OIKOS 38: 321–332. Copenhagen 1982

Biogeochemical cycle of nitrogen in a semi-arid savanna

France Bernhard-Reversat

Bernhard-Reversat, F. 1982. Biogeochemical cycle of nitrogen in a semi-arid savanna. – Oikos 38: 321–332.

The nitrogen cycle was studied in a savanna of north Senegal in the sahelian zone. Organic matter and N content of the soil were low and concentrated in the first centimeters of soil and increased under the trees. In situ N mineralization in the 0–10 cm layer was relatively high, ranging from 5 to 8% of total N per year, according to the relief. It occurred mainly from the beginning of the rainy season (July) to August, although rainfall occurred up to October. In vitro measurements showed that N mineralization was a function of the number of days during which the soil was wet, for a given temperature and N content. Prediction of in situ mineralization on this basis were in good agreement with in situ data.
N fluxes between vegetation and soil were higher in soil-tree systems than in the open, but litter-fall and canopy weathering accounted for a small part in N cycling, the major fluxes occurring via the herbaceous stratum.

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Исследовали круговорот азота в саванне северного Сенегала. Содержание органики и азота в почве, сосредоточенных в верхних сантиметрах почвенного слоя, низкое, под деревьями возрастает. In situ минерализация азота в слое 0-10 см относительно высока и составляет 5-8% от общего азота в год, в зависимости от характера рельефа. Она происходит в основном в период от начала сезона дождей (июль) до августа, хотя выпадение дождей наблюдается до октября. Определения in vitro показали, что минерализация азота - функция количества дней, в течение которых почва сохраняет влажность при данной температуре и содержании азота. Предсказание скорости минерализации in situ на этой основе хорошо совпадает с данными, полученными in situ.
Поток азота между растительностью и почвой выше в системе дерево-почва, чем в открытых местообитаниях, но продукты выщепачивания листового опада и крон играют незначительную роль в круговороте азота. Основную часть потока составляют продукты травянистого яруса.

Accepted 19 May 1981

1. Introduction

A large part of the sahelian zone is occupied by semi-arid savanna with pastoral vocation, where climatic hazards and overgrazing are frequent threats to the biological equilibrium, with soil degradation as a main effect. Consequently soil conservation is an important aim of management projects in the Sahel, with an emerging view that trees are a major factor in maintaining soil fertility.

In this scope the understanding of nitrogen cycling processes in relation to the occurrence of trees will contribute to the knowledge of the ecosystem function.

Soil organic matter and nitrogen were studies in relation to trees or shrubs in semi-arid environment by Russel et al. (1967), Garcia-Moya and McKell (1969), Jung (1970), Charley (1972), Charley and West (1977), Barth and Klemmedson (1978), and the increase of soil organic matter under the trees or shrubs was pointed out.

In the present study an attempt is made to estimate the impact of some trees on soil nitrogen distribution and nitrogen cycling via mineralization and plant uptake.

2. Site and methods

The study area, at Fete Ole, North Senegal, has been described by Bille et al. (1972). The vegetation cover consists of a steppic herbaceous layer, with scattered trees and shrubs. The landscape is a succession of flat dunes and depressions. Scarce on the dune tops and slopes, the herbaceous cover and the trees are more dense in the lower parts of slopes and depressions, where the herbaceous species composition is different (Cornet and Poupon 1977).

Differences between higher and lower parts of the landscape are related to the water balance, which is more favourable to plant growth in the lower zones, as was shown by Cornet (pers. comm.). The center of the depressions is occupied by a temporary pool on hydromorphic soil not included in the present study.

The soil developed on a sandy substratum is a weakly leached tropical ferrugineous soil (French classification; Psammentic ustropept: USDA classification), with a low clay content (less than 3%).

Mean annual precipitation is about 300 mm with large interannual variations. Rainfall occurs in July, August and September, the other months being dry with sometimes erratic showers. The temperature is high, with an annual mean maximum of 36.5°C (Poupon 1978).

Chemical analysis

The chemical methods of analysis were as follows: total N in soil and plants were analysed as NH_4-N, after sulfuric acid (Kjeldahl) digestion, with an autoanalyzer by the indophenol blue method. Soil C was determined by combustion in a Carmhograph®. NH_4-N was extracted by 10% NaCl and analyzed as previously stated for total N. NO_3-N was extracted with a 0.25% $CuSO_4$ – 0.06% $AgSO_4$ mixed solution and analyzed with the disulfonic acid method.

Soil sampling

Soil samples were taken every four weeks in the 0–10 cm layer, below 8 *Acacia senegal* and 8 *Balanites aegyptiaca* trees. The samples were taken either on dunes and higher part of slopes ("dunes") or on lower part of slopes ("l.s."), excluding hydromorphic soils. At the same sampling dates two samples (each from 10 mixed subsamples) were taken in the open, one on dunes and one on l.s.

These soil samples were used to measure total N, C, mineral N, in situ and in vitro N mineralization.

Additional sampling was done once during the dry season below 12 *Commiphora africana,* 14 *Boscia senegalensis,* and 11 *Adansonia digitata* for C and total N.

Below three *Acacia,* two *Balanites* and one *Adansonia* samples were taken at different depths and distances from the trunk to establish C, total N and mineralizable N distribution. Samples were taken each 25 or 30 cm between 0 and 120 cm from the trunk, and each 100 cm between 120 cm from the trunk and the canopy edge. The soil layers sampled were 0–2 cm, 2–10 cm, 10–30 cm, 30–50 cm, 50–70 cm.

Soil incubations

In situ incubations were done every four weeks. For each sample a PVC tube (20 cm long, 56 mm diam.), was filled with soil to 10 cm. It was closed by a 100 µm-mesh shieve at the bottom, and covered by a cap which allowed air but prevented direct humidification by rain. The tube was placed vertically in the soil, its bottom at 10 cm depth. After four weeks the soil was brought to the laboratory for mineral N determination, and a new sample was put in the tube.

