T. Rosswall (ed). 1980
Nitrogen Cycling in West African Ecosystems

MICROBIOLOGICAL CONSIDERATIONS OF THE NITROGEN CYCLE IN WEST AFRICAN ECOSYSTEMS

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Abstract

The review is an attempt to specify particular features of the biological processes involved in the nitrogen cycle as they occur in the following categories of West African ecosystems : flooded rice fields, rain-fed agroecosystems, and forests.

In rice fields in Senegal the nitrogen input through blue-green algae was reported to be in the range of 1–30 kg ha^{-1} yr^{-1}. Figures for heterotrophic rhizosphere N_2-fixation in the rice rhizosphere should be reassessed. In rain-fed ecosystems, symbiotic N_2-fixation is often impeded by such limiting factors as moisture stress (in semi-arid areas), nematode attacks, soil acidity and toxicity, mineral deficiencies (especially phosphorus deficiency), inadequacy of *Rhizobium* populations and competition between native and introduced strains. Inoculation with *Rhizobium* is futile if even one of the above-mentioned limiting factors is still operating. No reliable evaluation has been published thus far of N_2-fixation in forests.

Nitrification and denitrification are limited by soil acidity in rice soils as well as in non-fertilized rain-fed agrosystems. However, when nitrogen fertilizers are applied to the soil, losses through denitrification were reported to be ca. 30 %, whereas losses through leaching were only 10 %. In West African forest ecosystems, nitrification is potentially much more active than in temperate conditions. Data on denitrification is lacking.

Mineralization rates are high, except in acid rice fields, as long as the soil is flooded. In arid conditions, mineralization is slowed down but still persists as long as the soil pF is not higher than 5.2, which corresponds to relatively dry conditions.

Introduction

A voluminous amount of literature has been accumulated concerning nitrogen transformations in soil, but, unfortunately, most of the information is limited to temperate conditions. Many of the general concepts applicable to temperate soils are applicable to tropical soils, but the special conditions which prevail in tropical environments lead to considerable modifications of the transformation rates and nitrogen transfers. The present paper is a review of our current knowledge of the role of microorganisms in nitrogen transformations occurring in different ecosystems which are typical of West Africa, attempting to specify the particular features of the biological processes in such conditions.

Table 1. **Distribution of bacteria, fungi and actinomycetes in different fractions of a typical sandy soil (Dior) from Central Senegal (Panthier & Feller, unpublished data)**

Fractions	Weight (%)	Bacteria (%)	Fungi (%)	Actinomycetes (%)
Organic matter				
>2.0 mm	0.02	0.7	2.0	0.4
0.2–2.0 mm	0.33	20.0	33.3	4.3
0.2–0.05 mm	0.67	13.3	16.6	2.2
Total	**1.02**	**34.0**	**51.9**	**6.9**
Organo-mineral fraction				
(<0.05 mm)	15.41	66.0	47.1	92.9
Mineral fraction				
>2.0 mm	0	0	0	0
0.2–2.00 mm	33.50	0	0.5	0
0.2–0.05 mm	49.50	0	0.5	0.2
Total	**83.00**	**0**	**1.0**	**0.2**

Total number of bacteria, fungi and actinomycetes were respectively 3.3×10^6, 4.8×10^3, 1.3×10^4 per g (d.w.) soil.

Two preliminary remarks should be made here. The first relates to the soils. In West Africa, sandy to coarse loamy structures prevail in surface layers and the organic matter content is usually very low in cultivated soils. For example, in the AP horizon of a typical sandy soil from central Senegal (Dior Soil) the clay and carbon contents are respectively 3–6 % and 0.2–0.3 %. Since the microbial populations are mainly located on the organic and organo-mineral particles, which make up the organic and organo-mineral fractions (Table 1), and since the organic matter content of these sandy soils is low, the total microbial numbers are low (10^6–10^7 g^{-1}). But such data do not mean that there is less microbial activity than in temperate conditions. Actually, it can be very high (see examples below) but it is located in habitats which represent only a relatively small volume of the soil: (1) in soil organic and organo-mineral particles and (2) in plant rhizospheres, i.e., the soil-plant root interface, including the surface of the root tissues and the surrounding soil (Yoshida, 1975). Another characteristic of the sandy soils of West Africa is their normally high acidity, which is generally associated with low Ca, P and Mo contents and high Al and eventually a high Mn content. Acidity may be responsible for impeding some major processes, especially N_2-fixation and nitrification.

The second remark refers to the climate. Just as frost does in temperate conditions, drought in tropical climates can act as a major limiting factor, which is responsible for a differential slow-down (Fig. 6) and ultimately a blockage of microbial activities, except in irrigated ecosystems. In West Africa we can distinguish three classical kinds of climates (Charreau, 1974):

– the desert climates which have very few tropical months (one or two), a large number of arid months (eight to ten), and one or two temperate months,

- the equatorial climates which have a large number of tropical months, one or two arid months, and no temperate months,
- the tropical climates which are characterized by the lack of temperate months and a variable number of tropical and arid months, but more than one or two arid months.

If we consider the tropical climates, a further distinction can be made on the basis of the proportion of arid and tropical months and we can distinguish two classes:

- dry climates, characterized by 2–4 1/2 humid months,
- wet-dry climates having 4 1/2–7 humid months.

Since tropical, dry or wet, climates exist in large areas of West Africa, the aridity factor is deemed to play a major role from both a microbial as well as an agronomic point of view. This should not be overlooked.

Flooded rice fields

In contrast with the situation in India and the far-eastern countries (see, for instance: IRRI, 1979), few studies have been devoted thus far to the nitrogen transformations occurring in rice fields of West Africa. However, some data are available as far as nitrogen fixation and denitrification are concerned.

N_2-fixation

Three groups of organisms are believed to be responsible for the nitrogen input to rice fields: bluegreen algae, heterotrophic N_2-fixing bacteria, and *Azolla*.

N_2-fixation by bluegreen algae

It is difficult to estimate the biomass of N_2-fixing bluegreen algae in rice fields, not only because such estimations are time-consuming, but also because large variations occur during the cultivation cycle. Such variations were carefully observed by Roger & Reynaud (1976), who showed that bluegreen algae make up only a low percentage of the total algae biomass up to the heading stage. But during the last growth phase, if the plant cover is dense enough, N_2-fixing algae could represent 13–99 % of the total algae biomass (Table 2), which itself is generally never higher than $6 \cdot 10^3$ kg (f.w.) ha^{-1} in acidic P-deficient paddy soils, which are most frequently encountered in Senegal.

