ripening; release that is dependent on the resident time, diffusion, and transients in solution chemistry, water velocity, and water saturation; and microbial decay (first-order and Weibull) and growth (logistic and Monod) that is dependent on temperature, nutrient concentration, and/or microbial concentration. We highlight a two-region model to account for microbe migration in the vicinity of a solid phase and use it to simulate the coupled transport and survival of *Escherichia coli* species under a variety of environmentally relevant scenarios. This review identifies challenges and limitations of models to describe and predict microbial transport and survival. In particular, many model parameters have to be optimized to simulate a diversity of observed transport, retention, and survival behavior at the laboratory scale. Improved theory and models are needed to predict the fate of microorganisms in natural subsurface systems that are highly dynamic and heterogeneous.

A N UNDERSTANDING and ability to predict the transport and fate of microorganisms (viruses, bacteria, and protozoa) in the subsurface is needed for a wide variety of applications including bioremediation and bioaugmentation (Mishra et al., 2001; Vidali, 2001), microbially enhanced oil recovery (Banat, 1995), water treatment (Stuyfzand, 1989; Tufenkji et al., 2002; Ray et al., 2002; Schijven et al., 2003; Weiss et al., 2005), and assessing and mitigating the risk of pathogen contamination (Schijven and Hassanizadeh, 2000; Foppen and Schijven, 2006; Tufenkji, 2007). Considerable amounts of research have therefore been directed to this topic (see reviews by Herzig et al., 1970; McDowell-Boyer et al., 1986; McCarthy and Zachara, 1989; Ryan and Elimelech, 1996; Khilar and Fogler, 1998; Schijven and Hassanizadeh, 2000; Ginn et al., 2002; Harvey and Harms, 2002; Jin and Flury, 2002; DeNovio et al., 2004; Rockhold et al., 2004; Unc and Goss, 2004; Foppen and Schijven, 2006; Kanti Sen and Khilar, 2006; Bradford and Torkzaban, 2008; Pang, 2009; Bradford et al., 2013a).

The transport and survival of microorganisms are well known to depend on the processes of advection, dispersion, diffusion, size exclusion, retention and release from the solid–water (SWI) and/or air–water (AWI) interfaces, growth, death, and/or inactivation, as well as initial conditions and sources. Many of these processes are highly coupled to a wide variety of physicochemical, biological, and hydrodynamic factors. For example, microorganism retention and release on the SWI and AWI are highly sensitive to the microorganism size and surface properties; the porous medium size, pore structure, and surface properties; the solution chemistry; the water velocity and saturation; and the input concentration (Ginn et al., 2002; Harvey and Harms, 2002; Foppen and Schijven, 2006; Tufenkji et al., 2006; Bradford et al., 2013a). In addition, a wide variety of abiotic (temperature, metal oxides, salinity, water content, organic sources, nutrients, and electron donors and acceptors) and biotic (microbial community, quorum sensing, and biofilms) factors are known to influence microorganism growth, death, and inactivation (Schijven and Hassanizadeh, 2002; Harvey and Ryan, 2004; Berry and Miller, 2005; Torkzaban et

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Abbreviations: AWI, air–water interface; IS, ionic strength; PV, pore volumes; SWI, soil–water interface.

al., 2006a; Foppen and Schijven, 2006; Cook and Bolster, 2007). Furthermore, microbial population heterogeneity is known to influence both transport and survival (Binnerup et al., 1993; DeFlaun et al., 1997; Bolster et al., 2000; Fuller et al., 2000; Morohashi et al., 2007; Oliver, 2010; Foppen et al., 2010).

A dramatic increase in the number and sophistication of mathematical models for microbial transport and/or survival has occurred in the last several decades to reflect the research community's evolving understanding (e.g., Sim and Chrysikopoulos, 1996; Ginn, 2002; Murphy and Ginn, 2000; Rathfelder et al., 2000; Schijven and Šimůnek, 2002; Lenhart and Saiers, 2003; Saiers and Lenhart, 2003; Bradford et al., 2003, 2011a, 2012; Tufenkji et al., 2003; Scheibe and Wood, 2003; Chrysikopoulos and Vogler, 2004; Gabriel et al., 2005; Tufenkji and Elimelech, 2005b; Grolimund and Borkovec, 2006; Šimůnek et al., 2006; Cortis et al., 2006; Bradford and Toride, 2007; Mostafa and Van Geel, 2007; Šimůnek and van Genuchten, 2008; Wang et al., 2008; Cheng and Saiers, 2009; Chatterjee and Gupta, 2009; Tosco et al., 2009; Wang and Ford, 2009; Yukalov et al., 2009; Molin and Cvetkovic, 2010; Shapiro and Bedrikovetsky, 2010; Tosco and Sethi, 2010; Yuan and Shapiro, 2010, 2011; Russell et al., 2012; Zhang et al., 2012; Hosseini and Tosco, 2013; Landkamer et al., 2013). These models are based on different assumptions to conceptualize water flow and microbial transport, retention, release, and survival within a mathematical framework. There is presently no consensus on the best model formulation, and no single model is expected to accurately simulate all scenarios. Most models do not consider the full physical, chemical, and biological complexities of dynamic natural systems because of uncertainty in process descriptions, difficulty in parameter estimation, incomplete characterization of heterogeneity, and the strong coupling with hydrodynamic and physicochemical factors. In addition, models and research studies have mainly examined transport and survival processes separately due to their individual complexity, even though both processes are known to strongly influence microbial fate. Consequently, mathematical models are not always accurate predictors of reality but are only as good as their input parameters and modeling assumptions.

This review is divided into two main sections: (i) the conventional model; and (ii) alternative models. We outline the standard approach to simulate microbial transport, which shares many similarities with solute transport models, in the conventional model section. The alternative models section highlights existing model formulations to account for many microbial transport and survival processes that are neglected in the conventional model. In addition, we show the ability and challenges of one promising alternative to the conventional model (the two-region model) to simulate microbial transport, retention, release, and survival. In both sections, we identify gaps in knowledge and note model limitations. The information presented in this review is intended to be illustrative and is not exhaustive.

Conventional Model

Microbes are transported in the subsurface environment with water as a result of advection, diffusion, and mechanical dispersion. Models for microorganism transport and fate are commonly based on some form of the advection–dispersion equation, with terms for retention and release from the SWI and AWI (Harvey and Garabedian, 1991; Hornberger et al., 1992; Corapcioglu and Choi, 1996). Water flow is typically described using either Richards' equation (Richards, 1931) for the vadose zone or the Bousinesque equation for groundwater. An expression for microbe transport in the aqueous phase that includes exchange to the SWI and AWI can be given in one-dimensional form as

$$\frac{\partial \theta_w C}{\partial t} = \frac{\partial}{\partial z}\left(\theta_w D \frac{\partial C}{\partial z}\right) - \frac{\partial q_w C}{\partial z} - E_{sw} - E_{aw} + B_w \qquad [1]$$

where z [L] is the distance in the direction of flow, t [T] is time, C [N L^{-3}, where N is number] is the microbe concentration in the aqueous phase, θ_w [L^3 L^{-3}] is the volumetric water content, D [L^2 T^{-1}] is the hydrodynamic dispersion coefficient for microbes, q_w [L T^{-1}] is the Darcy water velocity, B_w [N L^{-3} T^{-1}] is the survival of the microbes in the water phase, and E_{sw} [N L^{-3} T^{-1}] and E_{aw} [N L^{-3} T^{-1}] are the exchange terms from/to the aqueous phase to/from the SWI and AWI, respectively. The first and second terms on the right-hand side of Eq. [1] account for the dispersive and advective fluxes of the microbes, respectively.

First-order kinetic expressions are frequently used to account for microbial retention and release. The solid-phase mass balance equation for microbes is commonly given as

$$\rho_b \frac{\partial S}{\partial t} = E_{sw} + B_s = \theta_w k_{sw} C - \rho_b k_{rs} S + B_s \qquad [2]$$

where S [N M^{-1}] is the solid-phase microbe concentration, ρ_b [M L^{-3}] is the bulk density, k_{sw} [T^{-1}] is the retention rate coefficient to the SWI, k_{rs} [T^{-1}] is the release rate coefficient from the SWI, and B_s [N L^{-3} T^{-1}] is the survival of microbes on the solid phase. The first and second terms on the right-hand side of Eq. [2] account for microbe retention and release, respectively. Each of these model parameters are discussed in detail below.

Filtration theory (Yao et al., 1971) attempts to predict k_{sw} as

$$k_{sw} = \frac{3(1-\theta_w)}{2d_{50}}\alpha\eta v \qquad [3]$$

where v [L T^{-1}] is the average pore water velocity, d_{50} [L] is the median grain diameter, η (dimensionless) is the single collector contact efficiency, and α (dimensionless) is the sticking efficiency. Mass transfer of microbes to the SWI is quantified by η. Correlation equations to predict η as a function of system variables (water velocity, microbe size and density, and collector size) have been developed from pore-scale simulations of colloid transport in simplified grain geometries under water-saturated conditions (e.g., Rajagopalan and Tien, 1976; Tufenkji and Elimelech, 2004; Nelson and Ginn, 2005; Ma et al., 2009).

Favorable attachment conditions occur in the absence of an energy barrier when $\alpha = 1$ (Eq. [3]). Conversely, unfavorable attachment conditions occur in the presence of an energy barrier to attachment. In this case, only a fraction of the microbes that are transported to the SWI will be retained and $\alpha < 1$. Several theoretical approaches have been developed to estimate α from the fraction of the solid surface area that is chemically favorable for deposition (Elimelech et al., 2000; Abudalo et al., 2005) or

the probability of diffusing microbes to be retained in a primary or secondary energy minimum (Spielman and Friedlander, 1974; Simoni et al., 1998; Shen et al., 2007). The kinetic energy model (also known as the Maxwell model) predicts that α rapidly increases with the depth of the secondary minimum (Simoni et al., 1998; Hahn and O'Melia, 2004; Shen et al., 2007), such that larger microbes will have much higher values of α than smaller microbes. Conversely, the energy barrier to the primary minimum increases with microbe size, and therefore the value of α that is associated with the primary minimum also decreases (Shen et al., 2007).

The value of α is well known to be sensitive to the solution chemistry (Tufenkji and Elimelech, 2005a; Shen et al., 2007) and the surface properties of the SWI and microbe (Kim et al., 2009a, 2010a, 2010b; Bolster et al., 2009, 2010; Foppen et al., 2010). Additional research also suggests that α will depend on the system hydrodynamics (Johnson et al., 2007; Torkzaban et al., 2007; Shen et al., 2010) and the input concentration (Bradford et al., 2009a). Innovative approaches are needed to predict the effects of all these factors on α. Due to all of these complexities, the value of α is frequently viewed as an empirical parameter that is obtained by fitting to measured transport data (Tufenkji and Elimelech, 2005a).

Figure 1 presents an illustrative example of the sensitivity of *E. coli* transport to the species type and physicochemical conditions. Breakthrough curves for *E. coli* D21g and *E. coli* O157:H7 are shown in Fig. 1a and 1b, respectively, when the solution ionic strength (IS) ranged from 1 to 100 mmol L^{-1} KCl. The breakthrough curves are presented as aqueous-phase normalized concentrations (C/C_o, where C_o is the influent concentration) as a function of the pore volumes (PV). The *E. coli* D21g and O157:H7 data have previously been reported by Torkzaban et al. (2008) and Kim et al. (2009a), respectively. Pronounced differences in the transport behavior of *E. coli* D21g and O157:H7 occurred with increases in solution IS. In particular, increasing the IS produced an increase in retention for D21g, whereas the opposite trend occurred for O157:H7. This behavior is primarily due to differences in the surface properties of the two *E. coli* strains, as well as physicochemical conditions. Standard interaction energy calculations (Derjaguin and Landau, 1941; Verwey and Overbeek, 1948) predict an increase in the depth of the secondary minimum with an increase in IS that will enhance cell retention. *Escherichia coli* D21g has

minimal amounts of extracellular polysaccharide on its surface (Walker et al., 2004), and it behaves in a manner consistent with this interpretation. Conversely, the amount of and conformation of the surface macromolecules on *E. coli* O157:H7 is much more complex (Kim et al., 2009b), and this produces pH- and IS-dependent electrosteric repulsion that decreases cell retention with increasing IS (Kim et al., 2009a). Other differences in Fig. 1 occurred as a result of the physicochemical conditions. For example, the *E. coli* D21g experiments were conducted in 205-μm ultrapure quartz sand at a Darcy water velocity of 0.66 cm min^{-1} and solution pH of 5.8. Conversely, the *E. coli* O157:H7 experiments were conducted in 275-μm ultrapure quartz sand at a Darcy water velocity of 0.1 cm min^{-1} and a solution pH of 9.2. Consequently, the results in Fig. 1 demonstrate that *E. coli* transport will be sensitive to the strain type and physicochemical properties, and that the surface macromolecules may have a large impact on retention under different solution chemistry conditions.

Under steady-state flow and solution chemistry conditions, k_{rs} has been reported to be a function of the diffusion coefficient, the adhesive interaction, and the boundary layer thickness (Ryan and Gschwend, 1994; Ryan and Elimelech, 1996). The strength of the hydrodynamic forces will also influence microbe release (Bergendahl and Grasso, 1998, 1999; Lenhart and Saiers, 2003; Torkzaban et al., 2007; Tosco et al., 2009). The value of k_{rs} has therefore been commonly viewed as an empirical fitting parameter, and additional research is warranted to predict this parameter.

Microbe retention and release under unsaturated conditions may also occur on the AWI in addition to the SWI. The value of E_{sw} will again be described in a manner similar to Eq. [2]. Under unsaturated conditions, however, the value of k_{sw} is not consistent with the assumptions used to develop filtration theory (Eq. [3]). The mass balance equation for microbes at the AWI may be described similar to Eq. [2] as (Šimůnek et al., 2006)

$$\frac{\partial A_{aw}\Gamma}{\partial t} = E_{aw} + B_a = \theta_w k_{aw} C - A_{aw} k_{ra}\Gamma + B_a \qquad [4]$$

where k_{aw} [T^{-1}] is the microbe retention coefficient on the AWI, k_{ra} [T^{-1}] is the release coefficient from the AWI, A_{aw} [L^2 L^{-3}] is the air–water interfacial area per unit volume, Γ [N L^{-2}] is the microbe concentration retained on the AWI, and B_a [N L^{-3}T^{-1}] is the survival of the microbes on the AWI.
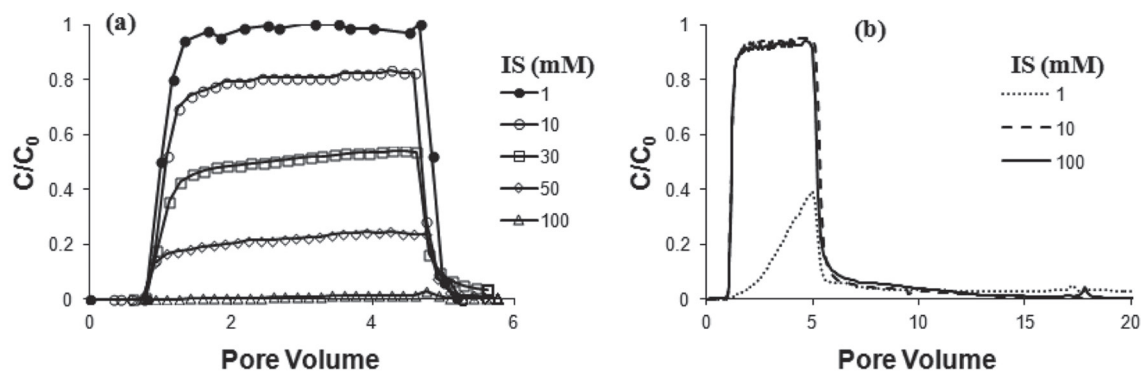

Fig. 1. Observed breakthrough curves for (a) *E. coli* D21g and (b) *E. coli* O157:H7 as a function of solution ionic strength (IS) (range 1–100 mmol kg^{-1} KCl). The *E. coli* D21g and O157:H7 data and experimental details were previously reported by Torkzaban et al. (2008) and Kim et al. (2009a).

No comprehensive theory is presently available to predict k_{aw} and k_{ra}. In general, hydrodynamic forces are expected to be more important for microbe retention on the AWI than the SWI due to differences in the boundary conditions. In particular, the SWI is typically considered to be a no-slip boundary condition (the water velocity is zero at the SWI), whereas the AWI is commonly assumed to be a partial-slip (non-zero water velocity at the AWI) or perfect-slip (the water velocity is unaffected by the AWI) boundary condition (Bird et al., 2002; Zheng et al., 2012). Adhesive interactions on the AWI are controlled by hydrophobic, electrostatic, and capillary forces. It should be noted that the van der Waals interaction with the AWI is repulsive and the AWI is negatively charged at pH values found in most natural environments (Bradford and Torkzaban, 2008).

Microbe retention tends to increase with a decrease in water content under given hydrodynamic and solution chemistry conditions due to: (i) sorption onto the AWI for positively charged or hydrophobic microbes (Wan and Wilson, 1994a, 1994b; Schäfer et al., 1998; Cherrey et al., 2003; Saiers and Lenhart, 2003; Torkzaban et al., 2006a, 2006b; Kim et al., 2008); (ii) physical restrictions imposed by thin water films (film straining) (Wan and Tokunaga, 1997; Veerapaneni et al., 2000); (iii) retention at the air–water–solid contact line (Crist et al., 2004, 2005; Chen and Flury, 2005; Zevi et al., 2005, 2009, 2012; Lazouskaya et al., 2006; Lazouskaya and Jin, 2008); (iv) immobilization in dead-end pores (Gao et al., 2006); (v) enhanced deposition onto the SWI due to a reduction in the diffusive length in partially filled pores (Torkzaban et al., 2006b); and (vi) a greater fraction of water flow in small pore spaces (Gargiulo et al., 2008).

