Geophysical Research Abstracts
Vol. 15, EGU2013-7897, 2013
EGU General Assembly 2013

Microscale effects on denitrification: does the ability of denitrifying bacteria to reduce N_2O depend on their position in the soil matrix?

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Soil is a heterogeneous matrix with a variety of microhabitats which probably select for organisms with distinct functional traits. The composition and functioning of soil denitrifier communities (DC) has been studied intensely over the last decades, primarily because of their role in the emission of N_2O from soil. The tacit assumption in such studies is that the soil microbial community is one "thing". In the present study, we challenge the concept of DC as a homogenous entity and suggest a stratification of denitrifier function based on the position within the soil matrix. We hypothesize that soil contains "inner" and "outer" habitats; the inner consisting of sites within crevices and cavities of the soil mineral material, structured organic materials and strong biofilms, the outer consisting of exposed surfaces and macropores within the soil matrix. We further believe that sequential dispersion/extraction by density gradient centrifugation (DGC) can be used to crudely separate the organisms residing in the two habitat types. We operationally define loosely attached cells (LAC) as those which are liberated from soil particles by moderate dispersion of soils. LAC were separated from the soil by DGC, and the pellets at the bottom of the gradients containing bacteria still attached to or embedded in soil material were then subjected to a stronger dispersion to release the more strongly attached cells (SAC) which were again separated from the soil by DGC. We hypothesized that SAC are cells situated deeper in biofilms or other protective structures within the soil matrix than LAC. We further hypothesized that the two habitats select for different characteristics regarding the regulation of denitrification. In short, SAC were expected to express N_2O-reductase earlier than LAC, because SAC experience anoxia and lack of NO_x more frequently than LAC. First results from incubations with LAC and SAC from different soils lend strong support to this hypothesis; in response to oxygen depletion, both denitrifying communities expressed similar apparent growth rates, both produced a mixture of NO, N_2O and N_2, but the relative amount of N_2O produced was much higher for LAC than SAC. This reemphasizes the significance of soil structure, habitable pore space, predation and bacteria-mineral interactions as regulating factors for N_2O emission in mineral soils and has implications for the understanding of selection pressures for sustained N_2O-reductase activity in soil.