Estimations of N_2-fixed by bluegreen algae in West Africa are few. Preliminary reports from Reynaud & Roger (1978) indicate that in this area the nitrogen input through bluegreen algae is between 1 and 30 kg ha^{-1} yr^{-1}. Low activities can be attributed to the effect of unfavourable climatic and/or edaphic factors. In the dry tropical conditions which prevail in Senegal, high light intensities reaching 70,000–80,000 lx are thought to be responsible for the relatively poor development of bluegreen algae, which are light sensitive (Roger & Reynaud, 1979a), whereas in equatorial conditions this limitation is not observed.

Temperature is not usually a limiting factor, except in the Sahelian zone during the dry season when a lower temperature at the beginning of the cultivation cycle inhibits bluegreen algae growth and favours eukaryotic algae (Roger & Reynaud, 1976). Other

Table 2. **Algal biomass in relation to rice development (40 rice soils studied) (Roger & Reynaud, 1978b)**

Stages of rice development	Nature	Dominant flora: % of total biomass Mean value	Max. value	Min. value	N_2-fixing algae: % of total biomass Mean value	Max. value	Min. value
Tillering	Diatoms, unicellular green algae	73	99	49	2	4	0.1
Panicle initiation	Filamentous green algae. Non-heterocystous blue-green algae	89	93	86	3	9	0.1
Heading to maturity; weak plant cover	Filamentous green algae. Non-heterocystous blue-green algae	70	91	62	8	14	0.2
Heading to maturity; dense plant cover	Bluegreen algae	71	99	16	38	99	13.0

major limiting factors in West Africa are related to soil characteristics, especially P deficiency and acidity. Biotic factors (predators and antagonists) may also influence the growth and activity of bluegreen algae, but their role has not yet been elucidated.

Heterotrophic N_2-fixation

Heterotrophic N_2-fixation occurs not only in the rhizosphere, but also in other soil micro-habitats, such as root litter, which provides heterotrophic N_2-fixing bacteria with favorable conditions for their activity (especially the presence of energy-yielding compounds and low pO_2 tension). Microorganisms involved have been shown to pertain to the usual genera that have been described elsewhere, i.e., *Spirillum, Clostridium, Enterobacter, Beijerinckia, Azotobacter, Desulfovibrio, Desulfotomaculum* (Rinaudo, 1974; Rinaudo *et al.*, 1977; Dommergues & Rinaudo, 1979).

Heterotrophic N_2-fixation in the rice rhizosphere is most difficult to investigate because of the interference of bluegreen algae and the occurrence of large variations during the rice growth cycle. According to Balandreau *et al.* (1974), N_2-(acetylene reducing activity)-fixation in a rice field in Ivory Coast (Lamto) was in the order of 72 kg ha^{-1} yr^{-1}, but considerably lower values have been reported by Rinaudo (pers. comm.), e.g., 0–20 kg ha^{-1} yr^{-1} in Senegal. These results must be cautiously interpreted and new *in situ* measurements are necessary along with long-term field experiments to reassess the quantitative significance of N_2-fixation in the rice rhizosphere.

One point is clear: the N_2-fixing system made up by the rice plant and the microorganisms associated with its rhizosphere is not a stable system in itself, since the composition of the rhizosphere populations is heterogeneous and changing. Moreover, this system is very sensitive to effects of soil factors which have already been mentioned as harmful to other systems (acidity, P deficiency, excess of inorganic nitrogen) and also to factors specific to the rhizosphere N_2-fixing system, especially an excess of O_2. No simple chemical or physical criterion can be used for predicting the N_2-fixing potential of a soil with planted rice. Thus, in a survey of 29 paddy fields from Senegal, Garcia *et al.* (1974) were unable to discover any significant correlation between N_2-fixing potential and the following soil characteristics: clay, loam, and sand content; C, N, S-SO_4^{2-}, or N-NO_3^- content. Laboratory experiments suggest that in some soils, such as newly reclaimed fields, the inadequacy of the N_2-fixing microflora could be held responsible for the low rhizosphere N_2-fixation.

Heterotrophic N_2-fixation occurring in microhabitats other than rhizospheres has been demonstrated by different authors, especially Matsuguchi (1979). This type of process has not yet been investigated in West Africa, but reports about the effects from ploughing under straw in rice fields in the Casamance (i.e., Beye, 1974) suggest that significant N_2-fixation could take place during the decomposition of straw in the soil, increasing the total soil nitrogen content and the crop yield.

N_2-fixation by *Azolla*

The *Azolla-Anabaena* association has been extensively studied for the last few years in India, in the Far East, and in the USA (IRRI, 1979). *Azolla* occurs in West Africa but, to the best of our knowledge, it has not yet been used in rice production as has been the case in China and Vietnam, for instance. *Azolla* grows well in the humid areas of West Africa, but in the semi-arid conditions which prevail in Senegal, its distribution seems to be mainly limited by desiccation and to a lesser extent by high light intensities, and by temperatures which are too high (Roger & Reynaud, 1979b).

Nitrification and denitrification

The surface layer of rice soils is known to be sufficiently aerobic to permit active nitrification. The nitrate produced in the aerobic layer readily diffuses to the underlying anaerobic layers, where it is rapidly denitrified (Focht, 1979). The nitrification potential of the surface layer of rice fields in West Africa has not been systematically studied, but in a recent survey, Garcia *et al.* (1974) found that the nitrification potential was moderately correlated with the soil pH and inversely correlated with salinity. To the best of our knowledge there has been no study published on the nitrifying microflora of West Africa.

Since denitrification depends primarily upon nitrate concentration, the results of Garcia *et al.* (1974) suggest that acidity and salinity might limit denitrification in acid and saline soils, which was actually verified *in situ*. Acid rice fields are far from being the exception in West Africa, and denitrification is presumed to be less important than in regions where neutral soils are more frequently found. However, laboratory studies indicate that denitrification may still occur in acidic conditions, nitrate being reduced to nitrite, which produces nitric oxide (NO) by a chemical reaction (Garcia, 1976). On the other hand, even in acidic or saline soils, denitrification can be enhanced by surface application of ammonium fertilizers (Mitsui, 1954). Moreover, denitrification is well known to be stimulated in a rice rhizosphere. This rhizosphere effect may be attributed to the development of anaerobic zones, the presence of roots exudates and large numbers of denitrifiers in the rhizosphere (Garcia, 1975; Raimbault *et al.*, 1977).

According to Gamble *et al.* (1977), *Pseudomonas fluorescens* biotype II and the "alcaligenes-like" group are the dominant denitrifiers. Many denitrifying strains of the *Bacillus* genus have, however, been isolated from rice soils in Senegal, using an enriched medium (Garcia, 1977b). Some of these organisms, which all tolerate high concentrations of nitrite during growth, can use nitric oxide as a respiratory substrate for growth (Garcia, 1977b; Pichinoty *et al.* (1978).

