The fate of nitrogen under maize and pasture cultivated on an alfisol in the western Llanos savannas, Venezuela

J.M. HÉTIER¹, G. SARMIENTO², T. ALDANA¹, M. ZUVIA¹, D. ACEVEDO² and J.M. THIÉRY³ ¹SOMOS Project ULA-ORSTOM, Mérida, Venezuela, ²Ecologia Tropical, Fac. Ci. ULA, Mérida, Venezuela and ³Service de Radioagronomie, CEN Cadarache, 13108 France

Received 6 May 1988, Revised November 1988

Key words: alfisol, immobilization, mineralization, nitrogen-15, savanna, tropical agrosystems

Abstract

A field experiment was designed to follow the fate of fertilizer nitrogen in an annual crop (maize) and a permanent meadow (*Digitaria decumbens*) cultivated on an alfisol under the tropical two-season-climate of the Venezuelan Llanos. ¹⁵N labelled urea equivalent to 150 kg N.ha^{-1} was added to field plots and to lysimeters of undisturbed soil.

Results obtained after the first year show that the accumulation of fertilizer nitrogen was twice as great in the aboveground parts of maize and accompanying weeds (29% of the added nitrogen) than in the aerial parts of grass (16%), while the reverse trend was shown by roots: about 2% of the added nitrogen was detected in corn roots and more than 4% in the underground biomass of the meadow. Leaching losses were less than 2% under maize and almost nil under pasture in spite of intensive leaching which occured during the rainy season.

The top-soil (0–40 cm) of the grassland retained about 50% of the fertilizer nitrogen while only about 25% remained in the top-soil of the maize plot. The loss of fertilizer could be explained, largely, either by volatilisation immediately after application, or denitrification during the following weeks. The relative proportions of fertilizer-N and soil-N in maize and grass suggest that, during this period, gross mineralization of soil-N in both agroecosystems attained a value almost equivalent to the total nitrogen added in the fertilizer. The implications of these results when converting natural savannas into cultivated regimes are very different in the case of permanent pasture, which can improve the organic status of these poor soils and annual crops, like maize, which induce an unavoidable deficit in the nitrogen balance.

Introduction

The Orinoco Llanos is an extensive savanna region covering more than 500,000 km² in Northern South America, half in Colombia and half in Venezuela. In both countries, the Llanos now represent the most mobile agricultural frontiers where original savannas are being increasingly replaced by commercial crops and cultivated pastures. The impact of this conversion of the original stable ecosystems (Sarmiento, 1983) into more productive agrosystems should be carefully considered, not only from the point of view of increasing productivity but for improving the organic status as a basis for developing the long term fertility of these poor soils (Pichot, 1983).

Annual crops, like maize, sorghum, or cotton, and improved pastures, are the two most widespread forms of land use intensification in the Llanos. Both require at least some NPK fertilization. To check the efficiency of this fertilization, a field experiment was carried out to follow the fate of the fertililzer-N in a maize culture and a permanent pasture of pangola grass (*Digitaria decumbens*) on an alfisol representative of the well drained and economically more attractive soils of the western

04 SEP. 1990 X N°: 30.487 ex1 Cote: B P

ORSTOM Fonds Documentaire

8183

295

Table 1. Main soil features

Depth (cm)	pHH ₂ O	Sand (%)	Silt (%)	Clay (%)	C (%)	N (%)	C/N	C.E.C. (meq/100 g)	Base sat. (%)
0-20	5.6	69	12	18	0.7	0.06	12	2.4	60
20-30	5.5	61	5	33	0.6	0.05	12	2.4	56
30-60	5.9	53	23	24	0.5	0.04	12	2.3	79
6090	6.3	51	21	28	0.3	0.03	10	3.3	65
90-105	6.4	51	9	40	0.2	0.02	10	3.6	64

Venezuelan Llanos. Total nitrogen and ¹⁵N were measured after the first year of cultivation in order to ascertain the Coefficient of Real Utilization (CRU) of the fertilizer by the crops, the Nitrogen Derived From Fertilizer (NDFF) in the plant parts, organic matter, and leaching losses under the heavy rainfall conditions of this tropical climate.