In vitro incubations were done in 250 ml conic flasks, covered non-hermetically with aluminium sheet. 70 g of soil humidified to 7% was incubated 20 d at 32°C. The choice of 20 d was empirical as it was observed that in vitro mineralization rate decreased sharply after 10–15 days but was never reduced to zero.

Plant material sampling

For each of five *Acacia* and three *Balanites,* a sample of about 50 leaves, and another of about 20 twigs were taken every four weeks for N determination.

The herbaceous layer was sampled for biomass and N determination at the end of the rainy season (October), by taking all the aerial parts on 0.125 m^2 plots. In 1976, 8 samples were taken below *Acacia,* 7 below *Balanites* and 4 in the open. In 1978 the number of samples was 8, 8 and 11, respectively.

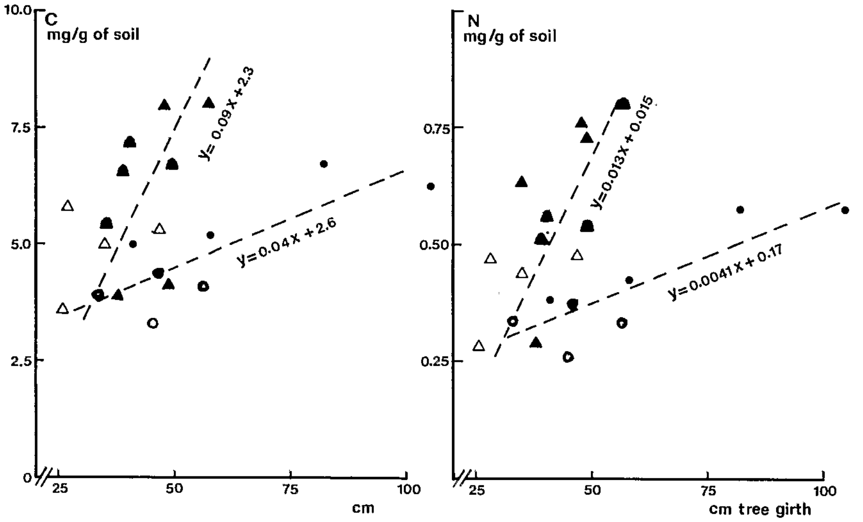

Fig. 1. C and N content of soil (0–10 cm) under tree canopy versus tree girth. △▲: *Acacia senegal* (C: r=0,54, P=90%. N: r=0.71, P=99%). ○●: *Balanites aegyptiaca* (C: r=79, P=95%. N: r=0.84, P=99%). ○△: Dunes, ●▲: lower part of slopes (L.S.).

In 1976 a soil core, 20 cm depth and 620 cm³ in volume, was taken in each plot for root extraction. Root samples were pooled according to vegetation cover for N determination.

3. Results and discussion

3.1. Nitrogen and organic matter distribution in soil

In semi-arid environments, soil organic matter is known to be concentrated in the surface soil (Charley and Cowling 1968), the amount of precipitation having an over-all influence on soil organic matter status (Birch and Friend 1956). Hence in the present study the spatial distribution of nitrogen was studied mainly in the 0–10 cm layer of soil.

Nitrogen and organic matter distribution in the surface soil

In the open the soil content in C and total N was low, specially on the dunes (Tab. 1), and lower than the mean N value for Nigerian sahelian savannas estimated by Singh and Balasubramanian (1980), 0.34 mg per g of soil.

Tab. 1. N and C content of the 0–10 cm soil in the open.

Situation	Content mg g^{-1} soil	Annual mean	Annual range
Dune	N	0.18	0.09–0.27
	C	2.2	1.7 –3.1
l.s.	N	0.30	0.19–0.43
	C	3.7	2.4 –5.0

Tab. 2. N and C content of the 0–10 cm soil, mg g^{-1} soil. Mean ($\bar{x}$) and standard (s.e.) error of the mean, and significant differences.

Species	*Commiphora africana*	*Balanites aegyptiaca*	*Acacia senegal*	*Boscia senegalensis*	*Adansonia digitata*
Number of trees sampled	12	18	18	14	11
C $\bar{x}$	4.2	5.8	6.2	7.0	8.1
s.e.	0.4	0.3	0.4	0.5	0.6
N $\bar{x}$	0.38	0.52	0.56	0.55	0.69
s.e.	0.03	0.03	0.04	0.03	0.05
Adansonia digitata	+++	++	++		
	○○○	○○	○	○	
Boscia senegalensis	+++	+			
	○○			Significance	
Acacia senegal	++			C	N
	○○			+	○ 95%
Balanites aegyptiaca	++			++	○○ 99%
	○○			+++	○○○ 99,9%

Tab. 2 emphasizes the increase in organic matter and N content below the tree canopy, except for *Commiphora africana.* The high variability is partly due to differences in tree age. As shown (Fig. 1) for two species, the organic matter enrichment below a tree increases throughout its life. This was probably the reason for the high organic matter content below *Adansonia,* the trees sampled being very old. The comparison of the means shows highly significant differences between the species, which may be related to the mean age of trees and to the amount of litter and its N content.

Nitrogen and organic matter distribution below the trees

The profile of organic matter and N distribution was established below some trees according to depth and distance from the trunk. Fig. 2 shows a steep gradient with depth, and another gradient with distance from the trunk, as observed earlier by Charley (1972) below *Atriplex vesicaria* and by Barth and Klemmedson (1978) below *Prosopis juliflora* and *Cercidium floridum.* However below *Acacia* and *Balanites* the horizontal gradient was observed from the trunk to about 1 m off. In the