In order to decrease denitrification, deep placement of ammonium has invariably been shown to be superior to surface placement (Mitsui, 1954; Abichandani & Patnaik, 1955). This was confirmed in pot experiments with rice growing in a Senegalese soil by measuring N_2O reduction rates (Garcia, 1977a). The slow release nitrogen fertilizer, sulfur-coated urea (SCU), which appeared to be a promising nitrogen fertilizer for the tropical regions, was tested successfully in the same experiment. Deep placement of SCU appears to be a good way to reduce losses by denitrification. The extra cost of SCU (30 %) would be compensated by (1) saving nitrogen fertilizer and by (2) eliminating the different split applications which are necessary when using conventional fertilizers.

Mineralization of organic nitrogen

Mineralization rates in acid rice soils are surprisingly low as long as the soil is flooded (Fig. 1), but there is some presumptive evidence that this activity is restored when the water content decreases.

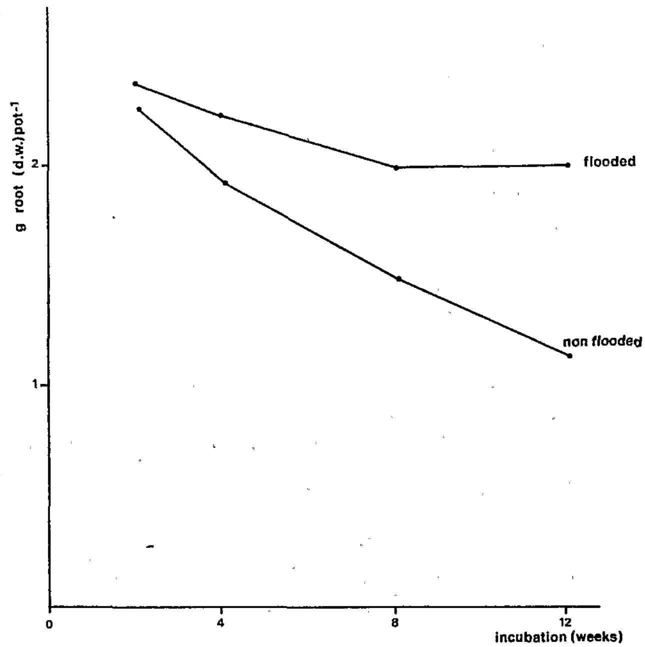

Figure 1. Time course of decomposition of rice roots introduced in flooded and rain-fed soil ("sol gris" from the Casamance) and incubated at 25°–28°C for 12 weeks. Root weight is expressed as g root (d.w.) per pot. Decomposition was much less in flooded than in rain-fed soil (Bernhard-Reversat, unpublished data).

Rain-fed agroecosystems

N_2-fixation

N_2-fixation by *Rhizobium* associated with legumes

Legumes are largely responsible for the nitrogen input in tropical rain-fed agroecosystems. The amount of N_2 fixed by *Rhizobium* associated with the legumes varies widely (Hainnaux, 1979), however, not only according to the legume-*Rhizobium* association under study, but also according to environmental conditions, which can be a much more important cause of variation than is usually assumed. Therefore, our discussion of the microbiology of symbiotic N_2-fixation will be mainly devoted to the factors which limit this process (Table 3).

The soil *Rhizobium* population is inadequate (1) when specific *Rhizobium* are absent or sparse, (2) when indigenous *Rhizobium* are ineffective or partially effective in N_2-fixation. Response to inoculation can be expected when such a situation exists, which mainly occurs with introduced legumes. Thus at the International Institute of Tropical Agriculture at Ibadan, seed inoculation increased the N_2-fixation (acetylene reducing activity) and nitrogen content of soybean, but did not affect cowpea which is an indigenous legume (Table 4). It should be noted that populations of *Rhizobium* specific to indigenous legumes may be abnormally low in some cases, such as recently cleared forest soils and leached acid soils. Table 5 illustrates the latter situation where inoculation was found to increase N_2-fixation by groundnut in Senegal.

Table 3. Major factors limiting symbiotic N_2-fixation in West Africa; proposed means of controlling their effect

Limiting factor	Control
1. Moisture stress	– irrigation – search for drought registing cv of legumes; and drought resisting *Rhizobium* (survival) – stimulating VA-mycorrhizal infection
2. Nematodes [1]	– fumigation by nematicides – biological control
3. Soil acidity and toxicity	– liming – addition of organic matter (farmyard manure; green manure; compost)
4. Mineral deficiencies especially phosphorus deficiency	– addition of phosphorus – stimulating VA-mycorrhizal infection
5. Inadequacy of native *Rhizobium* populations and competetion between native and introduced strains	– inoculation

[1] Some pests and diseases may become serious in some circumstances

Table 4. Effects of seed inoculation on nitrogenase activity and nitrogen content of tops of cowpea and soybean in two soils (Ayanaba, 1977)

Legume	Inoculant [1]	Apomu soil		Egbeda soil	
		N(%)	C_2H_4 (μmole g^{-1} nod. h^{-1})	N(%)	C_2H_4 (μmole g^{-1} nod. h^{-1})
Cowpea	None	3.80	2.17	3.57	34.05
	EL	5.95	1.32	4.37	32.34
Soybean	None	2.60	11.64	3.93	0.00
	S	3.15	20.14	4.30	366.90
	Nitrogerm	3.20	17.24	4.40	10.28

[1] EL and S are inoculants of the Nitragin Co., USA. Nitrogerm inoculant is Australian.

Table 5. Estimation (A value) of N_2-fixed by field-grown groundnut at the Bambey Agronomic Research Center, Central Senegal (Ganry, 1975, 1976, unpublished data)

Year	Rainfall(mm)	kg N_2-fixed ha^{-1}	
		Inoculated	Non-inoculated
1974	458 [3]	52	56
1975	521 [1]	84	67
1976	403 [2]	26	16

[1] Satisfactory distribution within the rainy season

[2] Unfavorable distribution

[3] Intermediate distribution

Thus far, no characteristic failure of nodulation due to microbial antagonism has been reported in West Africa. Thus, groundnut chlorosis due to a decrease of nodulation which occurs frequently in Senegal, could not be related to the antagonism of actinomycetes, since the number of actinomycetes antagonistic to a *Rhizobium* cowpea strain was similar in sites where chlorosis occurred and in nearby sites where no chlorosis was seen (J.J. Panthier, pers. comm.). It is obvious that further research is necessary to improve our knowledge of the different categories of microbial antagonism, including interstrain competition. Plant pathogens, such as virus, insects, and nematodes, are known to be potential antagonists to symbiosis. Parasitic attacks by nematodes are probably responsible for the reduction of N_2-fixation and for low yields of groundnuts and soybeans in many semiarid soils. Thus, a field experiment recently carried out in Central Senegal showed that soil fumigation with a nematicide (1,2-dibromo-3-chloropropane) not only reduced dramatically the nematode (*Scutellonema cavenessi*) population, but also markedly increased the N_2-fixing activity (acetylene reducing activity, Fig. 2); seed yields expressed

