

Expanding the Frontiers of the Virosphere: Viruses in the Subsurface

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Viruses are the most abundant biological entities on Earth and have been identified everywhere that life has been found. In surface environments, viruses are known to be mediators of global biogeochemical cycling by infecting and killing host cells, thereby releasing biomass-bound carbon, nitrogen, and other elements. However, the role that viruses play in subsurface systems remains poorly understood. Viral infection of subsurface microbial communities may be widespread as shown by the presence of viral sequences, integrated prophage, as well as CRISPR (Clustered Regularly Interspaced Short Palindromic Repeat) sequences. Full genomes of 56 Bacteria and Archaea isolates from various subsurface environments were analyzed for viral genes and CRISPR sequences. Integrated viral genes were detected in 50% of subsurface genomes, and CRISPR sequences were detected in 79%, suggesting that viral infection may be prevalent and may play an important role in the subsurface. The activity of subsurface viruses is also likely correlated with the local geochemical conditions which influence host metabolism. Viruses and cells were enumerated in groundwater from a shallow aquifer at Rifle, Colorado (USA). Viruses and cells were positively correlated (Spearman's $r_s=0.46$, $p<0.05$ and $r_s=0.54$, $p<0.05$; respectively) to dissolved organic carbon (DOC) concentrations, with both being more abundant in organic-rich regions of the aquifer. Experimental stimulation of microbial activity within a section of the aquifer through the injection of oxygenated groundwater resulted in an increase in virus-to-cell ratio by 1.8-3.4 times, indicating that subsurface viruses are responsive to changes in geochemical conditions. A possible consequence of subsurface viral infection may be cell lysis, which would result in a flux of organic matter from biomass to environmental pools of dissolved organic matter/particulate organic matter (DOM/POM). As a result, viruses have the potential to influence carbon biogeochemistry in subsurface systems. This process may be especially important in deep subsurface environments where energy and nutrients are limiting. In order to expand the frontiers of the virosphere, it will be necessary to determine the nature of viruses under conditions of extreme energy limitation in the deep subsurface and how viruses may be playing a role in the functioning of the deep subsurface ecosystem.

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