Materials and methods

Study site

The experimental plots were established in the Botanical Garden of the University of the Llanos (UNELLEZ) in Barinas (8"37'N, 70"12'W, 180 m.a.s.l.). The tropical climate of this station shows a sharp contrast between the rainy season, when monthly precipitation may attain 400 mm and an almost rainless dry season from December to March. Annual rainfall slightly exceeds 1700 mm. The mean annual temperature is about 26°C with very small variations.

The soil (Barinas series Table 1) is a 2.5 m deep oxic Tropustalf, rather acid (pH 5) with very low CEC (less than 1 meq) that corresponds to the mainly kaolinitic clay content.

The original savanna grassland on these soils is dominated by perennial bunch grasses of low nutritive value but more valuable African species like

Hyparrenia rufa and Panicum maximum easily replace natural savannas after human disturbance.

Experimental design (Fig. 1)

Maize. A 360 m^2 maize plot (var. *Eto amarillo* from CIMMYT) was sown on May 22, 1986, with a

density of 50,000 plants.ha⁻¹. Within this plot, six randomly chosen microplots (each consisting of three rows 2 m long, spaced 0.9 m apart, *i.e.* 27 plants) were labelled and fertilized (150 kg N.ha⁻¹) 19 days later at the 3 to 5 leaves stage. The labelled urea solution was applied to each plant (E = 2.5%, 3 g N per plant, by four 15 ml applications).

The corn was harvested 99 and 145 days after sowing (*i.e.*, 82 and 127 days after labelling). The final yield was established on the basis of 700 unlabelled plants, and the ¹⁵N balance on 30 labelled plants from the central line of each labelled microplot. Living roots were also sampled within a soil volume of $20^2 \times 40$ cm. These samples were used to



Fig. 1. Experimental design. Notice the two field plots adjoining the large pit where the collectors from the six lysimeters were placed.

1

z

measure the total nitrogen and ^{15}N concentration, but the total root biomass was calculated on the basis of a root/shoot ratio of 15%, classical in maize (Hétier *et al.*, 1986). The soil under maize was sampled during the dry season using the same procedure.

Pasture. Stolons of Digitaria decumbens were uniformly planted (April 11, 1986) on a 500 m² plot. Six 1.44 m² microplots were randomly selected to be labelled with ¹⁵N urea. After two months (June 10, 1986) the newly grown pasture was harvested and each microplot was labelled by mean of 169 applications of 20 ml of urea in solution (15 g N/m², E = 2.5%), avoiding any contamination of the remaining area. The pasture was harvested again, 98, 154, and 252 days after labelling and fertilizing (150 kg N.ha⁻¹). For ¹⁵N determinations, only the central 1 m² surface of each labelled microplot was sampled.

One year after labelling, on the same day of the fourth harvest, one plot was destroyed and the topsoil was sampled (three replicates of $20 \times 25 \times 40$ cm volume divided into four 10 cm layers).

Lysimetric device

يون.

Along and near (150 cm) the two contiguous edges (Fig. 1) of a 25 m^2 square pit, six galvanized steel cylinders (1.2 m) high, diameter 0.56 m) were slowly forced into the soil to a depth of 110 cm without disturbing the inner soil core. The bottoms of the soil cylinders were set on a sand gravel base contained in a steel cone fixed to the cylinder by an asphalt gasket, allowing a controllable water outflow without any loss. The drained water was collected in 30-L plastic beakers (Roose, 1981, Dodwell and Webster, 1980).

Three of these lysimeters were sown with *Digitaria decumbens* and the other three with one grain of maize. One lysimeter of each group was labelled with ¹⁵N urea on the same day as the labelled plots, but with a more strongly labelled solution (E = 12%).

Every fortnight, the volume of water collected in the 30-litre plastic beaker of each lysimeter, was measured and a 2-L sub-sample was saved for analysis.

Analytical procedure

Dry weight was always expressed on an oven-dry basis (60°C). After weighing, each sample was finely ground to pass a 0.2 mm sieve and thoroughly homogenized before sub-sampling for analysis. Plant and soil samples were analyzed using the Kjeldahl-Olsen procedure as modified by Guiraud and Fardeau (1977) for previous reduction of nitrates. Water samples were first acidified and concentrated by gently boiling and then analyzed for ammonium, nitrate, and total nitrogen content by Bremner's method described by Guiraud (1984). The isotopic excess was measured by an optical spectrometer SOPRA GS1, after oxidation to N₂ by lithium hypobromide within a vacuum device derived from that of Ross and Martin and adapted by Guiraud (1984).

