Oxidation of Fe(II)-bearing smectite by *Sideroxydans lithotrophicus* in low oxygen conditions

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Fe(II)-bearing smectite, a major weathering product of basalt, is widespread in the subsurface and may serve as a large, solidphase electron donor for microbial communities. However, the potential of Fe(II)-smectite to be oxidized by microbes has not been well studied because most prior research on smectites has focused on the microbial reduction of Fe(III)-substitutions. In this study, we explored whether trioctahedral Fe(II)-bearing smectite can support the growth of Fe(II)-oxidizing bacteria (FeOB) by acting as an electron donor. We observed growth of a representative microaerophilic FeOB Sideroxydans lithotrophicus ES-1 on chemical synthesized Fe(II)-smectite and 2% oxygen as the electron donor and acceptor, respectively. Sequential extraction of different Fe(II) species in clays shows that the microbes primarily oxidize Fe(II) on the sheet edges but can also partially access the interior, structural Fe(II). Further mineral characterization by X-ray absorption spectroscopy and Mössbauer spectroscopy shows that ES-1 can increase the extent of Fe(II) oxidation relative to the abiotic control under our experimental condition. However, the resulting Fe(III) remains in the smectite structure, as no secondary minerals were detected in either the biotic or abiotic oxidation products. Comparative gene expression and proteomics of ES-1 grown on Fe(II)-smectite and Fe(II)-citrate show different expression patterns of the candidate Fe(II) oxidases in ES-1, indicating that microbes might use distinct pathways to access solid and aqueous Fe(II) sources. These results suggest that FeOB could use the large solid Fe(II) reservoir in the subsurface and may be a key driver of mineral transformations in ocean crust and other weathered basalts.