Computation of the Electrical Double Layer Properties of Semipermeable Membranes in Multicomponent Electrolytes

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A methodology is presented for calculating the surface potential, Donnan potential, and ion concentration profiles for semipermeable microbial membranes that is valid for an arbitrary electrolyte composition. This model for surface potential, Donnan potential, and charge density was applied to recently reported experimental data for gram-positive bacteria, including Bacillus brevis, Rhodococcus opacus, Rhodococcus erythropolis, and Corynebacterium species. These calculations show that previously unconsidered trace amounts of divalent and trivalent cations at very low concentrations (10^-10 M) can have significant effects on the calculated surface and Donnan potentials, at ionic strengths of I ≤ 0.01 M, and that these effects need to be considered in accurate modeling of microbial surface. In addition, the calculated ion concentration profiles show that owing to the relatively high surface charges that can develop in microbial membranes, electrostatic effects can act to significantly concentrate divalent (factors of 5 x 10^3) and trivalent (factors of 2 x 10^4) cations within the bacterial cell wall. Comparison of the calculated concentration factors with those derived from experiments shows that a significant fraction of the uptake of metal by bacteria can be explained by the proposed electrostatic model.

Characterization of the electrical double layer of bacterial surfaces has been the subject of a great deal of recent research efforts owing to the fact that the bacterial surface charge and electrical double layer properties affect many important environmental properties of bacteria including attachment-detachment of bacteria, metal binding, mobility, and zeta potential (1–8, 10–13, 16–21). As a result, models of the charge potential relationships at bacterial surfaces and across bacterial cell walls have been studied extensively (9, 10, 13, 14, 17, 18, 21), usually by assuming Donnan equilibrium deep within the membrane and then solving the Poisson-Boltzmann equation for a specific electrolyte type and concentration with fixed boundary conditions to obtain the surface potential distribution. All of the proposed numerical or analytic solutions of these equations to obtain the relationships among the Donnan potential, surface potential, and charge density for microbial membranes are strictly valid only for pure 1-1 electrolytes (see, for example, reference 17) or at most mixtures of 1-1 and 2-1 electrolytes (14). Unfortunately, natural geochemical systems often contain a complex mixture of different chemical components and ionic species, and the question as to the applicability of equations derived for simple mixtures to complex multicomponent natural systems arises.

In this paper, a solution procedure to the Poisson-Boltzmann equation for a semipermeable membrane that is valid for any arbitrary mixture of charged ions is presented. The importance of considering all ions in the calculation of surface and Donnan potentials for microbial membranes in dilute solutions is demonstrated by using surface charging data for bacterial membranes reported recently in by van der Wal et al. (17). The results show that the presence of trace amounts of divalent or trivalent cations in relatively dilute solutions (I, ≤0.01 M) can significantly alter both the calculated surface and Donnan potential as well as the distribution of counter and co-ions within the membrane.

This model does not account for metabolism in the bacteria. However, the rate at which the thermodynamic equilibrium described by this model is reached is likely to be significantly higher than the rate of metabolism.

Abbreviations used. For a complete list of abbreviations and units used in notation of equations, see Table 1.

Computational procedure. Equations for the Donnan potential, surface potential, and the potential profiles across a planar ion-penetrable membrane have been published in the literature for several particular special cases. The most comprehensive treatment for mixed electrolyte solutions was presented by Ohshima and Kondo (14), who described 1-1 electrolytes, symmetric electrolytes, and a mixed solution of 1-1 and 2-1 electrolytes. In this paper, the treatment found is in that reference is extended to the case of an arbitrary electrolytic solution of charged species, and the validity of assumptions made to solve these equations is discussed. The published analytic solutions follow from our general equations as special cases.

Following earlier treatments (14, 17), the solution for the planar geometry with the only coordinate (x) perpendicular to the surface of the membrane is obtained. Use of a planar geometry is justified, since the radius of curvature of the cell (approximately 10^4 Å) is significantly greater than the thickness of the area in which a nonzero electrostatic field exists. An infinite thickness of the membrane and solution is also assumed. Once again, after solving the equations under this assumption we note that the electric field exists only in the area thinner than the membrane, justifying the infinite-thickness assumption.

