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INDEPENDENCE OF SAVANNA GRASSES FROM SOIL ORGANIC MATTER FOR THEIR NITROGEN SUPPLY[1]

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Abstract. In Lamto savanna (Côte d'Ivoire), grass $\delta^{15}N$ ($\approx -1.3‰$) is much lower (has a smaller absolute value) than soil organic matter $\delta^{15}N$ ($\approx +5‰$). In order to understand such a discrepancy, we have analyzed ^{15}N natural concentrations in the four major sources of mineral nitrogen that can meet the annual requirements of plants: bulk precipitation, mineralization of humified soil organic matter, atmospheric dinitrogen fixation, and decomposition of plant litter. The first source (negative $\delta^{15}N$) only contributes ≈7% of nitrogen requirements, as does the second ($\delta^{15}N \approx +7‰$) due to a very low humus mineralization rate. The third source ($\delta^{15}N = 0$) contributes up to 17%, due to nonsymbiotic N_2 fixation by microorganisms associated with grasses, legumes being almost absent from the savanna. All these processes cannot account for the low $\delta^{15}N$ of grasses, suggesting that most of the assimilated nitrogen originates from the decay of root material ($\delta^{15}N \approx -1.1‰$).

Key words: grasses; ^{15}N; nitrogen cycling; nonsymbiotic fixation; root decomposition; savanna; West Africa.

INTRODUCTION

In the humid savanna of Lamto (Côte d'Ivoire), nitrogen requirements of the herbaceous stratum have been estimated at 70 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Abbadie 1984). In the field, as well as during incubation under optimal conditions, net N mineralization rates are very low (≈5 $kg \cdot ha^{-1} \cdot yr^{-1}$), and nitrification does not occur (Abbadie and Lensi 1990). Even with increased ammonification in particular sites, where the soil has been processed by fauna (Abbadie and Lepage 1989), the mineralization of soil organic nitrogen cannot be the only source of nitrogen assimilated by grasses. Other sources of nitrogen (precipitation, leguminous fixation) are too low to account for the difference. Therefore, nonsymbiotic fixation or rapid litter mineralization must be important.

In some tropical savannas where legumes are not numerous, nitrogen fixation by microorganisms in the rhizosphere of grasses and trees may significantly contribute to the N requirements of the ecosystem (Hogberg 1986, Maasdorp 1987). Nonsymbiotic nitrogen fixation has also been reported to be a significant contribution to the nitrogen budget of West African savannas (Robertson and Rosswall 1986). Using the acetylene reduction assay on two grass species (*Loudetia simplex* and *Hyparrhenia diplandra*) that represent >50% of the biomass of the herbaceous stratum in Lamto savanna, a production of 10–80 nmol of C_2H_4 per hour per gram of dry roots has been measured during the vegetative period (Balandreau 1976). Comparable results had been found for Brazilian savanna grasses by De-Polli et al. (1977).

Natural ^{15}N abundance in soils is usually higher than in the atmosphere (Shearer et al. 1978). As a result, ^{15}N abundance in non-N_2-fixing plants, for which soil is the only source of nitrogen, is higher than in N_2-fixing plants, which assimilate nitrogen from both soil organic matter and atmosphere (Rennie et al. 1976, Shearer and Kohl 1978, Delwiche et al. 1979). When N_2 fixation is the major source of nitrogen assimilated, the natural ^{15}N abundance of plants is close to that of atmospheric N_2, only slightly modified by the low isotope effect associated with dinitrogen fixation (Mariotti et al. 1980, Shearer and Kohl 1986). For these reasons, ^{15}N abundance measurement constitutes a valuable method to identify N_2-fixing species in the field (Virginia and Delwiche 1982).

The aim of this paper is to assess the relative contribution of mineralization and nonsymbiotic N_2 fixation to the annual nitrogen assimilation by grasses at the ecosystem level. The approach chosen is to com-

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TABLE 1. Isotopic composition of nitrogen in soil, as δ^{15}N (‰). All values are means ± 1 SE. n is the number of analyzed samples.

Component	Depth (cm) 0–5	Depth (cm) 5–13
	δ^{15}N (‰)	
Total organic nitrogen	5.0 ± 0.2 ($n = 4$)	5.5 ± 0.2 ($n = 4$)
Soil-derived mineral nitrogen	7.3 ± 1.1 ($n = 2$)	7.0 ± 0.6 ($n = 2$)

pare natural ^{15}N abundance in soils, legumes, and grasses.

