Variability of the Influence of Physicochemical Factors Affecting Bacterial Adhesion to Polystyrene Substrata

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The role of electrostatic and hydrophobic interactions and solid and liquid surface tensions in the adhesion of four bacterial species (Pseudomonas fluorescens, Enterobacter cloacae, Chromobacterium sp., and Flexibacter sp.) to hydrophobic polystyrene petri dishes and to more hydrophilic polystyrene tissue culture dishes was measured for adhesion of the effects of different electrolyte solutions on attachment to and of different electrolyte and pH solutions on detachment from the polystyrene substrate. The significance of solid and liquid surface tensions and hydrophobic interactions was investigated by measuring the effects of different surfactants (including a concentration series of dimethyl sulfoxide) on adhesion and detachment. Adhesion varied with bacterial species, substratum, and electrolyte type and concentration, with no apparent correlation between adhesion and electrolyte valence or concentration. The influence of different pH and detergent solutions on bacterial detachment also varied with species, substratum, pH, and detergent type; however, the greatest degree of detachment of all strains from the surfaces was produced by detergent treatment. The results suggest that adhesion cannot be attributed to any one type of adhesive interaction. There was some evidence for both electrostatic and hydrophobic interactions, but neither interaction could wholly account for the data.

The adhesion of a bacterium to a solid surface is dependent upon attractive forces between the two surfaces (12, 17, 30, 31). At the same time, repulsive forces can occur which may offset the attractive interaction or even inhibit adhesion. These physicochemical forces of attraction and repulsion include long-range forces, e.g., electrostatic interactions and van der Waals forces, and short-range interactions, e.g., dipole interactions, chemical (electrostatic, covalent, hydrogen) bonding, and hydrophobic interactions. Electrostatic interactions were investigated by the Derjaguin-Landau-Verwey-Overbeek (DLVO) theory. (For a more detailed discussion of the theory and its application to bacterial adhesion, see references 19, 30, and 31.)

Long-range forces may prevent contact between the bacterial and solid surfaces. Most bacteria have a net negative charge (15), as do most solid surfaces. Thus, electrostatic repulsion between surfaces of like charge will tend to prevent close approach between surfaces (31). If repulsion is strong enough, the two surfaces will not come close enough for adhesion to occur. Whether repulsion thus prevents adhesion depends upon the balance between opposing attraction and repulsion forces, and this has been described by the Derjaguin-Landau-Verwey-Overbeek (DLVO) theory. (For a more detailed discussion of the theory and its application to bacterial adhesion, see references 19, 30, and 31.) If the bacterial and substrate surfaces come close together (ca. <0.4 nm), adhesion may occur if short-range attractive forces are sufficient. A short-range interaction which has been implicated in bacterial adhesion is hydrophobic "bonding," which involves the interaction of nonpolar groups on opposing surfaces (33). The short-range physicochemical forces of a surface can be indirectly evaluated by measuring its surface tension or surface free energy (3), and surface free energies or related parameters have been measured for both substratum (2, 21) and bacterial (2) surfaces.

A number of workers have tried to evaluate the role of long- and short-range forces in bacterial adhesion. The significance of long-range electrostatic interactions has been investigated by determining the effect of electrolytes or surface charges on attachment. Adhesion should be promoted by an increase in electrolyte concentration or a reduction in charge difference on the two opposing surfaces. Accordingly, the adhesion of some bacteria to some surfaces, e.g., Enterobacter sp. strain R8 to glass (19), Pseudomonas aeruginosa to stainless steel (32), and Vibrio alginolyticus to hydroxyapatite (14), has been increased by increasing the electrolyte concentration in the medium (23, 24). On the other hand, other studies have found no relationship between attachment and surface charge of particular bacteria (1) or electrolyte concentration (19).

The influence of short-range forces on bacterial adhesion has been investigated by determining the relationship between attachment and the surface energies of the substrata or bacterial surfaces. A number of studies have shown adhesion to be related to substratum surface energy (2, 10) or to related parameters (e.g., hydrophobicity [24], whereas others have found little relationship (34). Similarly, adhesion has been found to be related to the surface energy of the bacteria (evaluated by contact angle measurements on lawns of cells) (2), while other studies have found no relationship between attachment and bacterial surface energy (20).