The survival of microorganisms in the subsurface reflects the net rate of death or inactivation (referred to as *decay*) and growth. The relative importance of decay and growth can vary dramatically with the microorganism type. For example, pathogenic viruses and protozoa are obligate parasites that do not replicate outside their hosts, whereas pathogenic bacteria are capable of growth in the environment. The rates of microorganism growth and decay in the water, solid, and air phases are usually modeled using first-order kinetics as (Crane and Moore, 1986; Himathongkham et al., 1999; Pachepsky et al., 2006; Lang and Smith, 2007; Charles et al., 2008)

$$B_w = \theta_w \left(\Lambda_w - X_w \right) C \qquad [5]$$

$$B_s = \rho_b \left(\Lambda_s - X_s \right) S \qquad [6]$$

$$B_a = A_{aw} \left(\Lambda_a - X_a \right) \Gamma \qquad [7]$$

where X [T^{-1}] is a decay coefficient, Λ [T^{-1}] is the microbe growth coefficient, and the subscripts w, s, and a denote the water, solid, and air phases, respectively. The net survival rate $(\Lambda - X)$ may be determined in microcosm or batch experiments or by inverse fitting to available transport data. It is usually not feasible to separately determine rates for X and Λ in the water, solid, and air phases in these experiments. In addition, independent determination of microbial survival is hampered by irreversible microbial retention on the solid phase that produces mass balance errors (Bradford et al., 2006b). Incomplete mass balance information may be incorrectly attributed to decay.

Identical rates for X and Λ are commonly assumed for all phases; however, some research has indicated that rates of decay are higher or lower on the solid than in the water phase (Schijven and Hassanizadeh, 2000; Harvey and Ryan, 2004; Asadishad et al., 2011).

Solute transport models have historically served as the starting point for the conventional microbial transport model. Many model assumptions that are valid for solutes may be violated for microorganisms. For example, Eq. [1] assumes that transport occurs at the average pore water velocity and that all of the pore space is accessible, dispersion is a Fickian process, and water flow is unaffected by the presence of microbes. The above model also assumes that microbe retention, release, growth, and decay are first-order processes, primarily based on mathematical convenience (e.g., linear transport equations can be solved analytically) and ease of analyses (e.g., determination of rate coefficients from log–linear plots). In reality, these processes can be highly nonlinear. Consequently, considerable deviations have been observed between the transport and fate of microbes and conventional model simulations. In an attempt to account for some of these discrepancies, a variety of alternative model formulations have been developed. Several representative modeling classes are highlighted below.

Alternative Models
Advection and Dispersion
Sedimentation

Most microbes are neutrally buoyant. In some cases, however, the density of cultured microorganisms can be greater than water (Wan et al., 1995; Harvey et al., 1996). In this case, the transport velocity of microbes may be influenced by sedimentation. To account for sedimentation, q_w in Eq. [1] has been replaced with $q_w + \theta_w v_s$ (Wan et al., 1995; Murphy and Ginn, 2000), where v_s [L T^{-1}] is the component of the sedimentation velocity in the direction of q_w. The value of v_s may be determined from Stokes' law after correcting for the influence of the soil grains (Wan et al., 1995).

Size and/or Anion Exclusion

The conventional transport model assumes that microbes sample the full distribution of water velocities and are therefore transported at the same average pore-water velocity as solutes. Size and/or anion exclusion may limit microbes to larger portions of the pore space, which produces a higher average transport velocity than for solutes. Size exclusion occurs when microbes are physically excluded from some of the pore space (velocity distribution) by virtue of their size (Ryan and Elimelech, 1996). Anion exclusion may occur as a result of repulsive interactions between negatively charged ions and/or microbes and interfaces (SWI or AWI) that limit their approach to the interface and channel them to pore-throat centerlines (Krupp et al., 1972; Bolt and de Haan, 1979).

Several methods have been reported in the literature to account for the influence of size and/or anion exclusion on microbe transport (Ginn, 2002; Bradford et al., 2003; Scheibe and Wood, 2003). The models of Ginn (2002) and Scheibe and Wood (2003) are based on the truncation of the distribution of local dispersive displacements in a random-walk particle model.

The pore-water velocity and apparent dispersion in Eq. [1] were predicted to increase and decrease, respectively, as a result of exclusion (Scheibe and Wood, 2003). Bradford et al. (2003) related the microbe size to an excluded pore size that was used in existing hydraulic property models to predict the effects of exclusion on θ_w and q_w (Eq. [1]). Earlier breakthrough was predicted for greater amounts of exclusion (e.g., larger microbes and finer soil textures) and for more graded soils.

Chemotaxic Migration

Chemotaxic migration of motile microbes may occur in response to an increasing concentration gradient of a chemo-attractant (e.g., nutrients) or a decreasing concentration gradient of a chemo-repellant (Ford and Harvey, 2007). Chemotaxis requires energy to follow the chemical gradient through a complex network of pores and pore throats. Consequently, chemotaxis has been reported to be closely linked to growth processes and may be an important transport mechanism in low-nutrient environments (Murphy and Ginn, 2000). Chemotaxic migration may be simulated using Eq. [1] after modifying q_w and D (Ford and Harvey, 2007; Wang et al., 2008; Wang and Ford, 2009). In particular, the value of q_w is replaced with $q_w + \theta_w v_c$, where v_c [L T^{-1}] is the component of the chemotaxic velocity in the direction of q_w. The value of v_c may be determined as (Chen et al., 1998)

$$v_c = \frac{1}{3}\left[\chi_o \frac{K_c}{\left(K_c + a\right)^2}\frac{\partial a}{\partial z}\right] \qquad [8]$$

where χ_o [L^2 T^{-1}] is the chemotactic sensitivity coefficient, K_c [M L^{-3}] is the chemotactic binding constant, and a [M L^{-3}] is the chemo-attractant concentration. The diffusion coefficient for motile bacteria has been reported to be up to three orders of magnitude greater than nonmotile bacteria (Camesano and Logan, 1998). However, dispersion may dominate D under typical groundwater velocities (Ford and Harvey, 2007).

Physical Nonequilibrium

The conventional transport model assumes uniform flow and Fickian dispersion. Many laboratory and field experiments have demonstrated more complex flow and transport behavior because of spatial variations in soil texture and structure (e.g., fractured rock; cracks in clayey soils; macropores in agricultural soils from earthworms, animals, and/or decaying roots; or inter- and intraaggregate pore space) (Evans and Owens, 1972; Beven and Germann, 1982; Dean and Foran, 1992; Guber et al., 2005; Cey and Rudolph, 2009; Cey et al., 2009; Garbrecht et al., 2009; Jarvis, 2007; McGechan and Lewis, 2002; Pang et al., 2008; Passmore et al., 2010; Fox et al., 2012; Wang et al., 2013). For example, breakthrough curves for solutes and microbes in soils frequently exhibit early arrival and concentration tailing or multiple peaks (e.g., Wang et al., 2013). Transport models of varying complexity have been developed to simulate nonequilibrium flow and transport processes (Dhawan et al., 1993; McGechan and Vinten, 2003, 2004; Gharasoo et al., 2012; Guzman and Fox, 2011; Martins et al., 2013). Detailed reviews on nonequilibrium flow and transport models are available in the literature (Jarvis, 2007; Šimůnek and van Genuchten, 2008; Köhne et al., 2009) and are only briefly outlined below.

Physical nonequilibrium models include the mobile–immobile water model (e.g., van Genuchten and Wierenga, 1976), the dual-porosity model (Philip, 1968; Šimůnek et al., 2003), and the dual-permeability model (Gerke and van Genuchten, 1993a, 1993b; Šimůnek and van Genuchten, 2008). The mobile–immobile model assumes uniform water flow (the Richards equation) and solves separate transport equations for mobile and immobile water fractions with diffusive exchange between the domains. The dual-porosity model is similar to the mobile–immobile model but allows for exchange between the domains due to both advection and diffusion. The dual-permeability model considers separate water flow and transport equations for fracture (fast) and matrix (slow) domains and allows for exchange by advection and diffusion. The dual-permeability model has been further extended to include immobile water and diffusive exchange within the matrix domain (Pot et al., 2005; Köhne et al., 2006).

Alternatively, non-Fickian models for dispersion have been developed to account for physical nonequilibrium processes. Examples of these types of models include the fractional advection–dispersion equation (e.g., Benson et al., 2000) and the continuous-time random walk approach (Cortis et al., 2006; Shapiro, 2007; Yuan and Shapiro, 2010). The non-Fickian transport behavior of the continuous-time random walk approach can be simply approximated by including a temporal dispersion term (e.g., the second partial derivative of concentration with respect to time multiplied by a temporal dispersion coefficient) in Eq. [1] (Shapiro, 2007; Yuan and Shapiro, 2010).

Microbial Retention

Retention profiles for microbes and other colloids frequently exhibit a shape that is not exponential with depth as predicted by Eq. [2]. Rather, retention profiles have been observed to be hyperexponential (Albinger et al., 1994; DeFlaun et al., 1997; Baygents et al., 1998; Simoni et al., 1998; Bolster et al., 2000; Redman et al., 2001; Zhang et al., 2001; Bradford et al., 2003; Li et al., 2004), nonmonotonic (Tong et al., 2005; Bradford et al., 2006a), or uniform (Xu et al., 2006; Bradford et al., 2009a) with distance. Furthermore, breakthrough curves for microorganisms are sometimes retarded (Bales et al., 1991; Powelson et al., 1993) or exhibit a decreasing (blocking) or increasing (ripening) rate of retention with time (Deshpande and Shonnard, 1999; Bradford et al., 2006a; Tufenkji, 2007; Kim et al., 2010a). Consequently, a variety of alternative models for microbial retention have been developed.

Blocking

Equation [2] assumes that k_{sw} is a constant with time. Under unfavorable attachment conditions, only a small fraction of the SWI may contribute to retention (Bradford et al., 2009a). Consequently, k_{sw} may decrease with time as available retention sites become filled—a process known as *blocking*. In this case, Eq. [2] is rewritten as

$$\rho_b \frac{\partial S}{\partial t} = E_{sw} + B_s = \theta_w \psi_{sw} k_{sw} C - \rho_b k_{rs} S + B_s \qquad [9]$$

where ψ_{sw} is a dimensionless function. A similar modification can be made to Eq. [4] to account for blocking on the AWI. The Langmuirian dynamics (Adamczyk et al., 1994) and random

sequential adsorption (RSA) (Johnson and Elimelech, 1995) models have been developed to account for blocking phenomena. The Langmuir model assumes that ψ_{sw} is a linear function of S that is given as

$$\psi_{sw} = 1 - \frac{S}{S_{max}} \qquad [10]$$

where S_{max} [N M^{-1}] is the maximum retained solid-phase microbe concentration. Conversely, the RSA model assumes that ψ_{sw} is a nonlinear function of S. Breakthrough concentrations will increase with time and retention profiles will change from exponential to uniform in shape as S_{max} fills. If the value of k_{sw} is sufficiently large, retarded breakthrough curves may also occur when using Eq. [9] and [10] (Harmand et al., 1996; Torkzaban et al., 2010a, 2012). This filling process will be highly sensitive to the input pulse duration and concentration, solution chemistry, and flow velocity when values of S_{max} are small (Bradford et al., 2009a).

The value of S_{max} is commonly viewed as an empirical fitting parameter, but it may also be estimated from the fraction of the surface area (S_f) that contributes to retention. The value of S_f can be determined from a balance of applied hydrodynamic and resisting adhesive torques over a porous medium surface (Bradford et al., 2011b; Bradford and Torkzaban, 2012). Results from such calculations indicate that S_{max} will be sensitive to microbe deformation, the microbe size and surface charge, the solution chemistry, the amount of chemical heterogeneity, the flow velocity, the amount and size of the roughness, and the grain size and number of grain–grain contact points (Bradford et al., 2013b). In addition, competitive retention of other colloids (e.g., organic matter and clays) and solutes (e.g., phosphate ions and surfactants) may reduce or increase S_f in particular locations (Liang et al., 2013). The value of αS_f has been used to correct α for the influence of hydrodynamics (Shen et al., 2010; Bradford et al., 2012) or to correct S_f for the effect of diffusion (Bradford et al., 2013b).

Ripening

Microbes may experience an increase in the rate of retention with time as a result of attractive interactions between microbes in the aqueous phase and those retained on the solid phase that produces decreasing effluent concentrations with time following breakthrough (Chiang and Tien, 1985a, 1985b; Tien, 1989; Deshpande and Shonnard, 1999; Tufenkji, 2007). This process is known as *ripening*, and it can theoretically be described using a functional form of ψ_{sw} that increases with the retained microbe mass. For example, Hosseini and Tosco (2013) accounted for ripening using the following empirical expression:

$$\psi_{sw} = 1 + AS^{\beta} \qquad [11]$$

where A [M$^{\beta}$ N$^{-\beta}$] and β (dimensionless) are fitting parameters. Alternatively, ripening may also be modeled by adding a separate term to Eq. [9] as (Bradford et al., 2005b; Bradford and Bettahar, 2006)

$$\rho_b \frac{\partial S}{\partial t} = E_{sw} + B_s$$
$$= \theta_w \psi_{sw} k_{sw} C + \theta_w C \rho_b S k_{int} - \rho_b k_{rs} S + B_s \qquad [12]$$

where k_{int} [L^3 T^{-1} N^{-1}] is the microbe interaction rate coefficient. Enhanced retention as a result of ripening is simulated using the second term on the right-hand side of Eq. [12]. Similar to aggregation models (a review was given by Elimelech et al., 1995), this approach assumes that ripening is second order with respect to concentration and therefore proportional to the frequency of collisions between microbes in the aqueous phase ($\theta_w C$) and immobilized microbes on the collector surface ($\rho_b S$).

Figure 2 presents observed and simulated breakthrough curves for pathogenic *E. coli* O157:H7 in 275-μm ultrapure quartz sand when the Darcy water velocity was 0.1 cm min^{-1}, the IS = 0.01 mmol L^{-1} KCl, and the solution pH = 5.8. Other experimental details were provided by Kim et al. (2010a). In this case, ripening behavior was observed for the *E. coli* O157:H7 transport, and Eq. [1] and [12] were used to simulate the observed behavior. Transport parameters were obtained by inverse optimization to the data. Note that the model provides an excellent description of the observed breakthrough data that exhibits ripening and significant concentration tailing (coefficient of linear correlation >0.96).

Multiple Retention Rates

Different rates and strengths of microbial interaction with the SWI are possible for a variety of reasons. For example, strong primary minimum interactions may rapidly occur as a result of nanoscale physical (e.g., roughness) and/or chemical (e.g., mineral defects, isomorphic substitution, protonation–deprotonation of hydroxyl groups, and adsorption of different ions, organics, and clay particles) heterogeneity on the SWI and/or microbial suspension that locally reduces or eliminates the energy barrier (Duffadar and Davis, 2007, 2008; Bendersky and Davis, 2011) or because a fraction of the microbial population may possess sufficient kinetic energy to diffuse over the energy barrier to the primary minimum (Shen et al., 2007). Conversely, relatively slower and weaker interactions of microbes with the SWI may occur in a secondary minimum depending on the chemical and hydrodynamic conditions (Torkzaban et al., 2007, 2008; Kuznar and Elimelech, 2007). Two modeling approaches that have been developed to describe different rates and types of microbial retention are briefly discussed below.
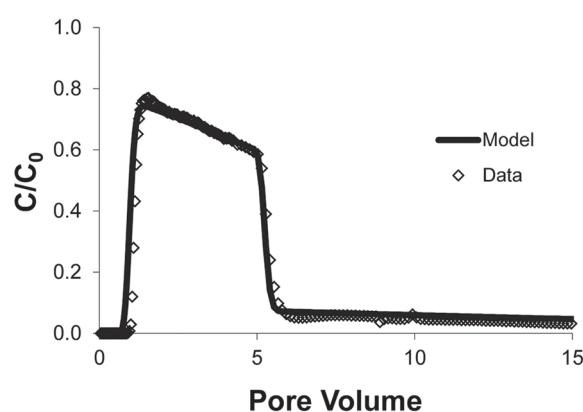

Fig. 2. Observed and simulated breakthrough curves for pathogenic *E. coli* O157:H7 in 275-μm ultrapure quartz sand when the Darcy water velocity was 0.1 cm min^{-1}, the solution ionic strength was 0.01 mmol L^{-1} KCl, and the solution pH was 5.8. Other experimental details were provided by Kim et al. (2010a). The conventional model was modified to simulate the observed ripening behavior using Eq. [12].

Retention models have considered two kinetic sites that are similar to Eq. [9] (Schijven and Hassanizadeh, 2000; Schijven and Šimůnek, 2002; Bradford et al., 2003; Gargiulo et al., 2007a). Both retention sites may be reversible (Schijven and Šimůnek, 2002), or one site may be irreversible and the second site reversible (Bradford et al., 2003). A faster rate is typically assumed for the irreversible site to be consistent with straining or primary minimum interactions, whereas a slower rate is used to represent attachment in a secondary minimum on the reversible site. One- and two-site kinetic models are mathematically equivalent when only a single value of k_{rs} is considered; however, differences in the simulated breakthrough curves and retention profiles occur when separate k_{rs} and/or ψ_{sw} terms are considered on each kinetic site.

Population heterogeneity (size or charge) of a microbial suspension can be simulated explicitly using multispecies transport models. In this case, separate transport equations (Eq. [1]) may be used for discrete or continuous distributions of microbial subpopulations (Baygents et al., 1998; Bolster et al., 1999; Tufenkji et al., 2003; Tufenkji and Elimelech, 2005b; Bradford et al., 2006a; Bradford and Toride, 2007; Chatterjee and Gupta, 2009; Shapiro and Bedrikovetsky, 2010; Landkamer et al., 2013). This approach increases the flexibility of the simulation output (allowing for hyperexponential, nonmonotonic, and uniform retention profiles) but requires knowledge of the population heterogeneity, exchange rates between the subpopulations, and retention coefficients for each subpopulation. Independent determination of all of these parameters is a daunting task. Consequently, most deterministic multispecies models consider only two discrete subpopulations (Bolster et al., 1999; Tufenkji and Elimelech, 2005b; Bradford et al., 2006a; Chatterjee and Gupta, 2009; Landkamer et al., 2013). In contrast, probabilistic modeling approaches use continuous single or joint probability density functions to generate input parameters that are iteratively used in a deterministic model (e.g., Tufenkji et al., 2003; Bradford and Toride, 2007). The model outputs can subsequently be analyzed statistically to determine mean values and confidence intervals.

