Research Signpost
37/661 (2), Fort P.O.
Trivandrum-695 023
Kerala, India

Recent Res. Devel. Soil Sci., 3 (2011): 1-33 ISBN: 978-81-308-0440-8

1. Savanna biomass production, N biogeochemistry, and cycling: A comparison between Western Africa (Ivory Coast and Burkina Faso) and the Venezuelan Llanos

Danilo López-Hernández[1], Michel Brossard[2] and Anne Fournier[3]
[1]*Laboratorio de Estudios Ambientales, Instituto de Zoología y Ecología Tropical*
Facultad de Ciencias, Universidad Central de Venezuela. Apdo 47058, Caracas
Venezuela; [2]*IRD, Umr 210 Eco&Sols, BP 64501, 34394 Montpellier cedex 5, France*
[3]*IRD (Institut de Recherche pour le Développement) Umr 208, 57 rue Cuvier*
75231 Paris Cedex 05, France

Abstract. Many studies examined the biomass accumulation, productivity and nutrient cycling of the grassy to woody savannas of Western Africa and the Venezuelan Llanos (Orinoco savannas). Yet, a comparative synthesis of that information for well extended territories on both sides of the Atlantic has not formally been presented. Those savannas, although strongly differing in soil parent material origin and human occupancy, are similar with respect to many features of soil-plant relationships, pedofauna activities, relief and climate.

Trachypogon spp., the dominant herbaceous component in Venezuelan well drained savannas is a genus well characterized by low productivity, lower nutritional, digestibility and palatability values

Correspondence/Reprint request: Dr. Danilo López-Hernández, Laboratorio de Estudios Ambientales, Instituto de Zoología y Ecología Tropical, Facultad de Ciencias, Universidad Central de Venezuela. Apdo 47058, Caracas Venezuela. E-mail: danilo.lopez@ciens.ucv.ve

and adaptation to acid, nutrient depleted soils. On the contrary, the African grasses such as *Andropogon spp.* present important nutritious and productive species. Fire is a management tool used in both savannas, it is often stated that the cumulative effect of small but persistent losses of nutrients by fire may decrease production. However, the existence of recurrent fires is a natural condition, and the N-depletion by fire is incompatible with the existence of savannas *per se*. Consequently, the idea of savanna as "natural" vegetation means they must have evolved under this constraint which, in turn, implies a positive or near to steady-state nitrogen budget. Research on nutrient cycling in savannas has been devoted to the fate or losses of nutrients during fires in local studies; practically no information exists on budgets, perhaps because of the complexity of the problem. In this contribution we have had the opportunity to gather information from International Biological Programs which allows us to present a comparison between savannas of West Africa and South America in an attempt to answer the following questions: Although, soil type and fertility present common features in savannas located north of the Equator on both continents, is there (or not) a strong difference in productivity (above-ground and subterranean) that could be related to the floristic composition (*Trachypogon sp.* vs *Andropogon sp.*) or pedologic, climatic features dominance? Can savannas be considered as a sink for atmospheric N due to biological fixation and can annual losses due to fire induce soil N depletion and a reduction in primary production?

Among the three studied regions higher primary production values were found in Ivory Coast savannas with a productivity that doubled the values of Burkina Faso and Venezuela. The higher production in Ivory Coast as compared to Venezuela savannas cannot be explained by differences in precipitation as it does not differ greatly between them. Therefore, the difference in production is related to soil fertility that is higher in Ivory Coast sites as compared with Venezuelan savannas. However, the lower precipitation in Burkina Faso can account for the biomass differences between Sudanese (Burkina Faso) and Guinean (Ivory Coast) savannas. Therefore, addressing the questions presented: There is a strong difference in productivity (aerial and subterranean) between Ivory Coast and Venezuelan savannas that corresponds to the dominance of *Andropogon sp.* instead of *Trachypogon sp.* On the other hand, with the information presented on the main N inputs and outputs, a comparative report on N budgets in well-drained savanna at Lamto, Ivory Coast and La Iguana, Venezuela is presented. In the African and South American savannas analyzed, N-fixation and the input in precipitation compensate for the fire loss and leaching. Therefore: the estimated amounts of dinitrogen fixation and deposition inputs seem to be enough to maintain plant production under periodic fires in both the African and the South American savannas analyzed here. Consequently, the vegetation in the natural savanna has evolved under fire constraint, therefore, implying a positive or near to steady-state nitrogen budget.

Introduction

Savannas are extensive to the north of the equator in the north of South America (Llanos of the Orinoco River) and in west central Africa. On both continents they are continuous ecosystems dominated by perennial grasses with variously scattered woody species and a typical isothermal climate with a seasonal rainfall distribution (April-October) which decreases according to a west-to-east gradient in the llanos of the Orinoco River [1], and with a south-to-north gradient in sub-Saharan West Africa [2].