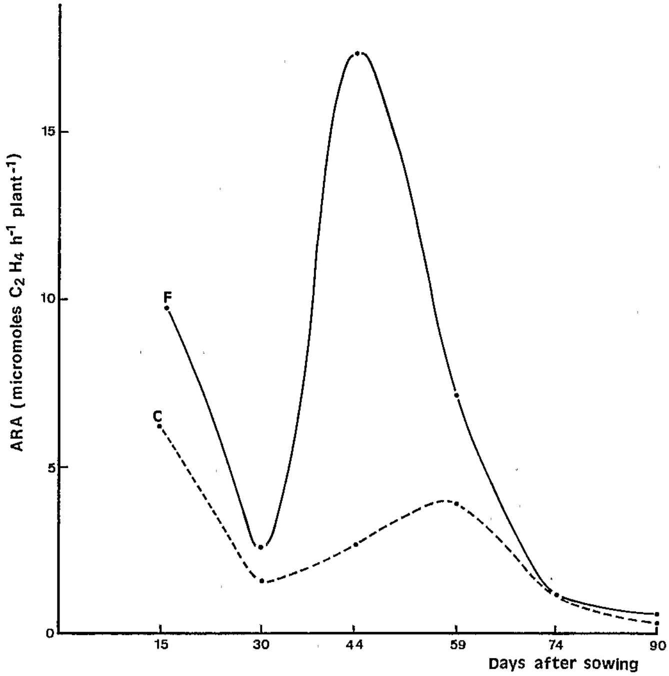

Figure 2. Influence of soil fumigation with 1,2-dibromo-3-chloropropane upon acetylene reducing activity (ARA) of field-grown groundnut. F: fumigated; C: control (non-fumigated) plot (Germani, unpublished data).

as kg N ha^{-1} were significantly increased (Germani *et al.*, 1978). Still unidentified biotic factors are probably responsible for the difference in N_2-fixing (C_2H_2) activity that are often observed *in situ*. Thus Dreyfus & Saint-Macary (unpublished data) found that soybeans growing in two adjacent plots, which did not differ in chemical soil properties and which had been similarly inoculated (10^9 *Rhizobium* per plant), exhibited large differences in acetylene reducing activity (Fig. 3).

High soil temperatures are often encountered in West African conditions during the dry season, but they seldom exceed 35°C during the rainy season. Such temperatures probably affect nodulation and N_2-fixation but, to the best of our knowledge, no specific field studies have been devoted to this problem.

By contrast, the influence of moisture stress on the *Rhizobium*-legume symbiosis has been given some attention at the Bambey Experimental Station in central Senegal over the last 3 or 4 years. N_2-fixation by groundnut (measured by the acetylene assay) was shown to be closely related to soil water content in 1976 and 1977 (Fig. 4). In 1977, nodulation was delayed by the low soil water content up to the 50th day, so that N_2-fixation started only after that date (Fig. 5). During the first 50 days the soil water content was high enough for the groundnut to grow, but too low for the infection process to take place.

Using the "A value method" (Fried & Middleboe, 1977), Ganry (1975, 1976, 1977)

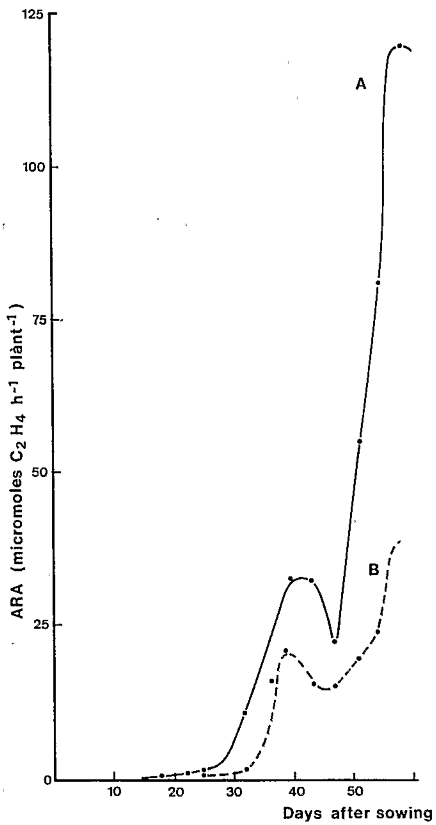

Figure 3. Acetylene reducing activity (ARA) of field grown soybean in two adjacent plots whose soil did not differ by any chemical or physical characteristic. Soybean had been massively inoculated (10^9 bacteria per plant) in both plots (Saint-Macary & Dreyfus, unpublished data).

found that N_2-fixation by field-grown groundnut at the Bambey Agronomic Research Center (central Senegal) depended largely on the rainfall (Table 5) and the distribution of rains within the rainy season. Thus, in 1976 the low overall rainfall (403 mm) and the occurrence of a period of relative aridity between August 15 and September 15 (the rainfall was only 65 mm, whereas the water requirement of the crop during this period was ca. 150 mm) caused a dramatic reduction in N_2-fixation (26 kg N_2 fixed ha^{-1}) in comparison with the satisfactory N_2-fixation (84 kg N_2 fixed ha^{-1}) that was recorded in 1975, when the rainfall was higher (521 mm) and precipitation well distributed. On the other hand, waterlogging, even if it is transitory, was noted to hinder nodulation and N_2-fixation of groundnut in the Casamance (south Senegal), where rainfall is higher than in central Senegal.

In conditions prevailing in West Africa, N_2-fixation by legumes is often restricted by unfavorable chemical characteristics, which have recently been reviewed by Kang *et al.* (1977). Soil acidity, which is known to inhibit nodulation by *Rhizobium*, is generally associated with Ca or P deficiency and Al or Mn toxicity. Therefore, the effect

