



Effects of livestock on nitrogen and carbon cycling in a savanna in Burkina Faso

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ABSTRACT

The nitrogen and carbon cycles are fundamental ecosystem processes influenced by several factors including soil type and other abiotic factors, plant species, grazing and soil organisms. Herbivores profoundly influence the functioning of ecosystems and the recycling of nutrients in interaction with plants in natural ecosystems. This study focuses on the effects of livestock on carbon and nitrogen cycling in a grazed savanna in Burkina Faso. Dominant grass species (aerial and root parts) and soil samples were collected under grasses and bare soil patches in 48 plots (24 protected and 24 unprotected plots), 18 months after setting up herbivores enclosures. Soil and grass ¹³C and ¹⁵N were used as integrative indicators of carbon and nitrogen cycles. The results revealed no significant effect of livestock on soil total carbon and nitrogen and on soil ^δ¹³C and ^δ¹⁵N values. Moreover, grazing had no significant effect on grass carbon and ^δ¹³C, while it significantly increased grass total nitrogen and ^δ¹⁵N. Therefore, our hypothesis that grazing would increase soil ¹³C and ¹⁵N values and plant biomass was only verified for grass ¹⁵N. Grass ^δ¹⁵N results suggest that grazing improves the immediate availability of nitrogen but could also increase nitrogen losses.

1. Introduction

The nitrogen and carbon cycles are fundamental ecosystem processes. They are influenced by several factors including soil type and other abiotic factors, plant species, grazing and soil organisms. Herbivores profoundly influence the functioning of ecosystems and the recycling of nutrients in interaction with plants (Wardle et al., 2001). Herbivores affect the soil physicochemical and biological characteristics through direct and indirect effects of trampling, plant cover modifications and urine and faeces inputs (Prieto et al., 2011). Plant defoliation by herbivores affects root distribution, biomass and activity, and also the root/shoot ratio (Wang and Ripley, 1997; Guitian and Bardgett, 2000). Root biomass generally decreases with grazing intensity (Han et al., 2008). The modification of the root system of plant species due to aboveground biomass consumption by herbivores can stimulate soil

organic matter mineralization (Han et al., 2008; Klumpp et al., 2009) due to increased microbial activity. In fact, herbivores, through plant defoliation, trigger root exudation, thus stimulating microbial mineralization of soil organic matter (Hamilton and Frank, 2001). Furthermore, herbivores can also directly or indirectly modify soil microbial communities and activity (Bardgett et al., 2001; Patra et al., 2005; Wang et al., 2006; Klumpp et al., 2009) which can lead to negative or positive effects on carbon and nitrogen mineralization (Bardgett and Wardle, 2003). Herbivores thus affect carbon and nutrient cycling through various mechanisms and can accelerate the carbon and nutrient cycles by increasing biomass renewal. Knowledge of the effects of livestock on nitrogen availability and recycling is therefore necessary to ensure the sustainable management of grazed ecosystems, especially in dry savannas of the Sudanian zone of West Africa that are prone to degradation (César, 1992), due to overgrazing (Wittig et al., 2002).

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^{15}N and ^{13}C abundances are commonly used to study the structural and functional characteristics of ecosystems and their responses to environmental changes and human activities because they are considered as good indicators of ecosystem functioning (Ehleringer et al., 2000; Robinson, 2001; Staddon 2004; Templer et al., 2007; Dijkstra et al., 2008). Soil ^{15}N and ^{13}C abundances can be used to determine the origin of soil organic matter and quantify its turnover rates (Balesdent et al., 1987; Danso et al., 1993; Boutton et al., 1998). Conversely, biomass ^{13}C provides information on the conditions under which photosynthesis has taken place while biomass ^{15}N provides clues about the origin of nitrogen. For example, nitrogen fixing legumes tend to have lower ^{15}N concentrations than other plants owing to symbiotic nitrogen fixation, and thus tend to decrease the soil ^{15}N concentration through their litter. C_4 (mostly tropical grasses) and C_3 plants have contrasting $\delta^{13}\text{C}$ signatures ($-12.5 \pm 2.5\text{‰}$ and $-25.5 \pm 4.5\text{‰}$ respectively) (Ehleringer et al., 2000). Furthermore, the isotopic fractionation due to the lower reactivity of ^{15}N and ^{13}C relative to ^{14}N and ^{12}C can be used to trace soil nitrogen and carbon fluxes. For example, rapid nitrogen cycling and nitrification are thought to increase ^{15}N abundance (Dijkstra et al., 2008), while tighter nitrogen cycling (e.g., less leaching and denitrification) should decrease ^{15}N abundance.