Savannas represent about 18 % of the world's vegetation and account for about 30 % of the primary production of all terrestrial vegetation [3]. At the global scale, climate is the principal determinant of savanna distribution [4,5], although at local level, soils and the type of vegetation may also have a predominant effect. Within savanna areas, amount and seasonality in precipitation have been known to have a determinant role on vegetation structure and production. Moreover, the specific growth patterns of savanna plants and their production are related to the existence of a well marked seasonality in the cycles of the wet and rainy seasons. The number of dry months in savanna varies from 3 to 8 according to region. Soil fertility and hydric characteristics can also differ within savanna types; however, very important parts of the savanna biome are located on poor, well weathered tropical soils. Another factor strongly associated with savannas is the regular burning of vegetation that currently is used as a management tool. Burning has been in the past an important element in the debate about savannas´ origin [4], but currently, the focus is more often on the influence of savanna burning in studies of regional, and possibly global, energy, water and carbon balances [3,5,6,7]. Although, fire frequency can be very variable (every 1 to 5 years) according to type of savannas and to human uses, its influence on carbon and also on nutrient cycling indeed can be remarkable [5,8,9,10]. Yet, in a wider approach integrating all these aspects, recent research led to the hypothesis that of a network of feedbacks between climate, fire and herbivores may play a prominent role in explaining the origin of C_4 savannas in the late Miocene [7].

The largest area of savannas in the world is located in Africa, where they occupy 43 to 50 % of continent territory. In South America, savannas cover a surface over 2.7×10^6 km^2, most of it in Brazil Cerrado (2.04×10^6 km^2) and the Llanos of Venezuela and Colombia (0.5×10^6 km^2) [11]; these American territories are characterized by low human density. In West Africa savannas occupy over one third of the territory ($1.3x10^6$ km^2) while the human population is today rather numerous and they have been involved in agriculture activities over millennia [12]. Although, the human presence in the savannas of Africa may be as old as the human species, the first agricultural activities in West Africa are thought to date from about 5000 BC, whereas cattle raising would be more recent – 3000 BC, particularly in Sudanese savannas [13]. Human settlements in the savannas of South America are newer; their presence has been reported from 7000 to 9000 BC in the savannas of the Orinoco River [14]. After the Columbian Encounter, and for centuries, the sparse human population used savannas only for extensive cattle raising instead of cultivation [15,16]. Since pastoral activities generally include the use of fire, they produced a much lighter disturbance on vegetation than cropping. It can, therefore be considered, that human activities had less effect on Latin American than on West African landscape.

The first use of fire by humans is probably linked to game activities that did not result in any deep mark. In Africa, the oldest ascertained vestiges of human fire use date from 60000 BC (upper Pleistocene, [17]), while in America the practice is clearly more recent. Thus human fires show a different history on the two continents.

Today fire is used to manage rangeland and protected areas maintaining a savanna environment by preventing bush encroachment and selecting for fire tolerant species. Fire has become a fundamental vegetation management tool used to eliminate grass material considered inedible by cattle, and also to stimulate regrowth of perennial grasses. At the same time, recurrent fires are usually considered an ecological factor, a determinant of the structure, floristic composition, production and nutrient cycling of savanna ecosystems [9,18]; however, before present practical uses, natural fires frequently occurred [7]. In fact, when fire is suppressed, vegetation develops from open savannas to densely wooded ecosystems, at least, in the most humid savannas [19,20,21]. Apart from tree densification, fire suppression induces, in turn, an increase in total soil carbon, nitrogen and available nutrients. Changes in soil fauna populations, soil enzymatic activities and microbial biomass also occur as soon as a savanna sector is protected from fire [22,23]. In addition, other factors may affect soil C and N contents in natural savannas, such as the recent increases in anthropogenic emissions and deposition of C and N [10,24,25]. When a savanna stand burns, the rapid combustion of the organic matter together with the ash dispersion and volatilization of the elements with gaseous cycles (e.g. N and S) induce a decline in the effective input of organic matter and nutrients to the soil [9,26]. Thus, N cycling is especially sensitive to frequent fires resulting in the loss of N. Attempts to clarify N cycling balance in savannas furnished contrasting results. In some Australian ecosystems, estimated rates of biological N fixation appear to be insufficient to replace the annual losses [27] inducing soil-N depletion and reduce productivity, whereas in neotropical savannas the estimated amounts of N fixation and deposition (bulk precipitation) inputs seem to be enough to maintain plant production despite periodic fires [28].

