



## Original article

# Contrasting impacts of grass species on nitrogen cycling in a grazed Sudanian savanna



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## ARTICLE INFO

## Article history:

Received 4 September 2014

Received in revised form

11 January 2015

Accepted 12 January 2015

Available online 20 January 2015

## Keywords:

<sup>15</sup>N

Nitrogen cycling

Savanna

Perennial grass

Annual grass

Herbivore

Burkina Faso

## ABSTRACT

We investigated the impact of perennial and annual grass species on nitrogen cycling in a Sudanian savanna of Burkina Faso. We also analysed how the local context in terms of grazing and soil properties modifies these impacts. We selected four plots differing both by the intensity of grazing by cattle and soil depth, and used soil and grass biomass <sup>15</sup>N as integrative indicators of N cycle. If perennials are able to foster a more efficient nitrogen cycling there should be lower <sup>15</sup>N abundances in their biomass and soil. If soil depth and cattle pressure significantly modify nitrogen fluxes, soil depth and cattle pressure should influence <sup>15</sup>N signatures. Our results suggest that perennial grasses are more conservative for nitrogen (inhibition of nitrification, less leaching via a perennial root system, slower cycling). The increase in leaf  $\delta^{15}\text{N}$  with N concentration is steeper in *Loudetia togoensis* than in the three other grasses. No significant difference was found between the <sup>15</sup>N signatures of the four plots. Our results on <sup>15</sup>N signatures and the fact that perennial grasses are much more abundant in the plots that are less grazed and have deeper soils, confirm that the switch from perennial to annual grasses is linked to a degradation in soil fertility and pasture quality. This suggests that <sup>15</sup>N signatures can be used as indicators of fertility.

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## 1. Introduction

Plants influence nutrient cycling and their long term availability (Chapman et al., 2006; Hobbie, 1992), and this feedbacks on their own growth and primary productivity. This is achieved through many mechanisms (Hobbie, 1992; Knops et al., 2002). This allows them to cope with abiotic constraints of ecosystems such as the lack of mineral nutrients and contrasting soil types and with biotic constraints such as herbivory or competition between plants (Craine, 2009; Grime, 2001). Among all possible strategies, the distinction between perennial and annual plants is particularly relevant in terms of nitrogen cycle and competitive ability (Grime, 1977, 2001). Annuals are viewed as opportunistic. They need to

acquire their resources as quickly as possible and benefit from the immediately available mineral resources. Perennials are more likely to influence local nutrient cycles and to benefit from such modifications because their root system, their root exudates and their litter (roots and leaves) interact for a longer period with the same patch of soil and soil micro-organisms living in this patch (Vinton and Burke, 1995). Perennials grow slower than annuals but may benefit from sparing soil mineral nutrient resources, from increasing the local availability of these resources and from decreasing nutrient losses. It has for example been shown in tropical savannas that many perennial bunch grasses are able to inhibit nitrification through the release of particular molecules from their root systems (Lata et al., 2004; Subbarao et al., 2007a, 2007b), which increases their own biomass (Boudsocq et al., 2009). As these grasses live for several tens of years, they build dense root systems where the close proximity between dead and live roots is likely to induce a very efficient nutrient recycling and reduce nitrogen losses (Abbadie and Lata, 2006; Abbadie et al.,

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1992). In this context, our primary goal was to compare, from the point of view of nitrogen cycling, two annual and two perennial bunch grasses growing in the same West African savanna.

To meet this goal, we measured the natural abundance in  $^{15}\text{N}$  of the biomass of these four grasses and of the soil penetrated by their root system. Indeed,  $^{15}\text{N}$  abundance is considered as a good indicator of ecosystem functioning (Dijkstra et al., 2008; Robinson, 2001; Staddon, 2004; Templer et al., 2007). First,  $^{15}\text{N}$  abundance is used to determine the origin of soil organic matter (Boutton et al., 1998; Danso et al., 1993). Similarly, the  $^{15}\text{N}$  of biomass gives hints on the origin of the nitrogen. For example legumes, due to symbiotic nitrogen fixation, tend to have lower concentrations in  $^{15}\text{N}$  than other plants and thus to decrease soil  $^{15}\text{N}$  concentration through their litter. Second, the isotopic fractionation due to the lower reactivity of  $^{15}\text{N}$  relatively to  $^{14}\text{N}$  allows tracing nitrogen fluxes in the soil. For example, rapid nitrogen cycling and nitrification are thought to increase  $^{15}\text{N}$  abundance (Dijkstra et al., 2008), while tighter nitrogen cycling (e.g. less leaching and denitrification) should lower  $^{15}\text{N}$  abundances. The difference between plant and soil  $^{15}\text{N}$  abundances gives hints on plant preference for ammonium vs. nitrate (Kahmen et al., 2008). Similarly, the discrepancy between the  $^{15}\text{N}$  signatures of the biomass of an African perennial bunch grass and bulk soil (lower  $^{15}\text{N}$  in the biomass than in the soil organic matter) (Abbadie et al., 1992) suggested that this grass fosters an efficient nitrogen cycling through the recycling of the nitrogen contained in the roots of its dense and localized root system. Taken together, we predict that our two perennial and two annual grasses should have different  $^{15}\text{N}$  signatures, which should in turn impact soil signatures. For the same reasons the universal positive correlation between leaf  $^{15}\text{N}$  signature and leaf N concentration (Craine et al., 2009b) should also be different between annual and perennial biomasses.