The problem is formally described as follows. The membrane (x < 0) has fixed charge density (charge in a unit volume) p_m and dielectric constant ε_m. The solution has N different aqueous ions, and its dielectric constant is ε_s. Each ion-
This equation is then solved for the Donnan potential. At this point, it is convenient to introduce the notation \( t = \exp\left(\frac{F\psi_D}{RT}\right) \) and reduce the numerical problem to finding the positive root of the following polynomial:

\[
\frac{p_m}{F} F t^{Z_{\text{max}}} + \sum_{i=1}^{N} C_i^0 Z_i t^{Z_{\text{max}} - Z_i} = 0 \quad (3)
\]

where \( Z_{\text{max}} \) is the maximum charge of the ion in the solution. The degree of this polynomial is \( Z_{\text{max}} - Z_{\text{min}} \), where \( Z_{\text{min}} \) is the minimum ionic charge (the formal charge of the most negatively charged anion). Algorithms and computer codes for finding the roots of a polynomial are readily available (15). We determined the Donnan potential by finding the single positive root of equation 3 (which takes a fraction of a second on a desktop computer) and then used \( t = \exp\left(\frac{F\psi_D}{RT}\right) \) to obtain the Donnan potential itself.

This expression is general, and the expression for the 1-1 electrolyte follows from equation 3 as a special case. In case of a 1-1 electrolyte, \( Z_{\text{max}} = 1 \) and \( Z_{\text{min}} = -1 \), while \( N = 2 \). Therefore, in this particular case equation 3 is a quadratic equation whose solution yields the well-known expression for the Donnan potential for the membrane in contact with a 1-1 electrolytic solution (14):

\[
y_D = \text{arcsinh}\left(\frac{p_m}{2C_0^0 F}\right) \quad (3')
\]

We never used equation 3’, since we always considered solutions with tracer species present. It is given here just to demonstrate consistency with the results of reference 14 for the special case treated therein.

**Potential profile across the membrane.** To obtain the potential profile across the membrane, we solved the Poisson equation \( \nabla^2 \psi = -\rho/(\varepsilon\varepsilon_0) \) (in SI units), where \( \rho/(\varepsilon\varepsilon_0) \) is the charge density and \( \varepsilon \) is the dielectric constant of the medium (Table 1). The zero of the \( x \) axis is located on the boundary between the membrane (\( x < 0 \)) and solution (\( x > 0 \)). The relative dielectric constant of the membrane is denoted \( \varepsilon_m \), and that of the solution is denoted \( \varepsilon_r \). Since we have only one spatial variable for the planar geometry, \( \nabla^2 = \frac{d^2}{dx^2} \). The charge density (\( \rho \)) consists of the fixed-charge density \( \rho_m \) (present only in the membrane) and the induced-charge density. The latter is determined from the Boltzmann distribution as in equation 1. Therefore, the Poisson equations for the membrane and the solution, respectively, have the following forms:

\[
\frac{d^2\psi}{dx^2} = -\frac{1}{\varepsilon_m\varepsilon_0}\left(\rho_m + \sum_{i=1}^{N} FC_i Z_i \exp\left(-\frac{ZF\psi}{RT}\right)\right) \quad \text{for } x < 0 \quad (4)
\]

\[
\frac{d^2\psi}{dx^2} = -\frac{1}{\varepsilon_r\varepsilon_0}\sum_{i=1}^{N} FC_i Z_i \exp\left(-\frac{ZF\psi}{RT}\right) \quad \text{for } x > 0 \quad (5)
\]

The boundary conditions for the potential are \( \psi(x = -0) = \psi(x = +0), \psi(x = -\infty) = \psi_D, \) and \( \psi(x = +\infty) = 0. \) The other boundary conditions involve the electric field \( E = -\frac{d\psi}{dx}. \) The only component of the electric field present in planar geometry is normal to the surface. This yields the boundary condition \( \varepsilon_r E(x = -0) = \varepsilon_r E(x = +0). \) Naturally, we expect the electric field to vanish far away from the boundary, \( E(x = -\infty) = E(x = +\infty) = 0. \)