It is often stated that the cumulative effect of small but persistent losses of nutrients by fire and agricultural activities may decrease production and, in turn, cause land degradation [29]. However, the existence of recurrent fires is a natural condition and N depletion by fire is incompatible with the existence of savannas *per se*. Consequently, savanna vegetations evolved under frequent fires which imply a positive or near to steady-state nitrogen budget. But most of the research on nutrient cycling in savannas has been devoted to the fate or losses of nutrients during fires in local studies; practically no information exists on budgets, perhaps because of the complexity of the problem and the lack of the effect of fire on nutrient data [28]. In this contribution we have had the opportunity to gather information from International Biological Programs (IBP) which offer the possibility to present a comparison between savannas of West Africa and South America in an attempt to answer the following question: can savannas be considered as a sink for atmospheric N due to biological fixation and can annual losses due to fire induce soil N depletion and a reduction in primary production? In a comparative way, information will be presented for both localities (West Africa and South America) on the main traits which affect the N-cycling: compartments (primary production, role of pedofauna) and transfers (input, outputs).

Following the wake of the IBP programs many studies have contributed our understanding of biomass accumulation, production and nutrient cycling of the grassy to woody savannas of Western Africa and the Venezuelan Llanos (Orinoco savannas). Although some of these studies showed the variation along regional environmental gradients, a comparative synthesis of that information on both sides of the Atlantic is still lacking. Although, strongly differing in soil parent material origin, flora, fauna and human occupancy, these savannas are similar in many of their features of soil-plant relationships, pedofauna activities, relief and climate (Tables 1 and 2).

The dominant herbaceous species in Venezuelan well drained savannas belong to the genus *Trachypogon*, well characterized by low production and adaptation to acid, nutrient depleted soils, especially in nitrogen and phosphorus [22,30,31,32]. This genus is also known because of its lower nutritional, digestibility and palatability values. In contrast, the dominant African grasses, mostly species of the *Andropogonae* tribe present important nutritious and productive species, and that is the reason for the conversion of neotropical forest and savannas to cultivated pastures dominated by African species, with the concomitant dramatic loss of native vegetation [16,22,24]. The *Trachypogon* savannas are indeed recognized as having among the lowest production in the world, and, the Venezuelan Llanos are possibly one of the more thoroughly analyzed and best known areas of neotropical savannas [18].

In this review we also present comparative information about primary production in well-drained seasonal regularly burned savannas, with a particular emphasis on the best known sites, namely *Trachypogon-Axonopus* savannas located at 6° 5’ – 10° 5’ N in the Orinoco Llanos of South America and *Andropogonae-Loudetia* savannas located at 6° N -12° N in the territories of Ivory Coast and Burkina Faso in Western Africa (Fig.1). The sites in Ivory Coast and Venezuela present similarities in climate, but they differ greatly in their soil parent material, whereas the sites in Burkina Faso and Ivory Coast differ strongly in climatic conditions (precipitation and temperature) (Tables 1 and 2).

The following questions will be addressed.

1) Concerning biomass production, to what extent does primary production differ in Venezuelan and African sites in its total amount and allocation between above and below-ground organs? Which floristic, pedologic and climate features are involved?
2) Concerning the ecosystem as a whole, how might these features contribute to the persistence of natural burned savannas?

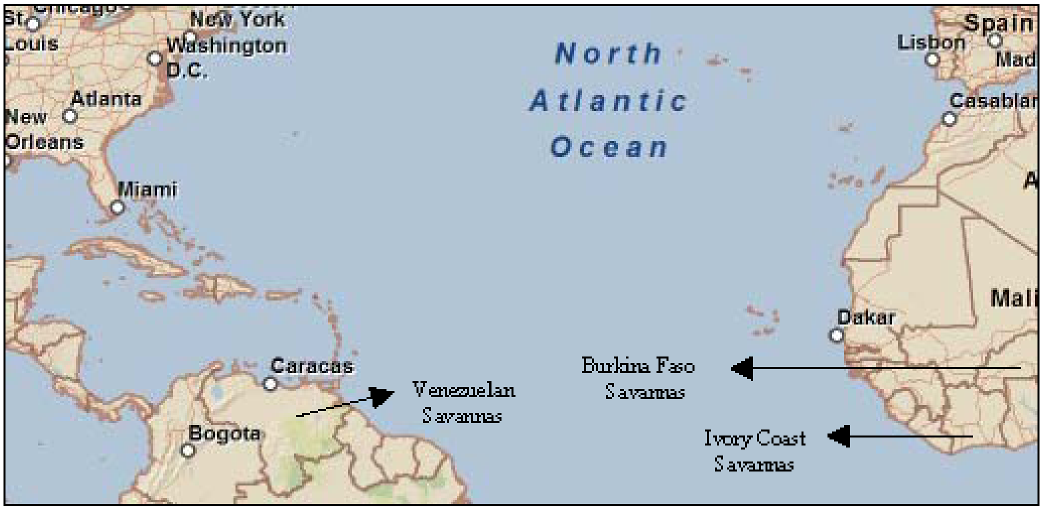

Figure 1. Location of the Western Africa (Ivory Coast and Burkina Faso) and the Venezuelan savannas.