The discrepancies in these data are difficult to resolve. Possibly, long-range effects are negligible when short-range factors are dominant, and vice versa, depending upon the experimental conditions. However, most studies have concentrated on only one of the two aspects, e.g., electrostatic or free-energy effects (exceptions are references 10 and 16), making a comparison of their relative significance impossible. Thus, the aim of this study was to investigate the significance of both electrostatic and hydrophobic interactions in the permanent adhesion of four freshwater bacteria to polystyrene surfaces. To evaluate the significance of

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**TABLE 1. Effect of electrolyte solutions on bacterial adhesion**

<table>
<thead>
<tr>
<th>Electrolyte and conc</th>
<th>P. fluorescens</th>
<th>E. cloacae</th>
<th>Chromobacterium sp.</th>
<th>Flexibacter sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PD</td>
<td>TCD</td>
<td>PD</td>
<td>TCD</td>
</tr>
<tr>
<td>0.01 M NaCl</td>
<td>1.67</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>0.1 M NaCl</td>
<td>1.90</td>
<td>1</td>
<td>1</td>
<td>0.76</td>
</tr>
<tr>
<td>0.01 M MgCl₂</td>
<td>1</td>
<td>0.68</td>
<td>0.61</td>
<td>0.67</td>
</tr>
<tr>
<td>0.1 M MgCl₂</td>
<td>1.38</td>
<td>1</td>
<td>0.70</td>
<td>0.41</td>
</tr>
<tr>
<td>0.1 M AlCl₃</td>
<td>2.52</td>
<td>0.67</td>
<td>0.72</td>
<td>0.64</td>
</tr>
</tbody>
</table>

* Results are expressed as Iₐ (index of attachment; see the text).

**MATERIALS AND METHODS**

**Adhesion assays.** Four freshwater isolates (27), *Pseudomonas fluorescens*, *Enterobacter cloacae*, *Chromobacterium* sp., and *Flexibacter* sp., were grown to stationary phase in 0.1% (wt/vol) bacteriological peptone-0.07% (wt/vol) yeast extract (PYE), pH 7.4, at 15°C. Cultures were harvested by centrifugation and washed once in 0.01 M HEPES (N-2-hydroxyethylpiperazine-N’-2-ethanesulfonic acid) buffer, pH 7.4 (Sigma Chemical Co., St. Louis, Mo.). The isolates were suspended to a concentration of 1 × 10⁸ to 3 × 10⁹ cells ml⁻¹ in solutions containing (i) 0.01 or 0.1 M NaCl, 0.01 or 0.1 M MgCl₂, or 0.1 M AlCl₃, all in 0.01 M HEPES buffer, pH 7.4, or (ii) dimethyl sulfoxide (DMSO; Fisons Scientific Equipment, Loughborough, England) at concentrations of 3, 6, 9, 12, 15, or 18% (vol/vol) in distilled water. Controls were suspended in buffer containing no electrolyte and no DMSO. The liquid surface tensions of the DMSO solutions, before addition of the bacteria, were measured by using a platinum loop and torsion balance (White Electrical Instruments, Malvern Link, England).

The method for evaluating bacterial attachment has been described previously (20). Briefly, 5-ml samples of each different cell suspension were placed in duplicate polystyrene PD (5 cm diameter; Sterilin, Teddington, England) or polystyrene TCD (5 cm diameter; Costar, Cambridge, Mass.), and bacteria were allowed to attach to substrata for 60 min at 15°C. The surfaces were then rinsed three times with 0.01 M HEPES (pH 7.4) to remove loosely attached bacteria, and the permanently attached cells were fixed with Bouin fixative and stained with crystal violet. Numbers of attached bacteria were indirectly estimated by measuring the A₉₀₀ of attached bacteria on four randomly selected areas of each substratum. Results were recorded as A₉₀₀ or, to normalize results, as an index of adhesion (20), i.e., PD/Iₐ or TCD-Iₐ. Iₐ values were calculated as ratios of A₉₀₀ of the test surface to that of the PD or TCD control surface, i.e., PD test/PD control. The 95% confidence limits of the means (n = 8) of A₉₀₀ values were calculated, and Iₐ values of unity were recorded for treatments in which the confidence limits of the experimental mean overlapped with those of the control. All of the adhesion experiments were repeated at least once.