Herbivores can influence plant ^{13}C signatures because they reduce the standing biomass, which should increase water availability. They can also have an impact on soil organic carbon and soil $\delta^{13}\text{C}$ (An and Li, 2015). The impacts of herbivores on nitrogen cycling and ^{15}N signatures have been studied extensively. On the one hand, herbivores can increase the efficiency of nitrogen cycling (reduce nitrogen losses), which could increase primary production in the long term (de Mazancourt et al., 1998). On the other hand, they can have an impact on many flows of mineral nitrogen (nitrification, denitrification, etc.), but the direction of these effects has been found more variable and probably depends on the ecosystems (McNaughton et al., 1997; Wardle et al., 2001). For example, cattle have been shown to increase nitrification, denitrification and the fixation of free nitrogen in temperate grasslands (Patra et al., 2006). Soil ^{15}N natural abundance can thus be modified by herbivores (Frank and Evans 1997; Frank et al., 2000; Aranibar et al., 2008; Craine et al., 2009a).

In the context of animal husbandry, it is therefore important to better analyze (i) how the interactions between plant cover and livestock affect nutrient recycling, and (ii) how these interactions influence nutrient availability in the long term and thereby the sustainability of husbandry. Mathematical models can help predict under what conditions herbivores or plants, through their impacts on nitrogen cycling, sustainably increase primary production by increasing nutrient recycling efficiency, i. e. by decreasing nitrogen losses (de Mazancourt et al., 1998, 1999; Boudsocq et al., 2009). In Burkina Faso, studies have mainly addressed the effects of livestock on vegetation and a few soil properties, but not on nutrient cycling (Savadogo et al., 2005; Yé et al., 2016; Savadogo et al., 2017). Consequently, the objective of this study is to determine the effects of livestock on the carbon and nitrogen cycles by setting up exclosures in a grazed savanna in the Bobo-Dioulasso area in Burkina Faso.

To achieve this objective, we measured the natural ^{15}N and ^{13}C abundances in whole plants (aerial and root parts) of the four dominant grass species and their soil because stable isotopes provide integrative measures of N and C cycling. We hypothesized that livestock would accelerate carbon and nitrogen cycling, which would result in increased heavy isotope natural abundance in soils and grass.

2. Materials and methods

2.1. Study site

The study site is a management unit of the protected forest of Dindéresso in the west region of Burkina Faso ($11^{\circ}12.494'$ north, $4^{\circ}24.159'$ west, altitude 390 m) (Yé et al., 2015). The climate is

south-Sudanian with a wet season from May to October and a dry season from November to April. The area is located between the 900- and 1200-mm isohyets. Some 1254 mm of rain fell in 2010; 831 mm in 2011 and 1089 in 2012 (Yé, 2013). The mean annual temperature was 28°C in 2012.

The whole forest lies on sedimentary rock, i.e., Bobo-Dioulasso coarse sandstone (BUNASOLS, 1985; FAO, 1994). According to the French soil classification (CPCS, 1967), soils are modal leached tropical ferruginous soils and indurated leached tropical ferruginous soils. They are Lixisols and Plinthosols according to the WRB classification (FAO, 2006). In general, they have low organic matter, N and phosphorus contents (BUNASOLS, 1985).

The vegetation consists of a shrub savanna grazed by livestock (cattle + sheep), characterized by the following dominant shrub or small tree species (C_3 plants) (Yé, 2013): *Vitellaria paradoxa*, *Terminalia laxiflora*, *Detarium microcarpum*, *Parkia biglobosa*, *Guiera senegalensis*, *Combretum nigricans* and *Gardenia ternifolia*. The herbaceous layer is dominated by grasses (C_4 plants). The main annual grasses include *Andropogon pseudapricus*, *Loudetia togoensis* and *Microchloa indica*. The main perennial grasses, all bunch grasses, include *Andropogon gayanus*, *Andropogon ascinioidis*, *Hyparrhenia subplumosa* and *Schizachyrium sanguineum*. Several legumes were present including *Cassia mimosoides*, *Indigofera trichopoda*, *Zornia glochidiata*, *Tephrosia pedicellata*, *Tephrosia bracteolata*, *Fimbristylis hispida* (Cyperaceae) and several other forbs (*Waltheria indica*, *Pandiaka heudelotii*, *Spermacoce stachydea*, *Striga hermonthica*) were also present. Grass aboveground biomass and necromass of the site as well as those of the two treatments were burnt every year by bushfires triggered by the population during the dry season.