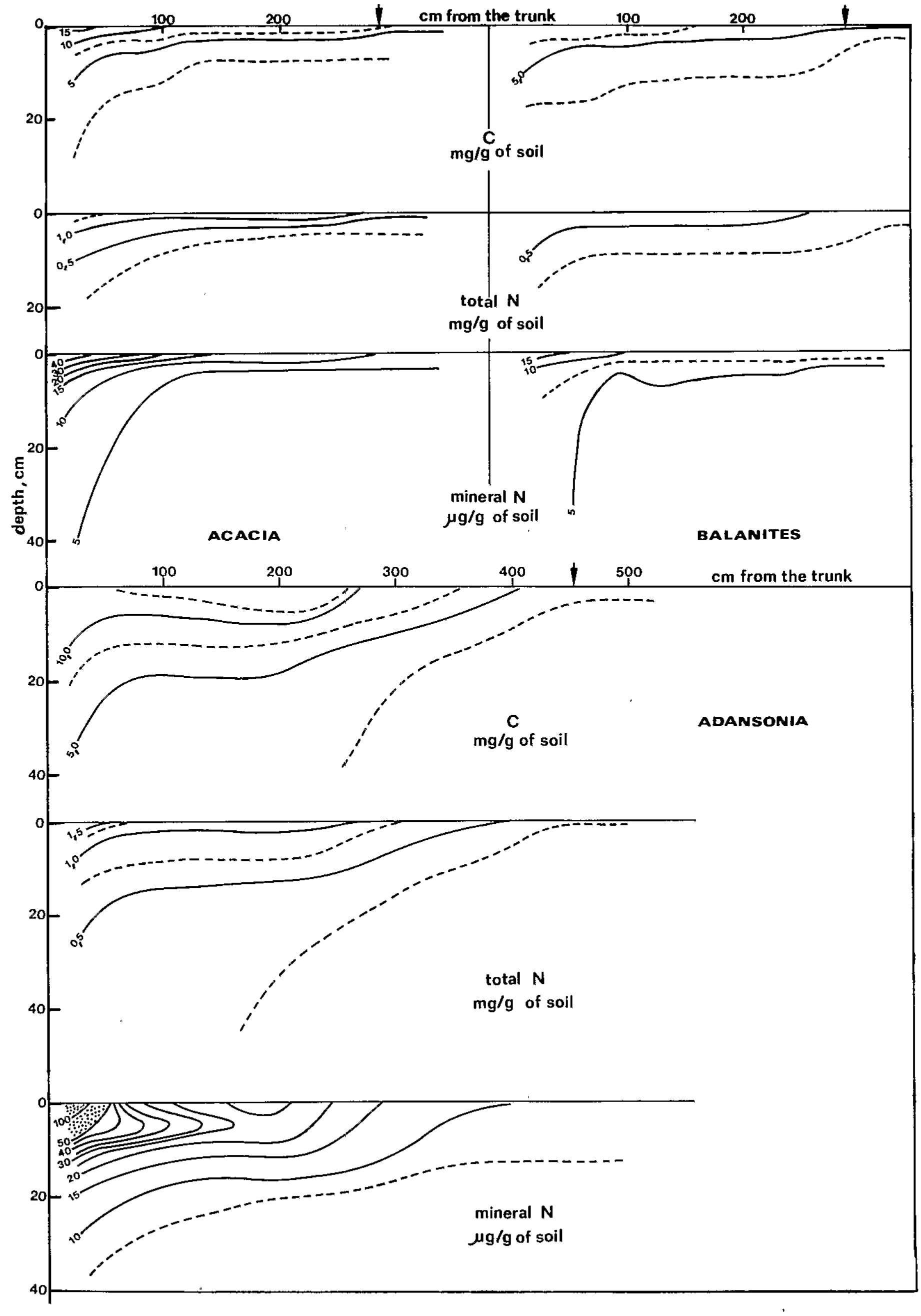

Fig. 2. Distribution of soil C and N under *Acacia senegal, Balanites aegyptiaca,* and *Adonsonia digitata,* from the trunk (left) to the canopy edge (arrow), and its variation with depth (cm).

peripherical part of the below-canopy area, nitrogen and organic matter were evenly distributed and the enrichment, as compared to the openfield, was superficial.

Charley and Cowling (1968) considered the accumulation in the surface soil below the trees as a possible redistribution with depletion of the deeper layers. This was not observed in the present study. The organic matter accumulation must be mainly due to an increased organic matter production by vegetation, and perhaps to a greater stability of organic matter derived from tree litter, as compared with the litter of Gramineae.

3.2. Nitrogen mineralization in soil

Mineralization in situ

The in situ mineralization was first studied in 1976 on a restricted samples of trees (Bernhard-Reversat 1977) and more extensively in 1977.

The results, obtained every four weeks, are shown in Fig. 3. Mineral N production decreased sharply in September, before the end of the rainy season. The occurrence of two peaks is related to rain distribution: there was an early rainfall in June and no rain in July. Total amounts of mineral N produced are given in Tab. 3.

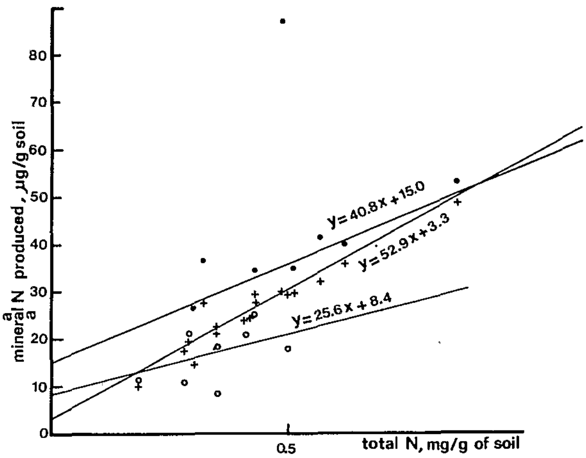

Fig. 4. Mean annual N mineralisation versus mean annual total N content of soil. In situ incubations: ○: dunes (r=0.50, not significant), ●: L.S. (r=0.80, p=98%). In vitro incubations: + (r=0.95, p=99%).