This boundary value problem can be solved numerically, but

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \psi )</td>
<td>Electrostatic potential (volts)</td>
</tr>
<tr>
<td>( \psi_D )</td>
<td>Donnan potential, the constant potential well inside the membrane</td>
</tr>
<tr>
<td>( \psi_0 )</td>
<td>Surface potential, ( \psi(x = 0) )</td>
</tr>
<tr>
<td>( \varepsilon_0 )</td>
<td>8.85419 \times 10^{-12} \text{ F/m}, vacuum permittivity</td>
</tr>
<tr>
<td>( \varepsilon_m )</td>
<td>Dielectric constant of the membrane (C/m³)</td>
</tr>
<tr>
<td>( \rho_m )</td>
<td>Fixed charge density in the membrane (C/m³)</td>
</tr>
<tr>
<td>( \varepsilon_r )</td>
<td>Dielectric constant of the solution</td>
</tr>
<tr>
<td>( C_i )</td>
<td>Concentration (mol/m³) of particular ionic species</td>
</tr>
<tr>
<td>( N )</td>
<td>Total number of different ionic species in solution</td>
</tr>
<tr>
<td>( Z_i )</td>
<td>Charge of ionic species (integer number)</td>
</tr>
<tr>
<td>( N_i )</td>
<td>Ionic strength of solution</td>
</tr>
<tr>
<td>( y )</td>
<td>Reduced potential (dimensionless number)</td>
</tr>
<tr>
<td>( y_D )</td>
<td>Reduced Donnan potential (dimensionless number)</td>
</tr>
<tr>
<td>( y_m )</td>
<td>Reduced surface potential</td>
</tr>
<tr>
<td>( F )</td>
<td>9.6485 \times 10^{-19} \text{ C/mol} (Faraday constant)</td>
</tr>
<tr>
<td>( R )</td>
<td>8.31451 \text{ J/(mol K)} (universal gas constant)</td>
</tr>
<tr>
<td>( T )</td>
<td>Temperature (300 K used)</td>
</tr>
<tr>
<td>( u )</td>
<td>( \frac{dy}{dx} ) (gradient of the reduced potential)</td>
</tr>
<tr>
<td>( I )</td>
<td>Ionic strength of solution</td>
</tr>
</tbody>
</table>
such solutions are inefficient for infinite-boundary conditions. As a result, the problem is transformed into an initial value problem by integrating equations 4 and 5 once and then applying the boundary conditions for the electric field. This procedure yields a single transcendental equation for the surface potential.

In solving equations 4 and 5, it is convenient to introduce the dimensionless (reduced) potential $y$ through $y = F\phi / RT$. Then, equations 4 and 5 are reduced to the following equations:

$$
\frac{dy}{dx} = -\frac{F}{RT\varepsilon_0} \left[ \rho_m + \sum_{i=1}^{N} FC_i^0 Z_i \exp(-Z_i y) \right] 
$$

(6)

$$
\frac{dy}{dx} = -\frac{F}{RT\varepsilon_0} \left[ \sum_{i=1}^{N} FC_i^0 Z_i \exp(-Z_i y) \right] 
$$

(7)

Since the right-hand side does not depend on $x$, equations 6 and 7 can be integrated by introducing new variables $u = dy/dx$, then

$$
\frac{d^2y}{dx^2} = \frac{du}{dx} = \frac{du}{dy} \frac{dy}{dx} = \frac{u du}{dy} 
$$

Integration of this equation yields the following expression for $u^2$ with the constant of integration $U_1$:

$$
\frac{1}{2} u^2 = \left\{ by - \sum_{i=1}^{N} a_i Z_i \exp(-Z_i y) \right\} + U_1 \text{, for } x < 0 
$$

(8)

where $b = \rho_m F / RT\varepsilon_0$ and $a_i = Z_i C_i^0 F^2 / RT\varepsilon_0$. To determine $U_1$, we note that as $x \to -\infty, y \to y_D$ and $u \to 0$. Substituting this in equation 8 yields

$$
U_1 = by_D - \sum_{i=1}^{N} a_i Z_i \exp(-Z_i y_D) 
$$

(9)

and the expression for the membrane is

$$
\frac{u^2}{2} = \sum_{i=1}^{N} a_i Z_i \exp(-Z_i y_D) - \left\{ by - \sum_{i=1}^{N} a_i Z_i \exp(-Z_i y) \right\} 
$$

(10)

For the solution, as $x \to \infty, y \to 0$ and $u \to 0$. A similar procedure yields the following equation for $x > 0$:

$$
\frac{u^2}{2} = \sum_{i=1}^{N} \frac{2F^2 C_i^0}{RT\varepsilon_0} \left\{ \exp(-Z_i y) - 1 \right\} 
$$

(11)