**Cell and solid surface tension estimation.** (i) **Cell surface tension.** *P. fluorescens*, *E. cloacae*, *Chromobacterium* sp., and *Flexibacter* sp. were grown to late stationary phase in PYE (pH 7.4, 15°C). The cells were harvested and washed (once in 0.15 M NaCl) by centrifugation. Each culture was suspended to approximately 10¹⁰ cells ml⁻¹ in 0.15 M NaCl. Liquid contact angles (θₛ) on lawns of these cells were then measured by the method of Absalom et al. (2). Contact angles of 10-μl drops of 0.15 M NaCl were measured with a vernier microscope with a goniometer eyepiece (Precision Optik and Instrument, Thornton Heath, England). θₛ values were recorded every 10 min, each with a freshly placed drop, until there were no further changes in contact angle; this plateaus value was recorded as θₛ. The surface tension of

**TABLE 2. Effect of electrolyte and DMSO concentrations on bacterial growth**

<table>
<thead>
<tr>
<th>Conc of electrolyte or DMSO</th>
<th>P. fluorescens</th>
<th>E. cloacae</th>
<th>Chromobacterium sp.</th>
<th>Flexibacter sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>No added electrolyte</td>
<td>0.400</td>
<td>0.400</td>
<td>0.600</td>
<td>0.097</td>
</tr>
<tr>
<td>0.01 M NaCl</td>
<td>0.550</td>
<td>0.303</td>
<td>0.079</td>
<td>0.175</td>
</tr>
<tr>
<td>0.1 M NaCl</td>
<td>0.637</td>
<td>0.228</td>
<td>0.110</td>
<td>0.204</td>
</tr>
<tr>
<td>0.01 M MgCl₂</td>
<td>0.630</td>
<td>0.378</td>
<td>0.317</td>
<td>0.296</td>
</tr>
<tr>
<td>0.1 M MgCl₂</td>
<td>0.431</td>
<td>0.402</td>
<td>0.193</td>
<td>0.099</td>
</tr>
<tr>
<td>0.1 M AlCl₃</td>
<td>0.117</td>
<td>0.126</td>
<td>0.145</td>
<td>0.099</td>
</tr>
<tr>
<td>0% DMSO</td>
<td>0.400</td>
<td>0.400</td>
<td>0.600</td>
<td>0.095</td>
</tr>
<tr>
<td>3% DMSO</td>
<td>0.445</td>
<td>0.385</td>
<td>0.330</td>
<td>0.095</td>
</tr>
<tr>
<td>6% DMSO</td>
<td>0.295</td>
<td>0.160</td>
<td>0.195</td>
<td>0.090</td>
</tr>
<tr>
<td>9% DMSO</td>
<td>0.070</td>
<td>0.075</td>
<td>0.002</td>
<td>0.075</td>
</tr>
<tr>
<td>12% DMSO</td>
<td>0.015</td>
<td>0.035</td>
<td>0.060</td>
<td>0.010</td>
</tr>
<tr>
<td>15% DMSO</td>
<td>0.015</td>
<td>0.010</td>
<td>0.030</td>
<td>0.010</td>
</tr>
<tr>
<td>18% DMSO</td>
<td>0.010</td>
<td>0.010</td>
<td>0.025</td>
<td></td>
</tr>
</tbody>
</table>

* Turbidity (A₄₅₀) was measured after 16 h of growth at 15°C.
cells from each culture was estimated from their respective \( \theta \) values by using an empirically derived equation (2).

(ii) Solid surface tension of PD and TCD. The surface tensions of the PD and TCD substrata were determined in the same way as were surface tensions of cells, except that the contact angles of distilled water on clean PD and TCD surfaces were measured.

Bacterial orientation at a hydrocarbon/water interface. The method used was based on that of Marshall and Cruickshank (18). The four isolates were grown in pure culture to late stationary phase in PYE (pH 7.4, 15°C) and harvested by centrifugation. The pellets were suspended to a concentration of \( 1 \times 10^7 \) to \( 3 \times 10^7 \) cells ml\(^{-1}\) in 0.01 M HEPES (pH 7.4). Drops of cell suspension were placed on a microscope slide and covered with a cover slip. Hexadecane (100 \( \mu \)l) was then applied at the edge of the cover slip so that it was drawn underneath by capillary action and formed an interface with the suspension. The orientation of cells at the interface was observed by phase-contrast microscopy.