Material and methods

Sites selection and methods

Sites and data selection

In order to compare primary production and N biochemistry and cycling in Africa and America sites, were needed directly comparable datasets from all sites. The IBP program [33,34] with research teams using common methods in sites distributed over the world offered the appropriate framework for such a selection. The primary production data selected come from the herbaceous layer from 12 vegetation stands in 3 localities in West Africa and from 14 vegetation stands in 6 localities in Venezuela. The N biochemistry and cycling data come from 5 vegetation stands, 3 in Ivory Coast and 2 in Venezuela**.** Data were collected following the same or very similar methods based on the assessment of biomass through harvesting.

Estimation of above and below ground herbaceous biomass and production from harvesting methods

One of the more direct and precise methods to study herbaceous primary production relies on plant harvesting, and different models derived from it have been used to evaluate primary production, particularly by IBP teams [12,35,36,37]. However, the assessment of biomass and primary production is a difficult task. Sources of errors remain i) in assessing the corresponding phytomass harvested by vertebrate or invertebrate primary consumers, ii) in taking account of the material turnover in the whole plant, iii) in the determination and separation of living roots from necromass through visual observations [12], and iv) in estimating the contribution of root exudates [12,38]. In spite of attempts to develop more sophisticated methods, production figures from classical harvesting methods are likely underestimated. There is no doubt that the primary production absolute values assessed by this group of methods are affected by some approximation, but the use of indirect methods entails no fewer problems. However, the selected data when obtained through similar methods can validly be compared. In this research, data were accessed from the literature and personal information from previous research of the authors, they include primary production assessments obtained through the detailed follow-up of the grass layer for each stand.

The estimation of the biomass of aerial parts was done by monthly harvesting and selecting of all plant material (green, dead and litter) in given sampling surfaces (4 to 10) and size (1 to 4 m^2) which allowed us to calculate reliable average values (the details of protocols can be found in the original publications). For the harvest of below-ground organs, monolith of soils or core samples were taken to a maximum depth of 30 cm (Venezuelan and Sudanese sites) to 1 m (Ivory Coast sites), according to the local characteristics of the topsoil that influence the vertical distribution of roots [12,39]. It is known that in Sudanese savannas 80 to 90% of roots are usually contained in the first 30 cm [12].

Net primary production for above-ground part of plants was calculated by summing separately the monthly increments of biomass (live organs) and necromass (dead organs) and taking carefully into account the process of mortality that transforms biomass into necromass [12]. For below-ground parts, due to the great difficulty to distinguish between live and dead materials the increments were summed without making any distinction between them.

Nitrogen cycling

The information presented here for N cycling comes from long-term studies at two experimental stations: Lamto, in Ivory Coast, and La Iguana, in Venezuela.

Lamto

Lamto Experimental Station is located in Ivory Coast (West Africa), at the edge of the rain forest (6° 13’ N and 5° 02’ W). Mean annual temperature is 27°C and rainfall averages 1200 $mm.yr^{-1}$, with a dry season between November and February. The density of large herbivores is presently very low in the whole zone. Three experimental plots were studied at Lamto [37]: i) Savanna of *Loudetia* (SL) on a sandy soil derived from granite, ii) Savanna of *Andropogon* (SA), also on a granitic sandy soil, and iii) Savanna protected from fire (SPF). In this last site, with no fire for more than 30 years, the grass species tend to disappear due to colonization by woody species, therefore the savanna is thus transformed into a forest. The soils of this experimental site are brown eutrophic black earths derived from amphibolites.

La Iguana

La Iguana Experimental Station (IES) is located in the southeast of Guarico state, Venezuela (8° 25’ N and 65° 24’ W). IES corresponds to savannas of the Venezuelan Central Plains, under the influence of the Orinoco River watershed. Well-drained savannas characterize the ecosystem. The region has a marked seasonality with a dry season from November to

May and a rainy season from June to October. The total annual precipitation is 1369 mm, and the mean annual temperature is 27ºC.

An experimental plot of one hectare was evenly divided into two subplots, one of which was burned at the end of the dry season (April of the first year and February of the second year). The other half of the plot had been protected from fire for two years previous to sampling. Large herbivores (mainly cows) were excluded from the experimental plot.

The information presented for N-cycling was collected at various times in a variety of experimental conditions. The main characteristics of the climate, soils and vegetation of both studied sites are presented in previous reports [8,28,37,40,41,42]. Estimates of nitrogen fixation by the acetylene reduction method (nitrogenase activity, NA) in the soil-plant system was determined with the field approach proposed by Balandreau [28,43,44], whereas nitrogen evaluation in the different compartments are presented in [40,41,45].