MATERIAL AND METHODS

Study site

Lamto is located in Côte d'Ivoire (West Africa), at the edge of the rain forest domain (6°13′ N, 5°02′ W). Mean annual temperature is 27°C and rainfall averages 1200 mm/yr, with a dry season lasting ≈2 mo between November and February. In 1988, the year in which the experiment was conducted, the first rain occurred on 20 January. The landscape ranges from pure grassland to densely wooded vegetation, but most of the area is covered by the very open shrub savannas in which the work was conducted. Soils are very sandy (80–90% sand) and characterized by low organic matter (≈1%) and nitrogen (≈0.5‰) contents; pH averages 5.8. Fire occurs each year in the dry season and burns the standing grass biomass. The maximum above- and belowground biomasses of the herbaceous cover, respectively, reach ≈7 and 14 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$. Perennial grasses make up 90% of total biomass. Legumes, mostly annuals, are unevenly distributed, scarce, and constitute <0.5% of total biomass (Menaut and César 1979).

Field sampling

In order to measure ^{15}N abundance of soil organic matter, six samples were excavated twice during the year from two humic layers (0–5 and 5–13 cm depth) between grass tufts to reduce, as far as possible, their content of living and dead roots. Six other samples were also excavated according to the same procedure beneath grass tufts to control for possible δ^{15}N spatial variation. Samples were air-dried. Each series of six samples was pooled. After homogenization, δ^{15}N was measured on the pooled samples.

Four types of plants were collected and dried at 60°C for determination of ^{15}N abundance: legumes, presumed to be active symbiotic fixers because they were nodulated; the four major perennial tuft grasses; a rhizomatous grass; and a grass with roots surrounded by a thick mantle of mycorrhizae.

To follow possible ^{15}N abundance variations in nitrogen assimilated by grasses during the year, 160 tufts of *Hyparrhenia smithiana* were selected just after fire occurred (15 January 1988). All new leaves were immediately marked with a spot of paint. Twice a month, during one year, all the leaves that appeared during the last 15 d were thus marked, the color of the paint changing every 15 d. At the same time, from the beginning of the experiment, six tufts were collected randomly and their leaves were sorted according to the color of their spot of paint (i.e., cohorts of different ages), and then dried at 60°C. In other words, all the remaining living cohorts of leaves of six tufts were collected every 15 d during a complete cycle of development.

Laboratory studies

Plant material was crumbled to 1-mm particles and digested by the modified Kjeldahl method for ^{15}N measurements at natural abundance level (Mariotti and Letolle 1978). The analyzed aliquots were chosen large enough (200–1000 mg) to obtain at least 2 mg of gaseous nitrogen. After digestion, ammonia was distilled and collected in dilute sulfuric acid, then oxidized with lithium hypobromite after evacuation to remove atmospheric N_2. Evolved dinitrogen was purified and analyzed on a mass spectrometer (Finnigan Delta E) fitted with triple ion collectors and a dual inlet system for rapid switching between reference and sample. The same method was applied to soil organic matter: δ^{15}N was measured on two aliquots (5 g) for each pooled soil sample. Native ammonia and nitrates were extracted with 2 mol/L KCl from two aliquots (200 g) for each pooled soil sample. In order to obtain sufficient quantities of N for the measurement, the four extracted solutes were pooled into two larger volumes, from which mineral nitrogen was collected by steam distillation in the presence of MgO and Devarda's alloy, then treated according to the above procedure.

Units

Results are expressed in relative δ^{15}N units: $\delta^{15}\mathrm{N} = [(^{15}R_{\mathrm{sample}} - {}^{15}R_{\mathrm{standard}}/{}^{15}R_{\mathrm{standard}}] \cdot 1000$, where ^{15}R is the nitrogen isotope ratio (^{15}N/^{14}N), the standard being the atmospheric dinitrogen, which has δ^{15}N = 0‰ by definition (Mariotti 1983). On a well-homogenized soil sample, the standard deviation of the measure does not exceed 0.1‰.

RESULTS

^{15}N abundance in soil organic nitrogen between grass tufts, whatever the depth, was significantly higher (≈+5‰) than in atmospheric N_2. The δ^{15}N of native mineral nitrogen (ammonium and nitrate together) in the soil was ≈+7‰, close to that of organic nitrogen (Table 1). Beneath grass tufts, δ^{15}N values of soil organic nitrogen only reached +3.4 ± 0.1‰.