Physical and Chemical Nonequilibrium Models

A growing body of experimental and theoretical evidence indicates that microbe retention is a combined chemical and physical nonequilibrium process. Many physical nonequilibrium processes can occur in homogeneous porous media. For example, pore-scale simulations of the flow field at grain–grain contacts, at large-scale roughness locations, and near the air–water–solid (AWS) triple point clearly show eddy zones that are hydrodynamically isolated from the bulk fluid flow (Taneda, 1979; Sheng and Zhou, 1992; Torkzaban et al., 2008; Cardenas, 2008; Li et al., 2010a, 2010b). Microbes that are weakly associated with the SWI and/or AWI can be funneled by hydrodynamic forces to locations where they can become immobilized (Torkzaban et al., 2007, 2008; Kuznar and Elimelech, 2007; Lazouskaya and Jin, 2008; Zevi et al., 2012). Enhanced microbe retention has been observed to occur where the hydrodynamic force is weaker (grain–grain contacts, surface roughness, and the AWS triple point) or the adhesive force is stronger (chemical heterogeneity) (Crist et al., 2004, 2005; Bradford et al., 2005a, 2006a; Gao et al., 2006; Li et al., 2006a,

2006b; Yoon et al., 2006; Xu et al., 2006; Choi et al., 2007; Gaillard et al., 2007; Lazouskaya and Jin, 2008; Tong et al., 2008; Zevi et al., 2005, 2009, 2012; Zhang et al., 2010).

Two-region models have been used to simulate different rates of microbial transport that occur in the bulk aqueous phase (Region 1) and in low-velocity regions (Region 2) adjacent to the SWI in homogeneous porous media (Bradford et al., 2009b, 2011a, 2012; Yuan and Shapiro, 2011). Rigorous derivation of the two-region model by volume averaging still has not appeared in the literature. Nevertheless, the two-region transport model is mathematically equivalent to the well-established dual-permeability transport model, and these names have been used interchangeably in the literature. The microbial mass balance equations for Regions 1 (bulk fluid) and 2 (adjacent to the solid phase) are given for saturated conditions (no AWI) as

$$\frac{\partial(\theta_{w1}C_1)}{\partial t} = -\frac{\partial J_1}{\partial z} - \theta_{w1}\alpha_i k_{12}C_1 + \theta_{w2}(1-\alpha_i)k_{21}C_2 + B_{w1} \qquad [13]$$

$$\frac{\partial(\theta_{w2}C_2)}{\partial t} = -\frac{\partial J_2}{\partial z} + \theta_{w1}\alpha_i k_{12}C_1 - \theta_{w2}(1-\alpha_i)k_{21}C_2 - E_{sw} + B_{w2} \qquad [14]$$

where subscripts 1 and 2 denote the respective regions, J [N L^{-2} T^{-1}] is the microbe flux (sum of the advective and dispersive fluxes), k_{12} [T^{-1}] is the mass transfer coefficient for microbes from Regions 1 to 2, k_{21} [T^{-1}] is the mass transfer coefficient for microbes from Regions 2 to 1, and α_i (dimensionless) is an interaction efficiency. The value of E_{sw} is given in the two-region model in a similar manner to Eq. [9] as

$$\rho_b \frac{\partial S}{\partial t} = E_{sw} + B_s = \theta_{w2}\psi_{sw}k_{sw}C_2 - \rho_b k_{rs}S + B_s \qquad [15]$$

where the parameter $k_{sw} = v_2/d_{uf}$ (Bradford et al., 2011a), where v_2 [L T^{-1}] is the pore-water velocity in Region 2 and d_{uf} [L] is the average distance that the microbes travel in Region 2 before they find a retention location.

Bradford et al. (2011a) demonstrated that hyperexponential, exponential, nonmonotonic, and uniform retention profiles occurred when using the two-region model depending on the hydrodynamic, solution chemistry, and input concentration conditions. Various combinations of irreversible (solid phase) and reversible (Region 2) retention are achieved depending on the values of α_i, k_{21}, and k_{sw}. Favorable attachment conditions (irreversible retention) occur when $\alpha_i = 1$ and k_{sw} is high (immobilization is instantaneous). Unfavorable, irreversible retention is achieved in the model when $\alpha_i < 1$ and k_{sw} is high; e.g., results are analogous to conventional filtration theory when $\alpha_i = \alpha$ and $\psi_{sw} = 1$. Unfavorable, completely reversible retention occurs when $\alpha_i < 1$ and $k_{sw} = 0$. In this case, microbes in Region 2 move slowly over the solid surface (reversibly retained on the solid) and the term k_{21} is multiplied by $(1 - \alpha_i)$ to account for the influence of the strength of the adhesive interaction on the release of mobile microbes in Region 2. The two-region model is therefore ideally suited to handle a blurred distinction between favorable and unfavorable conditions, which frequently occurs

in natural porous media. In addition, earlier breakthrough behavior (similar to size exclusion) sometimes occurred for larger microbes.

Figure 3 presents observed and simulated breakthrough curves (Fig. 3a) and final retention profiles (Fig. 3b) for pathogenic *E. coli* O157:H7 in various quartz sands (d_{50} = 710, 360, 240, and 150 µm) when the Darcy water velocity was approximately 0.1 cm min^{-1}. Figure 4 presents similar information in 150-µm quartz sand when the Darcy water velocity was 0.017, 0.102, and 0.177 cm min^{-1}. The experimental data were previously described in detail by Bradford et al. (2006a). In brief, the solution IS was 1 mmol L^{-1} NaBr, the solution pH was buffered to 6.7, and the porosity was about 0.35. The simulation results were obtained using the two-region model (Eq. [13–15]), and the retention profiles were plotted in terms of the total normalized concentration $[C_T = (\theta_{w1}C_1 + \theta_{w2}C_2 + \rho_b S)/C_o]$ as a function of dimensionless distance (z divided by the column length). The parameter k_{12} was determined using filtration theory (Eq. [3] with α = 1 and η determined with the correlation equation of Tufenkji and Elimelech [2004]). In contrast to the traditional dual-permeability model, only one flow equation needs to be solved to determine the total water content and flow rate in homogeneous porous media. The hydrodynamic parameters (water contents and velocities for both regions) were obtained from this information and scaling relations developed from pore-scale water flow simulations in sphere packs (Bradford et al., 2011b). The parameters that depend on adhesive interactions were obtained by inverse optimization to the transport data for the 150-µm sand when the Darcy water velocity was 0.1 cm min^{-1}

as α_i = 0.05, S_f = 0.007, k_{21} = 0, and k_{sw} = 0.01 min^{-1} and assumed to be constants for the other sand sizes and Darcy velocities. Consequently, the simulated transport behaviors in Fig. 3 when d_{50} = 710, 360, and 240 µm are independent predictions. Similarly, predictions are shown in Fig. 4 for Darcy velocities of 0.017 and 0.177 cm min^{-1}.

The two-region model correctly predicted the trend of decreasing cell retention with increasing grain size (Fig. 3) and increasing water velocity (Fig. 4). Some deviation in the observed and simulated retention profiles occurred because of experimental mass balance errors that occurred due to irreversible cell retention. However, the model was able to describe the general trends of the nonmonotonic retention profiles for different grain sizes and velocities, which cannot be simulated using the conventional approach (Eq. [1] and [2]). Collectively, Fig. 3 and 4 demonstrate that the two-region model is a promising approach to account for observed differences in microbe transport and retention for different grain sizes and velocities. Additional theory and innovative approaches are needed to predict the parameters of the two-region model. In particular, prediction of the adhesive parameters (α_i, S_f, k_{21}, and k_{sw}) for different chemical conditions and the hydrodynamic parameters for different soil types (grain size distributions, nonspherical shape, and roughness) and water contents remains a challenge.

Microbial Release

Residence Time

The strength of colloid and microbial adhesion to the SWI has been reported to increase with contact time (Kolakowski
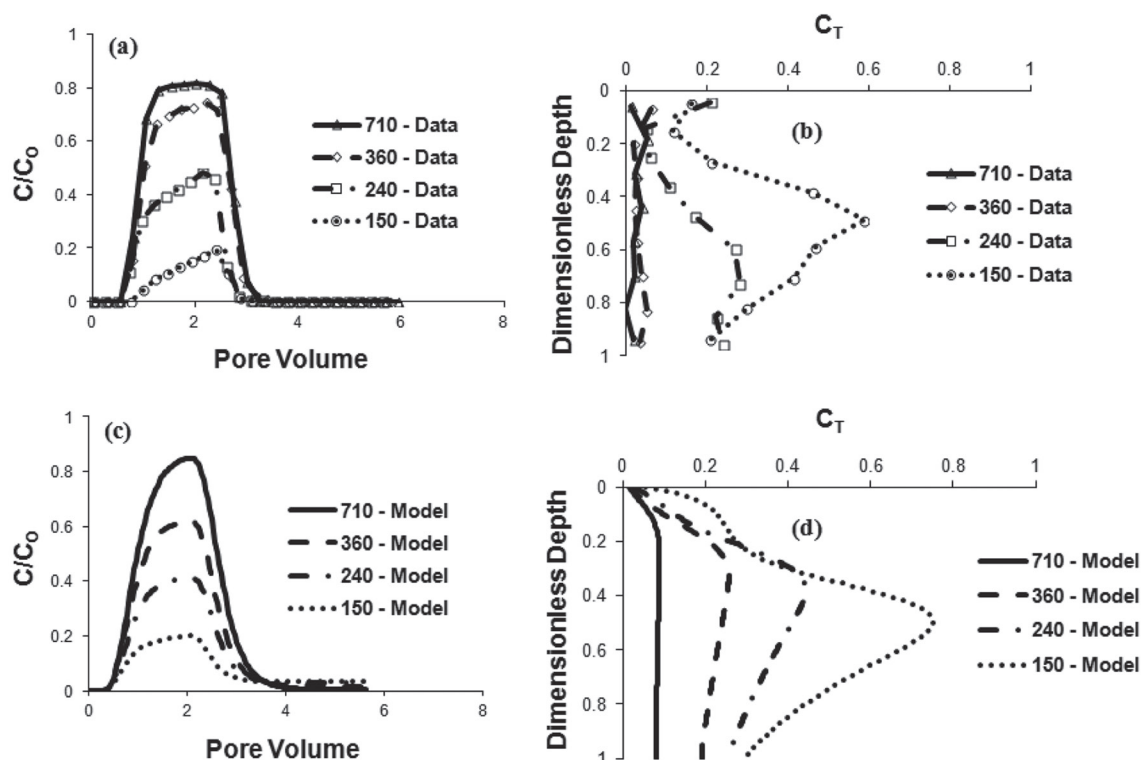

Fig. 3. Observed (top) and simulated (bottom) breakthrough curves (left) and final retention profiles (right) for pathogenic *E. coli* O157:H7 in various quartz sands (median grain size d_{50} = 710, 360, 240, and 150 µm). The experimental data were previously described in detail by Bradford et al. (2006a). The simulated results were obtained using the two-region model (Eq. [13–15]) with values of interaction efficiency α_i = 0.05, the fraction of the surface area that contributes to retention S_f = 0.007, mass transfer coefficient for microbes from Region 2 to 1 k_{21} = 0, and the retention rate coefficient to the solid–water interface k_{sw} = 0.01 min^{-1} fitted to 150-µm data and other parameters predicted.
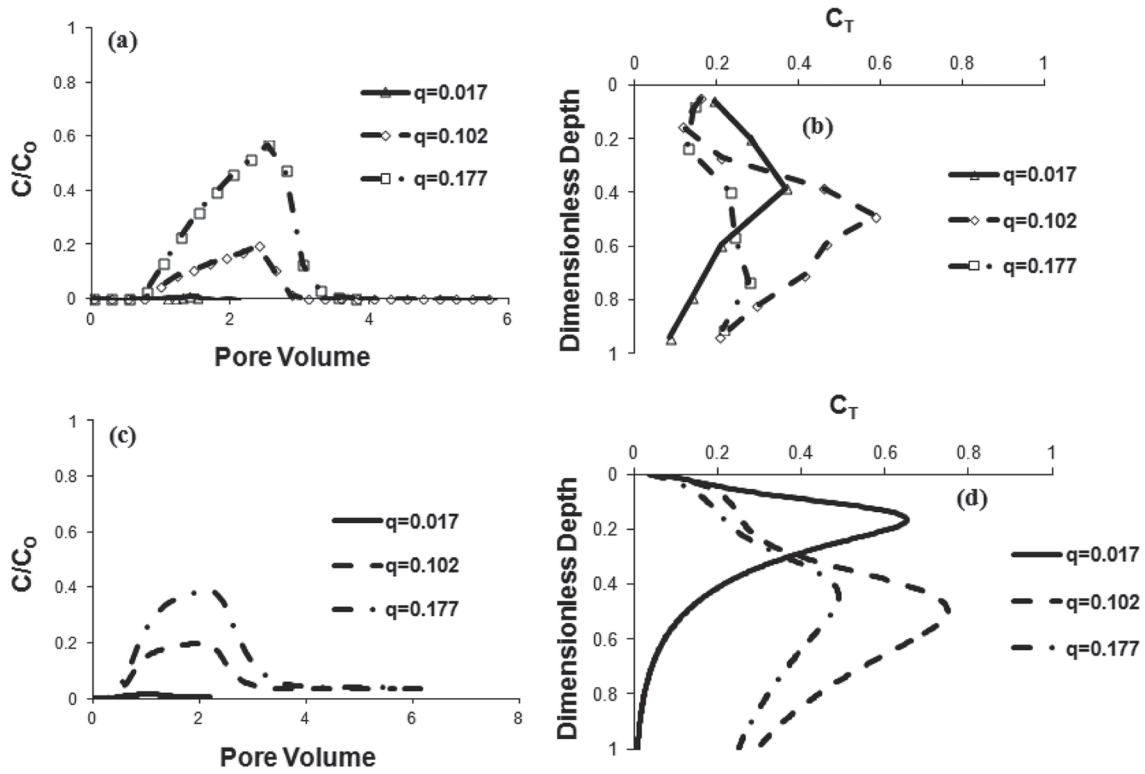
Fig. 4. Observed (top) and simulated (bottom) breakthrough curves (left) and final retention profiles (right) for pathogenic *E. coli* O157:H7 in 150-μm quartz sand under various Darcy water velocities (q = 0.017, 0.102, and 0.177 cm min⁻¹). The simulated results were obtained using the two-region model (Eq. [13–15]) with values of interaction efficiency α_i = 0.05, the fraction of the surface area that contributes to retention S_f = 0.007, mass transfer coefficient for microbes from Region 2 to 1 k_{21} = 0, and the retention rate coefficient to the solid–water interface k_{sw} = 0.01 min⁻¹ fitted to q = 0.102 cm min⁻¹ data and other parameters predicted. No additional parameter optimization was undertaken.

and Matijevic, 1979; Dabroś and Van De Ven, 1982; Weiss et al., 1998; Xu and Logan, 2006; Kumar et al., 2013). This has been attributed to plastic deformation that increases the contact area (Weiss et al., 1998; Kumar et al., 2013), water exclusion, protein rearrangement and conformation, and bond formation (Ginn et al., 2002; Xu and Logan, 2006), and cell-surface changes such as the production of extracellular polymeric substances (Williams and Fletcher, 1996; Jucker et al., 1997). Consequently, the release rate of microbes from the SWI may decrease with residence time (Johnson et al., 1995; Ginn, 2000a), and this effect probably contributes to the observed hysteresis in colloid and microbe release with transients in solution IS (Torkzaban et al., 2010b; Bradford and Kim, 2012; Bradford et al., 2012).

Ginn (2000ab) presented a modeling framework to simulate microbial release that is dependent on the residence time. This transport model is written for saturated conditions as

$$\frac{\partial \theta_w C}{\partial t} + \frac{\partial \theta_w v_{w\omega} C}{\partial \omega} = \frac{\partial}{\partial z}\left(\theta_w D \frac{\partial C}{\partial z}\right) - \frac{\partial q_w C}{\partial z} \\ - \theta_w \psi_{sw} k_{sw} C + \rho_b k_{rs}(\omega) S + B_w \quad [16]$$

$$\rho_b \frac{\partial S}{\partial t} + \rho_b \frac{\partial v_{s\omega} S}{\partial \omega} = \theta_w \psi_{sw} k_{sw} C - \rho_b k_{rs}(\omega) S + B_s \quad [17]$$

where ω [T] is the residence time, $v_{w\omega}$ (dimensionless) is the rate of displacement of aqueous-phase microbes in the resident time dimension, and $v_{s\omega}$ (dimensionless) is the rate of displacement of solid-phase microbes in the resident time dimension. Little

information is currently available on the proper functional form for $k_{rs}(\omega)$. Dabroś and Van De Ven (1982), Meinders et al. (1992), and Johnson et al. (1995) proposed that $k_{rs}(\omega)$ is a constant when $\omega < \omega^*$ and drops to a lower value when $\omega \geq \omega^*$, where ω^* [T] is a critical value of ω. This is implemented in the residence time model as follows. When the cumulative residence time on a surface controls the microbe release rate, there is a 1:1 correspondence between ω and the total time the microbe has spent on the SWI. In this case, the value of $v_{w\omega}$ = 0 and $v_{s\omega}$ = 1 (Ginn, 2000b). Conversely, a contiguous residence time description is needed when microbes do not retain any structural memory of changes induced on the SWI, in which case $v_{s\omega}$ = 1 and Eq. [16] is replaced with a form that has no ω coordinate and that assigns detaching microbial fraction at ω = 0 (Ginn, 2000b):

$$\frac{\partial \theta_w C}{\partial t} + \frac{\partial \theta_w v_{w\omega} C}{\partial \omega} = \\ \frac{\partial}{\partial z}\left(\theta_w D \frac{\partial C}{\partial z}\right) - \frac{\partial q_w C}{\partial z} - \theta_w \psi_{sw} k_{sw} C \\ + \delta(\omega) \int_0^\infty \rho_b k_{rs}(\omega) S(\omega) d\omega + B_w \quad [18]$$

Aqueous Chemistry

Microorganism release is known to be sensitive to temporal changes in solution chemistry (Lenhart and Saiers, 2003; Grolimund and Borkovec, 2006; Tosco et al., 2009; Bradford et al., 2012) and flow rate (Bergendahl and Grasso, 1998, 1999, 2000). The conventional release term in Eq. [9] is unable

to account for such observations because only a fraction of the deposited particles are released with a change in solution chemistry. Several models for microbe transport, retention, and release during transient solution chemistry conditions have been presented in the literature (Lenhart and Saiers, 2003; Grolimund and Borkovec, 2006; Tosco et al., 2009; Bradford et al., 2012). In general, microbe transport equations are coupled to the geochemistry by making relevant microbe retention parameters (e.g., α and S_{max}) functions of solute concentrations (e.g., ionic strength and/or adsorbed divalent cations). The transport equations for geochemistry and microbes are subsequently solved and microbe transport parameters are updated at each time step.