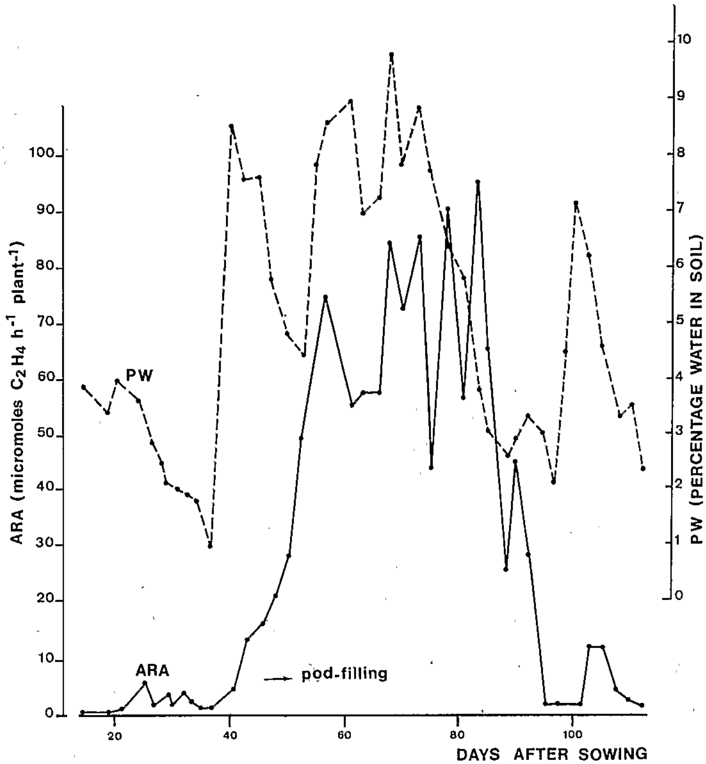

Figure 4. Variations of acetylene reducing activity (ARA per plant) of field-grown groundnut and of soil water content throughout the groundnut cycle (Ducerf, 1978).

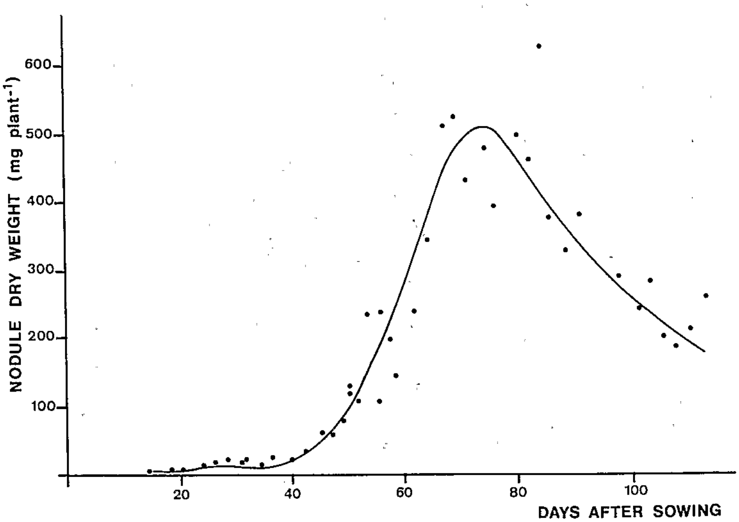

Figure 5. Time course of nodule weight of field-grown groundnut throughout the 1976 rainy season. For the first 45 days, the soil water content was high enough for the plant but too low for nodulation to occur (Ducerf, 1978).

Table 6. Effect of nitrogen application on N_2-fixation (estimated by A value method) by groundnut

Rates of application of nitrogen fertilizer (kg ha^{-1})	kg N_2-fixed ha^{-1}		
	Senegal[1]		Ghana [2]
	(1974)	(1975)	(1975)
15 at seeding	52.0	67.5	60.7
30 at seeding	56.0	75.4	69.3
30 split	–	67.2	38.2
60 at seeding	25.0	–	–

[1] Ganry (1976), trial carried out at Bambey Agronomic Research Center
[2] Kwakve & Afori (1977)

of limiting on N_2-fixation may be direct or indirect. Mn was reported to inhibit nodulation by Kang & Fox (1975) in Nigeria. Panthier (pers. comm.) hypothesized that excessive manganese uptake could be responsible for poor nodulation in soils of central Senegal (Thilmakha). By increasing pH through liming, exchangeable manganese is oxidized to manganic oxides, which are not assimilated by plants so that normal nodulation is restored. Phosphorus deficiency is well known in West Africa and upon the application of phosphorus in field trials increases in legume yield have been reported many times (e.g., Kang *et al.*, 1977).

By contrast, the beneficial role of sulfur is often overlooked. Some reports exist, however, such as that of Kang *et al.* (1977), indicating that sulfur application significantly stimulated nodulation of cowpea in a soil from West Nigeria.

Small additions of nitrogen fertilizer often, but not always, were shown to increase the yields of legumes and N_2-fixation. However, split application of 30 kg N ha^{-1} considerably reduced N_2-fixation of groundnut in Ghana (Table 6). Rates equal to or higher than 60 kg N ha^{-1} appeared to be detrimental to N_2-fixation in a sandy soil of central Senegal (Table 6).

Incorporating organic matter, particularly as farmyard manure, was reported to be generally most beneficial. The combination of liming, ploughing and farmyard manure application was reported to significantly increase groundnut yields, probably through increasing N_2-fixation, in central Senegal (Institut Sénégal de Recherches Agricoles, 1977).

At the present state of our knowledge, four major factors appear to limit symbiotic N_2-fixation in West Africa: moisture stress, nematode attacks, soil acidity and associated toxicity and the inadequacy of *Rhizobium* populations. Table 3 summarizes the means which are or could be recommended to control these limiting factors. We would like to stress here again that inoculation with even the best *Rhizobium* strain would be useless if just one of the other limiting factors were still operating.

Heterotrophic N_2-fixation

Nye & Greenland (1960), then Moore (1963) and Jaiyebo & Moore (1963) were the first investigators to draw attention to the possible importance of heterotrophic N_2-fixation in drained agroecosystems of West Africa. A recent review (Odu, 1977) has presented our current knowledge of this process for the area of Africa. It is well known that the main limiting factor for heterotrophic N_2-fixation is energy. Beside organic amendments, the two major sources of energy in the soil are (1) rhizosphere exudates and lysates, (2) and root litter.

Much experimental data has confirmed the role of living root systems as a source of energy for N_2-fixing bacteria, but this role has probably been over-estimated. There is increasing agreement that "root litter", or decaying root residues, may be a substantial source of energy for N_2-fixers, so that the contribution of "N_2-fixation in root litter" to the nitrogen input in the ecosystem could probably be more important that that resulting from "N_2-fixation on the living roots". Lysimeter measurements recently published (Ganry, 1977) show that nitrogen gains in a sandy acid soil of central Senegal (Dior soil), which had been enriched with chopped millet root (extrapolated rate: 15000 kg ha^{-1}), were as high as 88 kg ha^{-1} for a 4-month period.

Odu (1977) aptly drew attention to the strong influence of the water regime and specially to "the influence of alternating wet-and-dry cycles, with the attendant availability of carbon during flushes of decomposition accompanying the rewetting of dry soil, on N_2-fixation by free-living organisms". We do agree with his conclusion that it would be useful to assess the conditions that enhance heterotrophic fixation and to establish agronomic practices that would enhance such fixation. From our own experience, besides the control of the soil water regime, two factors should be dealt with in order to increase heterotrophic N_2-fixation: (1) acidity, which could be easily neutralized by liming, and (2) N_2-fixing micro-population, which could be achieved by proper inoculation methods.