General environmental characteristics of the studied savannas

Geology, relief and soils

West Africa is underlain by the geological units corresponding to a metamorphic and eruptive Precambrian basement which is, on average, a billion years old. The basement corresponds to crystalline, hard rocks, mainly granites and gneiss. Tectonic movements have been insignificant since Precambrian, which explain the flatness of the relief, mainly molded by erosion processes [46].

On the other hand, 65 million years ago (during the Paleocene), the territory corresponding to the Venezuelan Llanos was under the sea. At the end of that geological period, due to the raising of the Guayana Craton, a marine regression started with the consequent deposit of sediments [47]. The continuous rising of mountain chains along the Tertiary induced an increment in the sedimentation of this extended watershed that remains to the present [48]. The resulting relief is an almost flat topography with altitudes that do not exceed the 400 to 500 m (Table 1).

The soils present in the savannas of West Africa (Burkina Faso and Ivory Coast) are closely related to the underlying parent material (Table 1). In general there are well weathered tropical ferrugineous and ferralitic soils (i.e. Alisols, Acrisols, Ferralsols). Although, the less weathered Alfisols and Lithosols are also found. In the Venezuelan savannas well weathered soils also are present, within them Ultisols (Acrisols) are dominant and, to a lesser extent, Oxisols (Ferrasols). Less weathered Inceptisols and Entisols (Arenosols) are also found.

Table 1. Geology and soils.

Feature	Llanos Venezuela	Guinean savannas Ivory Coast	Sudanese savannas Ivory Coast and Burkina Faso
Original rock and sediments	Tertiary clays, Mesa Formation	Granite and schist Precambrian	Granite Precambrian
Tectonic	Important in the past	Negligible	Negligible
Relief	Flat, small hills	Flat	Flat, small hills
Soils	Acrisols, Arenosols, Nitisols, Lixisols, Ferralsols, Plinthosols	Acrisols, Ferralsols, Lixisols, Luvisols, Nitisols	Acrisols, Luvisols, Plinthosols, Vertisols

Table 2. Main climatic characteristics of the savannas studied.

Characteristic	Llanos (Venezuela)	Guinean savannas (Ivory Coast)	Sudanese savannas (Ivory Coast and Burkina Faso)
Latitude	6° 5’ - 10° 5’ N	6°- 9° N	9°- 12 N
Altitude, masl	100 – 300	300 - 500	300 – 500
Precipitation, mm	800 – 2400	1100 - 1600	800 – 1100
Potential Evapotranspiration, mm	1000 – 2400	1300 - 1500	1500 – 2500
Annual mean temperature, °C	26 – 27	27	27 – 28
Annual minimum temperature, °C	22	22	22
Annual maximum temperature, °C	33	32	34 – 35
Start and end of wet season	April - October	April – November (with a dryer period in August)	May – September or October
Duration of dryness (months)	6	5	6- 8

Climate

The savanna regions have a marked seasonality, variation occurs according to the regions (Table 2). In West African Guinean savannas the rainy season starts approximately in April and ends in November, with an annual average precipitation between 1100 and 1600 mm, a mean annual potential evapotranspiration between 1300 and 1500 mm, and an annual average temperature of about 27°C. In West African Sudanese savannas, the shorter rainy season begins in May and ends in September, the annual average precipitation is lower (800 to 1100 mm), but the potential evapotranspiration is higher (1500 to 2500 mm) and the annual average temperature is a little higher (28°C). In Venezuela the rainy season extends between April and October, mean annual precipitation ranges between 800 (Central Llanos) to 2400 mm (Amazonian savannas), mean annual evapotranspiration potential ranges between 1000 and 2400 mm and annual average temperature 26 to 27° C. The length of the dry season at the studied sites in Guinean savanna and the Llanos is rather similar, but longer in Sudanese savannas (Table 2).

Main features of vegetation

In most West African countries, the main vegetation types lie in strips more or less parallel to the Equator, which, in turn, mirrors the influence of precipitation [46].

The distribution of the undisturbed savanna vegetation types (floristic and physiognomic) in the landscape related to topography, each climatic region having its own communities. Grassy types are generally located on the shallower soils of hardpan and plateaus and in temporarily-flooded lowlands, while bush to tree and wooded types are found on the deeper and better drained lowland soils [12]. However, under human pressure this structure is altered and other vegetation types develop [49].

The Llanos of the Orinoco present a wide-range of vegetation physiognomic types affected by different climatic, soil characteristic and human interference [50].

The description of the study sites illustrates the diversity of vegetation facies in savanna (Tables 3 and 4).