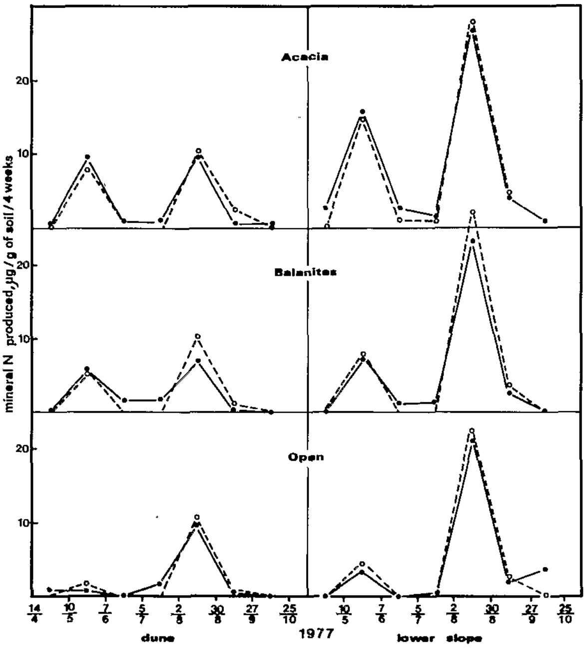

Fig. 3. In situ production of mineral N during the rainy season in the 0–10 cm layer of soil. ○: NO_3-N (nitrification). ●: NH_4-N + NO_3-N (ammonification).

Mineral N occurred mainly as NO_3-N. The measurements gave comparable results for the two years, although the rainfall was 330 mm in 1976 and 120 mm in 1977. However losses of NO_3-N during a heavy rainfall in 1976 has lowered the estimation of mineral N produced that year.

In 1979 some measurements were carried out with a reduced number of sampling locations. Mineral N produced was 3.7 g m^{-2} below the trees (l.s.) and 1.7 g m^{-2} in the open (dunes). These low values were related to low total N content. No attempt was made to relate this observation to a general trend or to sampling location particularities.

As shown previously for *Acacia senegal* (Bernhard-Reversat 1977), the variability of N production between trees was large. Mineralized N was related to total N content with a significant correlation ($r = 0.49$, $p = 95\%$). However the trend (Fig. 4) is that the relation is not the same for the dune and the l.s. samples. If the amount of mineralized N is expressed as per cent of total N, the mean is 5.1% for the dune samples and 8.2% for the l.s. samples, the difference being signifi-

Tab. 3. Total amounts of mineral N produced during the wet seasons of 1976 and 1977, in g m^{-2}. (0–10 cm layer of soil).

Tree cover	*Acacia senegal*		*Balanites aegyptiaca*		Open	
Situation	Dune	l.s.	Dune	l.s.	Dune	l.s.
1976	–	7.5	–	3.9	–	4.9
1977	3.6	8.9	2.6	5.9	2.2	4.4

Tab. 4. In situ mineralized N during the rainy seasons as per cent of total N.

Tree cover	*Acacia senegal*		*Balanites aegypriaca*		Open	
Situation	Dune	l.s.	Dune	l.s.	Dune	l.s.
1976 11/6–27/10	–	9.5	–	6.0	–	12.2
1977 10/5–27/9	5.5	10.4	4.6	7.2	7.6	9.8
1979 22/5–24/9	–	9.1	–	7.9	6.6	–

cant ($P = 98\%$). These values appeared to be relatively constant from year to year (Tab. 4), and they are of the same magnitude as the estimation of 5.5% by Wetselaar (1980) for a semi arid region of Australia with an annual rainfall of 900 mm.

When an erratic rainfall occurred during the dry season a fast mineralization followed: 1.4 to 5 g of mineral N m^{-2} was produced in the dry season of 1976.

No other data are known to be available for in situ mineralization in a sahelian savanna, but it appears that the amount of N produced below the trees is relatively high according to the environmental conditions. In a Guinean savanna, de Rham (1973) found an annual mineralization of 0.4–0.5 g m^{-2} below a clump of trees.

As a result of N mineralization and N uptake by vegetation, the mineral N content of the soil was high in the early stages of the rainy season, prior to herb growth, and decreased to a low level as soon as the herbaceous vegetation was developed (Fig. 5).

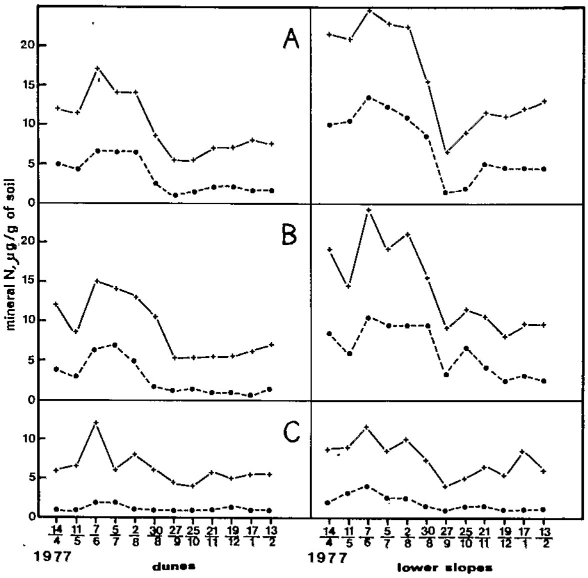

Fig. 5. Mineral N content of soil (0–10 cm) under *Acacia senegal* (A), *Balanites aegyptiaca* (B) and in the open (C). ●: NO_3-N, +: NH_4-N.

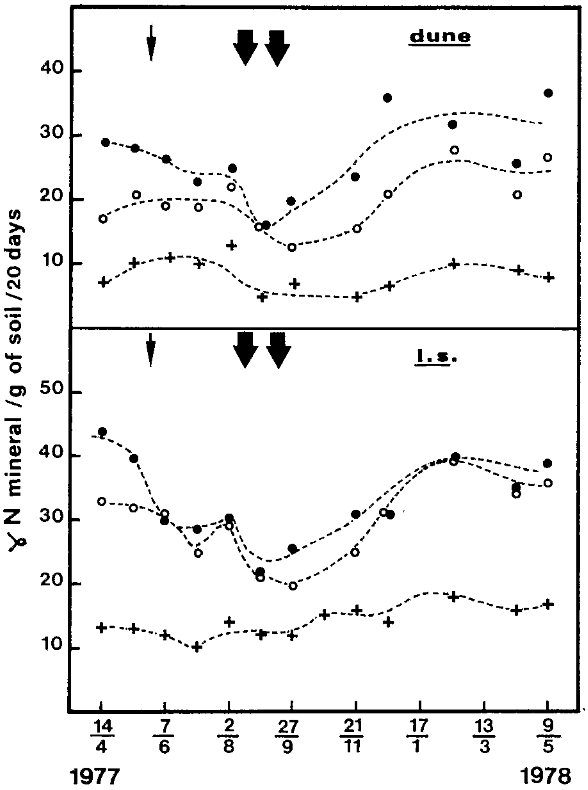

Fig. 6. Mineralizable N content of soil (0–10 cm) as measured by in vitro incubations. ●: under *Acacia senegal*, ○: under *Balanites aegyptiaca*, +: in the open. Precipitation is indicated by arrows.

