

The role of outer membrane *c*-type cytochromes in the adhesion of *Shewanella* to goethite

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The microbial iron reduction is the main driving force for iron biogeochemical cycle. Adhesion of dissimilatory iron-reducing bacteria to iron oxide has shown to determine the reduction efficiency, which facilitates the direct electron transfer between bacteria and mineral. For most *Shewanella* strains, OmcA and MtrC are the essential outer membrane proteins for the extracellular electron transfer pathway. Previous researches have demonstrated that these outer membrane *c*-type cytochromes form specific bonds with iron oxides. Meanwhile, whether they play a role in bacterial adhesion onto iron oxide surface remained vague. The objective of this study is to investigate the contribution of OmcA and MtrC to the adhesion of *S. oneidensis* MR-1 to goethite. The different adhesion processes of wild type and cytochrome-deficient mutants were recorded by quartz crystal microbalance with dissipation monitoring (QCM-D). The wild-type cells underwent three phases of adhesion processes and eventually displayed a Sauerbrey-type mass adsorption which developed a rigid layer on goethite surface. Comparing with wild-type *Shewanella*, less $\Delta mtrC$ cells adhered on goethite in the first stage of adhesion and $\Delta mtrC\text{-}\Delta omcA$ showed the minimum cell attachment. Two-dimensional correlation ATR-FTIR spectroscopy demonstrated that bacterial phosphate-moieties contributed significantly to the initial attachment and carboxyl groups involved in long-term bacteria-mineral interfacial reaction. The direct interaction force between *Shewanella* cells and goethite was further evaluated by AFM. The mechanical analysis revealed that OmcA dominated the interaction force which formed strong bonds with iron oxide. Consequently, MtrC played a vital role in the initial attachment and OmcA was crucial to develop a tight *Shewanella*-goethite interaction. Taken together, this study improved our understanding of the role of outer membrane cytochromes in *Shewanella* - mineral interaction.