The study site was divided into four blocks of approximately 1.5 ha each according to the dominance of perennial and annual grasses and grazing frequency: blocks 1 and 2 were co-dominated by two annual grasses (*A. pseudapricus* and *L. togoensis*) and were more grazed by cattle and sheep during the rainy season, while blocks 3 and 4 were co-dominated by two perennial grasses (*A. ascinioidis* and *A. gayanus*) and were less grazed during the rainy season. Blocks 1 and 2 were close to the main road, so that they were more easily reached by cattle and pastoralists, while blocks 3 and 4 were supposed to host an abundant population of tsetse flies during the rainy season, so that herdsmen tended to avoid this part of the study site to limit the risk of cattle infection by trypanosomiasis. Blocks 1 and 2 had shallower and indurated soils (at most 55 cm deep). This indurated layer was deeper in blocks 3 and 4, so the soils were deeper (at least 105 cm deep). Blocks 1 and 2 were contiguous, and so were blocks 3 and 4. Blocks 1-2 and blocks 3-4 were approximately 2000 m apart.

2.2. Experimental design

In order to determine the effects of livestock on carbon and nitrogen cycling in grazed savanna, twelve 16-m^2 plots were set up in each of the four blocks in May 2011. Grass species grew in rather homogeneous mono-specific patches. As blocks 1 and 2 were dominated by annual grasses and blocks 3 and 4 by perennial grasses, we chose 6 pairs of plots for each of the 2 dominant annual grasses in each of the two blocks dominated by annuals and 6 pairs of plots for each species of the 2 dominant perennial grasses in the two blocks dominated by perennials. Each pair of plots included one plot unprotected from livestock and one plot protected from livestock. Taken together, a total of 48 permanent plots (24 unprotected and 24 protected plots) were thus set up throughout the site. After 18 months of exclusion, we collected soil and grass samples in each of the 48 plots.

2.3. Soil and grass sampling

In each of the 48 plots, 5 soil samples were collected from the 0–10 cm layer using a 5-cm diameter auger under each dominant grass species. Similarly, 5 soil samples were also collected from bare areas

between the tufts. The 5 below-grass and bare soil samples were then combined respectively, which led to 2 composite soil samples (1 for grass species and 1 for bare soil) per plot and a total of 96 composite soil samples (48 for grass species and 48 for bare soil). After removing roots, these samples were then dried in the shade at ambient air temperature, and sieved to 2 mm.

All the grass individuals under which the soil samples had been taken were uprooted and grouped together to form a composite sample per plot. The roots of these plants were washed with water and then separated from the aerial parts (leaves + stems). Roots and aerial parts were oven-dried at 70 °C for 72 h. This gave a total of 96 composite samples (48 for aerial part and 48 for roots) for the 48 plots.

2.4. Soil and grass analyses

Soil and grass samples were ground to a powder and their contents in N, C, ^{15}N and ^{13}C were measured by EA-IRMS (Carlo-Erba NA-1500 NC Elemental Analyzer on line with a Fisons Optima Isotope Ratio Mass Spectrometer). ^{13}C and ^{15}N contents were expressed as relative differences in the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios between samples and international standards (Wang et al., 2010):

$$\delta^{15}\text{N} (\text{‰}) = ((^{15}\text{N}/^{14}\text{N})_{\text{sample}} / (^{15}\text{N}/^{14}\text{N})_{\text{standard}} - 1) * 1000,$$

$$\delta^{13}\text{C} (\text{‰}) = ((^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}} - 1) * 1000.$$

The international standard for N is atmospheric N_2 ($\delta^{15}\text{N}_{\text{N}_2} = 0$), while it is a fossil rostrum of belemnite (PDB) for C ($\delta^{13}\text{C}_{\text{PDB}} = 0$).

2.5. Statistical analysis

All statistical analyses were carried out using R software (R 3.3.1). All variables were analyzed using linear mixed-effects models with block as random effect. The null effect of enclosure was tested on soil and grass C, N, ^{13}C and ^{15}N . This null effect was tested based on the dominant species/or bare soil. When there was a significant effect, its direction was determined using the estimated model parameters and subsequent grouping of modalities (Crawley, 2007). Significant differences were $P < 0.05$. The interactions between species/or bare soil and enclosure were also tested. All interactions were not significant so were removed from the models and are not showed in the tables (Tables 1 and 2). For all linear models we checked for the normality and homoscedasticity of the residuals.