Estimation of mineralizable nitrogen

1. In vitro measurements of mineralization

The sharp decrease of in situ N mineralization before the end of the rainy season suggests that a form of organic nitrogen which is readily available occurred in limited amounts. An attempt to estimate the mineralizable N was made by in vitro incubation. The values decreased in August and increased in November (Fig. 6). The annual means calculated for each sampling location were highly correlated with the mean total N content (Fig. 4), and the mineralizable N expressed as per cent of total N (or mineralization coefficient) was

Tab. 5. Vertical gradient of N mineralization measured in vitro in two soil profiles.

Tree cover	depth cm	µg g^{-1} (20 d)$^{-1}$	% of total N
Acacia senegal	0–1.5	129	10.8
	1.5–5	35	4.5
	5–8	14	2.6
Open	0–1.5	71	10.3
	1.5–5	13	3.9
	5–8	1	0.5

relatively constant with a mean of 6.1%. The data exhibited no significant difference between the dune samples and the l.s. samples although such a difference was observed in situ.

Significant seasonal variation occurred and the mineralization coefficient was lower in August and September, but there was still an appreciable amount of mineralizable N in September soil samples, in constrast to the in situ results. The higher temperatures and the change between dry and wet periods in the field may be involved in the different behaviour of in vitro and in situ incubation.

When determinations were made on finer layers of soil, a sharp gradient in mineralizable N appeared (Tab. 5). The most active mineralization occurred in the first 2 cm of soil.

The profile of the distribution of mineralizable N was established below some trees. The pattern is the same as for total N (Fig. 7), with a vertical and an horizontal gradient. Expressed as per cent of total N the quantity of mineralizable N is higher in the 0–2 cm layer than in the deeper layers, and also higher near the trunk. This general pattern of two gradients, a vertical one and an horizontal one, was observed by Charley and West (1977) under shrubs in a semi-desert ecosystem.

2. Nature and formation of mineralizable N

The distribution of mineralizable N in various soil organic matter fractions was studied by a floatation and sieving methods; most of the mineralizable N was produced in the organo-mineral fraction (Bernhard-Reversat 1981). It was assumed from these results that fresh plant material had to be partly humified before mineral N might be released. However the nature of the organic N which undergoes mineralization is not known. Cameron and Posner (1979) among others suggested that mineral N is released mainly from dead microbial cells, microbial materials and microbial metabolites. Marumoto et al. (1977) showed that microbial cells and particularly cell-wall substances may contribute considerably to the soil organic matter becoming decomposable after soil drying.

In the studied area, the amount of easily mineralizable N was at a low level at the end of the rainy season. Soil samples taken in October, humidified and incubated in vitro, exhibited a weak mineral N production. However, soil samples taken in January and later, exhibited a high mineralizable N content. Since no rainfall occurs between October and January, the only addition which may affect soil organic matter was the input of dry dead plant material (litter and roots) which cannot affect the organomineral fraction. This observation suggested that mineralizable N could be produced through the lethal effect of a long dry period on microbial cells. However, Birch (1959) stated that the drying effect involves changes in the soil organic colloïds with increased exposed surface, and that the longer the dry period, the less reversible the cracking of the gel.

Prediction of in situ mineral N production

It was observed in another study that the two main factors, temperature and soil water content, could be accounted for with a simple relation, involving mean soil temperature for the rainy season, and the number of days where the soil was wet (Bernhard-Reversat 1980).

A curve of mineralization versus time was established in vitro for the 0–10 cm soil at 36°C and with alternating desiccation and wetting from one to five dry days per week. Only the "wet" periods were taken into account for the curve. Mineralized N was expressed as per cent of the 20 d mineralization, which was assumed to be the total mineralizable N, i.e. 6% of total N for dune soils and 8% of total N for l.s. soils.

Other data required were the mean total N content,

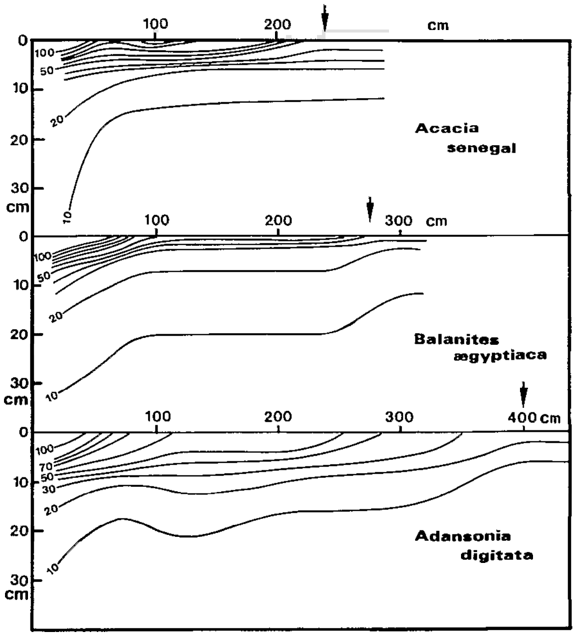

Fig. 7. Distribution of mineralizable N under *Acacia senegal*, *Balanites aegyptiaca*, and *Adansonia digitata*, from the trunk (left) to the canopy edge (arrow) and its variation with depth (cm), µgN g^{-1} of soil.

Tab. 6. Comparison between calculated (C) and observed (O) in situ N mineralization during the rainy season under three canopies (0–10 cm, μgN g^{-1} of soil).