The ^{15}N abundance of grasses (leaf material) was very different from that of soil mineral nitrogen; it was significantly lower, with $\delta^{15}N$ values lying between −0.3 and −2.0‰, regardless of plant species (Table 2). On the same plants, root material gave an average $\delta^{15}N$ value of −1.1 ± 0.3‰. The isotope composition of nitrogen in the leaves of *Hyparrhenia smithiana* was constant during the year, with no clear variation occurring either with season or age of cohorts, except in those cohorts that appeared at the very beginning of the rainy season (Table 3).

Legumes (Table 2) showed typical $\delta^{15}N$ values for N_2-fixing plants, i.e., close to the $\delta^{15}N$ of atmospheric N_2, modified by the isotope effect associated with dinitrogen fixation (−2.0 ± 0.3‰). Grass $\delta^{15}N$ values were close to those of legumes.

DISCUSSION

The four possible major sources of nitrogen are: (1) soil organic matter (humified fractions), (2) dead plant matter newly incorporated into the soil and mineralized, (3) atmospheric dinitrogen via biological fixation, and (4) precipitation.

1) The slightly lower $\delta^{15}N$ values obtained below grass tufts ($\approx +3.4$‰), as compared to between-tufts values ($\approx +5$‰), probably come from the presence of inconspicuous rootlets ($\delta^{15}N \approx -1.2$‰), and from the influence of rhizodeposition of dead cells or exudates (with expected similar $\delta^{15}N$ values). The ^{15}N abundance in soils reported here, for organic or mineral forms, is similar to other published data (Shearer et al. 1978, Ledgard et al. 1984). It has been shown that isotope fractionation during nitrate nitrogen assimilation by mature plants is small (Kohl and Shearer 1980, Mariotti et al. 1980). No information is available on isotope fractionation associated with ammonium nitrogen assimilation by plants. However, at any time during the growing period, the pool of available mineral nitrogen in the soil is very small as compared to plant needs. In such a situation, the isotope effect associated with soil nitrogen assimilation, if it exists, cannot be expressed in the plant by an isotope enrichment between the mineral source and plant organic nitrogen. Thus, if soil-derived nitrogen was the source of nitrogen to the plant, the $\delta^{15}N$ of the total nitrogen of plants should reflect the $\delta^{15}N$ of the mineralized soil nitrogen. We did not observe this.

TABLE 2. Isotopic composition of nitrogen, as ‰ $\delta^{15}N$, in leaf material of some grasses (mean ± 1 SE = −1.3‰ ± 0.3‰) and legumes (−2.0 ± 0.3‰) of Lamto savanna.

Species	$\delta^{15}N$ (‰)
Perennial tuft grasses	
Loudetia simplex C. E. Hubbard	−2.0
Andropogon schirensis Hochst	−1.9
Hyparrhenia diplandra Stapf.	−1.3
Hyparrhenia smithiana Stapf.	−1.3
Rhizomatous grass	
Imperata cylindrica Beauv.	−0.3
Grass with mycorrhizae	
Brachiaria brachylopha Stapf.	−1.1
Legumes	
Cassia mimosoïdes Linn.	−2.1
Desmodium ramosissimum G. Don.	−2.0
Desmodium tortuosum (S. W.) D. C.	−1.0
Eriosema griseum Bak.	−2.9
Eriosema molle Hutch. ex Milne-Redhead	−3.9
Indigofera paniculata Vahl.	−1.0
Indigofera polysphaera Bak.	−1.3
Pseudarthria hookeri Wight & Arn.	−2.6
Tephrosia elegans K. Schum.	−2.5
Teramnus buettneri (Harms) Bak. F.	−1.0

TABLE 3. Temporal variation of the isotopic composition of nitrogen in the leaves of *Hyparrhenia smithiana*, Poaceae, collected in 1988 (two cohorts analyzed for each date; expressed as ‰ $\delta^{15}N$ [mean ± 1 SE = −1.6 ± 0.1‰]).

