Role of extracellular electron transfer in the nitrogen cycle

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Extracellular electron transfer impacts the nitrogen cycle by enhancing microbial processes and connecting to other biogeochemical cycles. Understanding EET mechanisms provides insights into ecosystem functioning and potential advancements; Arpita Bose and Zhecheng (Robert) Zhang explain

Nitrogen is a fundamental element required by all living species. It can be found in amino acids, proteins, and nucleic acids. The nitrogen cycle promotes nitrogen transformation and transit across the environment, making it available for biological activity. Key steps in the cycle include nitrogen fixation (conversion of atmospheric nitrogen to ammonia), nitrification (oxidation of ammonia to nitrate), denitrification (reduction of nitrate to nitrogen gas), and anaerobic ammonium oxidation (anammox), which then converts ammonium and nitrite directly to nitrogen gas. Extracellular electron transfer (EET) is the mechanism by which microorganisms transmit electrons from their cells to accept electrons from external donors. This ability allows microorganisms to interact with insoluble substrates, which, in turn, influences a variety of biogeochemical cycles, including the nitrogen cycle. Understanding EET's function sheds light on microbial ecology and environmental processes.

Direct and indirect electron transfer

Extracellular electron transfer is carried out by two mechanisms: direct and indirect electron transfer. Direct electron transfer requires physical connections between the microbial cell and the electron acceptor or donor. Bacteria such as *Geobacter sulfurreducens* develop filamentous structures known as conductive pili, otherwise known as nanowires. These structures emerge from the cell's surface, enabling electrons to pass directly to external acceptors such as metals or other microbial cells. The makeup of these pili is designed to conduct electricity, allowing for more efficient electron transport. In addition, outer membrane cytochromes are proteins located in the cell membrane that also contribute to EET. They serve as electron transporters, facilitating the transport of electrons from within the cell and from external donors. In the context of the nitrogen cycle, cytochromes are essential in the steps of denitrification, where they transport electrons to nitrate or nitrite molecules. On the other hand, indirect electron transport is dependent on soluble molecules known as electron shuttles. *Shewanella oneidensis* and other microorganisms release chemicals such as flavins and quinones into their surroundings. As a result, these shuttles collect electrons from their cell and deliver them to electron acceptors elsewhere. This process allows for electron transmission over longer distances and presents an alternative where direct contact with acceptors is restricted.

Anammox bacteria perform EET via routes involving multi-heme cytochromes and other electron transfer proteins. When conventional electron acceptors like nitrite or nitrate are not available, anammox bacteria can transfer electrons to insoluble extracellular acceptors like graphene oxide or electrodes in microbial electrolysis cells (MECs). This ability indicates that anammox bacteria have the structural and functional elements required for EET.

The role of EET in the nitrogen cycle

EET plays a variety of roles within the nitrogen cycle. The nitrogen cycle is a repeating cycle of processes during which nitrogen moves through both living and non-living things. Denitrification, the microbial conversion of nitrate (NO_3-) to nitrogen has (N_2), is a process to return nitrogen to the atmosphere. EET improves anaerobic denitrification by allowing for more efficient electron transfer to nitrate or nitrite. Also, microorganisms like *Shewanella oneidensis* uses EET to transfer electrons externally, improving nitrate reduction efficiency and potentially reducing nitrous oxide (N_2O) buildup, that is a greenhouse gas. Moreover, anammox bacteria directly convert ammonium (NH_4+) and nitrite (NO_2-) to nitrogen gas. The cytochrome c proteins found in these bacteria indicate that EET processes are involved. In the anammoxosome, a specialized organelle where the anammox process takes place, EET might help with electron balance. This mechanism is important for the anammox bacteria to function efficiently and conserve energy.

Recent research showed that ammonium may be oxidized to nitrogen gas by anammox bacteria utilizing EET without the use of nitrite or nitrate as electron acceptors. Instead, they send electrons to insoluble extracellular electron acceptors. The EET-dependent anammox mechanism uses hydroxylamine (NH_2OH) as an intermediate. Additionally, the electrons produced during ammonium oxidation were transported through routes similar to those found in metal-reducing bacteria. Genes encoding multi-heme cytochromes and other EET-related proteins are increased in anammox bacteria during EET-dependent ammonium oxidation, according to comparative transcriptomic analysis. Thus, anammox bacteria may contribute to nitrogen loss in settings without soluble electron acceptors.