Year	Period		10 may – 5 Jun		5 Jun – 2 Aug		2 – 30 Aug		30 Aug – 27 Sep	
1977	Number of "wet" days		1				5		5	
	Tree cover		C	O	C	O	C	O	C	O
	Acacia senegal	dune	6.4	9.3	0	0	11.1	9.4	3.0	0.6
		l.s.	11.2	15.4	0	0	19.4	20.0	5.2	3.9
	Balanites aegyptiaca	dune	5.0	5.5	0	0	8.6	6.8	2.3	0
		l.s.	10.0	7.4	0	0	17.3	23.0	4.6	2.6
Year	Period		22 May – 19 Jun		19 Jun – 31 Jul		31 Jul – 26 Aug		26 Aug – 24 Sep	
1979	Number of "wet" days		1		1.5		3		7	
	Tree cover		C	O	C	O	C	O	C	O
	Acacia senegal	l.s.	8.6	10.8	6.9	6.8	7.3	11.0	7.4	7.7
	Balanites aegyptiaca	l.s.	7.2	6.8	5.9	6.4	6.2	8.8	6.3	6.3

and the number of "wet" days in situ, which were estimated from the pluviometric readings[1].

The number of "wet" days was applied to the mineralization curve and the amount of mineralized N calculated for each period.

The results obtained (curve A, Fig. 8) were compared to the in situ measurements. There was a relatively good agreement between calculated and observed data for the tree-covered soils in 1977 and 1979 (Tab. 6). It should be emphasized that the two main factors were total N content and duration of soil humidity. Moreover these results indicate that the in situ mineralization rate is controlled by a definite relation for the whole rainy season.

For the open-field soils the curves obtained in vitro exhibited large variations between replications, and the mean curve (B, Fig. 8) did not agree with the observed in situ mineralization.

A curve (C, Fig. 8), drawn empirically, should agree with the observed results (Tab. 7). It showed that in the open, nitrogen mineralization started slowly and was achieved in a few days. The reason for the discrepancy between curves B and C are not understood.

These models would be improved by a more precise knowledge of the relations between precipitation and duration of surface soil humidity, and between mineralizable N and total N. Particularly the causal factor of the different behaviour of dune and l.s. soils in respect to the percentage of total N which is abailable should be looked for.

[1] On the following basis: rainfall, mm: 5, 5–10, 10–15, 15–25, 25–35, 35–45; "wet" days: 0, 0,5, 1, 1,5, 2, 3.

3.3. Nitrogen cycling by vegetation

Nitrogen utilization and cycling by trees

1. Nitrogen content of leaves

N content of leaves and its change during the year were measured together with that of the twigs. The variability between trees of the same species was relatively low (Fig. 9). In *Acacia,* the leaf N content exhibited a constant decrease during the life of leaves, although, according to Poupon (1980) the dry weight of leaves is

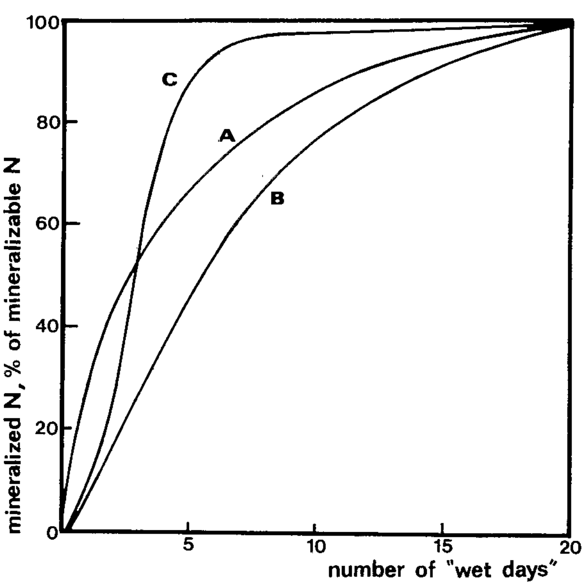

Fig. 8. Mean curves for N mineralization versus time, measured during in vitro incubation of under-canopy (*Acacia* and *Balanites*) soils (A) or "open" soils (B). C: estimated relation for in situ mineralization in the open (see text for further explanations).

Tab. 7. Comparison between calculated (C) and observed (O) in situ N mineralization during the rainy season in the open (0–10 cm, μgN g^{-1} of soil).

Year	Period		10 May – 5 Jun		5 Jun – 2 Aug		2 – 30 Aug		30 Aug – 27 Sep	
1977	Numbe of "wet" days		1				5		5	
			C	O	C	O	C	O	C	O
		dune	0,7	0.7	0	0	8.9	9.6	0.4	0.4
		l.s.	1.5	1.3	0	0	18.8	21.0	0.9	2.3
Year	Period		22 May – 19 Jun		19 Jun – 31 Jul		31 Jul – 26 Aug		26 Aug – 24 Sep	
1979	Number of "wet" days		1		1.5		3		7	
			C	O	C	O	C	O	C	O
		dune	0.9	1.7	4.0	5.5	7.1	7.4	0.9	

stabilized soon after their appearance. The leaching of leaves by rain might occur in August and September, but withdrawal accounted for most of the decrease in N content. Nitrogen withdrawn did not accumulate in the twigs as shown by their steady N content, but could

