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Carbon and nitrogen limitation explain the contrasting responses of rhizospheric N-cycling microbial communities to maize inoculation by Azospirillum lipoferum CRT1

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Introduction
Maize inoculation with the plant-growth promoting rhizobacterium Azospirillum stimulates root growth and carbon, C, exudation, thereby enabling a better exploitation of soil and enhancing plant uptake of nitrogen, N. This can modulate the availability of N in the rhizosphere, by enhancing plant-microbe competition for N and modifying rhizosphere environmental variables important for N-cycling microbial communities, i.e. the amount of soil mineral N and oxygen availability. We tested the hypothesis that inoculation-induced stimulation of root N uptake and C exudation would enhance plant competition over microorganisms for N while increasing C availability for heterotrophs, thus leading to (i) a decrease of nitrifier abundance and activity, and (ii) a decrease or increase of denitrifier abundance and activity depending on the level of denitrifier limitation by N and C.
Methods
The extent of inoculation-induced changes in microbial activities (potential nitrification and denitrification), abundances and diversity of (de)nitrifiers as well as in root functional traits was assessed at 4 dates over two consecutive years in a multi-site field trial. Measurements were performed for the 6- and 12-leaves maize stages. In a second experiment, we artificially altered the level of denitrifier limitation by N and C in a greenhouse pot experiment by applying synthetic root exudates to inoculated and non-inoculated maize plants. Inoculation-induced response to nutrient limitation on microbial N-related activities and abundances was assessed for the 6-leaves stage maizeplants.
Results
Inoculation resulted in an idiosyncratic response of nitrification and nitrifier (AOA, AOB) abundance, which varied from one sampling date to another at a given site, and between sites and treatments at a given date. Modifications of water balance and soil moisture rather than increased plant-nitrifiers competition for soil NH4+ were the main drivers of nitrification. Conversely, inoculation-induced changes in denitrifier activity and abundance (nirK, nirS) were consistent across sites and ranged from -23% to +84% depending on sites. Particularly, in soils with high C limitation levels, inoculation increased nirS-denitrifier abundance and denitrification, likely by stimulating root C exudation. Conversely, in soils with lower C limitation, the stimulating effect of inoculation on root C exudation was less critical for denitrifiers whereas the increased competition between roots and denitrifiers for NO_3- became prominent, thus resulting in slightly decreased nirS-denitrifier abundance and denitrification. Pot experiment results revealed that the inoculation effect on denitrification decreased with increased amount of root exudates-like amended to soil.
Discussion
Maize seed inoculation with the beneficial Azospirillum lipoferum CRT1 can be a sustainable, though soil-specific, agricultural practice providing both beneficial agronomic and environmental effects. Our findings may indicate that the crop seed inoculation practice would increase potential N2O losses from agricultural soils where denitrifiers are highly C-limited. However, our results also demonstrate that the responses of nitrite reducers and N2O reducers to inoculation are tightly coupled, and that inoculation thus does not necessarily represent a risk for increased N2O losses from C-limited soils. Finally, the nirS-denitrifier abundance to microbial basal respiration ratio could be successfully used as a proxy of gaseous-N losses through denitrification from the soil-plant system following inoculation.