Bradford et al. (2012) outlined such an approach for transient IS conditions. In this case, the solid-phase mass balance equation is given as

$$\rho_b \frac{\partial S}{\partial t} = E_{sw} + B_s$$
$$= \theta_w \psi_{sw} k_{sw} C \qquad [19]$$
$$- \rho_b k_{rs} (S - f_c S_i) H_o (S - f_c S_i) + B_s$$

where S_i [N M^{-1}] is the value of S before a change in chemical composition, f_c (dimensionless) is the fraction of retained microbes that are not released with a change in chemical composition, and $H_o(S - f_c S_i)$ is the Heaviside function that is equal to 1 when $S > f_c S_i$ and 0 when $S \leq f_c S_i$. The value of f_c is given as

$$f_c = \frac{S_f}{S_{if}} = \frac{S_{max}}{S_{imax}} = \frac{S_{eq}}{S_i} \qquad [20]$$

where S_{if} (dimensionless) is the value of S_f before the change in chemistry, S_{imax} [N M^{-1}] is the value of S_{max} before the change in chemistry, and S_{eq} [N M^{-1}] is the equilibrium value of S at the end of the chemical perturbation. When these equations are written in terms of S_f, the amount of microbes that is released is directly related to changes in the balance of the applied hydrodynamic and resisting adhesive torques. Consequently, this approach applies to both transient solution chemistry and hydrodynamic conditions. As mentioned above, a wide variety of factors are known to influence S_f.

Figure 5 presents the observed and simulated breakthrough and release curves for *E. coli* D21g under transient IS conditions. The experimental data and simulation were previously presented by Bradford et al. (2012). In brief, the transport experiment was conducted in 360-μm Ottawa sand at a Darcy water velocity of around 0.1 cm min^{-1}. A pulse of *E. coli* D21g was flushed through the column in 106 mmol L^{-1} NaCl solution at pH = 10, and then the IS of the cell-free eluting solution was decreased in steps of 106, 56, 31, 6, and 0 mmol L^{-1} NaCl. The simulation result was obtained using the two-region model (Eq. [13], [14], and [15]), with release modeled using the second term on the right-hand side of Eq. [19]. The determination of the two-region model parameters was already outlined above. The parameters α_i and S_f were functions of the simulated IS (1:1 electrolyte) that were determined from experimental results, and other model parameters were either predicted or obtained from a sensitivity analysis (Bradford et al., 2012). Results demonstrated that cell release was especially sensitive to
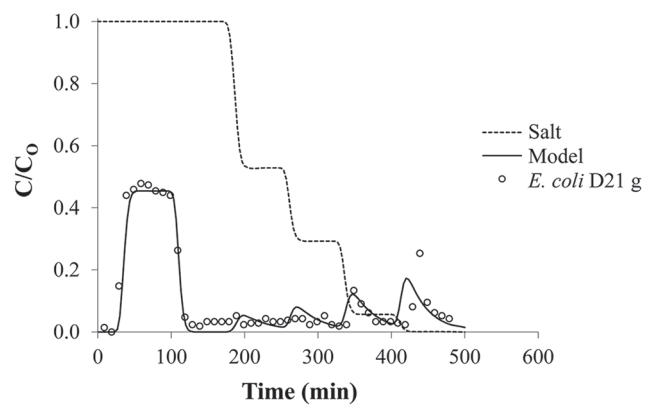

Fig. 5. Observed and simulated breakthrough and release curves for *E. coli* D21g under transient ionic strength (IS) conditions. The experimental data and simulation were previously presented by Bradford et al. (2012). A pulse of *E. coli* D21g was flushed through the column in 106 mmol L^{-1} NaCl solution at pH = 10, and then the IS of the cell-free eluting solution was decreased in steps of 106, 56, 31, 6, and 0 mmol L^{-1} NaCl. The simulation result was obtained using the two-region model with release modeled using the second term on the right-hand side of Eq. [19].

low solution IS. There is currently a need to develop predictive procedures to determine the effects of solution chemistry, aging time, and nanoscale heterogeneity on α_i and S_f. This is especially true for microorganisms that exhibit electrosteric repulsion (Fig. 1b).

Water Saturation

Transients in water content commonly occur in the vadose zone as a result of infiltration and drainage events, evapotranspiration, and fluctuations in the water table height and/or surface water levels (waves, tides, and river stage). Several mathematical models have been developed to simulate the substantial amounts of colloid and microbe release that have been observed with changes in water saturation (Saiers and Lenhart, 2003; Cheng and Saiers, 2009; Zhang et al., 2012; Russell et al., 2012). Saiers and Lenhart (2003) simulated colloid release using a kinetic expression that included a dependence on the pore-water velocity. Zhang et al. (2012) simulated virus interactions at the AWI using a linear equilibrium partition coefficient and retardation factor. Cheng and Saiers (2009) and Russell et al. (2012) used a kinetic expression that was a function of temporal changes in water content ($\partial \theta_w / \partial t$) to represent the propagation of the AWI at a particular location. Release was turned on by a distribution of snap-on/snap-off pressure heads in the model of Cheng and Saiers (2009), whereas positive values of $\partial \theta_w / \partial t$ (imbibition) turned on release in the model of Russell et al. (2012). Equation [9] may be rewritten to include the release model of Russell et al. (2012) as

$$\rho_b \frac{\partial S}{\partial t} = E_{sw} + B_s$$
$$= \theta_w \psi_{sw} k_{sw} C - \rho_b k_{rs} S \qquad [21]$$
$$- \rho_b k_{rt} S \frac{\partial \theta_w}{\partial t} H_o \left(\frac{\partial \theta_w}{\partial t} \right) + B_s$$

where k_{rt} (dimensionless) is the release rate coefficient associated with transients in water content and $H_o(\partial \theta_w / \partial t)$ is the Heaviside function that is equal to 1 when $\partial \theta_w / \partial t > 0$ (imbibition) and

0 when $\partial\theta_w/\partial t \leq 0$ (drainage). Additional experimental and modeling research is needed to directly relate microbial release during transient saturation conditions with changes in the AWI area and the adhesive force.

Microbial Survival

Survival is an extremely complex process that depends on a wide variety of abiotic and biotic factors that may not always be independent, including: nutrient levels, degree of water saturation, temperature, pH, dissolved and particulate organic C, ionic strength/salinity, redox conditions, presence or absence of biofilms, environmental microbial diversity and ecology, physicochemical characteristics of the solid phase, and nature of the rhizosphere (Schijven and Hassanizadeh, 2002; Harvey and Ryan, 2004; Berry and Miller, 2005; Foppen and Schijven, 2006; Cook and Bolster, 2007; Bradford et al., 2013a). Consequently, mechanistic modeling of microorganism survival using simple first-order expressions (Eq. [5–7]) is frequently inadequate to describe the observed behavior (Petterson et al., 2001; John and Rose, 2005; Charles et al., 2008; de Roda Husman et al., 2009). Potential models to quantify the effects of temperature, population heterogeneity, nutrients, and competition on the survival parameters X_w and Λ_w (Eq. [5]) are discussed below. Similar expressions may be developed for the solid and air phases.

Decay

Temperature is widely recognized to be one of the most critical factors in determining microorganism decay, and its effect may be described using the Arrhenius equation (Stumm et al., 1981):

$$X_w(T_k) = X_r \exp\left[\frac{E_a(T_k - T_r)}{RT_kT_r}\right] \qquad [22]$$

where T_k is temperature (K), R (8.3144621 J mol^{-1} K^{-1}) is the universal gas constant, E_a (J mol^{-1}) is the activation energy, and X_r [T^{-1}] is the reference decay rate at a reference temperature (T_r, K). Equation [22] requires knowledge of the temperature at a given location and time. Heat movement can be modeled using numerical or analytical solutions of an advection–dispersion-type equation (e.g., Šimůnek et al., 2008).

A number of studies have indicated the presence of microbial subpopulations that are more or less persistent under environmental conditions (Besnard et al., 2002; Kussell et al., 2005; Proctor et al., 2006; Cook and Bolster, 2007; Morohashi et al., 2007; Oliver, 2010; Rotem et al., 2010). Intrapopulation variability is evident in the ability of some bacteria to form robust spores (Morohashi et al., 2007) or to enter a pseudo-dormant viable but nonculturable state (Kussell et al., 2005; Proctor et al., 2006; Oliver, 2010). The effects of population heterogeneity on decay have been modeled using time-dependent, pseudo-first-order rate coefficients (Sim and Chrysikopoulos, 1996; Peleg and Cole, 1998; Chrysikopoulos and Vogler, 2004; Molin and Cvetkovic, 2010). For example, the Weibull model (e.g., Peleg and Cole, 1998) describes the time dependency of the decay coefficient as

$$X_w(t) = \mu n t^{n-1} \qquad [23]$$

where μ [T^{-n}] and n (dimensionless) are empirical parameters. Additional inactivation models are discussed in the literature (Oliver et al., 2006, 2010).

Growth

Expressions from Monod (1942), Tessier (1942), Contois (1959), or Andrews (1968) are commonly used to simulate microbial growth These models relate specific growth rates with substrate concentrations using saturation kinetics. For example, the Monod model relates the microbial population growth rate to the concentration of a limiting nutrient (N_g [M L^{-3}]) as (Monod, 1942)

$$\Lambda_w = \frac{\Lambda_{max}N_g}{K_N + N_g} \qquad [24]$$

where Λ_{max} [T^{-1}] is the maximum specific growth rate when $N_g \gg K_N$, and K_N [M L^{-3}] is the value of N_g when $\Lambda_w/\Lambda_{max} = 0.5$. Monod expressions may be further modified to account for the utilization of electron donors, electron acceptors, multiple substrates, yield coefficients, and inhibition functions (Bailey and Ollis, 1977; Rathfelder et al., 2000; Mohamed et al., 2007).

Microbial survival in microcosm experiments has frequently been simulated using the logistic model (Semenov et al., 2009) and its variants (Verhulst, 1838; Gabriel et al., 2005; Yukalov et al., 2009). The logistic model considers the effects of both growth and competition on microbial survival:

$$\Lambda_w(C) = \Lambda_o\left(1 - \frac{C}{C_{max}}\right) \qquad [25]$$

where Λ_o [T^{-1}] is the growth rate in the absence of competition and C_{max} [N L^{-3}] is the maximum microbe concentration that is associated with the upper limit of population growth. The logistic model predicts that microbe concentrations will increase when $C < C_{max}$ reaches a plateau at $C = C_{max}$ and will decrease when $C > C_{max}$. Theoretically, the value of C_{max} is expected to change with the biogeochemical conditions, and the logistic model has been extended for this purpose (Yukalov et al., 2009). The logistic model has been reported to provide a superior description of pathogen survival in manure-amended soils than linear, exponential, or Weibull survival models (Semenov et al., 2009).

Coupled Transport and Survival

Most models and research studies have separately examined transport and survival processes due to their individual complexity. In reality, transport and survival processes for microbes may be highly coupled. This is especially true for bacteria that can undergo growth and/or decay. For example, dynamic nutrient fronts can promote the division of retained "mother" cells and induce the transport of "daughter" cells, a process referred to as *cell-division-mediated transport* (Reynolds et al., 1989; Sharma et al., 1993; Murphy and Ginn, 2000). Changes in the metabolic activity of cells with age and nutrient availability may also produce differences in cell surface properties that promote release or enhance retention (Sanin et al., 2003; Gargiulo et al., 2007b). Models can be useful tools to better understand the complex coupling between microbial

transport and survival processes, which otherwise might be experimentally intractable. For example, Murphy and Ginn (2000) simulated the transport and dynamic partitioning of a consortium of anaerobic bacteria in response to a pulse of growth substrate. Gargiulo et al. (2007b) simulated the transport and deposition of metabolically active and stationary-phase *Deinococcus radiodurans* in unsaturated sand. Below we present several illustrative examples of simulated microbial transport and survival at the column scale.

Figure 6 presents simulated breakthrough curves (Fig. 6a) and retention profiles (Fig. 6b, 6c, and 6d) for *E. coli* O157:H7 in 150-μm sand when considering Weibull decay (Eq. [23]). Figure 6a also shows the sinusoidal temperature fluctuations at the soil surface that were used to simulate the soil temperature distribution with an analytic solution (Jury et al., 1991). The two-region model (Eq. [13–15]) was used in these simulations, using transport and retention parameters that were given in Fig. 3. Three conditions were considered: (i) no death; (ii) Weibull decay (Eq. [23]); and (iii) Weibull decay (Eq. [23]) that used Eq. [22] to account for a temperature dependency on μ. The same Weibull model parameters ($\mu = 1.67 \times 10^{-8}$ min^{-n} and $n = 2.02419$) were used for Regions 1 and 2 of the aqueous phase and the solid phase. The retention profiles in Fig. 6b, 6c, and 6d are shown after 1.0, 3.9, and 5.8 PV of eluting solution. The effects of decay on breakthrough curves were rather minimal for these small scale and short duration simulations. In contrast, consideration of decay had a large impact on the amount and shape of the retention profile, especially at larger PV, and temperature fluctuations further accentuated these

effects. These hypothetical results demonstrate that decay will have a controlling influence on transport behavior at larger temporal scales and that neglecting these effects will lead to inaccurate model output and conclusions. However, the relative importance of decay to transport and retention will depend on the magnitudes of the model parameters. Consequently, model simulations that consider transport, retention, and decay are useful tools to understand these factors and to make informed decisions.

Figure 7 presents simulated breakthrough curves (Fig. 7a) and retention profiles (Fig. 7c and 7d) for *E. coli* O157:H7 in 150-μm sand when considering logistic growth and/or death (Eq. [25]). The two-region model (Eq. [13–15]) was again used in these simulations, using transport and retention parameters that were given for Fig. 3. The logistic growth and/or death model (Eq. [25]) was used in terms of C_T; e.g., Eq. [25] was rewritten as $\Lambda_T(C_T) = \Lambda_o(1 - C_T/C_{Tmax})$, where the subscript T is used to denote variables associated with C_T. Three values of C_{Tmax} were considered, namely: (i) $C_{Tmax} = 1$; (ii) $C_{Tmax} = 0.1$; and (iii) C_{Tmax} that was determined by the transport of a hypothetical nutrient and/or substrate shown in Fig. 7b. The value of Λ_o was set equal to 0.012 min^{-1} in all cases. The retention profiles in Fig. 7c and 7d are shown after 1.0, 3.9, and 5.8 PV of eluting solution. The simulation results demonstrate a strong coupling between transport and retention behavior and the value of C_{Tmax}. Very complex breakthrough curves and tailing behavior were obtained when considering the logistic model. In particular, periods of growth ($C_T < C_{Tmax}$) and death ($C_T > C_{Tmax}$) occurred depending on the relative values of C_T
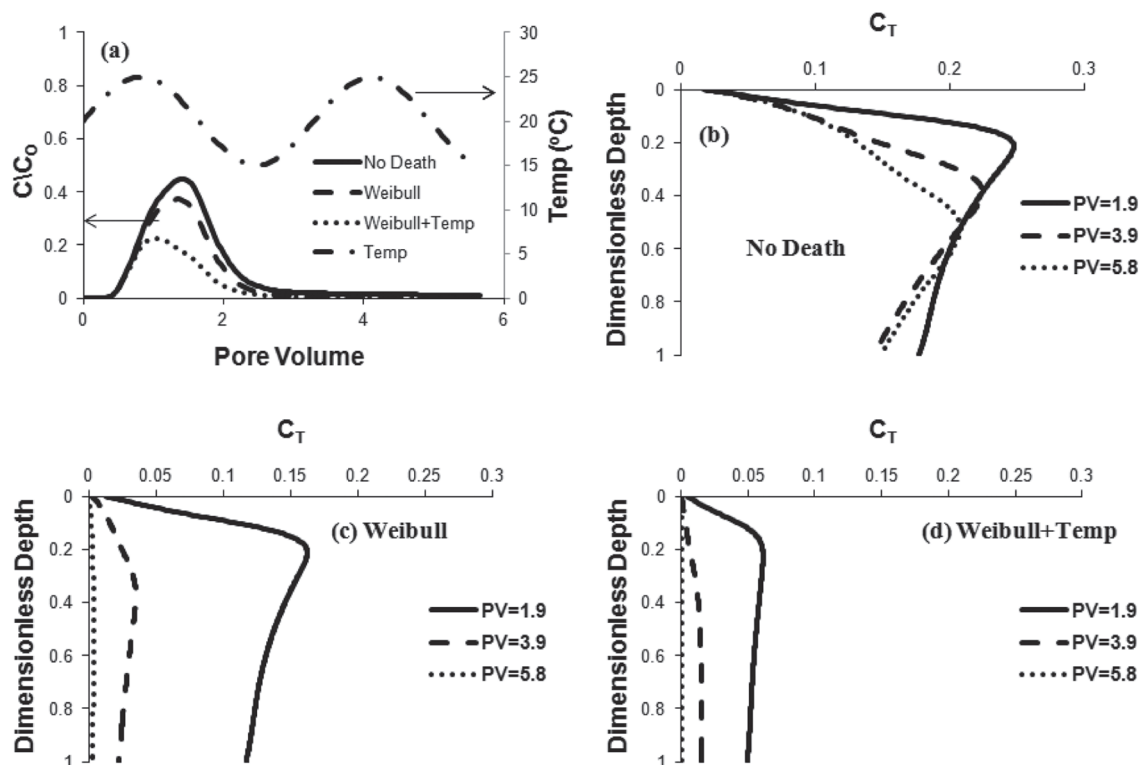