Results

Soluble nitrogen balance (Fig. 2)

Total precipitation during the annual cycle (May 26, 1986 to May 28, 1987) amounted to 1721 mm, 1192 mm of which fell during the period of maize cultivation (May 28, 1986 to October 10, 1987). About 90% of the precipitation reached the soil surface, 47% leached through under maize and 31% under pasture.

The total annual nitrogen outflow (90% of which was mineral-N during the cultivation period) was about 13 kg.ha^{-1} under maize and 1.5 kg.ha^{-1} under Digitaria.

On average, the nitrogen concentration was about 1 mg.L^{-1} under pasture and 2 mg.L^{-1} under maize. But this soluble nitrogen was weakly labelled and the leached fertilizer-N was less than 2% of the labelled nitrogen under maize and too low to be measured under pasture.

After the dry season following the final harvest the proportion of the fertilizer nitrogen leached from the maize lysimeter increased, but the amounts were so low that the total losses of fertilizer-N during the whole year remained at about 2%. Under meadow, the nitrogen outflow was almost nil during this 6-month period.





Fig. 2. Water and nitrogen outflows from maize and pasture as measured with the lysimeters. The fertilizer leaving the meadow was negligible.

Maize (Table 2, Fig. 3). Corn yield reached 5.2 t.ha^{-1} with 94 kg of nitrogen (29 kg of which was derived from the fertilizer). The stubble remaining on the field had a dry weight of 6.5 L.ha^{-1} with 34 kg of nitrogen (12 kg of which came from the fertilizer). As a whole, the maize harvest accumulated a total of 138 kg N.ha⁻¹, of which 41 kg came from the urea (CRU 29%) and 97 kg from the pre-existent stock of soil nitrogen.

The dry weight of weeds collected aboveground between the maize rows at harvest attained. 4.25 t.ha^{-1} and contained 71 kg of nitrogen, only 2 kg of which came from the fertilizer. This fact may be explained by the poor lateral diffusion of the applied urea fertilizer and the delayed growth of the weeds.



Fig. 3. Fertilizer-N (*left values*) and total nitrogen (*right values*) in the compartments of the maize culture after the first year (values in kg N.ha⁻¹, rainfalls according to Sarmiento, 1984).

In the labelled lysimeter, the maize plant still remained green at harvest time, though the grain was mature and well formed. But the amount of ureic nitrogen was nearly 50% higher than in the field (68 kg.ha^{-1} compared to 43 kg.ha^{-1}). Although there was no replicate, this difference is considered as significant and attributed to the spatial limitation of root development within the lysimeter. As the roots were not able to extend towards the unlabelled zones of the soil and thus they explored more intensively the lower horizons enriched by leached ureic nitrogen.

At the end of the annual cycle of maize, the apparent losses reached about 40% (see balance in Fig. 3). The distribution of these apparent losses are detailed in the discussion.

Pasture (Table 3 and Fig. 4). The total harvest of grass during the first year was approximately 12.75 t.ha^{-1} of dry matter, excluding the preliminary harvest before labelling. 116 kg N.ha^{-1} were accumulated in this grass biomass, 22 kg of which came from the fertilizer, *i.e.* 14% of the fertilizer input. So the sward was apparently using the fertilizer inefficiently at least in the cropped above-ground parts. The crowns left after cutting contained about 1% of the fertilizer-N, while the underground biomass (0–40 cm) attained 4.4 t.ha⁻¹ at

,

Plant and soil samples:	Dry matter (t.ha ⁻¹) ^a	N° (%)	1ot. N (kg.ha ⁻¹)	(kg.ha ⁻¹)	NDFF (%) ^b	CRU (%)	
Maize at heading	(99 days after sowin	1g)					
Grains	4	1.5	53	18	34	12	
sd [%]	15	2	i.		5	. •	
Stubbles	12	0.7	85	34	39	-23	
sd [%]	18	3			6		
Roots	2	0.5	9	3'	36	2.	
sd [%]	25	4		ł	10		
Total	18	0.83	147	55	39	38	
sd [%]	19	3.5			6.5		
Maize at harvest	(145 days after sowi	ina)		i			
Grains	5 2	18	94	29	31	19.4	
sd [%]	15	2			5		
Stubbles	6.5	0.52	34	12	36	8	
sd [%]	18	3	• ·		6		
Roots	1.9	0.6	11	2	20	1.4	
sd [%]	25	4			10		
Total	13.6	1.02	139	43	31	28.8	
sd [%]	19	3.5			6.5	- 1	
Maiza lugimatar							
Graine	4.6	1.6	73	42	57	28	
ed [%]	U	2	15	-12	5	20	
Stubbles	8.7	0.51	44	26	59	17 ·	
Weeds	43	17	72	2	3	T	
sd [%]	30	3	12	2	6	* ,	
Soil						,	
0-40 cm	5550	0.05	2920	39	1.3	26	
sd [%]	10 .	5	· · · · · · · · · · · · · · · · · · ·		20		