Date	Age of the cohort (d)			
	15	30	45	60
19 Feb 1988	−1.6	−3.5	no cohort	no cohort
6 Mar 1988	−1.5	−2.0	−5.4	no cohort
19 Mar 1988	−1.3	−1.0	−1.0	dead
1 Apr 1988	−1.3	−1.3	−0.8	dead
9 May 1988	−1.5	−1.1	−0.9	dead
2 Jul 1988	−1.8	−1.3	−1.7	−1.6
2 Oct 1988	−1.6	−1.2	−1.3	−1.5
31 Oct 1988	−2.0	−1.3	−1.7	−1.3
1 Dec 1988	−1.5	−1.8	−1.8	−2.0
15 Dec 1988	−0.7	−1.6	−1.1	−1.8
30 Dec 1988	−1.4	−1.3	−2.1	−1.1

On the contrary, $\delta^{15}N$ values of grasses were much lower (−1.3 ± 0.3‰ for whole plants, Table 2; −1.6 ± 0.1‰ for cohorts of leaves of *Hyparrhenia smithiana*, Table 3) than those of mineralized soil nitrogen $\delta^{15}N$ (+7.1 ± 0.4‰). Even lower $\delta^{15}N$ values were found in the very first cohort appearing after fire. This can be explained by one of the following processes: (1) a strong fractioning effect during the first phase of nitrification is fully documented (Feigin et al. 1974, Bremner and Hauck 1982). Herman and Rundel (1989) reported that, after fire in chaparral, there was a rapid accumulation of ^{15}N-depleted inorganic nitrogen from nitrification. However, the increase in nitrification after fire is still debated in chaparral (Debano et al. 1979) and has not been observed in savannas (Frost and Robertson 1987). Meiklejohn (1955) had found that nitrifying bacteria were either killed, or reduced to very few, by burning in Kenyan savannas. Adedeji (1983) also reported that, in Nigerian savanna soils, nitrification rates were initially reduced by fire. It is thus unlikely that the depletion in ^{15}N observed in the very first cohort would come from a rapid flush of plant-available nitrate after burning, even with a low $\delta^{15}N$. Anyhow, in Lamto savannas, in the field and during incubation, nitrification does not occur (Abbadie and Lensi 1990). If it did, the ^{15}N-depleted nitrogen absorbed by the first cohort could not be, by far, in a sufficient amount to "pollute" the isotope composition

TABLE 4. Tentative nitrogen budget at plant level.

Category	N flux ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Citation
Requirements of grasses	70	Abbadie 1984
Inputs		
Mineral nitrogen in rain	5	Villecourt and Roose 1978
Mineral nitrogen in ashes	1	Delmas 1982
Humus mineralization	5	De Rham 1973
Dinitrogen fixation	12	Balandreau 1976
Dead root mineralization	40	
Total	63	
Outputs		
Fire	20	Abbadie 1984
Consumption by invertebrates	5	Menaut and César 1979
Root mortality	40	Abbadie 1984
Total	65	

of the plant during its full cycle. All other cohorts showed $\delta^{15}N$ values close to those of the whole plant (Tables 2 and 3); (2) the alternation of dry and wet periods mimics the early stage of an incubation when a depletive effect on $\delta^{15}N$ is noticed (Feigin et al. 1974); (3) the first rains following a dry spell are often reported to be depleted in ^{15}N (Freyer 1978) and may act as a mineral nitrogen source for the plant; (4) the low activity of nitrate reductase at the onset of leaf growth is known to induce a strong isotopic effect and a ^{15}N depletion in the younger parts of the plant (Mariotti et al. 1982).

The difference in ^{15}N abundance between grasses and soils is such that savanna grasses are not likely to take up significant quantities of the nitrogen mineralized in the bulk of the soil. In addition, we know that humus N mineralization in Lamto is not quantitatively important ($\approx 5 \ kg \cdot ha^{-1} \cdot yr^{-1}$; De Rham 1973) because of its high degree of condensation (Delmas 1967) and the lack of carbon assimilable by bacteria (Darici et al. 1986).

2) Dead plant litter is the second major potential source of mineral nitrogen. During the early stages of plant matter decomposition, it has been shown that no significant nitrogen isotopic fractionation occurs (Mariotti 1982). Mineralized nitrogen from plant matter decomposition should thus present an isotopic composition close to that of the plant ($\approx -1.3‰$ in Lamto). As the annual bush fire destroys the major part of stems and leaves, most of the litter originates from root decomposition. Dead root mineralization mostly occurs in the first 20 cm of the soil under the tufts, where dead and living roots are concentrated: living roots stimulate the decay of dead roots by exudation of carbonaceous compounds. The residence time of the mineral N originating from mineralization of dead roots is probably very short: as soon as this mineral N is produced, it is taken up by living roots, and is subsequently not accessible to measurement. This process may produce $\approx 40 \ kg \cdot ha^{-1} \cdot yr^{-1}$ N (Abbadie 1984), and accounts for the low $\delta^{15}N$ grass values.