Fig. 6. Simulated (a) breakthrough curves and (b,c,d) retention profiles for *E. coli* O157:H7 in 150-μm sand when considering: (b) no death; (c) Weibull survival (Eq. [23]); and (d) Weibull survival that used Eq. [22] to account for a temperature dependency of the empirical parameter μ. Figure 6a also shows the sinusoidal temperature fluctuations at the soil surface. The two-region model was used in these simulations, using interaction efficiency $\alpha_i = 0.05$, the fraction of the surface area that contributes to retention $S_f = 0.007$, mass transfer coefficient for microbes from Region 2 to 1 $k_{21} = 0$, and the retention rate coefficient to the solid–water interface $k_{sw} = 0.01$ min^{-1}.
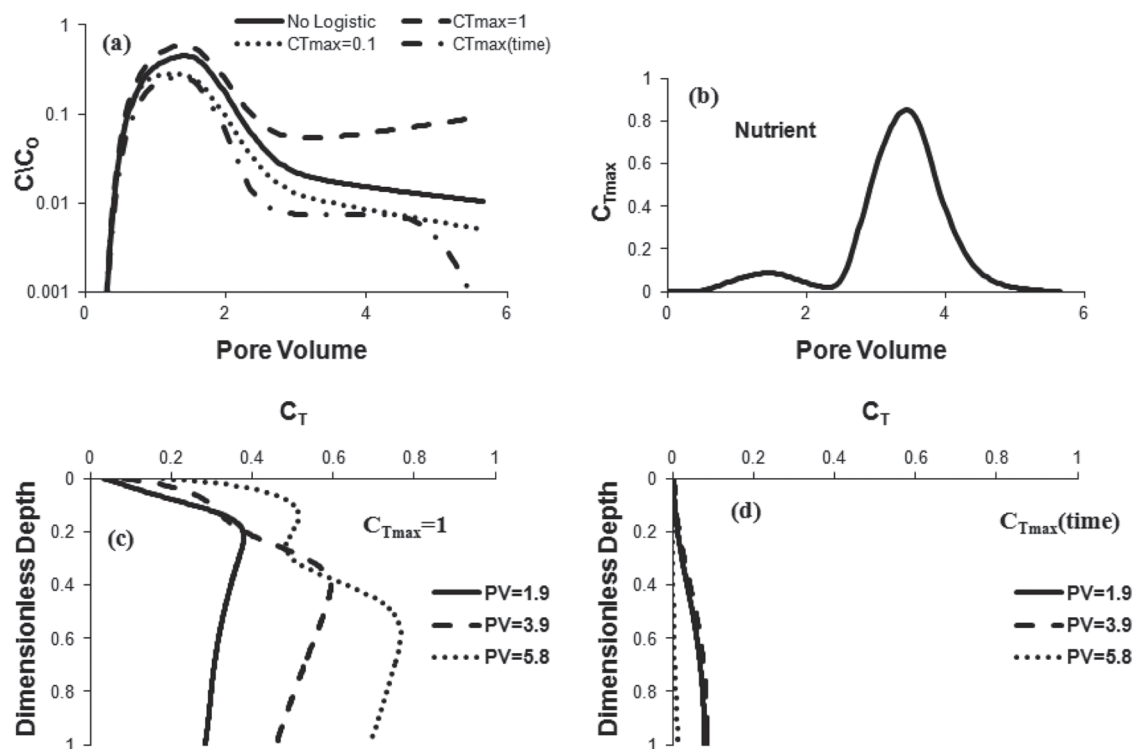
Fig. 7. Simulated (a) breakthrough curves and (c,d) retention profiles for *E. coli* O157:H7 in 150-μm sand when considering no growth or death, logistic survival (Eq. [25]) with maximum total concentration $C_{Tmax} = 1$; logistic survival with $C_{Tmax} = 0.1$, and logistic survival with C_{Tmax} determined by the transport of a hypothetical nutrient and/or substrate shown in (b). The two-region model was again used in these simulations using interaction efficiency $\alpha_i = 0.05$, the fraction of the surface area that contributes to retention $S_f = 0.007$, mass transfer coefficient for microbes from Region 2 to 1 $k_{21} = 0$, and the retention rate coefficient to the solid–water interface $k_{sw} = 0.01$ min^{-1}.

and C_{Tmax}. The results shown in Fig. 7 demonstrate the potential for strongly nonlinear dynamic effects on the transport and fate of microorganisms that is dependent on biological factors (competition) and growth conditions (C_{Tmax}).

There is presently a need to study and predict microbial transport and survival throughout a range of environmentally relevant conditions at the laboratory scale. An understanding and ability to simulate these effects at the field scale is even more complex due to the spatial and temporal variability of conditions and parameters in the heterogeneous environments of the soil surface, the root zone, the vadose zone, and aquifers. Consequently, deterministic modeling of microbial transport and survival through the collective transport pathways will be exceedingly difficult.

Clogging

A reduction in soil porosity and permeability frequently occurs in porous media due to the retention and release of colloids and microorganisms, and/or biological growth (reviews have been given by Herzig et al., 1970; McDowell-Boyer et al., 1986; Baveye et al., 1998; Khilar and Fogler, 1998; Pérez-Paricio and Carrera, 1999; Mays and Hunt, 2005). As discussed above, these clogging processes will strongly depend on a wide variety of physical, chemical, and biological properties that influence retention, release, and growth. In turn, microbial retention, release, and survival are expected to change in a nonlinear manner as clogging progresses (Ives, 1970). Below we provide a brief overview of clogging models.

A large number of empirical and theoretical models for clogging have appeared in the literature (Ives and Pienvichitr, 1965; O'Melia and Ali, 1978; Taylor et al., 1990; Kildsgaard and Engesgaard, 2002; Thullner et al., 2002a, 2002b, 2004; Mostafa and Van Geel, 2007; Wissmeier and Barry, 2009; Tosco and Sethi, 2010). Empirical clogging models have established correlations between the time evolution of pressure buildup (permeability decline) and key soil and water quality properties. Most of these correlations have been developed for infiltration rates at the soil surface and are site specific. A detailed list of empirical clogging models was provided by Pérez-Paricio and Carrera (1999). The soil permeability has also been inversely related to some function of S, denoted as $f(S)$. Various forms for $f(S)$ have also appeared in the literature (Herzig et al., 1970; McDowell-Boyer et al., 1986; Mays and Hunt, 2005). A large class of these models can be approximated when $f(S)$ is a polynomial function (McDowell-Boyer et al., 1986). Theoretical clogging models are more sophisticated than empirical correlations but are based on a number of assumptions, and they require additional information on model parameters. These clogging models have been developed based on the Kozeny–Carman equation (Ives and Pienvichitr, 1965; Taylor et al., 1990; Tosco and Sethi, 2010), pore network models (Kildsgaard and Engesgaard, 2002; Thullner et al., 2002a, 2002b, 2004), and pore-size distribution models (Mostafa and Van Geel, 2007; Soleimani et al., 2009; Wissmeier and Barry, 2009).

Kozeny–Carman type models relate changes in the soil porosity and specific surface area with S to the saturated hydraulic conductivity as (e.g., Baveye et al., 1998)

$$K_s(S) = K_{so} \left[\frac{\varepsilon(S)}{\varepsilon_o} \right]^3 \left[\frac{A_{so}}{A_s(S)} \right]^2 \qquad [26]$$

where K_s [L T^{-1}] is the saturated hydraulic conductivity, K_{so} [L T^{-1}] is the initial saturated hydraulic conductivity, ε (dimensionless) is the porosity, ε_o (dimensionless) is the initial porosity, A_s [L^2 M^{-1}] is the specific surface area of the soil, and A_{so} [L^2 M^{-1}] is the initial specific surface area of the soil. Values of $\varepsilon(S)$ and $A_s(S)$ in Eq. [26] may be determined as (e.g., Tosco and Sethi, 2010)

$$\varepsilon(S) = \varepsilon_o - \frac{\rho_b}{\rho_m} S \qquad [27]$$

$$A_s(S) = A_{so} + f_A A_m \frac{\rho_b}{\rho_m} S \qquad [28]$$

where ρ_m [M L^{-3}] is the bulk density of the retained microbes, A_m [L^2 M^{-1}] is the specific surface area of the microbes, and f_A (dimensionless) is the fraction of A_m that contributes to the increase in the surface area of the soil.

Clogging models based on the Kozeny–Carman equation implicitly assume that microorganisms uniformly coat the grain surfaces with a constant thickness at a particular location. Experimental evidence indicates that this assumption may not be valid in many instances (Baveye et al., 1998). Pore-size distribution models may potentially overcome some of these limitations by allowing for different microbial distributions in the pore space under saturated or unsaturated conditions. For example, Mostafa and Van Geel (2007) related S to a microbial saturation [$S_m = (\rho_b / \varepsilon_o \rho_m) S$] and then used this value in existing pore-size distribution models (Burdine, 1953; Mualem, 1976; Parker and Lenhard, 1987) to determine the water relative permeability for various microbial distributions.

Conclusions

We have reviewed existing model formulations to simulate microbial transport and survival in the subsurface. The conventional model is based on the solution of the advection–dispersion equation, with first-order kinetic terms for survival and exchange with the SWI and AWI. This model is frequently used to describe microbial transport experiments in which only the breakthrough curve was measured. The limitations of this model may not be apparent under such circumstances because the full mass balance (e.g., the soil) was not quantified. When experiments have been designed to achieve mass balance, then the conventional model has frequently proven to be inadequate, even when the model parameters were obtained by inverse optimization.

Alternative model formulations were highlighted to describe the observed kinetic retention on the SWI and AWI; blocking and ripening; release that is dependent on the resident time, diffusion, and transients in solution chemistry, water velocity, and water saturation; and microbial decay and growth that is dependent on temperature, nutrient concentration, and/or the microbial concentration. In particular, we demonstrated that the two-region model can be modified with appropriate terms for microbial retention, release, and survival to describe a wide variety of observed behavior. Nevertheless, parameter optimization was frequently required to obtain a meaningful description of the experimental data, and independent predictions at the column scale are still not feasible. Consequently, model calibration under site-specific conditions is highly recommended before making predictions. In such cases, simulation results are useful in predicting outcomes under given assumptions, testing hypotheses, identifying conditions of vulnerability, development of treatment strategies, and for informing management decisions. Models are especially useful for understanding the potential effects of complex interactions that occur during microbial transport and survival that are experimentally intractable.

There is still a critical need to improve our understanding and description of many fundamental microbial transport, retention, and survival processes and especially in independently determining model parameters for dynamic natural environments. In saturated systems, the retention and release parameters are known to be strong functions of the system hydrodynamics (q_w, d_{50}, and colloid size), the microbial concentration, and the chemistry of the aqueous phase, the solid phase, and the microbe. Few methods currently exist to predict the dependency of retention parameters on these factors. In addition, under unsaturated conditions, the rates of microbial mass transfer and retention on the SWI and AWI have not yet been quantified, and temporal changes in water saturation will further complicate microbial retention and release. Accurate determination of survival parameters is hampered by mass balance errors that may arise from irreversible microbial retention. Furthermore, microbial decay and growth are strongly coupled to a wide variety of biotic and abiotic factors that are imperfectly characterized.

Acknowledgments

References

Abudalo, R.A., Y.G. Bogatsu, J.N. Ryan, R.W. Harvey, D.W. Metge, and M. Elimelech. 2005. Effect of ferric oxyhydroxide grain coatings on the transport of bacteriophage PRD1 and *Cryptosporidium parvum* oocysts in saturated porous media. Environ. Sci. Technol. 39:6412–6419. doi:10.1021/es050159h

Adamczyk, Z., B. Siwek, M. Zembala, and P. Belouschek. 1994. Kinetics of localized adsorption of colloid particles. Adv. Colloid Interface Sci. 48:151–280. doi:10.1016/0001-8686(94)80008-1

Albinger, O., B.K. Biesemeyer, R.G. Arnold, and B.E. Logan. 1994. Effect of bacterial heterogeneity on adhesion to uniform collectors by monoclonal populations. FEMS Microbiol. Lett. 124:321–326. doi:10.1111/j.1574-6968.1994.tb07303.x

Andrews, J.F. 1968. Mathematical model for the continuous culture of microorganisms utilizing inhibitory substrates. Biotechnol. Bioeng. 10:707–723. doi:10.1002/bit.260100602

Asadishad, B., G. Subhasis, and N. Tufenkji. 2011. Method for the direct observation and quantification of survival of bacteria attached to negatively or positively charged surfaces in an aqueous medium. Environ. Sci. Technol. 45:8345–8351. doi:10.1021/es201496q

Bailey, J.E., and D.F. Ollis. 1977. Biochemical engineering fundamentals. McGraw-Hill, New York.

Bales, R.C., S.R. Hinkle, T.W. Kroeger, K. Stocking, and C.P. Gerba. 1991. Bacteriophage adsorption during transport through porous media: Chemical perturbations and reversibility. Environ. Sci. Technol. 25:2088–2095. doi:10.1021/es00024a016

Banat, I.M. 1995. Biosurfactant production and possible uses in microbial enhanced oil recovery and oil pollution remediation: A review. Bioresour. Technol. 51:1–12. doi:10.1016/0960-8524(94)00101-6

Baveye, P., P. Vandevivere, B.L. Hoyle, P.C. DeLeo, and D.S. de Lozada. 1998. Environmental impact and mechanisms of the biological clogging of saturated soils and aquifer materials. Crit. Rev. Environ. Sci. Technol. 28:123–191. doi:10.1080/10643389891254197

Baygents, J.C., J.R. Glynn, O. Albinger, B.K. Biesemeyer, K.L. Ogden, and R.G. Arnold. 1998. Variation of surface charge density in monoclonal bacterial populations: Implications for transport through porous media. Environ. Sci. Technol. 32:1596–1603. doi:10.1021/es9707116

Bendersky, M., and J.M. Davis. 2011. DLVO interaction of colloidal particles with topographically and chemically heterogeneous surfaces. J. Colloid Interface Sci. 353:87–97. doi:10.1016/j.jcis.2010.09.058

Benson, D.A., S.W. Wheatcraft, and M.M. Meerschaert. 2000. Application of a fractional advection–dispersion equation. Water Resour. Res. 36:1403–1412. doi:10.1029/2000WR900031

Bergendahl, J., and D. Grasso. 1998. Colloid generation during batch leaching tests: Mechanics of disaggregation. Colloids Surf. A 135:193–205. doi:10.1016/S0927-7757(97)00248-3

Bergendahl, J., and D. Grasso. 1999. Prediction of colloid detachment in a model porous media: Thermodynamics. AIChE J. 45:475–484. doi:10.1002/aic.690450305

Bergendahl, J., and D. Grasso. 2000. Prediction of colloid detachment in a model porous media: Hydrodynamics. Chem. Eng. Sci. 55:1523–1532. doi:10.1016/S0009-2509(99)00422-4

Berry, E.D., and D.N. Miller. 2005. Cattle feedlot soil moisture and manure content: II. Impact on *Escherichia coli* O157. J. Environ. Qual. 34:656–663. doi:10.2134/jeq2005.0656

Besnard, V., M. Federighi, E. Declerq, F. Jugiau, and J.-M. Cappelier. 2002. Environmental and physico-chemical factors induce VBNC state in *Listeria monocytogenes*. Vet. Res. 33:359–370. doi:10.1051/vetres:2002022

Beven, K., and P. Germann. 1982. Macropores and water flow in soils. Water Resour. Res. 18:1311–1325. doi:10.1029/WR018i005p01311

Binnerup, S.J., D.F. Jensen, H. Thordal-Christensen, and J. Sørensen. 1993. Detection of viable, but non-culturable *Pseudomonas fluorescens* DF57 in soil using a microcolony epifluorescence technique. FEMS Microbiol. Ecol. 12:97–105. doi:10.1111/j.1574-6941.1993.tb00021.x

Bird, R.B., W.E. Stewart, and E.N. Lightfoot. 2002. Transport phenomena. 2nd ed. John Wiley & Sons, New York.

Bolster, C.H., K.L. Cook, I.M. Marcus, B.Z. Haznedaroglu, and S.L. Walker. 2010. Correlating transport behavior with cell properties for eight porcine *Escherichia coli* isolates. Environ. Sci. Technol. 44:5008–5014. doi:10.1021/es1010253

Bolster, C.H., B.Z. Haznedaroglu, and S.L. Walker. 2009. Diversity in cell properties and transport behavior among 12 different environmental isolates. J. Environ. Qual. 38:465–472. doi:10.2134/jeq2008.0137

Bolster, C.H., A.L. Mills, G.M. Hornberger, and J.S. Herman. 1999. Spatial distribution of deposited bacteria following miscible displacement experiments in intact cores. Water Resour. Res. 35:1797–1807. doi:10.1029/1999WR900031

Bolster, C.H., A.L. Mills, G. Hornberger, and J. Herman. 2000. Effect of intra-population variability on the long-distance transport of bacteria. Ground Water 38:370–375. doi:10.1111/j.1745-6584.2000.tb00222.x

Bolt, G.H., and F.A.M. de Haan. 1979. Anion exclusion in soils. In: G.H. Bolt, editor, Soil chemistry: B. Physico-chemical models. Elsevier, Amsterdam. p. 233–257.

Bradford, S.A., and M. Bettahar. 2006. Concentration dependent transport of colloids in saturated porous media. J. Contam. Hydrol. 82:99–117. doi:10.1016/j.jconhyd.2005.09.006

Bradford, S.A., and H. Kim. 2012. Causes and implications of colloid and microorganism retention hysteresis. J. Contam. Hydrol. 138–139:83–92. doi:10.1016/j.jconhyd.2012.06.007

Bradford, S.A., H.N. Kim, B.Z. Haznedaroglu, S. Torkzaban, and S.L. Walker. 2009a. Coupled factors influencing concentration-dependent colloid transport and retention in saturated porous media. Environ. Sci. Technol. 43:6996–7002. doi:10.1021/es900840d

Bradford, S.A., V.L. Morales, W. Zhang, R.W. Harvey, A.I. Packman, A. Mohanram, and C. Welty. 2013a. Transport and fate of microbial pathogens in agricultural settings. Crit. Rev. Environ. Sci. Technol. 43:775–893. doi:10.1080/10643389.2012.710449

Bradford, S.A., J. Šimůnek, M. Bettahar, Y.F. Tadassa, M.Th. van Genuchten, and S.R. Yates. 2005a. Straining of colloids at textural interfaces. Water Resour. Res. 41:W10404. doi:10.1029/2004WR003675

Bradford, S.A., J. Šimůnek, M. Bettahar, M.Th. van Genuchten, and S.R. Yates. 2003. Modeling colloid attachment, straining, and exclusion in saturated porous media. Environ. Sci. Technol. 37:2242–2250. doi:10.1021/es025899u

Bradford, S.A., J. Šimůnek, and S.L. Walker. 2006a. Transport and straining of *E. coli* O157:H7 in saturated porous media. Water Resour. Res. 42:W12S12.