Detachment assays. The isolates were grown to stationary phase in PYE (pH 7.4, 15°C), centrifuged, washed, and suspended (as above) in 0.01 M HEPES (pH 7.4) to an optical density of 0.1 at 540 nm (approximately \( 1 \times 10^7 \) to \( 3 \times 10^7 \) cells ml\(^{-1}\)). The organisms were then allowed to adhere to PD and TCD surfaces for 60 min by the adhesion assay procedure (see above). One set of duplicate plates of PD and TCD was washed to remove loosely attached bacteria before being fixed and stained, and these served as controls. Remaining duplicate surfaces were then exposed for 60 min at 15°C to 5 ml of either 0.01 M HEPES buffer (pH 5, 7, or 9) or 0.01 M HEPES buffer (pH 7) solution containing one of the following: 0.1 M NaCl, 0.1 M MgCl\(_2\), 0.1% (vol/vol) sodium dodecyl sulfate (BDH, Poole, England), 0.1% (vol/vol) RBS 25 [Chemical Concentrates (RBS) Ltd., London, England] or 0.1% (vol/vol) Tween 80 (Sigma). The surfaces were then washed and stained, and numbers of attached cells were estimated as described above. The results were expressed as an index of detachment (PD-I\(_D\), TCD-I\(_D\)), where I\(_D\) represents numbers of cells after a 1-h detachment period, divided by numbers of attached cells on control surface. The detachment experiments were repeated at least once.

Growth of electrolyte and DMSO PYE media. Duplicate 5-ml tubes of PYE media, buffered at pH 7.4 with 0.01 M HEPES, were inoculated with 100 \( \mu \)l of stationary-phase cells of the isolates. The PYE media contained the concentrations of electrolytes and DMSO used for the adhesion assays (see above). After growth at 15°C for 16 h, values of A\(_{540}\) of the cultures were measured to estimate growth.

**RESULTS**

Effect of different electrolytes on adhesion to PD and TCD. The concentration and type of electrolyte influenced the adhesion of the bacterial isolates to PD and TCD surfaces, and the effect varied with bacterial species and with solid substratum (Table 1). The electrolyte solutions affected the growth of all isolates (Table 2), but there was no apparent relationship between growth and bacterial adhesion in the solutions (Tables 1 and 2).

**Effect of liquid and solid surface tensions on adhesion to PD and TCD surfaces.** The liquid surface tension (\( \gamma_{LV} \)) values for the DMSO solutions were 7.2, 7.1, 6.9, 6.8, 6.5 \( \mu \)J cm\(^{-2}\) for 0, 3, 6, 9, 12, 15, and 18% (vol/vol) DMSO, respectively. The only isolate whose adhesion changed considerably with differences in suspending liquid \( \gamma_{LV} \) (Table 3) was *E. cloacae* (Fig. 1), in that its adhesion to both PD and TCD decreased with decreasing \( \gamma_{LV} \). The relationship between adhesion and \( \gamma_{LV} \) was also different for the two surfaces. With all isolates and both substrata, there was no apparent relationship between change in adhesion, \( \gamma_{LV} \), and surface tension of the bacterial surface (\( \gamma_{YSV} \)) of the cells (Fig. 1; Table 3). In general, the comparative suitability of the substrate for attachment was largely unaltered over the \( \gamma_{LV} \) range used; e.g., *P. fluorescens* cells attached more to TCD than to PD at most \( \gamma_{LV} \) values (Fig. 1). There was no correlation between the influence of \( \gamma_{LV} \) on adhesion and the progressive inhibition of growth of all isolates by increasing concentrations of DMSO (Table 2).