Sites of study

The studies were carried out on different natural savanna sites located in Burkina Faso, Ivory Coast and Venezuela, all of them under frequent burning but light grazing. Nowadays plant harvesting principally occurs from local wildlife (ungulates and invertebrates) in African sites, whereas in Venezuelan sites it is mainly from extensive cattle ranching and invertebrate consumption. While not quite negligible [12] this harvesting by primary consumers can be considered light and similar in all study sites.

West African sites

In West Africa Burkina Faso information comes from two phytogeographical regions. Five stands belong to the Sudanese sector, in the sites of Nazinga (Burkina Faso), an experimental Game Ranch (not fenced), and Ouango-Fitini (Ivory Coast) next to the Parc National de la Comoé. The seven other stands in Lamto Research Station are included in the climatically more humid Guinean sector.

Table 3. Vegetation and soils of the studied sites in West Africa.

Site	**Type of vegetation**	**Grass vegetation (dominant species)**	**Ligneous vegetation (cover and dominant species)**	**Soils**
Nazinga 11°09'N, 01°36'W				
• Nazinga 1	Grassy savanna	*Andropogon chinensis* *Schizachyrium sanguineum*	< 5% *Terminalia avicennioides* and diverse species	Lixisols
• Nazinga 2	Bush savanna	*Andropogon chinensis* *Schizachyrium sanguineum*	5% *Gardenia erubescens* *Terminalia laxiflora* *Ximenia americana*	Haplic Lixisols
• Nazinga 3	Tree savanna	*Andropogon chinensis* *Hyparrhenia smithiana*	20% *Detarium microcarpum* *Terminalia laxiflora*	Dystric Plinthosols
• Ouango-Fitini 1	Grassy savanna	*Loudetia simplex*	< 5% *Acacia dudgeoni* *Annona senegalensis*	Alisols
• Ouango-Fitini 2	Bush savanna	*Andropogon chinensis* *Hyparrhenia smithiana* *Andropogon schirensis*	30% *Detarium microcarpum* *Vitellaria paradoxa* *Daniellia oliveri* *Terminalia laxiflora*	Alisol
• Lamto 1	Grassy savanna	*Loudetia simplex* *Andropogon schirensis*	< 5% *Borassus aethiopum*	Deep pseudogley on sand
• Lamto 2	Transition grassy savanna	*Hyparrhenia diplandra* *Andropogon schirensis* *Loudetia simplex*	< 5% *Cochlospermum planchonii*	Transition between pseudogley and lixisol
• Lamto 3	Grassy savanna	*Hyparrhenia spp* *Andropogon spp.*	absent	Acrisol
• Lamto 4	Transition bush savanna	*Hyparrhenia smithiana* *Hyparrhenia diplandra*	25% *Borassus aethiopum* and diverse species	Transition between pseudogley and lixisol
• Lamto 5	Bush savanna clearing	*Hyparrhenia diplandra* *Hyparrhenia smithiana*	<25% diverse species	Lixisol
• Lamto 6	Bush savanna	*Imperata cylindrica* *Sorghastrum bipennatum* *Hyparrhenia diplandra*	5% < > 25% *Crossopteryx febrifuga* *Piliostigma thonningii* *Bridelia ferruginea* *Cussonia arborea* *Borassus aethiopum*	Acrisol

Table 3. continued

• Lamto 7	Tree savanna	*Imperata cylindrica* *Hyparrhenia diplandra*	80% *Borassus aethiopum* *Terminalia glaucescens* *Erytrophleum guineense* *Vitex doniana*	Acrisol

Venezuelan sites

In the Venezuelan savannas, six different sites located from 5°47´ N to 9°45’N were chosen. Sites differ according to soil type. However, the vegetation (herbaceous and ligneous components) was, in general, less diverse than in the African sites (Table 4).

Table 4. Vegetation and soils of the sites studied in Venezuela.

Site	Grass vegetation	Ligneous vegetation	Soils
Calabozo 8°56’N, 67°25’W	*Trachypogon plumosus, Hyparrhenia rufa*	*Curatella americana, Byrsonimia crassifolia, Bowdichia virgilioides*	Ferralsols
Jusepín 9°45’N, 63°31’W	*Trachypogon plumosus, Hyparrhenia rufa*	*Curatella americana, Byrsonimia crassifolia, Bowdichia virgilioides*	Acrisols
Dos Caminos 9°30’N, 66°34’W	*Trachypogon vestitus, Paspalum carinatum, Andropogon angustatus,Aristida sp., Bulbostylis sp.*	*Cassia moschata, Genipa caruto, Godmania macrocarpa*	Ferrasols, Acrisols
Cabruta 5°47’N, 67°30’W	*Trachypogon vestitus, Axonopus canescens*	*Curatella americana, Byrsonimia crassifolia, Bowdichia virgilioides, Palicourea rigida*	Ferralsols
La Iguana 8°25’N, 65°25’W	*Trachypogon vestitus, Axonopus canescens*	*Curatella americana, Byrsonimia crassifolia, Bowdichia virgilioides*	Arenosols, Acrisols
Puerto Ayacucho 5°47N, 67°30´W	*Trachypogon vestitus, Axonopus canescens, Paspalum carinatum, Bulbostylis paradoxa, B. capillaris*	*Byrsonima crassifolia*	Arenosols