Nitrification and denitrification

Nitrification is reportedly low in most West African soils, especially in acid soils (Ayanaba & Kang, 1976; Feller, 1977). In sandy soils of central Senegal, populations of nitrifiers are generally low (10^2–10^3 g^{-1} of soil) except in the rhizosphere of some plants (millet) where their numbers can be as high as 10^4 g^{-1} (Ganry, unpublished data). However, there is some indication that nitrification could be active in soils such as those from banana plantations or rain-fed maize or rice-crops (Chaballier, 1976) in the Ivory Coast, where large applications of ammonium fertilizer or urea seem to boost this activity.

It is well known that losses through denitrification are likely only when there is a large supply of both nitrate and energy-providing compounds in the soil. According to Greenland (1959), "high levels of nitrate usually exist for short periods following the dry season and it seems probable that at these times significant losses occur". Saturation or near saturation, conditions consecutive to heavy rains, obviously enhance the process, but in drained soils denitrification may also occur in anaerobic microsites (e.g., root debris), which are distributed in the soil profile. Recent lysimeter investigations on a typical sandy soil from Senegal (Dior Soil) indicate that losses through denitrification were ca. 30 % of the nitrogen fertilizer applied, whereas losses through leaching did not exceed 10 % (Ganry *et al.*, 1978).

Mineralization and immobilization of nitrogen

In the tropics, mineralization rates of organic nitrogen are generally high, because of favorable soil temperatures. This process is known to be enhanced in the rhizosphere (Blondel, 1971) and in sandy soils which occur most frequently in West Africa, the clay content being too low to protect the soil organic matter (humus and plant residues) against microbial attacks.

In arid conditions, it could be predicted that drought would stop mineralization. In fact, this process is somewhat slowed down but still persists after the rains have stopped, because many microorganisms are still active in the range of pF 4.2–5.2. Whereas nitrification is impeded when pF reaches 4.2, ammonification continues so that within the range of pF 4.2–5.2, the ammonium content increases (Fig. 6).

Consequently, the pool of organic matter in West African soils is usually very low (Charreau, 1974). On the other hand, immobilization of nitrogen in the form of humic compounds or microbial biomass is very limited. The microbial biomass is usually low (e.g., Table 1), so that amounts of nitrogen tied up in the soil microflora are negligible. But it seems possible to increase immobilization of nitrogen in the soil by increasing the input of plant residues. Thus, Ayanaba *et al.* (1976) showed that the heavy returns of organic matter from Guinea grass maintained and even increased both the total nitrogen and biomass in different Nigerian soils.

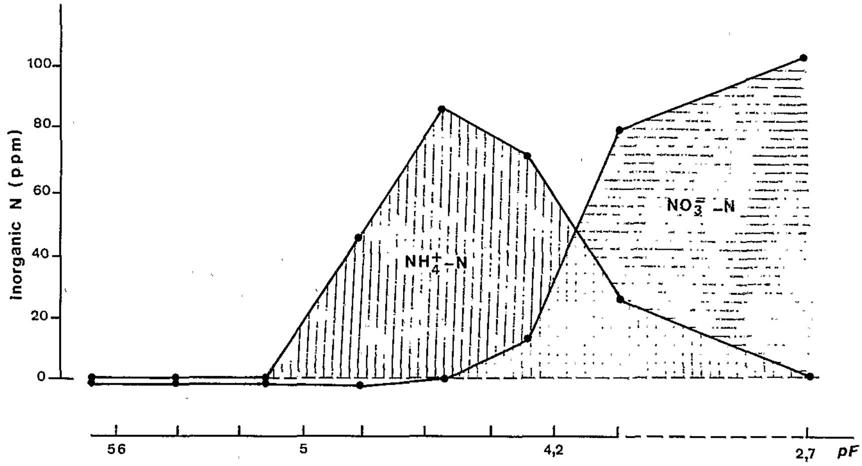

Figure 6. Influence of soil pF on the build-up of inorganic nitrogen after a 28-day incubation. Ammonification is favored by high pF (high water potential) whereas nitrification is favored by low pF (Dommergues, 1977).

Forest ecosystems

N_2-fixation

According to Greenland (1977), the humid tropical forest ecosystem of West Africa could accumulate 120 kg N_2 ha^{-1} yr^{-1} minus any gains from rainfall, dust, or collection from sub-soil sources. There has been much speculation about the source of the nitrogen accumulated.

In the semi-arid and arid zone different species of *Acacia* have been thought to contribute actively to N_2-fixation. Actually, although *Acacia albida* (Jung, 1967, 1969), or *Acacia senegal* (Bernhard-Reversat & Poupon, 1979) are nodulated when they are at the seedling stage at the laboratory or in nurseries, they seldom bear nodules as adults. This lack of nodules in the field was attributed by Bernhard-Reversat & Poupon (1979) to an active nitrate production in the soil. Drought may also be an important limiting factor of symbiotic fixation in forest ecosystems as it is in agroecosystems. *Casuarina equisetifolia*, a non-leguminous nodule-bearing tree, largely used for reforesting sandy soils on the coasts of West Africa, was reported to fix as much as 60 kg N ha^{-1} yr^{-1} in the Cap-Vert peninsula (Dommergues, 1963).

More investigations are obviously needed to obtain reliable data on the nitrogen input through non-symbiotic and symbiotic N_2-fixation in tropical forests.

Nitrification and denitrification

In contrast to the well-established concept that nitrification is slowed down in temperate forests, nitrification appears to be potentially active either in the humid forest such as the Banco and Yapo forests in the Ivory Coast (Bernhard-Reversat, 1974, 1975), in less humid conditions that prevail in the Casamance (Dommergues, 1956), or in the Sahelian savanna under *Acacia senegal* (Bernhard-Reversat, 1977). The nitrifying organisms which are involved in these acid soils have yet to be studied; investigations in that field should be initiated using the methodology proposed by Schmidt (1978).

Quantitative reports on denitrification in forests are lacking, but there is some presumptive evidence that losses through denitrification could occur rapidly, especially when soils are saturated (Moureaux, 1967; Bernhard-Reversat, 1975).

Mineralization of organic nitrogen

According to Bernhard-Reversat (1977), the mineralization rate in a Sahelian savanna in northern Senegal is considerable. She estimated that the amount of nitrogen mineralized under *Acacia senegal* and *Balanites aegyptiaca* during the period from January to November was 126 kg and 66 kg ha^{-1}, respectively. Such values compare well with data which have been reported for tropical humid forests of the Ivory Coast (Bernhard-Reversat, 1974).

Conclusion

For the last 5 years, qualitative and quantitative studies on biological N_2-fixation have been developed. But our knowledge of the ecology of this process is still inadequate and more investigations are urgently needed in order to elucidate vital problems such as that of the quantification of nitrogen fluxes attributable to biological N_2-fixation, competition between *Rhizobium*, interactions between *Rhizobium* and Vesicular-Arbuscular mycorrhizae, effects of aridity upon N_2-fixation.