^a field standard deviation.

- 1

\$

^b analytical standard deviation

the end of the annual cycle, containing 32 kg.ha^{-1} of nitrogen, 9.6 kg of which were derived from the fertilizer.

The grass roots were more evenly labelled than those of the maize and the soil under meadow was also more uniformly labelled, as could be expected from the labelling procedure. The whole soil (0 to 40 cm) retained about 50% of the ureic-N. Thus, the apparent losses of fertilizer-N under meadow are lower than under maize (31% compared to 44%, as shown by the fertilizer balance displayed on Tables 2 and 3).

Discussion

These results will be discussed in terms of gross

mineralization and immobilization processes, which corresponded to the total production during a given time. Each gross process should be clearly distinguished from the corresponding net result, *i.e.* the instantaneous difference between mineralization and immobilization, as explained by Dommergues (1970). In an open system such as a fertilized agrosystem, the gross mineralization process generally overrides the gross immobilization. Thus, we have a net mineralization result which is approximately represented by the soil nitrogen content of the harvest.

The soil had a low initial total carbon and nitrogen content: 0.7 and 0.06% respectively in the top-soil, giving a C/N ratio of about 12 (Table 1). According to these values and the very low soluble nitrogen content of the soil solution and leached

300 Hétier et al.

Table 3. Total-N and fertilizer-N in plants and soil in the pasture plot

Pasture and soil samples:	Dry matter (t.ha ⁻¹) ^a	N (%) ^b	Tot. N (kg.ha ⁻¹)	Fert. N (kg.ha ⁻¹)	Fert. N/Tot. N NDFF (%) ^b	Fert. Bal. CRU (%)
Successive harvests						
0 (labelling day)	3	1.3	40			
1 (98 days aft. lab.)	7	1.1	77	17	23	12
2 (170 days aft. lab.)	3	0.8	23	3	12	2
3 (323 days aft. lab.)	2	0.7	·16	2	4	1
Total $(1 + 2 + 3)$	13	0.91	116	22	19	15
sd [%]	24	3			6	ι.
Pasture in lysimeter	9	1.03	93	25	27	17
sd [%]		3			6	
Roots after last harvest					·	
0–10 cm	4	0.74	30	4.8	16	3.2
sd [%]	20	4			5	
10-20 cm	0.3	0.5	1.5	0.15	11	0.1
sd [%]	25	5			7	
20–30 cm	0.1	0.6	0.6	0.06	10	0.05
sd [%]	30	5			7	
30–40 cm	0.1	0.6	0.6	0.06	10	0.05
sd [%]	30	5			7	
Total	4.5	0.73	32.7	5.07	15.5	3.4
Soil						
0–40 cm	5550	0.06	3575	77	2.1	51
sd [%]	10	5			20	

^a field standard deviation.

^b analytical standard deviation.



Fig. 4. Fertilizer-N (*left values*) and total nitrogen (*right values*) in the compartments of the grass plot after the first year (values in kg N.ha⁻¹).

waters, we may suppose that the mineralization rate of the native organic matter was very low.

Considering the plant biomass as an extracting agent of soil mineral nitrogen, we had a total exportation of 116 kg N under pasture, 22 kg of which came from the fertilizer (Fig. 4). In addition, at the end of the annual cycle, we had 32 kg N in the roots, almost 10 kg of which came from the fertilizer and about 7 kg in the crowns (6 kg of which were derived from the soil). The net annual production of mineral nitrogen by the soil was then at least 122 kg.ha^{-1} (154 within the plant minus 32 from the fertilizer), since we did not know if the ureic nitrogen had indeed been organically transformed and remineralized before absorption by the plant.