3. Results

3.1. Effects of grazing on soil parameters

All parameters except C/N ratio showed significant differences among species (Table 1). Total carbon and total nitrogen contents were higher under *A. asciodis* than under other grass species and in bare soil (Fig. 1). Soil $\delta^{15}\text{N}$ values were higher under the two annual species (*A. pseudapricus* and *L. togoensis*) and bare soil than under the perennials *A. asciodis* and *A. gayanus* (Fig. 1). Soil $\delta^{13}\text{C}$ values did not appear to be related to the grass type (annual or perennial species) but were higher under *A. asciodis*. Enclosure did not significantly affect any of the parameters (Table 1).

Table 1

Analysis of variance of soil total carbon, total nitrogen, the C/N ratio, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ as a function of enclosure and grass species or bare soil.

	DF	Total nitrogen	Total carbon	C/N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Species and bare soil	4	7.02***	7.50***	2.13 ^{ns}	2.70*	3.95**
Enclosure	1	0.12 ^{ns}	0.81 ^{ns}	1.40 ^{ns}	0.85 ^{ns}	0.03 ^{ns}
Direction of effects		Aa > Ag, Ap, Lt, BS	Aa > Ag, Ap, Lt, BS		Aa, Ag < Ap, Lt, BS	Aa > Ag, BS > Ap, Lt

Table 2

Analysis of variance of the total carbon and nitrogen contents, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in grass as a function of enclosure and grass species.

	DF	Total nitrogen	Total carbon	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Species	3	8.92***	9.29***	11.06***	42.22***
Enclosure	1	16.18***	0.51 ^{ns}	24.95***	0.00 ^{ns}
Direction of effects		Aa, Lt < Ag, Ap NP>P	Aa > Ag, Lt > Ap	Aa, Ag, Lt < Ap NP>P	Aa, Lt < AP < Ag

The effects of species, bare soil and enclosure on soil parameters are given with F values with the following significance levels (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = no significant effect). Origin = grass species or bare soil. Aa (*A. asciodis* - perennial); Ag (*A. gayanus* - perennial); Ap (*A. pseudapricus* - annual); Lt (*L. togoensis* - annual); BS (bare soil).

Species were Aa (*A. asciodis* - perennial); Ag (*A. gayanus* - perennial); Ap (*A. pseudapricus* - annual) and Lt (*L. togoensis* - annuals); BS (bare soil). Different letters (a, b, c) denote significant differences among treatments at a 0.05 level.

3.2. Effects of grazing on grass parameters

These results show significant differences among the four species of grasses for all parameters (Table 2). These differences do not appear to be related to the grass type (annual or perennial), as *A. asciodis* and *L. togoensis* showed the lowest total nitrogen and $\delta^{13}\text{C}$ values (Fig. 2). The highest total carbon and $\delta^{15}\text{N}$ values were measured in the perennial grass *A. asciodis* and the annual grass *A. pseudapricus*, respectively. A significant difference between protected (ungrazed) and unprotected (grazed) plots for each grass species was also observed for total nitrogen and $\delta^{15}\text{N}$ (Table 2). The values of these two parameters were higher outside enclosures (Fig. 3).

The effects of species and enclosure on grass parameters are given with F values and the following indicators of significance (*** $P < 0.001$; ns = no significant effect). Aa (*A. asciodis* - perennial); Ag (*A. gayanus* - perennial); Ap (*A. pseudapricus* - annual); Lt (*L. togoensis* - annual). P (protected plot); NP (unprotected plot).

Aa (*A. asciodis* - perennial); Ag (*A. gayanus* - perennial); Ap (*A. pseudapricus* - annual); Lt (*L. togoensis* - annual). Different letters (a, b, c) denote significant differences among treatments at a 0.05 level.

P (protected plot); NP (unprotected plot). Different letters denote significant differences among treatments at a 0.05 level.

4. Discussion

Our results revealed significant differences among grass species for all measured soil parameters, except for the C/N ratio. This is consistent with studies showing that plant species differently influence soil total nitrogen, total carbon (Somé et al., 2006, 2007; Yé et al., 2017), $\delta^{15}\text{N}$ (Nadelhoffer et al., 1996; Yé et al., 2015; Barthelemy et al., 2017), and $\delta^{13}\text{C}$ (Boutton et al., 1998).