Data related to nitrification, denitrification, humification and mineralization of nitrogen is still very scarce. Since it is not possible to initiate all the desirable investigations in these latter fields, we would like to suggest with Paul (1976) that, in the near future, the main effort be devoted to the evaluation of denitrification, together with other processes leading to losses of nitrogen (ammonia volatilization, leaching) in a number of typical ecosystems.

References

Abichandani, C.T. & Patnaik, S. 1955. Mineralising action of lime on soil nitrogen in waterlogged rice soils. – Int. Rice Comm. Lett. 13: 11–13.

Ayanaba, A. 1977. Toward better use of inoculants in the humid tropics. – In: Ayanaba, A. & Dart, P.J., (eds.) Biological Nitrogen Fixation in Farming Systems of the Tropics, pp. 181–187. New York: John Wiley.

Ayanaba, A. & Kang, B.T. 1976. Urea transformation in some tropical soils. – Soil Biol. Biochem. 8: 313–316.

Ayanaba, A., Tuckwell, S.B. & Jenkinson, D.S. 1976. The effects of clearing and cropping on the organic reserves and biomass of tropical forest soils. – Soil Biol. Biochem. 8: 519–526.

Balandreau, J.P., Millier, C.R. & Dommergues, Y.R. 1974. Diurnal variations of nitrogenase activity in the field. – Appl. Microbiol. 27: 662–665.

Bernhard-Reversat, F. 1974. L'azote du sol et sa participation au cycle biogéochimique de la fôret ombrophile de Côte d'Ivoire. – Rev. Ecol. Biol. Sol. 11: 263–282.

Bernhard-Reversat, F. 1975. Recherches sur l'écosystème de la forêt subéquatoriale de basse Côte d'Ivoire VI. Les cycles des macroéléments. – Terre et Vie 29: 229–254.

Bernhard-Reversat, F. 1977. Observations sur la minéralisation *in situ* de l'azote du sol en savane sahélienne (Sénégal). – Cah. ORSTOM Sér. Biol. 12: 301–306.

Bernhard-Reversat, F. & Poupon, H. 1979. Nitrogen cycling in a soil tree system in a Sahelian savanna. Example of *Acacua senegal*. – In: Rosswall, T. (ed.) Nitrogen Cycling in West African Ecosystems, pp. 363–369. Stockholm: SCOPE/UNEP International Nitrogen Unit, Royal Swedish Academy of Sciences.

Beye, G. 1974. Etude comparative de l'action de la potasse et de la paille enfouie sur le développement du riz, sur sol argileux de basse Casamance. – Agron. Trop. 29: 803–811.

Blondel, D. 1971. Rôle de la matière organique libre dans la minéralisation en sol sableux: relation avec l'alimentation azotée du mil. – Agron. Trop. 26: 1372–1377.

Chaballier, P.F. 1976. Contribution à la connaissance du devenir de l'azote du sol et de l'azote engrais dans un système sol-plante. Thèse, Faculté des Sciences, Université d'Abidjan, No. 33.

Charreau, C. 1974. Soils of tropical dry and dry-wet climatic areas of West Africa and their use and management. – Agron. mimeo, 74–26. Ithaca: Cornell University.

Dommergues, Y.R. 1956. Etude de la biologie des sols des forêts tropicales sèches et de leur évolution après défrichement. VIe Congr. Sci. Sol Paris 5: 6-5–610.

Dommergues, Y.R. 1963. Evaluation du taux de fixation de l'azote dans un sol dunaire reboisé en Filao (*Casuarina equisetifolia*). Agrochimica 7: 335–340.

Dommergues, Y.R. 1977. La biologie des sols. Que-sais-je? – Paris: Presses Universitaires de France, 128 pp.

Dommergues, Y.R. & Rinaudo, G. 1979. Factors affecting N_2-fixation in the rice rhizosphere. – In: Nitrogen and Rice, pp. 241–260. Los Banos: IRRI.

Ducerf, P. 1978. Synthèse des travaux effectués sur la modélisation de la fixation d'azote d'une culture d'arachide au Sénégal (années 1976–1977) Institut Sénégalais de Recherches Agricoles, CNRA, Bambey, Doc. mimeo, 42 pp.

Feller, C. 1977. Evolution des sols de défriche récente dans la région des Terres-Neuves (Sénégal Oriental). Aspects biologiques et caractéristiques de la matière organique. – Cah. ORSTOM sér. Pedol. 15: 291–302.

Focht, D.D. 1979. Microbial kinetics on nitrogen losses in paddy soils. – In: Nitrogen and Rice, pp. 119–134. Los Banos: IRRI.

Fried, M. & Middleboe, V. 1977. Measurement of amount of nitrogen fixed by a legume crop. – Plant Soil 47: 713–715.

Gamble, T.N., Betlach, M.R. & Tiedje, J.M. 1977. Numerically dominant denitrifying bacteria from world soils. – Appl. Environ. Microbiol. 33: 926–939.

Ganry, F. 1975. Action de la dose et de la date d'application de l'azote sur la fixation symbiotique et le rendement de l'arachide. Rapport provisoire sur l'expérimentation réalisée au Sénégal en 1974. Centre National de Recherches Agronomiques de Bambey, Doc. mimeo, 30 pp.

Ganry, F. 1976. Action du fractionnement de l'azote et de la date d'inoculation sur la fixation symbiotique et le rendement de l'arachide. Rapport sur l'expérimentation réalisée au Sénégal en 1975. Centre National de Recherches Agronomiques de Bambey, Doc. mimeo, 20 pp.

Ganry, F. 1977. Etude en microlysimètres de la décomposition de plusieurs types de résidus de récolte dans un sol tropical sableux. – Agron. Tropic. 32: 51–65.

Ganry, F., Guiraud, G. & Dommergues, Y.R. 1978. Effect of straw incorporation on the yield and nitrogen balance in the sandy soil-pearl millet cropping system of Senegal. – Plant Soil. 50: 649–664.

Garcia, J.L. 1975. Effet rhizosphère du riz sur la dénitrification. – Soil Biol. Biochem. 7: 139–141.

Garcia, J.L. 1976. Production d'oxyde nitrique dans les sols de rizière. – Ann. Microbiol. (Inst. Pasteur) 127: 401–414.

Garcia, J.L. 1977a. La dénitrification en sol de rizière: influence de la nature et du mode d'épandage des engrais azotés. – Cah. ORSTOM Sér. Biol. 12: 83–87.

Garcia, J.L. 1977b. Analyse de différents groupes composant la microflore dénitrifiante des sols de rizière du Sénégal. – Ann. Microbiol. (Inst. Pasteur) 128: 433–446.

