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Review Paper

Contrasting effects of grasses and trees on microbial N-cycling in an African humid savanna

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ABSTRACT

African humid savannas are highly productive ecosystems, despite very low soil fertility, where grasses and trees coexist. Earlier results showed that some perennial grass species are capable of biological nitrification inhibition (BNI) while trees likely influence differently on nitrogen cycling. Here we assessed the impact of the dominant grass and tree species of the Lamto savanna (Ivory Coast) on soil nitrifying and denitrifying enzyme activities (NEA and DEA, respectively) and on the abundances of archaeal and bacterial ammonia oxidizers (AOA and AOB, respectively) and nitrite reducers. This is one of the first studies linking nitrifying and denitrifying activities and the abundances of the involved groups of microorganisms in savanna soils. NEA was 72-times lower under grasses than under trees while AOA and AOB abundances were 34- and 3-times lower. This strongly suggests that all dominant grasses inhibit nitrification while trees stimulate nitrification, and that archaea are probably more involved in nitrification than bacteria in this savanna. While nitrite reducer abundances were similar between locations and dominated by *nirS* genes, DEA was 9-times lower under grasses than trees, which is likely explained by BNI decreasing nitrate availability under grasses. The *nirS* dominance could be due to the ferruginous characteristics of these soils as *nirS* and *nirK* genes require different metallic co-enzymes (Fe or Cu). Our results show that the coexistence of grasses and trees in this savanna creates a strong heterogeneity in soil nitrogen cycling that must be considered to understand savanna dynamics and functioning. These results will have to be taken into account to predict the feedbacks between climate changes, nitrogen cycling and tree/grass dynamics at a time when savannas face worldwide threats.

1. Introduction

Savannas are characterized by the coexistence of two contrasting plant types, trees and grasses, and cover 12–13% of global terrestrial areas (Rutten et al., 2016). This coexistence is traditionally explained by disturbances or resource partitioning (Barot and Gignoux, 2004; Sankaran et al., 2004): in nutrient-limited ecosystems, tree-grass coexistence could also be explained by positive plant-soil feedbacks (Bonanomi et al., 2008) creating heterogeneity in soil resources (Brandt et al., 2013). Some perennial grass species of savannas (e.g. *Brachiaria* spp., *Sorghum bicolor, Hyparrhenia diplandra)* are known to inhibit nitrification (Lata et al., 1999, 2000, 2004; Subbarao et al., 2009). In particular, *Hyparrhenia diplandra*, the dominant species in the Lamto savanna in Ivory Coast, is the first species for which such an ability has been documented (Lata et al., 2004, 1999, 2000). The mechanism allowing nitrification inhibition has been described for *Brachiaria humidicola* (Subbarao et al., 2009): roots release exudates into the soil that can block the bacterial ammonia oxidation pathway (Subbarao et al.,

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2009). The ability of grass to inhibit nitrification has probably a strong influence on savanna functioning as it decreases the availability of nitrate and the subsequent possible losses of nitrogen (N) by denitrification and nitrate leaching, which is likely to increase primary production through a plant-soil feedback (Boudsocq et al., 2009). This has also broad implications for tropical pastures as African grasses have been exported worldwide and are widely used in pastures e.g. in Brazil, the largest beef exporter in the world (Del' Alamo Guarda and Del' Alamo Guarda, 2014). However, it is not yet known whether biological nitrification inhibition (BNI) or at least very low nitrification rates in rhizospheric soils, is a common trait among African tropical perennial grasses.

Concerning trees, previous results obtained in Lamto savanna showed that mineralization rates and soil organic matter content were higher under tree canopies than under grasses (Mordelet et al., 1993). This suggests that nitrification could also be enhanced under trees if all microbial activities are enhanced by the higher availability in organic matter. However, tree canopy effect on soil functioning is complex and likely depends on tree species characteristics (Mordelet et al., 1993). Modelling results (Boudsocq et al., 2012) suggest that such differences in nitrification rates and possible differences between trees and grasses in their preference for the absorption of ammonium vs. nitrate could contribute to their coexistence. Our first objective was thus to compare nitrification rates under dominant tree species and grasses in Lamto savanna to test whether these two plant types can lead to contrasting types of N cycling.

The impact of grasses and trees on the various fluxes involved in N cycling are likely linked to variations in the abundance of the involved microbial groups. A first issue is the identification of the major microbial groups involved in N fluxes in savanna soils. Since the discovery of their role in nitrification, ammonia oxidizing archaea (AOA) have been found to be more abundant than ammonia oxidizing bacteria (AOB) in most temperate soils (Prosser and Nicol, 2012; Sterngren et al., 2015). However, the relative importance of AOA and AOB for nitrification likely depends on soil characteristics (Hatzenpichler, 2012). Therefore, a growing number of articles have documented the actual importance of archaea in the realization of ammonia oxidation. Significant AOA activities have been found in acidic soils and soils with low ammonium concentration (Nicol et al., 2008; Prosser and Nicol, 2012). On the contrary, AOB are important drivers of nitrification in soils with high ammonium concentrations and in response to N fertilization (Ma et al., 2016; Simonin et al., 2015; Verhamme et al., 2011). However, very few studies have been published on nitrification and nitrifiers in savanna soils (Catão et al., 2016; Rughöft et al., 2016; Wild, 2016; Assémien et al., 2017). Moreover, to our knowledge, no study has assessed the denitrifying activity and its link with denitrifying microorganisms in savanna soils.