The high carbon and total nitrogen content measured under the perennial *A. asciodis* suggest that it could help maintain and/or improve the accumulation of these elements better than the others species. Studies have indeed showed increased soil total carbon and total nitrogen under *A. asciodis* fallows (Somé et al., 2006).

Soil $\delta^{15}\text{N}$ values were lower under the perennial grasses *A. asciodis* and *A. gayanus* than under annual grasses and bare soil. These results confirm grass life cycle (annual and perennial) influence nitrogen cycling differently. Perennial grasses might better control nitrogen recycling and limit losses by inhibiting nitrification, leaching and slowing down recycling (Yé et al., 2015). The high values of soil $\delta^{15}\text{N}$ observed under annual grasses (*A. pseudapricus* and *L. togoensis*) and bare soil can be considered as an indication of high nitrogen recycling rates

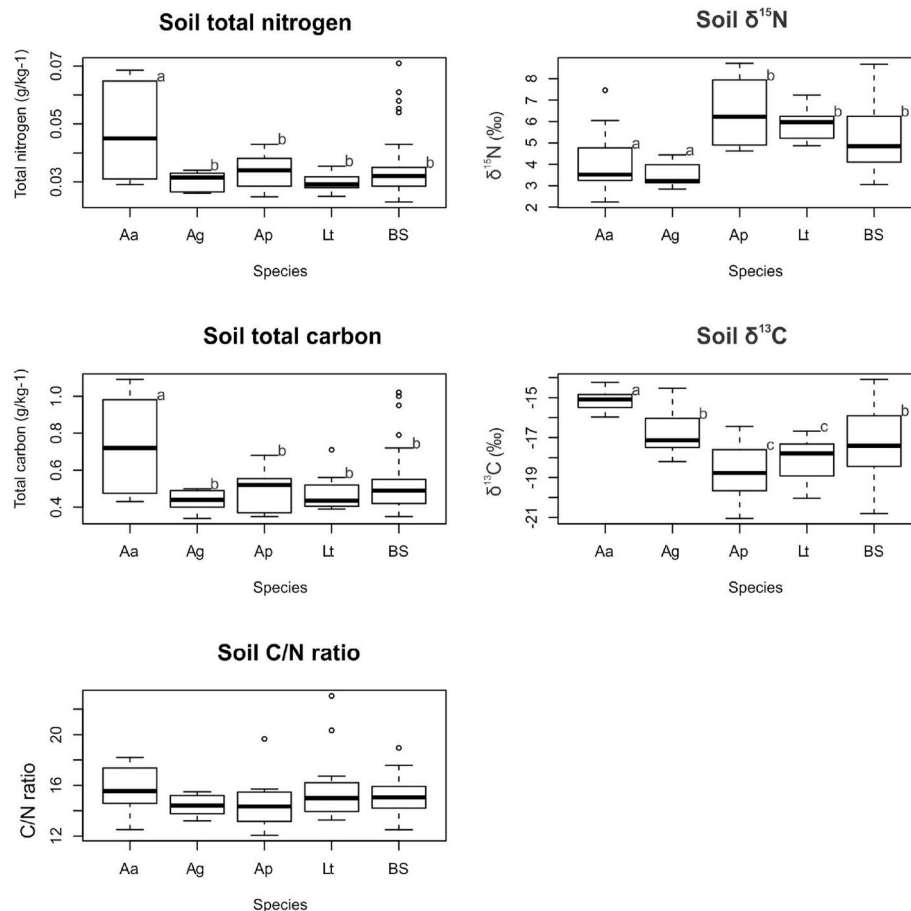


Fig. 1. Soil total carbon, total nitrogen, C/N ratio, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ under grass species or bare soil.

(mineralization, nitrification and denitrification), which also favor nitrogen losses (Nacro et al., 2004; Templer et al., 2007, 2008). Indeed, along the many transformations undergone by nitrogen, isotopic fractionation is likely to enrich the residual pool in ^{15}N because ^{14}N (the lighter of the two stable isotopes) is more reactive (Mariotti et al., 1981). Thus, in the case of an increased rate of nitrogen cycling, ^{14}N is more likely to be lost by denitrification and leaching, which leads to an increase in soil $\delta^{15}\text{N}$.