Garcia, J.L., Raimbault, M., Jacq, V., Rinaudo, G. & Roger, P. 1974. Activités microbiennes dans les sols de rizières du Sénégal: relations avec les caractéristiques physico-chimiques et influence de la rhizosphère. – Rev. Ecol. Biol. Sol 11: 169–185.

Germani, G., Diem, H.G. & Dommergues, Y.R. 1978. Influence of 1.2-dibromo-3-chloropropane fumigation on nematode population, mycorrhizal infection, N_2-fixation and yield of field-grown groundnut. – In: Proc. International Workshop on Tropical Mycorrhiza Research, Kumasi, September 1978.

Greenland, D.J. 1959. Nitrogen gains and losses in tropical coils. – Troisième Conférence Interafricaine des Sols 1: 531–535.

Greenland, D.J. 1977. Contribution of microorganisms to the nitrogen status of tropical soils. – In: Ayanaba, A. & Dart, P.J., (eds.), Biological Nitrogen Fixation in Farming Systems of the Tropics, pp. 12–25. New York: John Wiley.

Hainnaux, G. 1979. Le cycle de l'azote dans les agro-systèmes de l'Afrique de l'Ouest. – In: Rosswall, T. (ed.) Nitrogen Cycling in West African Ecosystems, pp. 115–129. Stockholm: SCOPE/UNEP International Nitrogen Unit, Royal Swedish Academy of Sciences.

Institut Sénégalais de Recherches Agricoles, 1977. Division de biochimie du sol. Rapport de synthèse 1976. Centre National de Recherches Agronomiques de Bambey, Doc. mimeo, 12 pp.

IRRI, 1979. Nitrogen and Rice. Las Banos: IRRI, 499 pp.

Jaiyebo, E.O. & Moore, A.W. 1963. Soil nitrogen accretion under different covers in a tropical rainforest environment. – Nature (London) 197: 317–318.

Jung, G. 1967. Influence de l'*Acacia albida* (Del) sur la biologie des sols Dior, ORSTOM, Dakar, Doc. mimeo, 63 pp.

Jung, G. 1969. Cycles géochimiques dans un écosystème de région tropicale sèche: *Acacia albida*-sol ferrugineux tropical peu lessivé (Dior). – Oecol. Plant 4: 195–210.

Kang, B.T. & Fox, R.L. 1975. Influence of soil fertility on the protein and sulfur contents of grain legumes. – In: Proc. Collaborators Meeting Grain Legume Improvement, Ibadan, Nigeria: International Institute of Tropical Agriculture.

Kang, B.T., Nangju, D. & Ayanaba, A. 1977. Effects of fertilizer use on cowpea and soybean nodulation and nitrogen fixation in the lowland tropics. – In: Ayanaba, A. & Dart, P.J. (eds.) Biological nitrogen fixation in farming systems of the tropics, pp. 205–216. New York: John Wiley.

Kwakye, P.K. & Ofori, C.S. 1977. The use of isotopes in fertilizer efficiency studies on groundnuts (*Arachis hypogaea*) and cowpeas (*Vigna unguiculata*). Research Contract No. 1230/RB. Soil Res. Inst. Kwadaso-Kumasi, Ghana, Doc. mimeo, 25 pp.

Matsuguchi, T. 1979. Factors affecting heterotrophic nitrogen fixation in submerged rice soils. – In: Nitrogen and Rice, pp. 207–222. Los Banos: IRRI.

Mitsui, S. 1954. Inorganic Nutrition, Fertilization and Soil Amelioration for Lowland Rice, Tokyo: Yokendo Press. 107 pp.

Moore, A.W. 1963. Nitrogen fixation in latosolic soil under grass. – Plant Soil 10: 127–138.

Moureaux, C. 1967. Influence de la température et de l'humidité sur les activités biologiques de quelques sols ouest-africains. – Cah. ORSTOM, Sér. Pédol. 5: 393–420.

Nye, P.H. & Greenland, D.J. 1960. The Soil under Shifting Cultivation. U.K.: Commonwealth Agricultural Bureau.

Odu, C.T.I. 1977. Contribution of free-living bacteria to the nitrogen status of humid tropical soils. – In: Ayanaba, A. & Dart, P.J. (eds.) Biological Nitrogen Fixation in Farming Systems of the Tropics, 257–266. New York: John Wiley.

Paul, E.A. 1976. Nitrogen cycling in terrestrial ecosystems. – In: Nriagu, J.O. (ed.) Environmental Biogeochemistry, 1: 225–243. Ann Arbor: Ann Arbor Science.

Pichinoty, F., Garcia, J.L., Mandel, M., Job, C. & Durand, M. 1978. Isolement de bactéries utilisant en anaérobiose l'oxyde nitrique comme accepteur d'électrons respiratoires. – C.R. Acad. Sci. (Paris), série D 286: 1403–1405.

Raimbault, M., Rinaudo, G., Garcia, J.L. & Boureau, M. 1977. A device to study metabolic gases in the rice rhizosphere. – Soil. Biol. Biochem. 9: 193–196.

Reynaud, P.A. & Roger, P.A. (1978). N_2-fixing algal biomass in Senegal rice fields. – Ecol. Bull. (Stockholm) 26: 148–157.

Rinaudo, G. 1974. Fixation biologique de l'azote dans trois types de sols de rizières de Côte d'Ivoire. –Rev. Ecol. Biol. Sol. 11: 149–168.

Rinaudo, G., Hamad-Fares, I. & Dommergues, Y.E. 1977. Nitrogen fixation in the rice rhizosphere: methods of measurements and practices suggested to enhance the process. – In: Ayanaba, A. & Dart. P.J. (eds.) Biological Nitrogen Fixation in Farming Systems of the Tropics, pp. 313–322. New York: John Wiley.

Roger, P.A. & Reynaud, P.A. 1976. Dynamique de la population algale au cours d'un cycle de culture dans une rizière sahélienne. – Rev. Ecol. Biol. Sol 13: 545–560.

Roger, P.A. & Reynaud, P.A. 1979a. Ecology of blue-green algae in rice fields. – In: Nitrogen and Rice, pp. 287–310. Los Banos: IRRI.

Roger, P.A. & Reynaud, P.A. 1979b. Premières données sur l'écologie d'*Azolla africana* en zone sahélienne. – Oecol. Plant. 14: 75–83.

Schmidt, E.L. 1978. Nitrifying microorganisms and their methodology. Microbiology 1978, pp. 288–291. Washington D.C.: American Society for Microbiology.

Yoshida, T. 1975. Microbial metabolism of flooded soils. – In: Paul, E.A. & MacLaren, A.D. (eds.), Soil Biochem. 3: 83–115. New York: Marcel Dekker, Inc.