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NEW INSIGHTS INTO MICROBIAL WAX ESTER BIOSYNTHESIS, NATURAL OCCURRENCE AND ADAPTIVE ROLE

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Introduction

Many prokaryotes accumulate lipophilic compounds as intracellular inclusions in response to environmental stress or growth under imbalanced conditions. The accumulation of storage lipids is advantageous for cell survival in natural habitats and the capability for their synthesis may provide a strong advantage during evolution. Wax esters (WE) are a major class of storage lipid compounds synthesized by bacteria in which they can have different physiological functions such as energy and carbon storage, deposit for toxic or useless cellular metabolites and resistance towards desiccation (Steinbüchel and Wältermann, 2020).

So far, the potential for WE biosynthesis by prokaryotes has been mostly investigated in aerobic bacteria, and this metabolic capacity is considered not to have arisen in archaea (Wang et al., 2019). Additionally, the use of WE in geochemical and environmental studies has been overlooked due to their apparent rapid hydrolysis during early diagenesis. However, some reports have documented a possible formation of WE by facultative (Rontani et al., 1999) or phototrophic (van der Meer et al., 2010) anaerobic bacteria, and WE have been reported in up to 40,000 years old lacustrine sediments (Cranwell, 1986), suggesting their possible formation in anoxic environments and preservation in the geological record under adequate conditions. Here, we present a combination of recent data demonstrating i) the potential of some strict anaerobic bacteria to produce WE and sulfurized derivatives, ii) the production of specific WE in a polyextreme environments by new (yet unknown) groups of anaerobic bacteria and, iii) the recycling of archaeal biomass in the form of WE as a microbial strategy to survive in the deep biosphere.

Results and discussion

The study of the anaerobic biodegradation of *n*-alkyl substrates by pure strains of sulfate-reducing bacteria (SRB) grown under laboratory conditions showed the formation of series of long-chain WE which distributions appeared substrate-dependent (Grossi et al., in prep.). Thiowax esters (TWE) were also produced during growth on some unsaturated substrates, indicating that, in addition of being used as carbon and energy sources, part of the substrates can be sulfurized and serve as building blocks for TWE biosynthesis. This is the first report of the biosynthesis of WE by SRB and of the bacterial formation of TWE from non-sulfur substrates. Our results further demonstrate that abiotic and biotic sulfurization processes can concomitantly occur during microbial sufate-reduction, and that sulfurization of OM can lead to the formation of organosulfur compounds that, in turn, can potentially fuel microbial communities.

In parallel to laboratory experiments, WE were observed to be specifically produced below the aphotic and euxinic haloclines of a contemporaneous stratified haloalkaline lake. Lipid depth profiles combined with phylogenetic analyses of the microbial diversity suggest that other



types of non-phototrophic anaerobic bacteria belonging to the Firmicutes and/or Bacteroidetes phyla can also biosynthesize WE, thus expanding this metabolic capacity among anaerobic Bacteria (Sala et al., submitted). Another biogeochemical investigation of unconventional sedimentary ecosystems showed the presence of isoprenoid WE in extreme evaporitic facies of the Dead Sea deep sediments. These WE were mostly derived from the recombination of hydrolyzed moieties of archaeal membrane lipids and were retrieved in gypsum and/or halite sedimentary deposits down to 243 meters below the lake floor (Thomas et al., 2019). Such isoprenoid WE attest for the recycling of archaeal cell wall constituents by deep subsurface microbial communities, which can build up intracellular carbon stocks and gain access to free water in this deprived environment (Fig. 1).

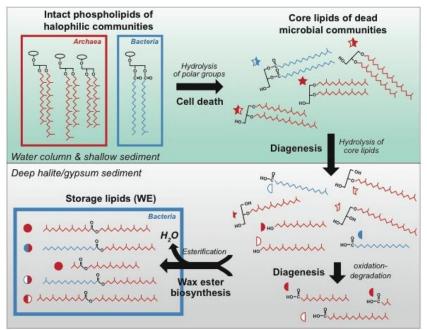


Figure 1 Schematic pathway for the formation of isoprenoid WE from membrane lipids of dead archaeal and bacterial biomass in deep Dead Sea sediments (from Thomas et al., 2019).

Conclusions

Our laboratory and field studies demonstrate that WE can be biosynthesized in various anoxic environments by several families of anaerobic bacteria and that such storage lipids may be specifically important for some microbial communities to survive in environments experiencing harsh environmental conditions. Our data also describe original interactions between abiotic and biotic processes that can occur during OM diagenesis and show that WE can constitute an interesting molecular tool to decipher carbon transformation pathways in the geosphere.

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