Soil $\delta^{13}\text{C}$ values varied significantly among grass species. However, these variations did not appear to be linked to grass type (annual or perennial species). They were higher under *A. ascinodis*. This could be linked to differences in carbon mineralization rates or to the origin of the organic matter (Mariotti et al., 1981; Desjardins et al., 1991). Since the four grass species were all C_4 plants, the high $\delta^{13}\text{C}$ values under *A. ascinodis* would indicate higher carbon mineralization below this plant, possibly linked to an efficient rhizosphere priming effect (Shahzad et al., 2015).

Our results revealed no significant difference between protected (ungrazed) and unprotected (grazed) plots for all measured soil parameters regardless of the grass species. This may be explained by the relatively short length of the experiment. Grazing has been found to have no significant effect on soil total carbon and total nitrogen contents in the short term, even if a slight decrease in soil organic matter content was found over two years (Silveira et al., 2013). However, in the long term, grazing can modify carbon and nitrogen accumulation in the soil depending on the plant species (Derner et al., 1997). Grazing can decrease soil total carbon and nitrogen content (Derner et al., 1997; Han et al., 2008; Prieto et al., 2011). On the other hand, it can also increase the soil carbon content (Reeder and Schuman, 2002). Contrary to our hypothesis, our results showed that grazing had no significant effect on

soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This might again be due to the short duration of enclosure, and is comparable to studies showing that grazing intensity does not affect the soil ^{13}C signature (Han et al., 2008). However, other studies show that herbivores have an impact on soil organic carbon and increase soil $\delta^{13}\text{C}$ (An and Li, 2015). In addition, cattle's grazing has been shown to increase soil processes such as nitrification, denitrification and free nitrogen fixation (Patra et al., 2006). Consequently, the modification of these fluxes (nitrification, denitrification, etc.) can affect ^{15}N signatures and may either increase (Frank and Evans 1997) or decrease (Frank et al., 2000) soil ^{15}N abundance. Thus, high values of soil $\delta^{15}\text{N}$ have been observed on heavily grazed sites compared to lightly grazed ones (Barthelemy et al., 2017). However, herbivores may most often have an impact on $\delta^{15}\text{N}$, which indicates changes in the nitrogen cycle (Frank and Evans, 1997; Frank et al., 2000; Aranibar et al., 2008; Craine et al., 2009a). In fact, herbivores impact the nitrogen cycle and aboveground-belowground link (i) directly through changes in plant growth and physiology and through alterations of the quality and quantity of mineral and organic resources, and (ii) indirectly through changes in the functional composition of vegetation (Bardgett and Wardle, 2003).

Our results highlight significant differences between the four grass species for all measured grass parameters unrelated to grass type (annual or perennial). These results are consistent with the results of several studies showing that the nitrogen, carbon and ^{13}C and ^{15}N signatures of plant biomass vary according to plant species, plant photosynthetic type (C_3 , C_4 , CAM) and nutrient availability in the soil (Mariotti et al., 1981; Joffre, 1990; Nadelhoffer et al., 1996; Aranibar et al., 2008; Craine et al., 2009b, 2012; Wang et al., 2010; Yé et al., 2015). In our case, all four grass species had a C_4 photosynthesis type, so that differences were bound to be related to other factors including