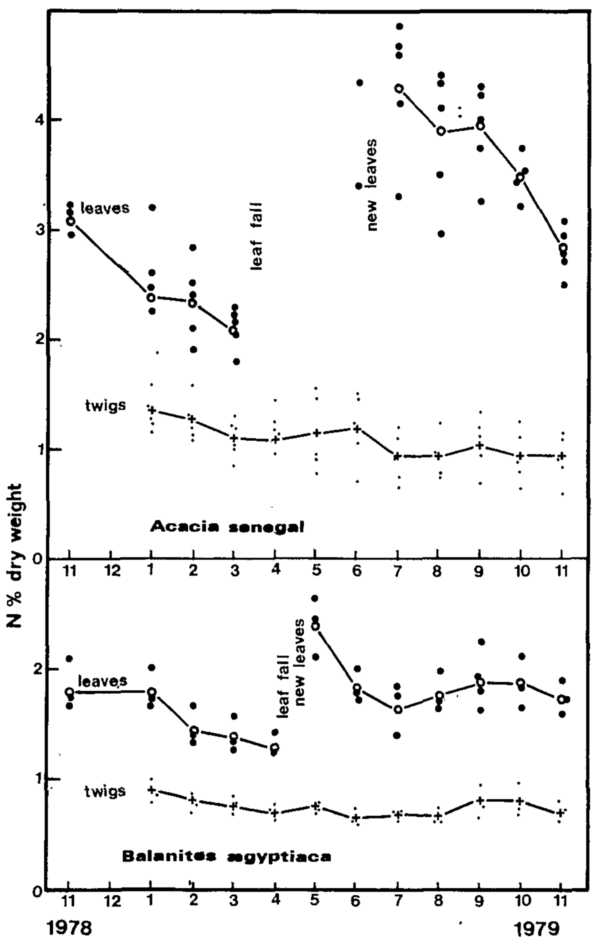

Fig. 9. N content of tree leaves and twigs during the year. ● · : individual trees, ○+: mean.

account partly for wood growth when the growth of herbs competed with trees for N uptake. However the decrease of leaf N content, from January to March, when no water was available for wood growth, must be associated with a reserve accumulation and allowed a new-leaf building-up at a low N cost, as suggested by Montes and Medina (1977). In *Balanites,* N content of leaves was approximatively constant from June, soon after leaf appearance, to January, and then showed a slight decrease before leaf fall. However, N withdrawal was lower than in *Acacia.* According to Hirose and Monsi (1975), the development of an internal N recycling system allows the plants to be less dependent on the environment. This aspect of the N cycle ought to be more extensively studied.

2. Nitrogen cycling by trees

Few data have been worked out on N immobilization and cycling by trees, except for *Acacia senegal* for which results have been stated previously (Bernhard-Reversat and Poupon 1980). Immobilization in woody parts of trees will not be discussed here, but only the participation of trees in short-term cycles.

The amount of leaves can be calculated for each tree with the leaf biomass versus tree girth relations established by Poupon (1980). In order to relate leaf N to the present soil N study, this amount was calculated for a "mean tree", i.e. for the mean trunk circumference among the individuals sampled for soil N. N input into soil was calculated from annual leaf production and N content of leaves before leaf-fall. The results were as follows (in g m^{-2} below canopy):

	Acacia	*Balanites*
leaf weight	33	59
N input with leaf-fall	0.70	0.76

Some measurements of the N content of leaves of other species and the values given by Bille (1977) suggested that N input below their canopies was of the same order of magnitude.

Tab. 8. Nitrogen input to the soil by rain and throughfall in 1977, g m^{-2}.

Tree species	*Acacia*	*Balanites*
N in rain	0.04	0.04
N in throughfall	0.57	0.71
leached	0.53	0.67

Tab. 9. N content of aerial parts of herbaceous vegetation (N%, oven dry weight) for 1976 and 1977 samples.

Tree cover	*Acacia*	*Balanites*	Open
Number of replications	16	15	15
Mean	1.20	0.95	0.77
Standard error of the mean	0.02	0.01	0.01

The leaching of N from the canopy by rain was studied in 1977 under seven *Acacia* and six *Balanites* (Tab. 8). Total precipitation was 124 mm. In throughfall water, 30–40% of N was mineral N, against 50–60% in rain. Leached N might originate from dust deposit on the trees, but no attempt was made to estimate the magnitude of this process.

Nitrogen cycling through the herbaceous stratum

The herbaceous layer consisted of annual plants exclusively, and N immobilized during plant growth was released each year as dead organic material.

N content of aerial parts was measured in 1976 and 1977. Slight differences were observed between years and between dune and l.s. samples. The main differences are linked to plant cover (Tab. 9).

The differences between vegetation cover types were all significant (p = 98% between *"Acacia"* and *"Balanites"* samples and between *"Balanites"* and "open" samples), and agree with differences in soil N content.

N content changes during the growth season were measured in 1979 in a few locations. Unfortunately in 1979 plant growth began very late (mid-August) and a few sampling could be done. The results (Fig. 10) showed different behaviour in the open, where there was a sharp decrease, and under the trees, where N content decreased more slowly. These observations are in agreement with the N mineralization pattern shown in Tabs 7 and 8 for 1979.

Amounts of immobilized N were calculated. The precision of such data is weak because of the high spatial variability of the standing-crop biomass. Large interannual variations occurred as the standing crop biomass was highly dependent on amount and repartition of precipitations (Cornet 1979). Amount of N and standing crop were larger under the trees than in the open (Tab. 10).

Comparison with the results of Tab. 9 points out the fact that the herbaceous stratum accounted for most of the annual N cycling under the trees, at least when receiving the "normal" amount of precipitations.

4. Discussion and conclusions

In the steppic semi-arid ecosystem studied, the estimation of a nutrient balance is very difficult, mainly because of spatial and interannual variations in vegetation cover.

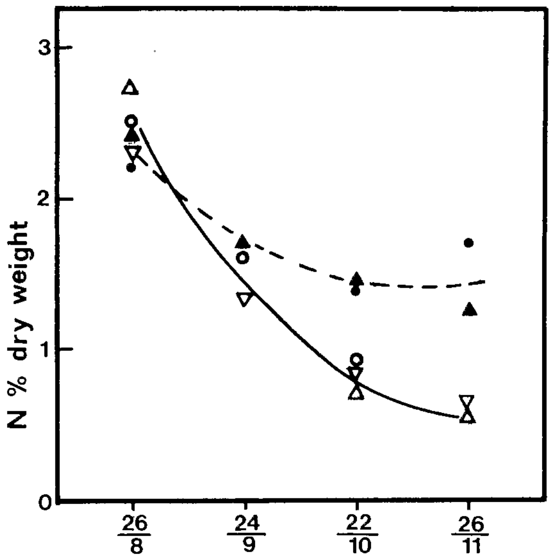

Fig. 10. N content of the herbaceous stratum during the rainy season: ▲●: under the trees, △△○: in the open.