3) The third potential source of nitrogen is biological N_2 fixation. The $\delta^{15}N$ values of the grasses ($-2‰$ to $0‰$) are consistent with the hypothesis that grass nitrogen is being derived from N_2 fixation (Kohl and Shearer 1980, Mariotti et al. 1980). However, it is very unlikely that N_2 fixation could account for 100% of the nitrogen assimilated by grasses. Even legumes in pure stands only meet 40–60% of their nitrogen requirements through N_2 fixation (Shearer and Kohl 1986). Through direct field measurements, Balandreau (1976) estimated nonsymbiotic nitrogen fixation at 12 $kg \cdot ha^{-1} \cdot yr^{-1}$. Even if the method is considered to give underestimated values of actual N_2 fixation, the process, on a yearly basis, cannot account for the negative values of $\delta^{15}N$ measured in the savanna grasses. However, it has to be noticed that, over a long period of time, the isotopic composition of a partially fixing plant necessarily tends toward that of atmospheric nitrogen if nitrogen in plant dead matter is efficiently recycled into new plant growth, and if the contribution of soil native nitrogen is rather negligible.

4) The fourth potential source of mineral nitrogen is bulk precipitation. $\delta^{15}N$ precipitation has not been measured in Lamto, "but long-term measurements all have yielded negative $\delta^{15}N$ values for both ammonium and nitrate" in different parts of the world, including the Tropics (Vitousek et al. 1989). Lamto precipitation only contains $\approx 5 kg \cdot ha^{-1} \cdot yr^{-1}$ mineral nitrogen (Villecourt and Roose 1978). Such a low amount should not significantly affect, in the short term, grass $\delta^{15}N$. However, the process adds up to the isotopic effect of biological N_2 fixation, and in the long term contributes to lower $\delta^{15}N$ values in grasses, if plant dead matter is efficiently mineralized.

CONCLUSION

It is thus clear that a unique source of mineral nitrogen cannot account for the nitrogen content of the grass layer. Given the relative values of the $\delta^{15}N$ of the possible sources of mineral nitrogen, we propose the following as the probable sources of nitrogen to the system: (1) only a very small part (≈ 5 kg·ha^{-1}·yr^{-1}) through the weak mineralization of the soil organic matter; (2) an equivalent part (≈ 5 kg·ha^{-1}·yr^{-1}) from bulk precipitation; (3) about double this (≈ 12 kg·ha^{-1}·yr^{-1}) through nonsymbiotic fixation in the rhizosphere; and (4) mainly through the recycling of the nitrogen stock of the dead roots, before humification (≈ 40 kg·ha^{-1}·yr^{-1}).

The tentative nitrogen budget presented in Table 4 incorporates results obtained on the same savanna site in different years. However, interannual climatic variations were not such that they could induce significant changes in the relative importance of the various components of the budget. Details on plant production and nitrogen uptake estimates (measurements and results for both above- and belowground parts) have been described in Menaut and César (1979) and in Abbadie (1984). Total N outputs from the plant compartment amount to ≈ 65 kg·ha^{-1}·yr^{-1}. This value rather closely compares with the annual requirements of grasses in nitrogen (≈ 70 kg/ha^{-1}). Measured N inputs to the plant compartment only reach ≈ 23 kg·ha^{-1}·yr^{-1}. Whatever the accuracy of the absolute values, the nitrogen budget of the savanna cannot be balanced, even roughly, if most of the nitrogen mineralized from dead roots (≈ 40 kg·ha^{-1}·yr^{-1}) is not taken up by plants. If such is the case, total annual N inputs amount to 63 kg/ha^{-1}, close to grass requirements. Both δ^{15}N measurements in various nitrogen sources and the values obtained for setting up a tentative nitrogen budget lead us to conclude that N mineralization from dead roots constitutes the major source of nitrogen to grasses in this savanna.

Such results confirm that nitrogen is mostly internally recycled within the vegetation–soil system, but not as much (73 vs. 95%) as shown by Rosswall (1976) at global level. A substantial portion of plant nitrogen originates from the atmosphere (dinitrogen fixation and precipitation), making up for the losses due to the annual bush fires. They particularly show that in this savanna, as in some temperate prairies, "nitrogen that enters the soil humus is very slowly recycled into new plant growth" and that the annual N grass requirements are largely met by mineralization of litter material (Clark 1977).

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