**Detachment of attached bacteria by electrolyte, surfactant, and pH treatments.** The additional 1-h incubation in buffer (pH 5, 7, or 9) or in NaCl or MgCl\(_2\) solutions resulted in no or little detachment of all strains tested (Table 4). Treatment with each of the detergents either increased bacterial detachment from the substrata or had no effect, depending on the species and attachment surface (Table 4). *P. fluorescens* cells detached markedly under all the detergent treatments, although to a lesser extent under the RBS treatment. In all cases the effect on detachment was greatest with PD.
4). Tween 80 and sodium dodecyl sulfate increased detachment of *E. cloacae* from both PD and TCD (Table 4). *Chromobacterium* sp. and *Flexibacter* sp. responded similarly to treatment with sodium dodecyl sulfate and RBS, detaching from the PD surface but not from TCD. Tween 80 increased detachment of *Chromobacterium* sp. from PD but had no effect on *Flexibacter* sp.

**Orientation of bacteria at a hydrocarbon/water interface.** *Flexibacter* cells became oriented perpendicular to the hydrocarbon interface in an "end-on" arrangement. Once associated with the hexadecane phase, the *Flexibacter* sp. did not desorb from the interface, and there was no observable exchange between the interface and the aqueous phase. When small droplets of hexadecane were dispersed in the aqueous phase, some accumulated at the poles of *Flexibacter* cells.

*P. fluorescens*, *E. cloacae*, and the *Chromobacterium* sp. demonstrated neither adhesion to the interface nor any characteristic orientation; cells tended to stream along the interface or to exchange between the interface and the bulk phase.

**DISCUSSION**

Previous reports have suggested that long-range electrostatic repulsion forces can influence bacterial adhesion to surfaces (10, 19). In such cases, adhesion to like-charged surfaces (such as TCD) should be facilitated in the presence of electrolytes (30, 31). In the present study, although electrolytes clearly influenced attachment, there was no apparent relationship between electrolyte concentration or valency and adhesion. Promotion of adhesion was uncommon (e.g., *P. fluorescens* on PD), and in many cases electrolytes inhibited adhesion (Table 1). Similarly, the effect of pH (which would affect electrostatic interactions [35]) on desorption of attached cells showed no consistent pattern (Table 4). This suggests that there is more than one mechanism by which the solutions with various electrolytes and pHs affected adhesion and, accordingly, that the molecular interactions responsible for adhesion differed with given combinations of organism, surface, and electrolyte. Alternative ways in which electrolytes could affect adhesion are through influencing bacterial physiological processes (20), adhesive conformation and efficiency, or hydrophobic interactions; these are considered in turn below.

First, the physiological status of bacteria can affect their adhesion to surfaces, since adhesiveness has been shown to depend upon growth phase (7), nutrient concentration (5, 16), and medium composition (20). The electrolyte solutions used in this study influenced growth (Table 2), and, accordingly, cell surface components (and thus adhesive ability) could also have been altered. However, there is no apparent correlation between growth and adhesive ability. Thus, it is unlikely that physiological effects wholly account for the adhesion differences observed with the different electrolytes.

Second, electrolytes could have a direct effect on adhesion interactions either by influencing short-range electrostatic interactions (e.g., by screening or cross-linking charged groups [8]) or by modifying the conformation of extracellular cell surface adhesives (29). Either process could promote or inhibit adhesion, depending upon adhesive characteristics. Alternatively, cations could promote attachment by cross-linking anionic groups on the bacterial and substrate surfaces (22). Cross-linking could explain the increased adhesion of *P. fluorescens* and *Chromobacterium* sp. in the presence of Al³⁺.

Third, electrolytes could influence adhesion through their effect on hydrophobic interactions, since, within limits, increased electrolyte concentrations tend to increase the strength of interaction (26). Hydrophobic interactions have been implicated in bacterial adhesion to inert substrata (11, 12, 18, 28), and the surfaces used in this investigation, particularly PD, are largely hydrophobic (27). However, if this were the basis for the observed electrolyte effect on adhesion, then an increase in adhesion with electrolyte concentration would be expected. Moreover, the effect could be more apparent with the more hydrophobic of the two surfaces, PD. Thus, the data do not support this explanation.

On the other hand, evidence for hydrophobic interactions was provided by experiments with surfactants measuring the detachment of cells; detergents desorbed all of the isolates from at least one of the test substrata (Table 4). Moreover, the removal of bacteria was more pronounced with PD, the more hydrophobic of the two surfaces. However, detergents were not always effective in removal of attached cells (e.g., *Chromobacterium* sp. and *Flexibacter* sp. with TCD), demonstrating that hydrophobic interactions cannot be the primary basis for all adhesive interactions of these organisms.