Nitrate-dependent iron oxidation is another example of the EET in the nitrogen cycle processes; in this process, bacteria oxidize ferrous iron (Fe^2+), using nitrate as an electron acceptor. Electrons from Fe^2+ are transferred to nitrate through EET routes. This interaction connects the nitrogen and iron cycles, which affects nutrient availability and metal mobility in the environment. Thus revealing how EET-capable microorganisms can affect many biogeochemical cycles at once. Lastly, EET enhances interactions between the nitrogen cycle and other cycles, such as sulfur and carbon. In the sulfur cycle, EET allows for the oxidation and reduction of sulfur compounds, often associated with nitrogen transformations. Since EET modifies the breakdown of nitrogen-containing organic molecules, it affects nitrogen availability through the decomposition of organic matter in the carbon cycle.

In addition, different microbial species and various communities are involved as a part of EET. *Shewanella oneidensis* is a multipurpose bacterium that may use a variety of electron acceptors, such as metal oxides and nitrate. The bacterium uses both direct and indirect EET processes, including electron shuttles and outer membrane cytochromes, to aid in metal reduction and denitrification. Furthermore, a common organism in sedimentary settings, *Geobacter sulfurreducens* is recognized for its ability to produce conductive pili. These pili are essential for nitrate-dependent iron oxidation and other activities because they allow direct electron transmission to external acceptors like iron oxides.

Anammox bacteria, such as *Candidaus Brocaidia anammoxidans*, have also been discovered to build biofilms on electrode surfaces. By giving the bacterial cells and the insoluble electron acceptors a bigger surface area for electron transfer, the biofilms improve the EET process. According to SEM imaging, anammox bacteria may bind to electrode surfaces without the requirement for call appendages such as pili, meaning a new way of direct electron transfer might exist. Furthermore, metagenomic explorations confirmed the prevalence of anammox bacteria in the biofilms, which implicates them as the main source of the electrochemical activity. Organized and embedded microbial populations in an extracellular matrix are known as biofilms. By improving electron transport and nutrient exchange, they are able to foster an atmosphere favorable to EET. Microbes can form syntrophic connections within biofilms, working together to perform metabolic tasks that would otherwise be energetically unfavorable for each individual.

In addition, long-distance electron transfer is a capability of filamentous organisms called cable bacteria. They alter redox gradients in sediments by forming centimeter-long conductive structures. This capacity impacts processes such as sulfide oxidation and can indirectly affect the nitrogen cycle by changing the chemical environment. In the case of EET-dependent anammox, biofilm growth on electrodes speeds up the process by providing a wide surface area for electron transfer.

The broader implications of EET

Moving into the broader implications of EET, evidence suggests that EET processes can be helpful to induce environmental impact and have biotechnological applications. By altering the rates of nitrogen transformations, EET affects the cycling of nutrients. In water bodies, enhanced denitrification with EET can lower nitrate pollution, hence reducing eutrophication and related issues, such as hypoxia and algal blooms. Furthermore, by controlling nitrous oxide (N2O) generation during denitrification, EET-capable microorganisms provide possible solutions for reducing greenhouse gas emissions and thereby contributing to climate change mitigation. In terms of biotechnological applications, leveraging EET-capable microorganisms can improve the effectiveness of nitrogen removal in wastewater treatment. Considering that EET is used by bioelectrochemical systems, such as EET (MFCs), to treat nitrogenous waste and produce energy, the dual functionality could provide a long-term solution for both energy production and trash management. On top of that, EET mechanisms are also being investigated in bioremediation efforts to clean up nitrogen-contaminated areas. Using EET-capable microorganisms' inherent capabilities can help create environmentally acceptable methods of cleaning up pollution for the future.

EET-dependent anammox processes effectively remove ammonium without accumulating nitrite or nitrate. When combined with renewable energy sources that power the electrode, EET-dependent anammox presents a viable method for energy-efficient wastewater treatment. To add, partial nitrification, or the conversion of the ammonium to nitrite, is no longer needed when electrodes are used as electron acceptors, which simplifies the entire process and lowers costs. Furthermore, the energy generated during ammonium oxidation may be collected as electrical currents and utilized to generate hydrogen gas via microbial electrolysis cells (MECs).

Ultimately, through the enhancement of important microbial processes, and its connection to other biogeochemical cycles, extracellular electron transfer has a profound impact on the nitrogen cycle. In addition to offering chances for environmental and technical breakthroughs, understanding EET mechanisms and the functions of certain microbes offers important insights into how ecosystems function. Additional research on EET-dependent anammox can improve knowledge of the nitrogen cycle in anoxic ecosystems and provide new approaches for nitrogen removal in settings with limited availability of conventional electron acceptors. Future research should focus on understanding the complexity of EET-mediated microbial interaction and finding practical applications that promote sustainability and address environmental concerns.

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