Besides plant influence on nitrogen cycling, other factors such as herbivory and soil properties are likely to impact these cycles, which should in turn modify  $^{15}\text{N}$  isotopic signatures. Cattle or wild herbivores indeed quicken carbon and nutrient cycling by increasing the turnover of the biomass. Herbivore impact on nutrient cycling has been extensively studied. On the one hand, an important issue is to determine whether herbivores could increase the efficiency of nitrogen cycling (decrease nitrogen losses), which could increase primary production on the long term (de Mazancourt et al., 1998). On the other hand, they have been shown to impact many fluxes of mineral nitrogen but the direction of these effects is likely to be case dependent (McNaughton et al., 1997; Wardle et al., 2001). For example, cattle have been shown to increase nitrification, denitrification and free nitrogen fixation in a temperate grassland (Patra et al., 2006). In turn, the modification of these fluxes impacts  $^{15}\text{N}$  signatures and may either increase (Frank and Evans, 1997) or decrease (Frank et al., 2000) soil  $^{15}\text{N}$  abundances. Similarly, soil properties such as soil depth, soil compaction, soil texture or soil organic matter content are likely to impact biomass and soil  $^{15}\text{N}$  signatures (Abadín et al., 2010) through their effects on soil capacity to retain mineral nutrients, or through their effects on microbial biomass and activities.

Taking into account these interactive impacts of plant species and soil type/herbivores on nitrogen cycling and detecting these interactions using  $^{15}\text{N}$  signatures is interesting in two contrasted ways. On the one hand, such complex interactions could strongly increase the variability in isotopic signatures, which could blur potential effects of targeted treatments (here the plant species). Documenting these interactions and their effects on isotopic signatures is thus methodologically useful to help designing and interpreting other experiments or field samplings. On the other hand, isotopic signatures might allow analysing the impact of herbivores and different soil types on nitrogen cycling and might

help disentangling the interactions between herbivores or soil types and plant species.

For these reasons, we compared two annual and two perennial grasses in a West African savanna where both soil depth and cattle pressure are varying. Taken together, we make the following predictions. If perennials are able to foster a more efficient nitrogen cycling, (1) there should be lower  $^{15}\text{N}$  abundances in their biomass and soil and (2) the relation between  $^{15}\text{N}$  signature and N concentration should be different between annual and perennial leaf biomass. If soil depth and cattle pressure significantly modify nitrogen fluxes, (3) soil depth and cattle pressure should influence  $^{15}\text{N}$  signatures, (4) plant species and soil depth or cattle pressure should affect  $^{15}\text{N}$  signatures in an interactive way, i.e. the impact of each species should depend on soil depth and cattle pressure.

## 2. Material and methods

### 2.1. Study site

The study site is the third management unit of the protected forest of Dindéresso (FCD) in the West of the town of Bobo-Dioulasso, at the altitude of 390 m (11°12.494' north, 4°24.159' west). The climate is South-Sudanian: there is a wet season from May to October and a dry season from November to April. The area is located between the 900 and 1250 mm isohyets. 1254 mm of rain fell in 2010 but only 831 mm in 2011. The mean annual temperature is 28 °C. The whole forest lies on sedimentary rocks and our own study area lies on Bobo-Dioulasso sandstone. Soils are tropical ferruginous leached soils indurated or not. Vegetation consists in a shrub savanna grazed by cattle. It is characterized by the following dominant shrub/small tree species: *Vitellaria paradoxa*, *Terminalia laxifolia*, *Detarium microcarpa*, *Parkia biglobosa*, *Guiera senegalensis*, *Combretum nigricans*, *Gardenia ternifolia*. The herbaceous layer is dominated by grasses. The main annual grasses are *Andropogon pseudapricus*, *Loudetia togoensis*, *Microchloa indica*. The main perennial grasses are *Andropogon gayanus*, *Andropogon ascinodis*, *Hyparrhenia subplumosa*, *Schizachyrium sanguineum* and they are all bunch grasses. There are some legumes (*Cassia mimosoides*, *Indigofera trichopoda*, *Zornia glochidiata*, *Tephrosia pedicelata*, *Tephrosia bracteolata*), Cyperaceae (*Fimbristylis hispidula*) and other forbs (*Waltheria indica*, *Pandiaka heudelotii*, *Spermacoce stachydea*, *Striga hermonthica*). Grass aboveground biomass and necromass are burnt each year by bushfires.

The study site has been divided in four blocs of approximately 1.5 ha according to the dominance of perennial and annual grasses and the frequency of grazing: blocs 1 and 2 are dominated by annual grasses and are more grazed by cattle during the rainy season while blocs 3 and 4 are dominated by perennial grasses and are less grazed during the rainy season. Blocs 1 and 2 are indeed next to the main road, so that they are more easily reached by cattle and shepherds, and blocs 3 and 4 are supposed to host an abundant population of tsetse flies during the rainy season so that they are avoided to limit the risk of cattle infection by trypanosomiasis. Blocs 1 and 2 have shallower soils (at most 55 cm deep, they are indurated ferruginous leached soils). Blocs 3 and 4 have deeper soils (at least 105 cm deep, the indurated layer is deeper). Blocs 1 and 2 are contiguous and so are blocs 3 and 4. Blocs 1–2 and 3–4 are separated by a distance of about 2000 m.

### 2.2. Soil and biomass sampling

The study focusses on four of the dominant grass species: *Andropogon pseudapricus*, *Loudetia togoensis* (annuals), *Andropogon ascinodis* and *Andropogon gayanus* (perennial bunch grasses). The four grasses are caespitose but the tussocks of the two perennials

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