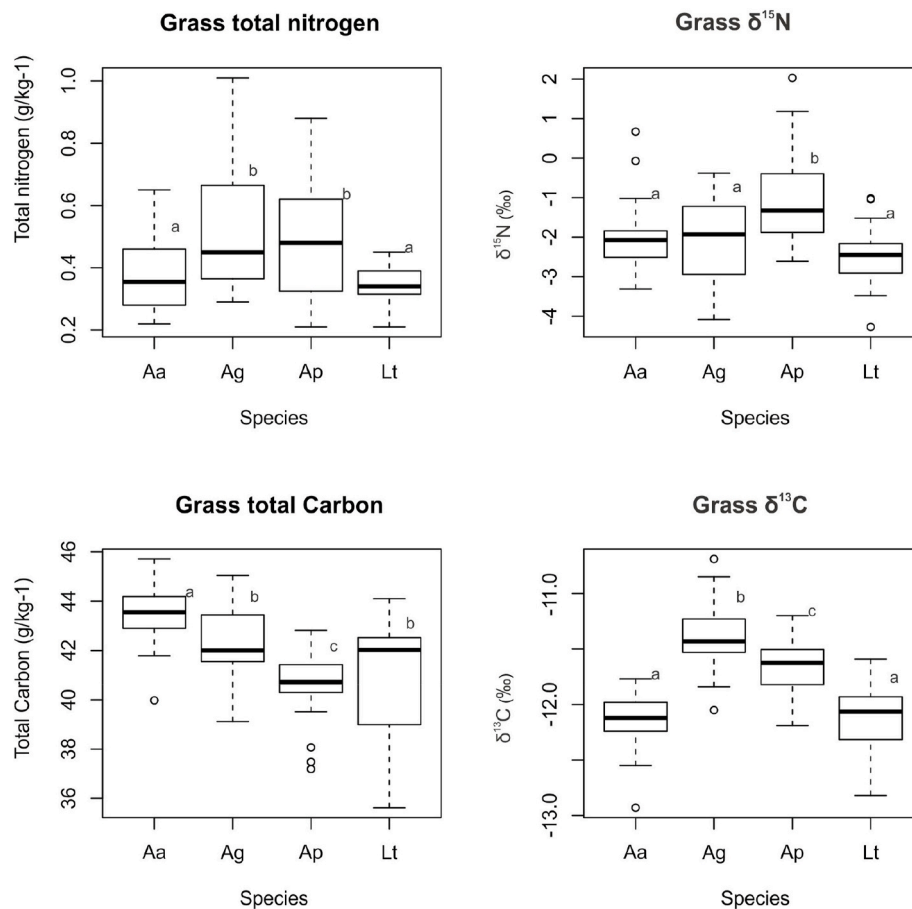


Fig. 2. Total carbon and nitrogen contents, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in grass.

species physiology, nutrient availability and soil properties. For example, a decrease in water use efficiency could lead to lower soil and plant biomass ^{13}C and ^{15}N levels (Peri et al., 2012). According to these authors, the differences in photosynthetic rates among grass species could explain variations in plant biomass $\delta^{13}\text{C}$. Grass nitrogen content was not linked to grass type (annual or perennial). They were higher for *A. gayanus* and *A. pseudapricus*, a perennial and an annual species, respectively. These findings are in contrast to other studies which found that annual species could display higher nutrient concentrations than perennial species (Garnier and Vancaeyzele, 1994). The observed differences in grass $\delta^{15}\text{N}$ values could be explained by isotopic fractionation during nitrogen transformation, differences in the sources and forms of absorbed nitrogen, e.g., according to rooting depth, mycorrhization and other factors controlling nitrogen absorption (Nadelhoffer et al., 1996; Kahmen et al., 2008; Craine et al., 2009b).

Our results show that grazing did not affect grass total carbon content and $\delta^{13}\text{C}$ values. Therefore, the presence of cattle did not seem to induce differences in the photosynthetic rates of the protected (ungrazed) and unprotected (grazed) plots, as any factor causing the modification of the photosynthetic rate would impact $\delta^{13}\text{C}$ values (Peri et al., 2012). On the other hand, grass total nitrogen content and $\delta^{15}\text{N}$ were higher in unprotected (grazed) than in protected (ungrazed) plots. This is consistent with results showing that grazing changes the plant biomass nitrogen content and the ^{15}N signature (Aranibar et al., 2008; Han et al., 2008; Craine et al., 2009a; Barthelemy et al., 2017). However, the increase in grass $\delta^{15}\text{N}$ was not consistent with the result obtained by Han et al. (2008). For these authors, the biomass total nitrogen content increased with grazing intensity, while the biomass $\delta^{15}\text{N}$ values of non-legume species decreased. Furthermore, Frank and Evans (1997) also found that plant $\delta^{15}\text{N}$ values were lower in grazed sites than in

ungrazed sites. Higher plant biomass total nitrogen and $\delta^{15}\text{N}$ values most likely reflected a relatively high availability of nitrogen for these grasses in the grazed plots (Craine et al., 2012). High $\delta^{15}\text{N}$ values could be related to higher nitrogen losses through denitrification and leaching that enrich the plant-available N pool in ^{15}N (Craine et al., 2009b). Absorption of this enriched nitrogen by grasses could therefore explain high ^{15}N values in their biomass. This is consistent with the idea that grazing generally promotes nitrogen loss (Frank and Evans, 1997), at least by increasing nitrogen mineralization (nitrification, denitrification) due to increased microbial activity (Frank et al., 2000; Le Roux et al., 2003; Patra et al., 2006). Many factors such as trampling, N returned in animal excreta, and/or modification of N uptake and C exudation by frequently defoliated plants could enhance microbial activity (Le Roux et al., 2003). Our results therefore suggest that grazing improves the immediate availability of nitrogen but could also increase nitrogen losses.