Tab. 10. Immobilization of nitrogen in the herbaceous layer, g m^{-2}.

Tree cover / Year	Situation	1976 Above ground	1976 Above ground + roots	1977 Above ground
Acacia senegal	dune	4.4	8.8	2.6
	l.s.			3.5
Balanites aegyptiaca	dune	4.5	7.3	1.8
	l.s.			2.5
Open	dune	–	–	0.3
	l.s.	2.5	4.7	1.2

Tab. 11. Estimation of some N fluxes under *Acacia* (A), *Balanites* (B) or in the open (O), g m^{-2}.

Year	1976			1977					
Tree cover	A	B	O		A	B		O	
Situation	l.s.	l.s.	l.s.	dune	l.s.	dune	l.s.	dune	l.s.
Mineralized in soil (0–10 cm)[1]	12.6	6.6	4.9	3.6	8.9	2.6	5.9	2.2	4.4
Uptake by vegetation[2]	9.5	8.1	4.7	5.9	8.4	3.4	5.8	0.6	1.2
Input into the soil[3]	–	–	–	–	10.1	–	8.8	–	4.7

[1] dry season mineralization is taken in account for 1976, in 1977 no rain occurred during the dry season.
[2] N amount in tree leaves + N amount in herbaceous stratum of the current year. (With 1977 root biomass estimated from 1976 shoot/root ratio).
[3] N amount in herbaceous stratum of the precedent year + N amount in tree leaves + throughfall N of the current year.

However some general trends are emphasized by the approximation of N balance of the Tab. 11. For soil-tree systems the results are assumed to represent a mean adult tree. Several fluxes were not taken in account: flower and fruit fall, wood growth, tree root turn-over.

The influence of trees

The occurrence of trees greatly increased the magnitude of fluxes between soil and vegetation, as a result of organic matter and nitrogen accumulation in soil, the origin of which is not well understood. It may be a primary effect of the tree litter, nutrients being concentrated from the rooting zone to the below canopy area, as suggested by Charley and Cowling (1968). Another hypothesis states that the primary effect is microclimatological, the reduced evapotranspiration rate allowing for a better plant growth. A mechanical effect of accumulation of wind-blown seeds near the trunk could occur (Cornet pers. comm.). These climatological and mechanical effects would result in an increased herb growth under the trees, responsible for soil organic matter accumulation and increased potentiality of nitrogen fixation in the Gramineae rhizosphere (Balandreau et al. 1976) and in the soil. The importance of the herb layer in the total N fluxes agrees with this hypothesis. Moreover it is noteworthy that a few trees were encountered that did not exhibit any soil organic matter accumulation below their canopies, where grass cover was not obviously more abundant than in the adjacent open area. Such soil-tree systems could not occur if the tree litter was the only factor involved in the building-up of organic matter accumulation.

Effect of drought

The immediate effect of the 1977 drought was to lower primary production and consequently N uptake by vegetation, sharply in the open (74%) and less below the trees (12–28%). The effect of drought on herbaceous plant growth is reduced below the trees as the water needs of herbs is decreased under shading and water efficiency increases with increasing N supply. In the open the decrease of N mineralization during the dry year is low compared to the decrease of N uptake: N mineralization is achieved with less water and originates from previous years' organic matter.

Inputs and outputs

Inputs and outputs to the ecosystem were not investigated but they are thought to be low. Input of N with rainfall is very low (Tab. 8) but input by dust deposit may be higher. N fixation must occur in leguminous herbs, as nodules were observed on most of them, but they account for only 12–14% of the herbaceous species (Bille et al. 1972, Cornet and Poupon 1977). The *Acacia* seem to have no nodules when they are adult trees (Bernhard-Reversat and Poupon 1980).

N losses by denitrification and leaching may occur, but cannot be important in rainy years when the herbaceous cover is well developed, as NO_3-N content of soil is low. Only dry years allow some NO_3-N losses when N uptake is lower than N mineralization, and NO_3-N may be denitrified or leached during the few heavy rainfalls that occur. However the water flow in the soil does not go deeper than 2 or 3 m, where the leached nutrient are still available to tree roots.

Conclusion

In conclusion, some characteristics of the N cycle in the studied sahelian ecosystem are to be emphasized: low level of soil N content and its concentration in the topsoil, and improvement of soil N status by the presence of trees. The organic N of dead plant material is involved in an edaphic cycle prior to its release as mineral N. This process is clearly controlled by the changes between dry and wet seasons. The dependence of organic matter and N cycles on the magnitude of the rainy season results in an unsteady state, as the sahelian zone is characterized by large climatic variations. Although the site under study is not degrading, the drought which has reigned from 1970 until now leads to a decrease of vegetation production and to the death of many trees, two factors that act upon N cycling. However a period of several rainy years should result in the reverse process.

Resumé

Le cycle de l'azote a été étudié dans une savane sahélienne du Sénégal. Le sol est pauvre en matière organique et en azote, qui sont concentrés dans les premiers centimètres du profil. Le taux de minéralisation de l'azote in situ est relativement élevé, allant, selon le relief, de 5 à 8% de l'azote total annuellement. La production d'azote minéral dans le sol sommence dès le début de la saison des pluies (juillet) et cesse presque complètement fin août alors que les pluies durent jusqu'en octobre.

Des mesures de la minéralisation de l'azote in vitro ont montré qu'elle était principalement fonction du temps pendant lequel le sol est humide, de la teneur du sol en azote total, et de la température. Avec ces données on peut calculer la minéralisation in situ.

Les flux d'azote entre la végétation et le sol sont plus importants sous les arbres qu'à découvert; cependant la litière de l'arbre et le pluviolessivage de sa couronne y participent pour une faible part, la plus grande part passant par la strate herbacée.

Acknowledgements – Analysis of C and N in soil and plant material were carried out at the Analysis Laboratory of ORSTOM, Dakar, under the control of C. Paycheng. Working with H. Poupon and A. Cornet allowed useful discussions on the ecosystem functioning. We thank I. Bodian for technical assistance and T. Maïga for drawing the figures.

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