Bacterial adhesion to surfaces can be analyzed in thermodynamic terms (9, 12, 13), and models with thermodynamic parameters have been used successfully to predict adhesion (2, 21). According to a model proposed by Absolom et al. (2), bacterial adhesion should increase with increasing surface tension of the substratum (γSV) if γLV is lower than γSV; if

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**TABLE 4. Detachment of bacteria after incubation in solutions of different pH or containing electrolytes**

<table>
<thead>
<tr>
<th>pH or electrolyte conc of solution</th>
<th><em>P. fluorescens</em></th>
<th><em>E. cloacae</em></th>
<th><em>Chromobacterium</em> sp.</th>
<th><em>Flexibacter</em> sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PD TCD</td>
<td>PD TCD</td>
<td>PD TCD</td>
<td>PD TCD</td>
</tr>
<tr>
<td>pH 5</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>pH 7</td>
<td>1</td>
<td>1</td>
<td>1.2</td>
<td>0.79</td>
</tr>
<tr>
<td>pH 9</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>0.1 M NaCl</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>0.1 M MgCl₂</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>0.1% SDS</td>
<td>0.11</td>
<td>0.31</td>
<td>0.14</td>
<td>0.67</td>
</tr>
<tr>
<td>0.1% RBS</td>
<td>0.34</td>
<td>0.8</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>0.1% Tween 80</td>
<td>0.02</td>
<td>0.5</td>
<td>0.63</td>
<td>0.69</td>
</tr>
</tbody>
</table>

* a: Detachment is expressed as Iₐ (index of detachment; see the text).
  b: SDS; Sodium dodecyl sulfate.
γLV is higher than γBV, adhesion should decrease. Some bacterial adhesion data from other studies have been consistent with this model (12). However, in the present study, there was no appreciable change in numbers of attached bacteria with change in γLV, and adhesion did not change as predicted by the model. This lack of consistency with the model could indicate that electrostatic interactions are making a significant contribution to the adhesive interaction, since it has been suggested (2) that electrostatic interactions can produce deviations from the predicted adhesive interactions. Other factors which could have contributed to the predictive failure of the model in this case were inherent difficulties in determining bacterial surface tensions from contact angles (4) and physiologically derived modifications of adhesive ability produced by DMSO (Table 2).

Thus, the data indicate that both electrostatic and hydrophobic interactions can play a role in adhesion, but that neither is dominant in all situations. This suggests that a bacterium may use alternative mechanisms for adhesion, depending upon conditions and surfaces. The possibility of separate adhesion mechanisms with PD and TCD was also suggested by studies with "Vibrio proteolytica." Triton X-100 removed cells attached to PD, but was ineffective with those attached to glass or TCD (25). Such potential for alternative adhesive mechanisms is likely, in view of the chemical and structural heterogeneity of the bacterial surface. For example, the behavior of P. fluorescens, E. cloacae, and the Chromobacterium sp. at the hydrocarbon/water interface indicated that none had a predominantly hydrophobic surface. With Flexibacter sp., hydrophobic regions were concentrated at the poles (as previously observed with Flexibacter aurantiacus [18]), although these cells lie lengthwise on the surface when permanently attached. Thus, with all four strains, the nonpolar groups which participate with hydrophobic surfaces in hydrophobic adhesive interactions are probably dispersed on the cell surfaces, along with the polar and charged groups which can enter into electrostatic or polar adhesive interactions with other, less hydrophobic surfaces.

In conclusion, adhesion to a solid surface could not be attributed to any one type of adhesive interaction. The evidence suggests that both electrostatic and hydrophobic interactions may contribute to adhesion but that the balance, and perhaps mutual reinforcement (6), of these interactions depends on the properties of the various components of the adhesive interaction. These include the bacterium and its associated physiological and surface adhesive properties, the surface, and environmental factors, such as electrolyte or surfactant concentration or pH. This probably accounts for the lack of agreement on the relative importance of thermodynamic and electrostatic factors reported in the literature.

ACKNOWLEDGMENTS

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LITERATURE CITED

PHYSICOCHEMICAL FACTORS AND BACTERIAL ADHESION

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