Bradford, S.A., Y.F. Tadassa, and Y. Jin. 2006b. Transport of coliphage in the presence and absence of manure suspension. J. Environ. Qual. 35:1692–1701. doi:10.2134/jeq2006.0036

Bradford, S.A., and N. Toride. 2007. A stochastic model for colloid transport and deposition. J. Environ. Qual. 36:1346–1356. doi:10.2134/jeq2007.0004

Bradford, S.A., and S. Torkzaban. 2008. Colloid transport and retention in unsaturated porous media: A review of interface-, collector-, and pore-scale processes and models. Vadose Zone J. 7:667–681. doi:10.2136/vzj2007.0092

Bradford, S.A., and S. Torkzaban. 2012. Colloid adhesive parameters for chemically heterogeneous porous media. Langmuir 28:13643–13651. doi:10.1021/la3029929

Bradford, S.A., S. Torkzaban, H. Kim, and J. Šimůnek. 2012. Modeling colloid and microorganism transport and release with transients in solution ionic strength. Water Resour. Res. 48:W09509. doi:10.1029/2012WR012468

Bradford, S.A., S. Torkzaban, F. Leij, J. Šimůnek, and M.Th. van Genuchten. 2009b. Modeling the coupled effects of pore space geometry and velocity on colloid transport and retention. Water Resour. Res. 45:W02414.

Bradford, S.A., S. Torkzaban, and A. Shapiro. 2013b. A theoretical analysis of colloid attachment and straining in chemically heterogeneous porous media. Langmuir 29:6944–6952. doi:10.1021/la4011357

Bradford, S.A., S. Torkzaban, and J. Šimůnek. 2011a. Modeling colloid transport and retention in saturated porous media under unfavorable attachment conditions. Water Resour. Res. 47:W10503. doi:10.1029/2011WR010812

Bradford, S.A., S. Torkzaban, and A. Wiegmann. 2011b. Pore-scale simulations to determine the applied hydrodynamic torque and colloid immobilization. Vadose Zone J. 10:252–261. doi:10.2136/vzj2010.0064

Bradford, S.A., M.Th. van Genuchten, and J. Šimůnek. 2005b. Modeling of colloid transport and deposition in porous media. In: S. Torkzaban and S.M. Hassanizadeh, editors, Proceedings of a Workshop on HYDRUS: Advanced modeling of water flow and solute transport in the vadose zone, Utrecht, the Netherlands. 17–19 Oct. 2005. Univ. of Utrecht, Utrecht, the Netherlands. p. 1–5.

Burdine, N.T. 1953. Relative permeability calculations from pore size distribution data. J. Pet. Technol. 5:71–78.

Camesano, T.A., and B.E. Logan. 1998. Influence of fluid velocity and cell concentration on the transport of motile and non-motile bacteria in porous media. Environ. Sci. Technol. 32:1699–1708. doi:10.1021/es970996m

Cardenas, M.B. 2008. Three-dimensional vortices in single pores and their effects on transport. Geophys. Res. Lett. 35:L18402. doi:10.1029/2008GL035343

Cey, E.E., and D.L. Rudolph. 2009. Field study of macropore flow processes using tension infiltration of a dye tracer in partially saturated soils. Hydrol. Processes 23:1768–1779. doi:10.1002/hyp.7302

Cey, E.E., D.L. Rudolph, and J. Passmore. 2009. Influence of macroporosity on preferential solute and colloid transport in unsaturated field soils. J. Contam. Hydrol. 107:45–57. doi:10.1016/j.jconhyd.2009.03.004

Charles, K.J., F.C. Souter, D.L. Baker, C.M. Davies, J.F. Schijven, D.J. Roser, et al. 2008. Fate and transport of viruses during sewage treatment in a mound system. Water Res. 42:3047–3056. doi:10.1016/j.watres.2008.02.032

Chatterjee, J., and S.K. Gupta. 2009. An agglomeration-based model for colloid filtration. Environ. Sci. Technol. 43:3694–3699. doi:10.1021/es8029973

Chen, G., and M. Flury. 2005. Retention of mineral colloids in unsaturated porous media as related to their surface properties. Colloids Surf. A 256:207–216. doi:10.1016/j.colsurfa.2005.01.021

Chen, K.C., R.M. Ford, and P.T. Cummings. 1998. Perturbation expansion of Alt's cell balance equations reduces to Segel's one-dimensional equations for shallow chemoattractant gradients. SIAM J. Appl. Math. 59:35–57. doi:10.1137/S0036139996301283

Cheng, T., and J.E. Saiers. 2009. Mobilization and transport of in situ colloids during drainage and imbibition of partially saturated sediments. Water Resour. Res. 45:W08414.

Cherrey, K.D., M. Flury, and J.B. Harsh. 2003. Nitrate and colloid transport through coarse Hanford sediments under steady state, variably saturated flow. Water Resour. Res. 39:1165. doi:10.1029/2002WR001944

Chiang, H.-W., and C. Tien. 1985a. Dynamics of deep-bed filtration: I. Analysis of two limiting situations. AIChE J. 31:1349–1359. doi:10.1002/aic.690310814

Chiang, H.-W., and C. Tien. 1985b. Dynamics of deep-bed filtration: II. Experiment. AICHE J. 31:1360–1371. doi:10.1002/aic.690310815

Choi, N.-C., D.-J. Kim, and S.-B. Kim. 2007. Quantification of bacterial mass recovery as a function of pore-water velocity and ionic strength. Res. Microbiol. 158:70–78. doi:10.1016/j.resmic.2006.09.007

Chrysikopoulos, C.V., and E.T. Vogler. 2004. Estimation of time dependent virus inactivation rates by geostatistical and resampling techniques: Application to virus transport in porous media. Stochastic Environ. Res. Risk Assess. 18:67–78. doi:10.1007/s00477-003-0130-z

Contois, D.E. 1959. Kinetics of bacterial growth: Relationship between population density and specific growth rate of continuous cultures. J. Gen. Microbiol. 21:40–50. doi:10.1099/00221287-21-1-40

Cook, K.L., and C.H. Bolster. 2007. Survival of *Campylobacter jejuni* and *Escherichia coli* in groundwater during prolonged starvation at low temperatures. J. Appl. Microbiol. 103:573–583. doi:10.1111/j.1365-2672.2006.03285.x

Corapcioglu, M.Y., and H. Choi. 1996. Modeling colloid transport in unsaturated porous media and validation with laboratory column data. Water Resour. Res. 32:3437–3449. doi:10.1029/95WR02693

Cortis, A., T. Harter, L. Hou, E.R. Atwill, A.I. Packman, and P.G. Green. 2006. Transport of *Cryptosporidium parvum* in porous media: Long-term elution experiments and continuous time random walk filtration modeling. Water Resour. Res. 42:W12S13.

Crane, S.R., and J.A. Moore. 1986. Modeling enteric bacterial die-off: A review. Water Air Soil Pollut. 27:411–439. doi:10.1007/BF00649422

Crist, J.T., J.F. McCarthy, Y. Zevi, P. Baveye, J.A. Throop, and T.S. Steenhuis. 2004. Pore-scale visualization of colloid transport and retention in partly saturated porous media. Vadose Zone J. 3:444–450. doi:10.2136/vzj2004.0444

Crist, J.T., Y. Zevi, J.F. McCarthy, J.A. Throop, and T.S. Steenhuis. 2005. Transport and retention mechanisms of colloids in partially saturated porous media. Vadose Zone J. 4:184–195. doi:10.2136/vzj2005.0184

Dabroś, T., and T.G.M. Van De Ven. 1982. Kinetics of coating by colloidal particles. J. Colloid Interface Sci. 89:232–244. doi:10.1016/0021-9797(82)90137-0

Dean, D.M., and M.E. Foran. 1992. The effect of farm liquid waste application on tile drainage. J. Soil Water Conserv. 47:368–369.

DeFlaun, M.F., C.J. Murray, W. Holben, T. Scheibe, A. Mills, T. Ginn, et al. 1997. Preliminary observations on bacterial transport in a Coastal Plain aquifer. FEMS Microbiol. Rev. 20:473–487. doi:10.1111/j.1574-6976.1997.tb00331.x

DeNovio, N.M., J.E. Saiers, and J.N. Ryan. 2004. Colloid movement in unsaturated porous media: Recent advances and future directions. Vadose Zone J. 3:338–351. doi:10.2136/vzj2004.0338

Derjaguin, B., and L. Landau. 1941. Theory of the stability of strongly charged lyophobic sols and of the adhesion of strongly charged particles in solutions of electrolytes. Acta Physicochim. URSS 14:633–662.

de Roda Husman, A.M., W.J. Lodder, S.A. Rutjes, J.F. Schijven, and P.F.M. Teunis. 2009. Long-term inactivation study of three enteroviruses in artificial surface and groundwaters, using PCR and cell culture. Appl. Environ. Microbiol. 75:1050–1057. doi:10.1128/AEM.01750-08

Deshpande, P.A., and D.R. Shonnard. 1999. Modeling the effects of systematic variation in ionic strength on the attachment kinetics of *Pseudomonas fluorescens* UPER-1 in saturated sand columns. Water Resour. Res. 35:1619–1627. doi:10.1029/1999WR900015

Dhawan, S., L.E. Erickson, and L.T. Fan. 1993. Model development and simulation of bioremediation in soil beds with aggregates. Ground Water 31:271–284. doi:10.1111/j.1745-6584.1993.tb01819.x

Duffadar, R.D., and J.M. Davis. 2007. Interaction of micrometer-scale particles with nanotextured surfaces in shear flow. J. Colloid Interface Sci. 308:20–29. doi:10.1016/j.jcis.2006.12.068

Duffadar, R.D., and J.M. Davis. 2008. Dynamic adhesion behavior of micrometer-scale particles flowing over patchy surfaces with nanoscale electrostatic heterogeneity. J. Colloid Interface Sci. 326:18–27. doi:10.1016/j.jcis.2008.07.004

Elimelech, M., J. Gregory, X. Jia, and R.A. Williams. 1995. Particle deposition and aggregation: Measurement, modeling, and simulation. Butterworth-Heinemann, Oxford, UK.

Elimelech, M., M. Nagai, C.-H. Ko, and J.N. Ryan. 2000. Relative insignificance of mineral grain zeta potential to colloid transport in geochemically heterogeneous porous media. Environ. Sci. Technol. 34:2143–2148. doi:10.1021/es9910309

Evans, M.R., and J.D. Owens. 1972. Factors affecting the concentration of faecal bacteria in land-drainage water. J. Gen. Microbiol. 71:477–485. doi:10.1099/00221287-71-3-477

Foppen, J.W., G. Lutterodt, W.F. Röling, and S. Uhlenbrook. 2010. Towards understanding inter-strain attachment variations of *Escherichia coli* during transport in saturated quartz sand. Water Res. 44:1202–1212. doi:10.1016/j.watres.2009.08.034

Foppen, J.W.A., and J.F. Schijven. 2006. Evaluation of data from the literature on the transport and survival of *Escherichia coli* and thermotolerant coliforms in aquifers under saturated conditions. Water Res. 40:401–426. doi:10.1016/j.watres.2005.11.018

Ford, R.M., and R.W. Harvey. 2007. Role of chemotaxis in the transport of bacteria through saturated porous media. Adv. Water Resour. 30:1608–1617. doi:10.1016/j.advwatres.2006.05.019

Fox, G.A., M.M. Marvin, J.A. Guzman, C.K. Hoang, R.W. Malone, R.S. Kanwar, and M.J. Shipitalo. 2012. *E. coli* transport through surface-connected biopores identified from smoke injection tests. Trans. ASABE 55:2185–2194. doi:10.13031/2013.42511

Fuller, M.E., H. Dong, B.J. Mailloux, T.C. Onstott, and M.F. DeFlaun. 2000. Examining bacterial transport in intact cores from Oyster, Virginia: Effect of sedimentary facies type on bacterial breakthrough and retention. Water Resour. Res. 36:2417–2431. doi:10.1029/2000WR900075

Gabriel, J.P., F. Saucy, and L.F. Bersier. 2005. Paradoxes in the logistic equation? Ecol. Modell. 185:147–151. doi:10.1016/j.ecolmodel.2004.10.009

Gaillard, J.-F., C. Chen, S.H. Stonedahl, B.L.T. Lau, D.T. Keane, and A.I. Packman. 2007. Imaging of colloidal deposits in granular porous media by X-ray difference micro-tomography. Geophys. Res. Lett. 34:L18404. doi:10.1029/2007GL030514

Gao, B., J.E. Saiers, and J. Ryan. 2006. Pore-scale mechanisms of colloid deposition and mobilization during steady and transient flow through unsaturated granular media. Water Resour. Res. 42:W01410. doi:10.1029/2005WR004233

Garbrecht, K., G.A. Fox, J.A. Guzman, and D. Alexander. 2009. *E. coli* transport through soil columns: Implications for bioretention cell removal efficiency. Trans. ASABE 52:481–486. doi:10.13031/2013.26841

Gargiulo, G., S. Bradford, J. Šimůnek, P. Ustohal, H. Vereecken, and E. Klumpp. 2007a. Bacteria transport and deposition under unsaturated conditions: The role of the matrix grain size and the bacteria surface protein. J. Contam. Hydrol. 92:255–273. doi:10.1016/j.jconhyd.2007.01.009

Gargiulo, G., S.A. Bradford, J. Šimůnek, P. Ustohal, H. Vereecken, and E. Klumpp. 2008. Bacteria transport and deposition under unsaturated flow conditions: The role of water content and bacteria surface hydrophobicity. Vadose Zone J. 7:406–419. doi:10.2136/vzj2007.0068

Gargiulo, G., S.A. Bradford, J. Šimůnek, H. Vereecken, and E. Klumpp. 2007b. Transport and deposition of metabolically active and stationary phase *Deinococcus radiodurans* in unsaturated porous media. Environ. Sci. Technol. 41:1265–1271. doi:10.1021/es062854a

Gerke, H.H. 2006. Preferential flow descriptions for structured soils. J. Plant Nutr. Soil Sci. 169:382–400. doi:10.1002/jpln.200521955

Gerke, H.H., and M.Th. van Genuchten. 1993a. A dual-porosity model for simulating the preferential movement of water and solutes in structured porous media. Water Resour. Res. 29:305–319. doi:10.1029/92WR02339

Gerke, H.H., and M.Th. van Genuchten. 1993b. Evaluation of a first-order water transfer term for variably saturated dual-porosity flow models. Water Resour. Res. 29:1225–1238. doi:10.1029/92WR02467

Gharasoo, M., F. Centler, P. Regnier, H. Harms, and M. Thullner. 2012. A reactive transport modeling approach to simulate biogeochemical processes in pore structures with pore-scale heterogeneities. Environ. Modell. Softw. 30:102–114. doi:10.1016/j.envsoft.2011.10.010

Ginn, T.R. 2000a. On the distribution of multicomponent mixtures over generalized exposure time in subsurface flow and reactive transport: Batch and column applications involving residence-time distributions and non-Markovian reaction kinetics. Water Resour. Res. 36:2895–2903. doi:10.1029/2000WR900171

Ginn, T.R. 2000b. On the distribution of multicomponent mixtures over generalized exposure time in subsurface flow and reactive transport: Theory and formulations for residence-time-dependent sorption/desorption with memory. Water Resour. Res. 36:2885–2893. doi:10.1029/2000WR900170

Ginn, T.R. 2002. A travel time approach to exclusion on transport in porous media. Water Resour. Res. 38(4). doi:10.1029/2001WR000865

Ginn, T.R., B.D. Wood, K.E. Nelson, T.D. Scheibe, E.M. Murphy, and T.P. Clement. 2002. Processes in microbial transport in the natural subsurface. Adv. Water Resour. 25:1017–1042. doi:10.1016/S0309-1708(02)00046-5

Grolimund, D., and M. Borkovec. 2006. Release of colloidal particles in natural porous media by monovalent and divalent cations. J. Contam. Hydrol. 87:155–175. doi:10.1016/j.jconhyd.2006.05.002

Guber, A.K., D.R. Shelton, and Y.A. Pachepsky. 2005. Transport and retention of manure-borne coliforms in soil. Vadose Zone J. 4:828–837. doi:10.2136/vzj2004.0097

Guzman, J.A., and G.A. Fox. 2011. Implementation of biopore and soil fecal bacteria fate and transport routines in the Root Zone Water Quality Model (RZWQM). Trans. ASABE 55:73–84. doi:10.13031/2013.41263

Hahn, M., and C.R. O'Melia. 2004. Deposition and reentrainment of equivalence of Brownian particles in porous media under unfavorable conditions: Some concepts and applications. Environ. Sci. Technol. 20:1123–1130.

Harmand, B., E. Rodier, M. Sardin, and J. Dodds. 1996. Transport and capture of submicron particles in a natural sand: Short column experiments and a linear model. Colloids Surf. A 107:233–244. doi:10.1016/0927-7757(95)03366-1

Harvey, R.W., and S.P. Garabedian. 1991. Use of colloid filtration theory in modeling movement of bacteria through a contaminated sandy aquifer. Environ. Sci. Technol. 25:178–185. doi:10.1021/es00013a021

Harvey, R.W., and H. Harms. 2002. Transport of microorganisms in the terrestrial subsurface: In situ and laboratory methods. In: C.J. Hurst et al., editors, Manual of environmental microbiology. ASM Press, Washington, DC. p. 753–776.

Harvey, R.W., D.W. Metge, N. Kinner, and N. Mayberry. 1996. Physiological considerations in applying laboratory-determined buoyant densities to predictions of bacterial and protozoan transport in groundwater: Results of in-situ and laboratory tests. Environ. Sci. Technol. 31:289–295. doi:10.1021/es960461d

Harvey, R.W., and J.N. Ryan. 2004. Use of PRD1 bacteriophage in groundwater viral transport, inactivation, and attachment studies. FEMS Microbiol. Ecol. 49:3–16. doi:10.1016/j.femsec.2003.09.015

Herzig, J.P., D.M. Leclerc, and P.L. Goff. 1970. Flow of suspensions through porous media: Application to deep filtration. Ind. Eng. Chem. 62:8–35. doi:10.1021/ie50725a003

Himathongkham, S., S. Bahari, H. Riemann, and D. Cliver. 1999. Survival of *Escherichia coli* O157:H7 and *Salmonella typhimurium* in cow manure and cow manure slurry. FEMS Microbiol. Lett. 178:251–257. doi:10.1111/j.1574-6968.1999.tb08684.x

Hornberger, G.M., A.L. Mills, and J.S. Herman. 1992. Bacterial transport in porous media: Evaluation of a model using laboratory observations. Water Resour. Res. 28:915–923. doi:10.1029/91WR02980

Hosseini, S.A., and T. Tosco. 2013. Transport and retention of high concentrated nano-Fe/Cu particles through highly flow-rated packed sand column. Water Res. 47:326–338. doi:10.1016/j.watres.2012.10.002

Ives, K.J. 1970. Rapid filtration. Water Res. 4:201–223. doi:10.1016/0043-1354(70)90068-0

Ives, K.J., and V. Pienvichitr. 1965. Kinetics of the filtration of dilute suspensions. Chem. Eng. Sci. 20:965–973. doi:10.1016/0009-2509(65)80094-X

Jarvis, N.J. 2007. Review of non-equilibrium water flow and solute transport in soil macropores: Principles, controlling factors and consequences for water quality. Eur. J. Soil Sci. 58:523–546. doi:10.1111/j.1365-2389.2007.00915.x

Jin, Y., and M. Flury. 2002. Fate and transport of viruses in porous media. Adv. Agron. 77:39–102.