Results and discussion

Principal features of the landscapes

Vegetation physiognomy and topography

In Western African undisturbed savannas, Fournier [12] emphasized a strong relationships between the savannas vegetation and topography. The savannas of the Orinoco do not necessarily present a similar physiognomic pattern, although a catena disposition of soil and vegetation is normally found in the seasonally flooded alluvial plains of the central Llanos [18,51], however vegetation of flooded savannas are not representative of *Trachypogon* savannas.

In Africa authors have remarked on a floristic enrichment from the most humid types of savannas to the Sudanese ones, figures were given along a south-north gradient from Lamto Experimental Station in the Southern part of Ivory Coast to Nazinga Ranch at Burkina-Faso [12]. That floristic enrichment particularly obvious among woody species is in close association with fire intensity. Due to the higher above-ground primary production, when fires occur in Lamto region their intensity is stronger than in Sudanese savannas, allowing only for a few very tolerant species to live in that humid savanna.

Soil fauna abundance and activities

In the savannas of Burkina Faso and Ivory Coast, termite mounds are very abundant, particularly of the grass-feeding *Trinervitermes*, and to a lesser extent the big mound builder *Macrotermes* [52,53,54]. Humivorous *Cubitermes* are also extensive, always associated with the lateritic hardpan. In West Africa there is an important variation of the different termite groups (plant debris-feeding or fungus cultivators) along the climatic gradient. The grass-feeding termites have their maximum presence in the drier environments, and then they are replaced by the fungus-growing termites that dominate above 500 mm precipitation. The trophic categories of wood and humus-feeding termites are found within the more humid environments [12].

In South American savannas (Colombia and Venezuela) termite mounds are also a significant feature of the landscape. Grass-feeding *Nasutes* are particularly important [55,56]; however, mound abundance is generally scarcer than in West African savannas.

The role of ants in the nutrient cycling in tropical savannas is scarcely known. Nonetheless, in a savanna-forest ecotone in the Venezuelan Amazonian, Netuzhilin et al. [57] have shown that ants were the most numerous and diverse group in all the ecosystems studied corresponding to about 65% of the macro arthropods captured.

Earthworms in both temperate and tropical ecosystems play a dominant role in the decomposition processes of organic matter, inducing changes in the physico-chemical and biological properties of the soil through the construction of galleries and the excretion of mucus and casts. Moreover, casts may be regarded as microsites of short-term mineral N and available P production and medium term soil organic matter accumulation [58]. However, in general they are less abundant in dry environments. In comparison with information for temperate environments, there is a lack of information concerning the species composition and structure of earthworm communities in tropical savannas. Studies are mainly from India and Ivory Coast [59,60] and recently from *Trachypogon* savannas [61,62]. Geophagus earthworms have a great capacity to ingest soil, which is thereby considerably transformed, particularly in terms of respiration rate and microbial activity. In the *Loudetia-Andropogon* savannas of Lamto (Ivory Coast), Lavelle and collaborators have studied the biology and ecology of tropical earthworms. There they reported the existence of large populations of earthworms (detritivores and geophagus) well adapted to the rainfall pattern (1276 mm) and temperature (27˚C) of the region [58,60]. In native neotropical savanna of *Trachypogon* and associated pasture (e.g. *Axonopus*, *Andropogon*), earthworm density and biomass are very low [61,62]. Earthworm populations however, significantly increase when natural savannas are transformed into improved pastures and agro ecosystems [61,62].

Plant production

Net primary production

The information obtained for the net primary production at the different sampled sites in West African and Venezuelan savannas showed that the above ground net primary production (APP, Table 5) ranges from 0.56 t ha^{-1} yr^{-1} in Cabruta 1 (Venezuela) to 10.36 t ha^{-1} yr^{-1} in Lamto 3 (Ivory Coast). The values were tested according with a Mann-Whitney test. Production is higher in West Africa than in Venezuela (Ua = 143.5, z = -3.03, P one tailed = 0.0012, P two tailed = 0.0024, and Fig. 3). In spite of the higher precipitation in Venezuelan than in the Sudanese sites of Nazinga and Ouango-Fitini (Table 2), production does not differ between them (Ua = 24.5, z = 0.93, P one tailed = 0.1762, P two tailed = 0.3524, and Fig. 2). In Ivory Coast savannas primary production indeed roughly doubled the values of Burkina Faso and Venezuela (Table 5). However, the precise relationship between precipitation and net primary production over large areas is difficult to assess: because of variations in the proportions of trees, shrubs and herbaceous plants as well as the soils chemical and physical characteristics [63].