5. Conclusion

Overall, our results reveal an absence of significant differences between protected (ungrazed) and unprotected (grazed) plots, regardless of the grass species, for all the soil parameters measured during this experiment. Moreover, livestock grazing did not affect grass total carbon content and $\delta^{13}\text{C}$ values. However, grazing significantly impacted grass total nitrogen and $\delta^{15}\text{N}$, which were higher in unprotected (grazed) than in protected (ungrazed) plots. This finding suggests that livestock altered the nitrogen cycle in the grazing sites toward faster recycling and possibly increased nitrogen losses. Although the denitrification rate and nitrate leaching were not measured, it is believed that grazing could increase nitrogen losses. This impact of livestock can stimulate short-

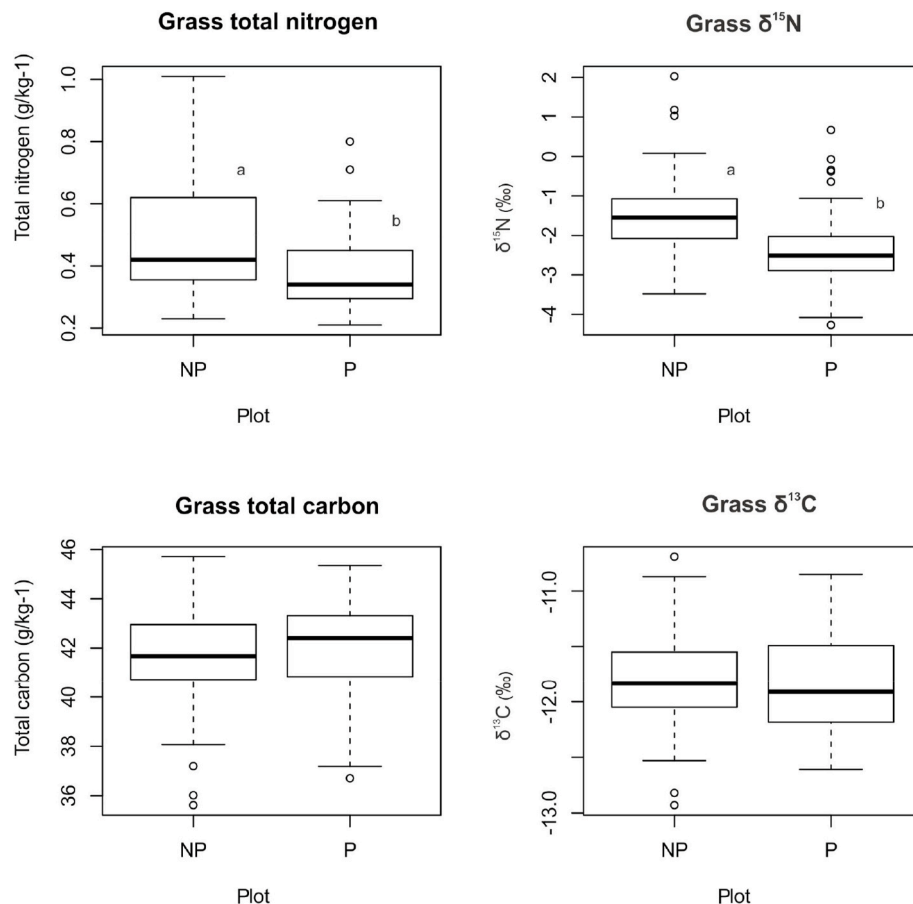


Fig. 3. Effects of enclosure on total carbon and nitrogen contents, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in grass.

term plant growth by increasing nitrogen availability. However, in the long term, nitrogen losses could also decrease nitrogen availability and decrease plant production, leading to pasture degradation. Testing this hypothesis would require keeping enclosures for a longer time and controlling the grazing pressure (intensity) on this site. We also hypothesize that the impact of grazing on grass $\delta^{15}\text{N}$ should result in a parallel change of this signature in the soil in the long term.

Authors' contributions

All the authors have contributed to the work presented. Lambiénou Yé carried out the field work and part of the measurements in the laboratory. Lambiénou Yé, Sébastien Barot, Hassan Bismarck Nacro, Dominique Masse and Jean-Christophe Lata designed the sampling, interpreted the results and were involved in writing the manuscript. They all approved the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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