Since $u$ is proportional to $E$,

$$
\varepsilon_0 \varepsilon_u u^2(x = -0) = \varepsilon_0 \varepsilon_u u^2(x = +0) 
$$

(12)

The transcendental equation for the reduced surface potential $y_0$ is obtained algebraically as follows:

$$
\frac{\varepsilon_0}{\varepsilon_1} \left\{ \rho_m (y_D - y_0) - \sum_{i=1}^{N} C_i^0 F \left[ \exp(-Z_i y_D) - \exp(-Z_i y_0) \right] \right\} 
$$

(13)

$$
= \sum_{i=1}^{N} C_i^0 F \left[ \exp(-Z_i y_D) - 1 \right] 
$$

This equation is solved by bracketing the root around $y_D$ and then using the Brent method (15).

Note that for the special case of a 1-1 electrolyte and with the additional assumption $\varepsilon_m = \varepsilon_1$ (which we believe is incorrect), the analytical expression $y_0 = y_D - \tanh \left( \frac{y_D}{2} \right)$ given in reference 14 follows from equations 13 and 3. We never used this expression, since it is inapplicable when the trace species are present; besides, in our case $\varepsilon_m \neq \varepsilon_1$. So we solved equation 13 numerically instead, which took approximately 1 s on a desktop computer.

To obtain the potential profile across the membrane, the initial value problem for differential equations 6 for $x < 0$ and 7 for $x > 0$ is solved. The initial values for the reduced potential $y(x = 0) = y_0$ are obtained by solving equation 13 for $y_0$ and $dy/dx |_{x=0}$ is calculated from equations 10 and 11, respectively. The sign of $u = dy/dx$ is determined from the following equation:

$$
sign[u(x = 0)] = -sign[y_u] 
$$

(14)

This initial value problem is solved numerically by the Runge-Kutta method with adaptive stepsize control as implemented by Press et al. (15).

The Fortran code that performs these calculations is available from the authors upon request.

**Application to bacterial surfaces.** In this section, the previously described model relating surface potential, Donnan potential, and charge density for an arbitrary ion composition is applied to the surface charging data for five gram-positive bacteria reported by van der Wal et al. (17). Use of data from the latter authors also allows a direct comparison of our results with their similar calculations for simple 1-1 electrolytes.

In calculating the potentials for different electrolytes, the only variables are the concentration and charge of each ion, the surface charge density, and the thickness of the cell wall. In the calculations that follow, the surface charge density at each ionic strength and the thickness of the cell wall were fixed at the values given in Table 2 of reference 17. These values correspond to neutral pH and are listed in that reference for three values of ionic strength, i.e., 0.1, 0.01, and 0.001 M. As the first approximation, the bulk charge density $\rho_m$ in the membrane was calculated by dividing the surface charge density by the cell wall thickness. We assumed $\varepsilon_m = 60$ as suggested by van der Wal et al. (17) and $\varepsilon_1 = 78$, which is the experimental dielectric constant of water. Since we are interested only in solutions at low concentrations, the difference between the dielectric constant of pure water and the solution is relatively small and does not affect the results significantly.

The effects on the surface and Donnan potentials of other ions present in minor concentrations were then calculated. The objective was to demonstrate the conditions (i.e., in terms of ionic strength and minor species charge and concentration) under which species present at low concentration need to be included in the calculations in order to obtain accurate representations of the surface and Donnan potentials. The calculations were performed at three different 1-1 electrolyte concentrations (i.e., 0.001, 0.01, and 0.1 M) with trace (i.e., $10^{-6}$ M) concentrations of divalent or trivalent ions added. The presence of such low concentrations of divalent or trivalent ions is very likely in groundwater systems.