ç,

ţ,

But the gross mineralization process included also the microbial absorption in competition with roots for mineral nitrogen. For maize and rye grass, the microbial-N accumulated during cultivation was measured in our previous study as equivalent to the root nitrogen (Chotte *et al.*, 1986; Hétier *et al.*, 1986). Based on this assumption, the microbial biomass should have used 32 kg of mineral nitrogen, 10 kg of which came from the fertilizer if we also admit that the isotopic composition of the roots at the end of the annual cycle reflected the mean composition of the soil solution during the same period. Thus, the gross annual mineralization can be estimated by this way as $144 \text{ kg}.\text{ha}^{-1}.\text{year}^{-1}$ (122 + 22).

1.10

Two further assumptions are needed to proceed: (1)- the N mineral content of the soil should not increase after introduction of the urea, for a period longer than one or two months after fertilization, and then should revert to its previous steady state.

(2)- once immobilized into organic compounds the nitrogen is not again mineralized during the considered period.

We need now to consider gross immobilization (I_n) : under pasture, 77 kg of ureic (Q_N) was accumulated in the soil organic matter at the end of the annual cycle. These 77 kg certainly did not reach the organic pool of the soil without being diluted by mineral nitrogen coming from the mineralization of the unlabelled initial roots and humic fractions. The fertilizer-N content of the grass harvests, which gives an estimation of the composition of the soil solution during cultivation, gave a good idea of this dilution. On the day of labelling, the isotopic composition of the solution corresponded to about 96% of the fertilizer isotopic excess, decreasing to about 18% at the first harvest. The nitrogen which passed through the solution during this first cultivation period can be about 57% derived from the fertilizer, *i.e.* a mean value half way between the initial ($E_i = 96\%$) and the final ($E_f = 18\%$) values of the nitrogen isotopic excess in the transit compartment. According to the calculation proposed by Guiraud (1984)

$$I_g = Q^{15} N/[(E_i - E_f)/2],$$

0

135 kg of mineral nitrogen passed through the soil solution during this time, 77 kg from the fertilizer and 58 kg from the soil. The following harvests were so weakly labelled that we may consider that the main part of the immobilization process occurred during the first week following the introduction of the fertilizer.

The same estimation of gross immobilization can be repeated for maize and gave a result of 58 kg

The fate of nitrogen under maize and pasture 301

(39 kg from the fertilizer and 19 kg from the soil), based on the third harvest result only. The apparent losses are much more important, since only 39 kg of the fertilizer-N was found in the first 40 cm of the soil. Thus the soil is conjectured to have given only 109 kg N (90 kg to the harvest + 19 kg to the soil) to dilute the fertilizer. The difference with pasture may be related to the effect of leaching already visible in the nitrogen output of the lysimeters.

Additional information can be obtained from the lysimetric data. We saw that under pasture, the nitrogen output was reduced almost to nil during the cultivation. After the onset of the rainy season, the water output of the grass lysimeter started three months later than that of the maize.

During these three months, the nitrogen output of the maize lysimeter became more and more concentrated and strongly labelled, suggesting that the leaching process was faster than the microbial immobilization which obviously needed an active rhizospheric development to be efficient.

The nitrogen balance was apparently slightly positive for maize (Fig. 3) but, if the stubble together with the weeds are burnt before the next crop cycle, as is usual in this area, the nitrogen balance becomes negative.

Furthermore, considering the leaching process and the volatilization or denitrification losses, this balance becomes even more unfavourable. The estimated deficit seems to be situated between 50 to 60 kg.ha^{-1} with 100 kg.ha⁻¹ total loss by volatilization, denitrification and burning.

At the end of the annual cycle, the nitrogen balance of the meadow system was positive for the soil. This enrichment can be estimated between 3 to 10 kg.ha^{-1} (Fig. 4) depending on the importance of gaseous losses (13 to 20 kg.ha^{-1} , respectively).

The difference in fertilizer utilization between maize and pasture suggested the presence of a strong A.N.I. (Added Nitrogen Interaction; see Jenkinson *et al.*, 1985, Hart *et al.*, 1986) under meadow. This apparent positive A.N.I. was obviously related to the intensification of the gross immobilization process occuring in the rhizosphere of grasses. In very different conditions (Mansell *et al.*, 1986), the possibility of such an enrichment had also been related to a good root biomass development.