A second issue is to determine the respective impacts of savanna trees and grasses on microbial communities, e.g. the abundances of nitrifiers and denitrifiers. These plants, by their likely different impacts on soil N functioning, could also modify the relative importance of different nitrifier and denitrifier groups. Indeed, nitrification is a key metabolic pathway for nitrifying bacteria and archaea with ammonia as the only source of energy, and BNI could modify the respective competitive abilities of nitrifying bacteria and archaea. BNI by decreasing the availability of nitrate under perennial grasses should also be detrimental to denitrifiers. Denitrification rates and denitrifier abundances should thus be lower under grasses than under trees. Taken together, by their impacts on organic and mineral N (nitrate and ammonium) trees and grasses likely impact all components of microbial communities. We expect these impacts to be particularly strong because perennial grasses inhibiting nitrification are long-lived tussock grasses, living as long as savanna trees (ca. 80 years; Abbadie et al., 2006).

We tested here whether the presence of grass *vs*. tree species, and possibly species identity, is associated to contrasting types of N cycling in their rhizospheric soil in the Lamto savanna. To do so, we compared soils under the influence of the four dominant perennial grass species and the four dominant tree species in terms of nitrifying and denitrifying enzyme activities (i.e. NEA and DEA), abundances of nitrifiers (i.e. AOA and AOB) and denitrifiers (*nirK*- and *nirS*-nitrite reducers), and soil physicochemical characteristics. The total abundances of bacteria and archaea were also quantified. The following hypotheses were tested: (1) The dominant savanna grass species are associated to very low soil NEA and low DEA due to direct and indirect impacts of BNI, respectively. (2) Contrary to grasses, dominant tree species are associated to higher soil NEA and DEA due to the absence of BNI activity under tree. (3) The differences in nitrifying and denitrifying activities between tree and grasses are linked to contrasting abundances in nitrifiers and denitrifiers due to the presence or absence of BNI. (4) The presence of trees and grasses modifies the relative abundance of the main groups involved in nitrification (i.e. AOA/AOB ratio) and denitrification (*nirS/nirK* ratio) in relation to the soil physicochemical characteristics (higher N, C contents and humidity under trees).

2. Material and methods

2.1. Study sites

The Lamto reserve is located in Ivory Coast, West Africa (6°13′N, 5°20′W). The vegetation is a mosaic of savannas with various tree densities, and gallery forests. Temperatures are relatively constant throughout the year (27 °C on average). Four seasons can be distinguished: (i) a long dry season from December to February; (ii) a long wet season from March to July; (iii) a short dry season in August; (iv) a short wet season from September to November. Annual precipitation in 2014 was 826 mm (data from the Geophysical Station of Lamto). The soils are composed of granites and derived sands and classified as tropical ferrugineous soils with a superficial gravelly horizon. The soils are sandy (ca. sands 77%; silts 14%; clays 9%) and with a bulk density of ca. 1.65 (Lata, 1999).

2.2. Soil sampling

Lamto savanna ecosystem is highly structured due to high environmental constraints (e.g. scarcity of nutrients, fire). Trees and grass individuals are spatially well separated (e.g. grass tussock individuals can be separated up to 70 cm distance). We therefore focused on the rhizospheric soil as the microbial processes are concentrated in the close vicinity of roots (Abbadie et al., 1992). Soil was sampled during the long wet season (April 2014) in the open shrub savanna under the tussocks of the four dominant perennial grass species: *Andropogon canaliculatus* (AC), *Andropogon schirensis* (AS), *Hyparrhenia diplandra* (HD) and *Loudetia simplex* (LS); and under the canopy of the four dominant tree species: *Bridelia ferruginea* (BF), *Cussonia barteri* (CB), *Crossopteryx febrifuga* (CF) and *Terminalia glaucescens* (TG). In total, these dominant species represent in this ecosystem a proportion of minimum 80% of individuals and biomasses for both grass and tree compartments (Abbadie et al., 2006).

Soil sampling below trees was achieved in patches of bare soil between grass tussocks. Grass tussocks were chosen to have similar basal diameter (ca. 20 cm) and trees were selected to have similar diameter at breast height (ca. 22.5 cm). The choice of plant individuals was made randomly on a surface of *ca*. 10 ha and local sources of heterogeneity (termite mounds, small depressions, rocks) were avoided. For each of the eight species, five replicated soil samples (about 1 kg, each of them composed of two pooled sub-samples) were collected from the top 15 cm with an auger (8 cm in diameter) and stored at 4 °C for a very short period during transport. Samples were subsequently sieved (2 mm), homogenised and 200 g of soil were stored at −20 °C for molecular biology analyses and the measurements of nitrifying/denitrifying enzyme activities. Freezing of soil samples was preferred to fresh or drying conservation methods because (i) the time between