As a first example, the potentials as a function of distance were calculated for Bacillus brevis (selected since it is a common microorganism in soil and vadose sediments) as a function of electrolyte concentration, with a minor charged $+3$ cation (actually 3-1 electrolyte) included in the solution at a fixed
concentration of $10^{-6}$ M (Fig. 1). As can readily be seen, at an electrolyte concentration of 0.1 M, the presence of such a minor concentration of trivalent cation has little or no effect on the surface and Donnan potentials, which are essentially identical to the values reported previously by van der Wal et al. (17). However, at ionic strengths of as low as 0.01 M, a detectable difference begins to appear, and at lower ionic strengths (0.001 M) the differences become marked, with the calculated electrostatic potentials being considerably lower than the calculated values in the absence of the trace trivalent cation. Divalent cations also can effect the calculated potentials at this lower ionic strength (Fig. 2), although the effect is not as large. Interestingly, however, the ion concentration plots for both trivalent and divalent cations present in the bulk solution at $10^{-6}$ M (Fig. 3), which show extremely large concentration effects relative to the concentrations in bulk solution (i.e., ~$2 \times 10^6$ for trivalents and $5 \times 10^5$ for divalents) at an ionic strength of 0.001 M. In fact, in these solutions 65% of the total surface charge is countered by trivalent cations. Clearly, including trace species in the calculation of the surface and Donnan potentials is necessary for accurate modeling of these parameters at these low ionic strengths. This model corresponds to the case of a small amount of bacteria in a significant volume of solution (infinite dilution with respect to the concentration of bacteria). Clearly, if an insufficient mass of the trace species is available, the concentration factor will be smaller. The calculations performed here were based on the values of the surface charge density for neutral pH. Increasing the pH of the solution makes the concentrating effect for the tracer divalent and trivalent cations more pronounced, since the magnitude of the charge density increases (although this effect may be compensated for by increased metal ion hydrolysis and reduced species charge). This effect decreases in acidic solutions. In addition, given the potentially high surface charges that develop under these conditions at bacterial cell surfaces (i.e., $-0.56$ C/m$^2$ for *B. brevis*), any accurate model of microbial metal uptake or charge development would need to include these factors. Similar calculations for all five bacteria
examined by van der Wal et al. (17) are given in Fig. 4. These results show that although there are certainly some differences among the various bacteria, the results for *B. brevis* are likely typical for gram-positive bacteria, and the following results are reported only for *B. brevis*.

With these factors in mind, it is also of interest to examine how the trace species can affect the ion concentration profiles of the bulk, singly charged, counter-, and co-ions (Fig. 5 and 6). These calculations show that the differences in potential calculated for the cell wall in the presence and absence of a trace trivalent cation in dilute electrolyte (Fig. 1) have marked effects on the ion concentration profiles for both the bulk cation (Fig. 5) and the bulk anion (Fig. 6). In the case of the bulk cation, the incorporation of significant concentrations of trivalent species significantly reduces the amount of sorbed bulk, singly charged cation. Correspondingly, the overall reduction in calculated surface and Donnan potentials in the presence of trace trivalent cation results in significant increases in adsorbed bulk co-ion (Fig. 6) compared to the case in which no trace cation is present. These large cation concentration effects make it of interest to determine the thickness of the area from which a membrane is able to concentrate the divalent and trivalent cations. Considering the thickness of the cell wall of *B. brevis* (750 Å) (17) and the concentrating effect of $2 \times 10^5$ found for trivalent cations, we estimated an upper bound of 1.5 mm for this distance. The same calculation for divalent cations yielded 0.375 mm. In other words, simple electrostatic considerations dictate that these microorganisms have the ability to scavenge trace species at length scales 1,000 times greater than the cell size.

Although consideration of minor highly charged species is certainly important, it needs to be pointed out that the very large concentration effects of minor divalent and trivalent species predicted for the microbial membranes is limited to more dilute solutions ($I \leq 0.01$ M). For example, comparing the predicted concentrations within the microbial membrane at the same concentration of trace trivalent cation ($10^{-6}$ M) between ionic strengths of 0.001 and 0.1 M (Fig. 7) shows that despite an increase in surface charge from $-0.56$ to $-1.25$ C/m$^2$ that occurs between these two solutions, the trivalent cation is concentrated by a factor of $10^3$ less in the 0.1 M solution than in the 0.001 M solution. Clearly, the electrostatic effects on trace metal ion are much more effective in dilute electrolytes than in concentrated electrolytes.

It is also of interest to compare the concentration factors predicted based on this electrostatic model with experimental data on bacterial metal uptake. Unfortunately, we are aware of no definitive study that measures all of the parameters (i.e., ionic strength, cell wall charge, pH, metal uptake, and cell wall volume) necessary to perform definitive calculations. Given these facts, the best data set available to test at least qualitatively the importance of electrostatics on the uptake of a wide range of metal ions is the data described by Beveridge and Murray (4), who measured the uptake of several divalent and trivalent metal ions on *B. subtilis* at a total metal concentration of $5 \times 10^{-3}$ M. Although the high metal concentrations used in these studies are not expected to result in large concentration factors, it is still of interest to contrast the experimental data with a model predicting metal uptake based solely on elec-

**FIG. 5.** Calculated ion concentration profiles for the bulk +1 counter ion and the trace trivalent cation ($10^{-6}$ M bulk concentration) in 0.001 M 1-1 electrolyte with and without considering the effects of trace trivalent cation concentration for *B. brevis*.