Conclusion

The implications of converting tropical savanna ecosystems into annual crops or permanent pastures are very different. In both cases fertilization induces a strong and short increase in nitrogen immobilization accompanied by a corresponding mineralization of the existing soil nitrogen.

But the permanent meadow, besides producing about 15 t.ha^{-1} of good quality forage, compared to 5 or 6 t.ha^{-1} of poor quality forage produced by the original savanna (Sarmiento, 1984), seemed to improve the organic matter content of the soil and its induced buffer capacity. This intensification does not imply a contamination of the phreatic or surface waters since the strong development of the root systems of perennial grasses induces the rapid immobilization of the added nitrogen. The organic status of these rather poor soils can thus be improved by the relatively inexpensive development of permanent meadows.

On the contrary, annual crops like maize need to be cultivated more cautiously, especially when the crop residues are burnt. Nitrogen immobilization is then much less intensive, allowing more volatilization and significant leaching losses towards the lower horizons. After the dry season, this nitrogen can be further leached out of the system by the first heavy rains. In this case, fertilization does not compensate the gaseous, burning and leaching losses.

Acknowledgements

This work is part of a collaborative programme between ORSTOM (France) and ULA (Venezuela) and received funding from CDCHT-ULA through projects C188-86 and F190-86. The analytical work was done by the ULA-ORSTOM staff in the Soil Laboratory of the Institute of Geography of the University of los Andes; the field work in the Botanical Garden of UNELLEZ.

The authors thank the directors and personnel of

both institutes for their most valuable help and also express their great indebtedness to I de Amaya for technical assistance with the istopic measurements and to Dr Jennifer Canva-Conley for carefully reading the manuscript.

` **

References

- Chotte J L, Hetier J M, Guiraud G and Andreux F 1986 Observation sur le devenir de l'azote organique du sol et des residus racinaires en présence d'une culture de mais. C.R. Acad. Sc. Paris t. 303 Série III no 7 269–272.
- Dodwell R J and Webster C P 1980 A lysimeter study using nitrogen-15 on the uptake of fertilizer nitrogen by perennial ryegrass swards and losses by leaching. J. Soil Sci. 31, 65–75.
- Dommergues Y and Mangenot E 1970 Ecologie microbienne du sol. Masson Paris 796 p. 180 fig, 101 tab.
- Guiraud G and Fardeau J C 1977. Dosage par la méthode Kjeldahl des nitrates contenus dans les sols et les végétaux. Ann. Agron. 28 (3) 329-333.
- Guiraud G 1984 Contribution du marquage isotopique à l'evaluation des Transferts d'Azote entre les Compartiments Organiques et Minéraux dans les Systémes Sol-Plante. Thése d'état Université Pierre et Marie Curie Paris VI, 336 p.
- Hart P B S, Rayner J H and Jenkinson D S 1986 Influence of pool substitution on the interpretation of fertilizer experiments with ¹⁵N. J. Soil Sci. 37, 389-403.
- Hetier J M, Andreux F, Schouller E and Marol C 1986 Organic matter inputs after growth of carbon 14-Nitrogen 15 labeled maize. Soil Sci. Soc. Am. J. 50, 76–80.
- Jenkinson D S, Fox R H and Rayner J H 1985 Interaction between fertilizer nitrogen and soil nitrogen: The so called "priming effect". J. Soil Sci. 1985, 36, 425-444.
- Mansell R S, Eiskell J G A, Calvert D V and Rogers J S 1986 Distribution of labelled nitrogen in the profile of a fertilized sandy soil. Soil Sci. 141, 2, 120–126.
- Pichot J 1983 Le bilan de l'azote dans quelques agrosystèmes tropicaux. Impact des relations sur l'intensification de l'agriculture pluviale en zone de savane. PLANALTINA 24.11 au 3.12 1983. Document roneo CIRAD.
- Roose E 1981 Dynamique actuelle des sols ferrallitiques et ferrugineux tropicaux d'Afrique occidentale. Travaux et documents de l'ORSTOM No 130 515 p.
- Sarmiento G 1983 The savanna of tropical America. In Tropical Savannas. Ed. F Bourlière. pp 245–288 Elsevier Amsterdam.
- Sarmiento G 1984 The ecology of neotropical savannas. In Tropical Savannas. G. Sarmiento, traduction O. SOLBRIG Harvard University Press Cambridge Massachussets and London England.