John, D.E., and J.B. Rose. 2005. Review of factors affecting microbial survival in groundwater. Environ. Sci. Technol. 39:7345–7356. doi:10.1021/es047995w

Johnson, P.R., and M. Elimelech. 1995. Dynamics of colloid deposition in porous media: Blocking based on random sequential adsorption. Langmuir 11:801–812. doi:10.1021/la00003a023

Johnson, W.P., K.A. Blue, B.E. Logan, and R.G. Arnold. 1995. Modeling bacterial detachment during transport through porous media as a residence-time-dependent process. Water Resour. Res. 31:2649–2658. doi:10.1029/95WR02311

Johnson, W.P., X. Li, and S. Assemi. 2007. Deposition and re-entrainment dynamics of microbes and non-biological colloids during non-perturbed transport in porous media in the presence of an energy barrier to deposition. Adv. Water Resour. 30:1432–1454. doi:10.1016/j.advwatres.2006.05.020

Jucker, B.A., H. Harms, S.J. Hug, and A.J.B. Zehnder. 1997. Adsorption of bacterial surface polysaccharides on mineral oxides is mediated by hydrogen bonds. Colloids Surf. B 9:331–343. doi:10.1016/S0927-7765(97)00038-6

Jury, W.A., W.R. Gardner, and W.H. Gardner. 1991. Soil physics. John Wiley & Sons, New York.

Kanti Sen, T., and K.C. Khilar. 2006. Review on subsurface colloids and colloid-associated contaminant transport in saturated porous media. Adv. Colloid Interface Sci. 119:71–96. doi:10.1016/j.cis.2005.09.001

Khilar, K.C., and H.S. Fogler. 1998. Migrations of fines in porous media. Kluwer Acad. Publ., Dordrecht, the Netherlands.

Kildsgaard, J., and P. Engesgaard. 2002. Tracer tests and image analysis of biological clogging in a two-dimensional sandbox experiment. Ground Water Monit. Rem. 22:60–67. doi:10.1111/j.1745-6592.2002.tb00313.x

Kim, H.N., S.A. Bradford, and S.L. Walker. 2009a. *Escherichia coli* O157:H7 transport in saturated porous media: Role of solution chemistry and surface macromolecules. Environ. Sci. Technol. 43:4340–4347. doi:10.1021/es8026055

Kim, H.N., Y. Hong, I. Lee, S.A. Bradford, and S.L. Walker. 2009b. Surface characteristics and adhesion behavior of *Escherichia coli* O157:H7: Role of extracellular macromolecules. Biomacromolecules 10:2556–2564. doi:10.1021/bm900516y

Kim, H.N., S.L. Walker, and S.A. Bradford. 2010a. Macromolecule mediated transport and retention of *Escherichia coli* O157:H7 in saturated porous media. Water Res. 44:1082–1093. doi:10.1016/j.watres.2009.09.027

Kim, H.N., S.L. Walker, and S.A. Bradford. 2010b. Coupled factors influencing the transport and retention of *Cryptosporidium parvum* oocysts in saturated porous media. Water Res. 44:1213–1223. doi:10.1016/j.watres.2009.09.041

Kim, M.K., S.B. Kim, and S.J. Park. 2008. Bacteria transport in an unsaturated porous media: Incorporation of air–water interface area model into transport modelling. Hydrol. Processes 22:2370–2376. doi:10.1002/hyp.6799

Köhne, J.M., S. Köhne, and J. Šimůnek. 2006. Multi-process herbicide transport in structured soil columns: Experiment and model analysis. J. Contam. Hydrol. 85:1–32. doi:10.1016/j.jconhyd.2006.01.001

Köhne, J.M., S. Köhne, and J. Šimůnek. 2009. A review of model applications for structured soils: A. Water flow and tracer transport. J. Contam. Hydrol. 104:4–35. doi:10.1016/j.jconhyd.2008.10.002

Kolakowski, J.E., and E. Matijevic. 1979. Particle adhesion and removal in model systems: 1. Monodispersed chromium hydroxide on glass. J. Chem. Soc., Faraday Trans. I 75:65–78. doi:10.1039/f19797500065

Krupp, H.K., J.W. Biggar, and D.R. Nielsen. 1972. Relative flow rates of salt and water in soil. Soil Sci. Soc. Am. Proc. 36:412–417. doi:10.2136/sssaj1972.03615995003600030016x

Kumar, D., S. Bhattacharya, and S. Ghosh. 2013. Weak adhesion at the mesoscale: Particles at an interface. Soft Matter 9:6618–6633. doi:10.1039/c3sm00097d

Kussell, E., R. Kishony, N.Q. Balaban, and S. Leibler. 2005. Bacterial persistence: A model of survival in changing environments. Genetics 169:1807–1814. doi:10.1534/genetics.104.035352

Kuznar, Z.A., and M. Elimelech. 2007. Direct microscopic observation of particle deposition in porous media: Role of the secondary energy minimum. Colloids Surf. A 294:156–162. doi:10.1016/j.colsurfa.2006.08.007

Landkamer, L.L., R.W. Harvey, T.D. Scheibe, and J.N. Ryan. 2013. Colloid transport in saturated porous media: Elimination of attachment efficiency in a new colloid transport model. Water Resour. Res. 49:2952–2965. doi:10.1002/wrcr.20195

Lang, N.L., and S.R. Smith. 2007. Influence of soil type, moisture content and biosolids application on the fate of *Escherichia coli* in agricultural soil under controlled laboratory conditions. J. Appl. Microbiol. 103:2122–2131. doi:10.1111/j.1365-2672.2007.03490.x

Lazouskaya, V., and Y. Jin. 2008. Colloid retention at air–water interface in a capillary channel. Colloids Surf. A 325:141–151. doi:10.1016/j.colsurfa.2008.04.053

Lazouskaya, V., Y. Jin, and D. Or. 2006. Interfacial interactions and colloid retention under steady flows in a capillary channel. J. Colloid Interface Sci. 303:171–184. doi:10.1016/j.jcis.2006.07.071

Lenhart, J.J., and J.E. Saiers. 2003. Colloid mobilization in water-saturated porous media under transient chemical conditions. Environ. Sci. Technol. 37:2780–2787. doi:10.1021/es025788v

Li, X., Z. Li, and D. Zhang. 2010a. Role of low flow and backward flow zones on colloid transport in pore structures derived from real porous media. Environ. Sci. Technol. 44:4936–4942. doi:10.1021/es903647g

Li, X., C.-L. Lin, J.D. Miller, and W.P. Johnson. 2006a. Pore-scale observation of microsphere deposition at grain-to-grain contacts over assemblage-scale porous media domains using X-ray microtomography. Environ. Sci. Technol. 40:3762–3768. doi:10.1021/es0525004

Li, X., C.-L. Lin, J.D. Miller, and W.P. Johnson. 2006b. Role of grain-to-grain contacts on profiles of retained colloids in porous media in the presence of an energy barrier to deposition. Environ. Sci. Technol. 40:3769–3774. doi:10.1021/es052501w

Li, X., T.D. Scheibe, and W.P. Johnson. 2004. Apparent decreases in colloid deposition rate coefficients with distance of transport under unfavorable deposition conditions: A general phenomenon. Environ. Sci. Technol. 38:5616–5625. doi:10.1021/es049154v

Li, Z., D. Zhang, and X. Li. 2010b. Tracking colloid transport in porous media using discrete flow fields and sensitivity of simulated colloid deposition to space discretization. Environ. Sci. Technol. 44:1274–1280. doi:10.1021/es9027716

Liang, Y., S. A. Bradford, J. Šimůnek, H. Vereecken, and E. Klumpp. 2013. Sensitivity of the transport and retention of stabilized silver nanoparticles to physicochemical factors. Water Res. 47:2572–2582. doi:10.1016/j.watres.2013.02.025

Ma, H., J. Pedel, P. Fife, and W.P. Johnson. 2009. Hemispheres-in-cell geometry to predict colloid deposition in porous media. Environ. Sci. Technol. 43:8573–8579. doi:10.1021/es901242b

Martins, J.M.F., S. Majdalani, E. Vitorge, A. Desaunay, A. Navel, V. Guiné, et al. 2013. Role of macropore flow in the transport of *Escherichia coli* cells in undisturbed cores of a brown leached soil. Environ. Sci.: Processes Impacts 15:347–356. doi:10.1039/c2em30586k

Mays, D.C., and J.R. Hunt. 2005. Hydrodynamic aspects of particle clogging in porous media. Environ. Sci. Technol. 39:577–584. doi:10.1021/es049367k

McCarthy, J., and J. Zachara. 1989. Subsurface transport of contaminants. Environ. Sci. Technol. 23:496–502.

McDowell-Boyer, L.M., J.R. Hunt, and N. Sitar. 1986. Particle transport through porous media. Water Resour. Res. 22:1901–1921. doi:10.1029/WR022i013p01901

McGechan, M.B., and D.R. Lewis. 2002. Transport of particulate and colloid-sorbed contaminants through soil: 1. General principles. Biosyst. Eng. 83:255–273. doi:10.1006/bioe.2002.0125

McGechan, M.B., and A.J.A. Vinten. 2003. Simulation of transport through soil of *E. coli* derived from livestock slurry using the MACRO model. Soil Use Manage. 19:321–330. doi:10.1079/SUM2003321

McGechan, M.B., and A.J.A. Vinten. 2004. Simulating transport of *E. coli* derived from faeces of grazing livestock using the MACRO model. Soil Use Manage. 20:195–202. doi:10.1079/SUM2004254

Meinders, J.M., J. Noordmans, and H.J. Busscher. 1992. Simultaneous monitoring of the adsorption and desorption of colloidal particles during deposition in a parallel plate flow chamber. J. Colloid Interface Sci. 152:265–280. doi:10.1016/0021-9797(92)90026-I

Mishra, S., J. Jeevan, C.K. Ramesh, and L. Banwari. 2001. In situ bioremediation potential of an oily sludge-degrading bacterial consortium. Curr. Microbiol. 43:328–335. doi:10.1007/s002840010311

Mohamed, M., K. Hatfield, and I.V. Perminova. 2007. Evaluation of Monod kinetic parameters in the subsurface using moment analysis: Theory and numerical testing. Adv. Water Resour. 30:2034–2050. doi:10.1016/j.advwatres.2007.04.006

Molin, S., and V. Cvetkovic. 2010. Microbial risk assessment in heterogeneous aquifers: 1. Pathogen transport. Water Resour. Res. 46:W05518.

Monod, J. 1942. Recherches sur la croissance des cultures bactériennes. Hermann, Paris.

Morohashi, M., Y. Ohashi, S. Tani, K. Ishii, M. Itaya, H. Nanamiya, et al. 2007. Model-based definition of population heterogeneity and its effects on metabolism in sporulating *Bacillus subtilis*. J. Biochem. 142:183–191. doi:10.1093/jb/mvm121

Mostafa, M., and P.J. Van Geel. 2007. Conceptual models and simulations for biological clogging in unsaturated soils. Vadose Zone J. 6:175–185. doi:10.2136/vzj2006.0033

Mualem, Y. 1976. A new model for predicting the hydraulic conductivity of unsaturated porous media. Water Resour. Res. 12:513–522. doi:10.1029/WR012i003p00513

Murphy, E.M., and T.R. Ginn. 2000. Modeling microbial processes in porous media. Hydrogeol. J. 8:142–158. doi:10.1007/s100409900043

Nelson, K.E., and T.R. Ginn. 2005. Colloid filtration theory and the Happel sphere-in-cell model revisited with direct numerical simulation of colloids. Langmuir 21:2173–2184. doi:10.1021/la048404i

Oliver, D.M., P.M. Haygarth, C.D. Clegg, and L. Heathwaite. 2006. Differential *E. coli* die-off patterns associated with agricultural matrices. Environ. Sci. Technol. 40:5710–5716. doi:10.1021/es0603249

Oliver, D.M., T. Page, A.L. Heathwaite, and P.M. Haygarth. 2010. Re-shaping models of *E. coli* population dynamics in livestock faeces: Increased bacterial risk to humans? Environ. Int. 36:1–7. doi:10.1016/j.envint.2009.08.006

Oliver, J.D. 2010. Recent findings on the viable but nonculturable state in pathogenic bacteria. FEMS Microbiol. Rev. 34:415–425.

O'Melia, C.R., and W. Ali. 1978. The role of retained particles in deep bed filtration. Prog. Water Technol. 10:167–182.

Pachepsky, Y.A., A.M. Sadeghi, S.A. Bradford, D.R. Shelton, A.K. Guber, and T. Dao. 2006. Transport and fate of manure-borne pathogens: Modeling perspective. Agric. Water Manage. 86:81–92. doi:10.1016/j.agwat.2006.06.010

Pang, L. 2009. Microbial removal rates in subsurface media estimated from published studies of field experiments and large intact soil cores. J. Environ. Qual. 38:1531–1559. doi:10.2134/jeq2008.0379

Pang, L., M. McLeod, J. Aislabie, J. Šimůnek, M. Close, and R. Hector. 2008. Modeling transport of microbes in ten undisturbed soils under effluent irrigation. Vadose Zone J. 7:97–111. doi:10.2136/vzj2007.0108

Parker, J.C., and R.J. Lenhard. 1987. A model for hysteretic constitutive relations governing multiphase flow: 1. Saturation–pressure relations. Water Resour. Res. 23:2187–2196. doi:10.1029/WR023i012p02187

Passmore, J.M., D.L. Rudolph, M.M.F. Mesquita, E.E. Cey, and M.B. Emelko. 2010. The utility of microspheres as surrogates for the transport of *E. coli* RS2g in partially saturated agricultural soil. Water Res. 44:1235–1245. doi:10.1016/j.watres.2009.10.010

Peleg, M., and M.B. Cole. 1998. Reinterpretation of microbial survival curves. Crit. Rev. Food Sci. Nutr. 38:353–380. doi:10.1080/10408699891274246

Pérez-Paricio, A., and J. Carrera. 1999. Clogging handbook. European Commonwealth, Brussels.

Petterson, S.R., P.F.M. Teunis, and N.J. Ashbolt. 2001. Modeling virus inactivation on salad crops using microbial count data. Risk Anal. 21:1097–1108. doi:10.1111/0272-4332.216178

Philip, J.R. 1968. The theory of absorption in aggregated media. Aust. J. Soil Res. 6:1–19. doi:10.1071/SR9680001

Pot, V., J. Šimůnek, P. Benoit, Y. Coquet, A. Yra, and M.-J. Martínez-Cordón. 2005. Impact of rainfall intensity on the transport of two herbicides in undisturbed grassed filter strip soil cores. J. Contam. Hydrol. 81:63–88. doi:10.1016/j.jconhyd.2005.06.013

Powelson, D.K., C.P. Gerba, and M.T. Yahya. 1993. Virus transport and removal in waste-water during aquifer recharge. Water Res. 27:583–590. doi:10.1016/0043-1354(93)90167-G

Proctor, R.A., C. von Eiff, B.C. Kahl, K. Becker, P. McNamara, M. Herrmann, and G. Peters. 2006. Small colony variants: A pathogenic form of bacteria that facilitates persistent and recurrent infections. Nat. Rev. Microbiol. 4:295–305. doi:10.1038/nrmicro1384

Rajagopalan, R., and C. Tien. 1976. Trajectory analysis of deep-bed filtration with the sphere-in-cell porous media model. AIChE J. 22:523–533. doi:10.1002/aic.690220316

Rathfelder, K.M., J.R. Lang, and L.M. Abriola. 2000. A numerical model (MISER) for the simulation of coupled physical, chemical and biological processes in soil vapor extraction and bioventing systems. J. Contam. Hydrol. 43:239–270. doi:10.1016/S0169-7722(00)00086-3

Ray, C., T.W. Soong, Y.Q. Lian, and G.S. Roadcap. 2002. Effect of flood-induced chemical load on filtrate quality at bank filtration sites. J. Hydrol. 266:235–258. doi:10.1016/S0022-1694(02)00168-3

Redman, J.A., S.B. Grant, T.M. Olson, and M.K. Estes. 2001. Pathogen filtration, heterogeneity, and the potable reuse of wastewater. Environ. Sci. Technol. 35:1798–1805. doi:10.1021/es0010960

Reynolds, P.J., P. Sharma, G.E. Jenneman, and M.J. McInerney. 1989. Mechanisms of microbial movement in subsurface materials. Appl. Environ. Microbiol. 55:2280–2286.

Richards, L.A. 1931. Capillary conduction of liquids through porous mediums. Physics 1:318–333. doi:10.1063/1.1745010

Rockhold, M.L., R.R. Yarwood, and J.S. Selker. 2004. Coupled microbial and transport processes in soils. Vadose Zone J. 3:368–383. doi:10.2136/vzj2004.0368

Rotem, E., A. Loinger, I. Ronin, I. Levin-Reisman, C. Gabay, N. Shoresh, et al. 2010. Regulation of phenotypic variability by a threshold-based mechanism underlies bacterial persistence. Proc. Natl. Acad. Sci. 107:12541–12546. doi:10.1073/pnas.1004333107

Russell, T.L., K.M. Yamahara, and A.B. Boehm. 2012. Mobilization and transport of naturally occurring enterococci in beach sands subject to transient infiltration of seawater. Environ. Sci. Technol. 46:5988–5996. doi:10.1021/es300408z

Ryan, J.N., and M. Elimelech. 1996. Colloid mobilization and transport in groundwater. Colloids Surf. A 107:1–56. doi:10.1016/0927-7757(95)03384-X

Ryan, J.N., and P.M. Gschwend. 1994. Effects of ionic strength and flow rate on colloid release: Relating kinetics to intersurface potential energy. J. Colloid Interface Sci. 164:21–34. doi:10.1006/jcis.1994.1139

Saiers, J.E., and J.J. Lenhart. 2003. Colloid mobilization and transport within unsaturated porous media under transient-flow conditions. Water Resour. Res. 39:1019.