**FIG. 6.** Calculated ion concentration profiles for the bulk –1 co-ion with and without considering the effects of trace trivalent cation concentration ($10^{-6}$ M bulk concentration) for *B. brevis* in 0.001 M 1-1 electrolyte.

**FIG. 7.** Calculated ion concentration profiles for trace trivalent cations ($10^{-6}$ M bulk concentration) in 0.001 and 0.1 M 1-1 electrolyte.
Electrostatic concentration effects. Unfortunately, the ionic strength of the solution, pH, and surface charge density were not reported by Beveridge and Murray (4). Therefore, in order to proceed, the following two assumptions are necessary: (i) the surface charge density is estimated from the data for B. brevis (17) and (ii) the solutions are assumed to be neutral (pH = 7).

Since the surface charge density is critical, we present the calculated concentration factors for three surface charge densities at different ionic strengths (Table 2). As a reference point, the ionic strengths of a $5 \times 10^{-2}$ M MeX$_2$ or MeX$_3$ solution would be 0.015 and 0.03 M, respectively, assuming that no additional components are present and no metal hydrolysis or precipitation occurred. The experimental data for several metals (4), expressed as dimensionless ratios of concentrations at different ionic strengths (Table 2), appear to explain the values vary dramatically between different cations but that the electrostatic calculations alone (Table 2) appear to explain the observations. The experimental data for several metals (4), expressed as dimensionless ratios of concentrations at different ionic strengths (Table 2). As a reference point, the ionic strengths of a $5 \times 10^{-2}$ M MeX$_2$ or MeX$_3$ solution would be 0.015 and 0.03 M, respectively, assuming that no additional components are present and no metal hydrolysis or precipitation occurred. The experimental data for several metals (4), expressed as dimensionless ratios of concentrations at different ionic strengths (Table 2), appear to explain the observations. The experimental data for several metals (4), expressed as dimensionless ratios of concentrations at different ionic strengths (Table 2), appear to explain the observations. The experimental data for several metals (4), expressed as dimensionless ratios of concentrations at different ionic strengths (Table 2), appear to explain the observations. The experimental data for several metals (4), expressed as dimensionless ratios of concentrations at different ionic strengths (Table 2), appear to explain the observations.

TABLE 2. Concentration factors for divalent and trivalent tracer cations as a function of surface charge calculated for B. brevis$^a$

<table>
<thead>
<tr>
<th>Cation</th>
<th>Concentration factor</th>
<th>Reason for concentration factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mg$^{2+}$</td>
<td>783</td>
<td>Specific binding</td>
</tr>
<tr>
<td>Ca$^{2+}$</td>
<td>38</td>
<td>Electrostatics (?)</td>
</tr>
<tr>
<td>Sr$^{2+}$</td>
<td>2.6</td>
<td>Electrostatics</td>
</tr>
<tr>
<td>Mn$^{2+}$</td>
<td>76.3</td>
<td>Specific binding</td>
</tr>
<tr>
<td>Ni$^{2+}$</td>
<td>10.2</td>
<td>Electrostatics</td>
</tr>
<tr>
<td>Pb$^{2+}$</td>
<td>1.9</td>
<td>Electrostatics</td>
</tr>
<tr>
<td>Cu$^{2+}$</td>
<td>285</td>
<td>Specific binding</td>
</tr>
<tr>
<td>Al$^{3+}$</td>
<td>0</td>
<td>Metal hydrolysis (?)</td>
</tr>
<tr>
<td>Fe$^{3+}$</td>
<td>341</td>
<td>Specific binding</td>
</tr>
</tbody>
</table>

$^a$ C$^o$ = 0.005 M. Charge densities for each ion strength and cell wall width (75 nm) are from van der Wal et al. (17).

$^b$ Concentration factor well within the cell wall, calculated from Donnan potential according to equation 1.

with improved experimental data on surface charge and metal binding, better understanding of the specific mechanisms of metal uptake can be obtained.

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