Sanin, S.L., F.D. Sanin, and J.D. Bryers. 2003. Effect of starvation on the adhesive properties of xenobiotic degrading bacteria. Process Biochem. 38:909–914. doi:10.1016/S0032-9592(02)00173-5

Schäfer, A., H. Harms, and A.J.B. Zehnder. 1998. Bacterial accumulation at the air–water interface. Environ. Sci. Technol. 32:3704–3712. doi:10.1021/es980191u

Scheibe, T.D., and B.D. Wood. 2003. A particle-based model of size or anion exclusion with application to microbial transport in porous media. Water Resour. Res. 39(4):1080. doi:10.1029/2001WR001223

Schijven, J.F., P. Berger, and I. Miettinen. 2003. Removal of pathogens, surrogates, indicators and toxins using riverbank filtration. In: C. Ray et al., editors, Bank filtration for water supply. Springer, New York. p. 73–116.

Schijven, J.K., and S.M. Hassanizadeh. 2000. Removal of viruses by soil passage: Overview of modeling, processes, and parameters. Crit. Rev. Environ. Sci. Technol. 30:49–127. doi:10.1080/10643380091184174

Schijven, J.F., and S.M. Hassanizadeh. 2002. Virus removal by soil passage at field scale and groundwater protection of sandy aquifers. Water Sci. Technol. 46:123–129.

Schijven, J.F., and J. Šimůnek. 2002. Kinetic modeling of virus transport at the field scale. J. Contam. Hydrol. 55:113–135. doi:10.1016/S0169-7722(01)00188-7

Semenov, A.V., L. van Overbeek, and A.H.C. van Bruggen. 2009. Percolation and survival of *Escherichia coli* O157:H7 and *Salmonella enterica* serovar Typhimurium in soil amended with contaminated dairy manure or slurry. Appl. Environ. Microbiol. 75:3206–3215. doi:10.1128/AEM.01791-08

Shapiro, A.A. 2007. Elliptic equation for random walks: Application to transport in microporous media. Physica A 375:81–96.

Shapiro, A.A., and P.G. Bedrikovetsky. 2010. A stochastic theory for deep bed filtration accounting for dispersion and size distributions. Physica A 389:2473–2494. doi:10.1016/j.physa.2010.02.049

Sharma, P.K., M.J. McInerney, and R.M. Knapp. 1993. In situ growth and activity and modes of penetration of *Escherichia coli* in unconsolidated porous materials. Appl. Environ. Microbiol. 59:3686–3694.

Shen, C., Y. Huang, B. Li, and Y. Jin. 2010. Predicting attachment efficiency of colloid deposition under unfavorable attachment conditions. Water Resour. Res. 46:W11526. doi:10.1029/2010WR009218

Shen, C., B. Li, Y. Huang, and Y. Jin. 2007. Kinetics of coupled primary- and secondary-minimum deposition of colloids under unfavorable chemical conditions. Environ. Sci. Technol. 41:6976–6982. doi:10.1021/es070210c

Sheng, P., and M. Zhou. 1992. Immiscible-fluid displacement: Contact-line dynamics and the velocity-dependent capillary pressure. Phys. Rev. A 45:5694. doi:10.1103/PhysRevA.45.5694

Sim, Y., and C.V. Chrysikopoulos. 1996. One-dimensional virus transport in porous media with time-dependent inactivation rate coefficients. Water Resour. Res. 32:2607–2611. doi:10.1029/96WR01496

Simoni, S.F., H. Harms, T.N.P. Bosma, and A.J.B. Zehnder. 1998. Population heterogeneity affects transport of bacteria through sand columns at low flow rates. Environ. Sci. Technol. 32:2100–2105. doi:10.1021/es970936g

Šimůnek, J., C. He, L. Pang, and S.A. Bradford. 2006. Colloid-facilitated solute transport in variably saturated porous media: Numerical model and experimental verification. Vadose Zone J. 5:1035–1047. doi:10.2136/vzj2005.0151

Šimůnek, J., N.J. Jarvis, M.Th. van Genuchten, and A. Gärdenäs. 2003. Review and comparison of models for describing non-equilibrium and preferential flow and transport in the vadose zone. J. Hydrol. 272:14–35. doi:10.1016/S0022-1694(02)00252-4

Šimůnek, J., and M.Th. van Genuchten. 2008. Modeling nonequilibrium flow and transport processes using HYDRUS. Vadose Zone J. 7:782–797. doi:10.2136/vzj2007.0074

Šimůnek, J., M.Th. van Genuchten, and M. Šejna. 2008. Development and applications of the HYDRUS and STANMOD software packages and related codes. Vadose Zone J. 7:587–600. doi:10.2136/vzj2007.0077

Soleimani, S., P.J. Van Geel, O.B. Isgor, and M.B. Mostafa. 2009. Modeling of biological clogging in unsaturated porous media. J. Contam. Hydrol. 106:39–50. doi:10.1016/j.jconhyd.2008.12.007

Spielman, L.A., and S.K. Friedlander. 1974. Role of the electrical double layer in particle deposition by convective diffusion. J. Colloid Interface Sci. 46:22–31. doi:10.1016/0021-9797(74)90021-6

Stumm, W., J.J. Morgan, and J.I. Drever. 1981. Aquatic chemistry. John Wiley & Sons, New York.

Stuyfzand, P.J. 1989. Hydrology and water quality aspects of Rhine bank groundwater in the Netherlands. J. Hydrol. 106:341–363. doi:10.1016/0022-1694(89)90079-6

Taneda, S. 1979. Visualization of separating Stokes flows. J. Phys. Soc. Jpn. 46:1935–1942. doi:10.1143/JPSJ.46.1935

Taylor, S.W., P.C.D. Milly, and P.R. Jaffé. 1990. Biofilm growth and the related changes in the physical properties of a porous medium: 2. Permeability. Water Resour. Res. 26:2161–2169. doi:10.1029/WR026i009p02161

Tessier, G. 1942. Croissance des populations bactériennes et quantité d'aliment disponible. Rev. Sci. Paris 3208:209–214.

Thullner, M., L. Mauclaire, M.H. Schroth, W. Kinzelbach, and J. Zeyer. 2002a. Interaction between water flow and spatial distribution of microbial growth in a two-dimensional flow field in saturated porous media. J. Contam. Hydrol. 58:169–189. doi:10.1016/S0169-7722(02)00033-5

Thullner, M., M.H. Schroth, J. Zeyer, and W. Kinzelbach. 2004. Modeling of a microbial growth experiment with bioclogging in a two-dimensional saturated porous media flow field. J. Contam. Hydrol. 70:37–62. doi:10.1016/j.jconhyd.2003.08.008

Thullner, M., J. Zeyer, and W. Kinzelbach. 2002b. Influence of microbial growth on hydraulic properties of pore networks. Transp. Porous Media 49:99–122. doi:10.1023/A:1016030112089

Tien, C. 1989. Granular filtration of aerosols and hydrosols. Butterworths, London.

Tong, M., X. Li, C.N. Brow, and W.P. Johnson. 2005. Detachment-influenced transport of an adhesion-deficient bacterial strain within water-reactive porous media. Environ. Sci. Technol. 39:2500–2508. doi:10.1021/es049013t

Tong, M., H. Ma, and W.P. Johnson. 2008. Funneling of flow into grain-to-grain contacts drives colloid–colloid aggregation in the presence of an energy barrier. Environ. Sci. Technol. 42:2826–2832. doi:10.1021/es071888v

Torkzaban, S., S.A. Bradford, and S.L. Walker. 2007. Resolving the coupled effects of hydrodynamics and DLVO forces on colloid attachment to porous media. Langmuir 23:9652–9660. doi:10.1021/la700995e

Torkzaban, S., S.M. Hassanizadeh, J.F. Schijven, and A.M. de Roda Husman. 2006a. Virus transport in saturated and unsaturated sand columns. Vadose Zone J. 5:877–885. doi:10.2136/vzj2005.0086

Torkzaban, S., S.M. Hassanizadeh, J.F. Schijven, and H.H.J.L. van den Berg. 2006b. Role of air–water interfaces on retention of viruses under unsaturated conditions. Water Resour. Res. 42:W12S14. doi:10.1029/2006WR004904

Torkzaban, S., Y. Kim, M. Mulvihill, J. Wan, and T. Tokunaga. 2010a. Transport and deposition of functionalized CdTe nanoparticles in saturated porous media. J. Contam. Hydrol. 118:208–217. doi:10.1016/j.jconhyd.2010.10.002

Torkzaban, S., H.N. Kim, J. Šimůnek, and S.A. Bradford. 2010b. Hysteresis of colloid retention and release in saturated porous media during transients in solution chemistry. Environ. Sci. Technol. 44:1662–1669. doi:10.1021/es903277p

Torkzaban, S., S.S. Tazehkand, S.L. Walker, and S.A. Bradford. 2008. Transport and fate of bacteria in porous media: Coupled effects of chemical conditions and pore space geometry. Water Resour. Res. 44:W04403. doi:10.1029/2007WR006541

Torkzaban, S., J. Wan, T.K. Tokunaga, and S.A. Bradford. 2012. Impacts of bridging complexation on the transport of surface-modified nanoparticles in saturated sand. J. Contam. Hydrol. 136–137:86–95. doi:10.1016/j.jconhyd.2012.05.004

Tosco, T., and R. Sethi. 2010. Transport of non-Newtonian suspensions of highly concentrated micro- and nanoscale iron particles in porous media: A modeling approach. Environ. Sci. Technol. 44:9062–9068. doi:10.1021/es100868n

Tosco, T., A. Tiraferri, and R. Sethi. 2009. Ionic strength dependent transport of microparticles in saturated porous media: Modeling mobilization and immobilization phenomena under transient chemical conditions. Environ. Sci. Technol. 43:4425–4431. doi:10.1021/es900245d

Tufenkji, N. 2007. Modeling microbial transport in porous media: Traditional approaches and recent developments. Adv. Water Resour. 30:1455–1469. doi:10.1016/j.advwatres.2006.05.014

Tufenkji, N., D.R. Dixon, R. Considine, and C.J. Drummond. 2006. Multi-scale Cryptosporidium/sand interactions in water treatment. Water Res. 40:3315–3331. doi:10.1016/j.watres.2006.07.036

Tufenkji, N., and M. Elimelech. 2004. Correlation equation for predicting single-collector efficiency in physicochemical filtration in saturated porous media. Environ. Sci. Technol. 38:529–536. doi:10.1021/es034049r

Tufenkji, N., and M. Elimelech. 2005a. Breakdown of colloid filtration theory: Role of the secondary energy minimum and surface charge heterogeneities. Langmuir 21:841–852. doi:10.1021/la048102g

Tufenkji, N., and M. Elimelech. 2005b. Spatial distributions of *Cryptosporidium* oocysts in porous media: Evidence for dual mode deposition. Environ. Sci. Technol. 39:3620–3629. doi:10.1021/es048289y

Tufenkji, N., J.A. Redman, and M. Elimelech. 2003. Interpreting deposition patterns of microbial particles in laboratory-scale column experiments. Environ. Sci. Technol. 37:616–623. doi:10.1021/es025871i

Tufenkji, N., J.N. Ryan, and M. Elimelech. 2002. The promise of bank filtration. Environ. Sci. Technol. 36:422A –428A. doi:10.1021/es022441j

Unc, A., and M.J. Goss. 2004. Transport of bacteria from manure and protection of water resources. Appl. Soil Ecol. 25:1–18. doi:10.1016/j.apsoil.2003.08.007

van Genuchten, M.Th., and P.J. Wierenga. 1976. Mass transfer studies in sorbing porous media: I. Analytical solutions. Soil Sci. Soc. Am. J. 40:473–480. doi:10.2136/sssaj1976.03615995004000040011x

Veerapaneni, S., J. Wan, and T.K. Tokunaga. 2000. Motion of particles in film flow. Environ. Sci. Technol. 34:2465–2471. doi:10.1021/es9912731

Verhulst, P.F. 1838. Notice sur la loi que la population suit dans son accroissement. Corresp. Math. Phys. 10:113–121.

Verwey, E.J.W., and J.T.G. Overbeek. 1948. Theory of the stability of lyophobic colloids. Elsevier, Amsterdam.

Vidali, M. 2001. Bioremediation: An overview. Pure Appl. Chem. 73:1163–1172. doi:10.1351/pac200173071163

Walker, S.L., J.A. Redman, and M. Elimelech. 2004. Role of cell surface lipopolysaccharides in *Escherichia coli* K12 adhesion and transport. Langmuir 20:7736–7746. doi:10.1021/la049511f

Wan, J., and T.K. Tokunaga. 1997. Film straining of colloids in unsaturated porous media: Conceptual model and experimental testing. Environ. Sci. Technol. 31:2413–2420. doi:10.1021/es970017q

Wan, J., T.K. Tokunaga, and C.-F. Tsang. 1995. Bacterial sedimentation through a porous medium. Water Resour. Res. 31:1627–1636. doi:10.1029/95WR01255

Wan, J., and J.L. Wilson. 1994a. Colloid transport in unsaturated porous media. Water Resour. Res. 30:857–864. doi:10.1029/93WR03017

Wan, J.M., and J.L. Wilson. 1994b. Visualization of the role of the gas–water interface on the fate and transport of colloids in porous media. Water Resour. Res. 30:11–23. doi:10.1029/93WR02403

Wang, M., and R.M. Ford. 2009. Transverse bacterial migration induced by chemotaxis in a packed column with structured physical heterogeneity. Environ. Sci. Technol. 43:5921–5927. doi:10.1021/es901001t

Wang, M., R.M. Ford, and R.W. Harvey. 2008. Coupled effect of chemotaxis and growth on microbial distributions in organic-amended aquifer sediments: Observations from laboratory and field studies. Environ. Sci. Technol. 42:3556–3562. doi:10.1021/es702392h

Wang, Y., S.A. Bradford, and J. Šimůnek. 2013. Transport and fate of microorganisms in soils with preferential flow under different solution chemistry conditions. Water Resour. Res. 49:2424–2436. doi:10.1002/wrcr.20174

Weiss, W.J., E.J. Bouwer, R. Aboytes, M.W. LeChevallier, C.R. O'Melia, B.T. Le, and K.J. Schwab. 2005. River filtration for control of microorganisms results from field monitoring. Water Res. 39:1990–2001. doi:10.1016/j.watres.2005.03.018

Weiss, M., Y. Lüthi, J. Ricka, T. Jörg, and H. Bebie. 1998. Colloidal particles at solid–liquid interfaces: Mechanisms of desorption kinetics. J. Colloid Interface Sci. 206:322–331. doi:10.1006/jcis.1998.5636

Williams, V., and M. Fletcher. 1996. Adhesion and transport through porous media of *Pseudomonas fluorescens* is affected by lipopolysaccharide composition. Appl. Environ. Microbiol. 62:100–104.

Wissmeier, L., and D.A. Barry. 2009. Effect of mineral reactions on the hydraulic properties of unsaturated soils: Model development and application. Adv. Water Resour. 32:1241–1254. doi:10.1016/j.advwatres.2009.05.004

Xu, L.C., and B.E. Logan. 2006. Adhesion forces between functionalized latex microspheres and protein-coated surfaces evaluated using colloid probe atomic force microscopy. Colloids Surf. B 48:84–94. doi:10.1016/j.colsurfb.2006.01.012

Xu, S., B. Gao, and J.E. Saiers. 2006. Straining of colloidal particles in saturated porous media. Water Resour. Res. 42:W12S16. doi:10.1029/2006WR004948

Yao, K.-M., M.T. Habibian, and C.R. O'Melia. 1971. Water and waste water filtration: Concepts and applications. Environ. Sci. Technol. 5:1105–1112. doi:10.1021/es60058a005

Yoon, J.S., J.T. Germaine, and P.J. Culligan. 2006. Visualization of particle behavior within a porous medium: Mechanisms for particle filtration and retardation during downward transport. Water Resour. Res. 42:W06417. doi:10.1029/2004WR003660

Yuan, H., and A.A. Shapiro. 2010. Modeling non-Fickian transport and hyperexponential deposition for deep bed filtration. Chem. Eng. J. 162:974–988. doi:10.1016/j.cej.2010.07.003

Yuan, H., and A.A. Shapiro. 2011. A mathematical model for non-monotonic deposition profiles in deep bed filtration systems. Chem. Eng. J. 166:105–115. doi:10.1016/j.cej.2010.10.036

Yukalov, V.I., E.P. Yukalova, and D. Sornette. 2009. Punctuated evolution due to delayed carrying capacity. Physica D 238:1752–1767. doi:10.1016/j.physd.2009.05.011

Zevi, Y., A. Dathe, B. Gao, W. Zhang, B.K. Richards, and T.S. Steenhuis. 2009. Transport and retention of colloidal particles in partially saturated porous media: Effect of ionic strength. Water Resour. Res. 45:W12403. doi:10.1029/2008WR007322

Zevi, Y., A. Dathe, J.F. McCarthy, B.K. Richards, and T.S. Steenhuis. 2005. Distribution of colloid particles onto interfaces in partially saturated sand. Environ. Sci. Technol. 39:7055–7064. doi:10.1021/es048595b

Zevi, Y., B. Gao, W. Zhang, V.L. Morales, M.E. Cakmak, E.A. Medrano, et al. 2012. Colloid retention at the meniscus–wall contact line in an open microchannel. Water Res. 46:295–306. doi:10.1016/j.watres.2011.09.046

Zhang, P., W.P. Johnson, T.D. Scheibe, K.-H. Choi, F.C. Dobbs, and B.J. Mailloux. 2001. Extended tailing of bacteria following breakthrough at the Narrow Channel Focus Area, Oyster, Virginia. Water Resour. Res. 37:2687–2698. doi:10.1029/2000WR000151

Zhang, Q., S.M. Hassanizadeh, A. Raoof, M.Th van Genuchten, and S.M. Roels. 2012. Modeling virus transport and remobilization during transient partially saturated flow. Vadose Zone J. 11(2). doi:10.2136/vzj2011.0090

Zhang, W., V.L. Morales, M.E. Cakmak, A.E. Salvucci, L.D. Geohring, A.G. Hay, et al. 2010. Colloid transport and retention in unsaturated porous media: Effect of colloid input concentration. Environ. Sci. Technol. 44:4965–4972. doi:10.1021/es100272f

Zheng, W., L.-P. Wang, D. Or, V. Lazouskaya, and Y. Jin. 2012. Role of mixed boundaries on flow in open capillary channels with curved air–water interfaces. Langmuir 28:12753–12761. doi:10.1021/la302833p