Below-ground primary production (BPP) was also found to vary widely within savannas (Table 5) ranging from 1.12 t ha^{-1} yr^{-1} in Calabozo (Venezuela) to 43.18 t ha^{-1} yr^{-1} in Lamto 2 (Ivory Coast). The highest values were found again in Ivory Coast savannas which roughly doubled the values of the drier Burkina Faso sites and were five fold the value of the Venezuelan sites (Table 5). The West Africa and Venezuela values differed significantly as well as Venezuelan and Sudanese West Africa savannas (Mann-Whitney Ua = 0, z = 3.19, P one tailed = 0.0007, P two tailed = 0.0014, and Fig. 3).

Table 5. Net primary production (t ha^{-1} yr^{-1}) of burned savannas

Sites	APP	BPP	TPP	A/B	References
West Africa Sudanese					
Nazinga 1	3.40	10.75	14.15	0.32	[12]
Nazinga 2	3.51	13.95	17.46	0.25	
Nazinga 3	5.39	13.27	18.66	0.41	
Ouango-Fitini 1	6.41	18.46	24.87	0.35	[12]
Ouango-Fitini 2	5.02	22.09	27.11	0.23	
West Africa Guinean					
Lamto 1	7.98	25.00	32.98	0.32	[12,64]
Lamto 2	7.33	43.18	50.51	0.17	
Lamto 3	10.36	25.95	36.31	0.40	
Lamto 4	9.71	34.04	43.75	0.28	
Lamto 5	7.05	20.42	27.47	0.35	
Lamto 6	9.08	17.96	27.04	0.51	
Lamto 7	7.11	12.65	19.76	0.56	
Venezuela					
Calabozo 1	1.75	1.61	3.36	1.08	[65]
Calabozo 2	3.51	2.92	6.43	1.20	[65]
Jusepín 1	2.99	5.80	8.79	0.52	[66]
Calabozo 3	5.70	2.27	7.97	2.51	[67]
Calabozo 4	1.98	2.29	4.27	0.87	[67]
Calabozo 5	6.35	1.20	7.55	5.29	[68]
Puerto Ayacucho	3.84	1.95	5.79	1.97	[69]
Dos Caminos	4.50	2.50	7.00	1.80	[70]
Cabruta 1	0.56	1.41	1.97	0.51	[71]
Cabruta 2	2.92	9.05	11.97	0.32	[72]
La Iguana 1	4.04	2.01	6.05	2.00	[40]
La Iguana 2	4.06	2.17	6.23	1.87	[40]
Calabozo 6	5.20	1.12	6.33	4.64	[66]
Calabozo 7	5.45	1.33	6.78	4.10	[66]

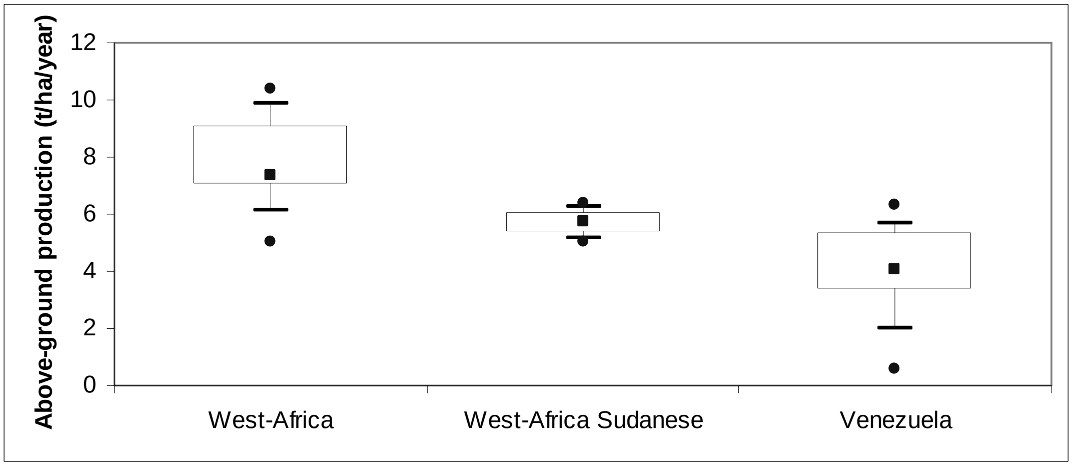

Figure 2. Above-ground primary production of the grass layer in 14 Venezuelan, 12 West African, and 5 West African Sudanese vegetation stands.

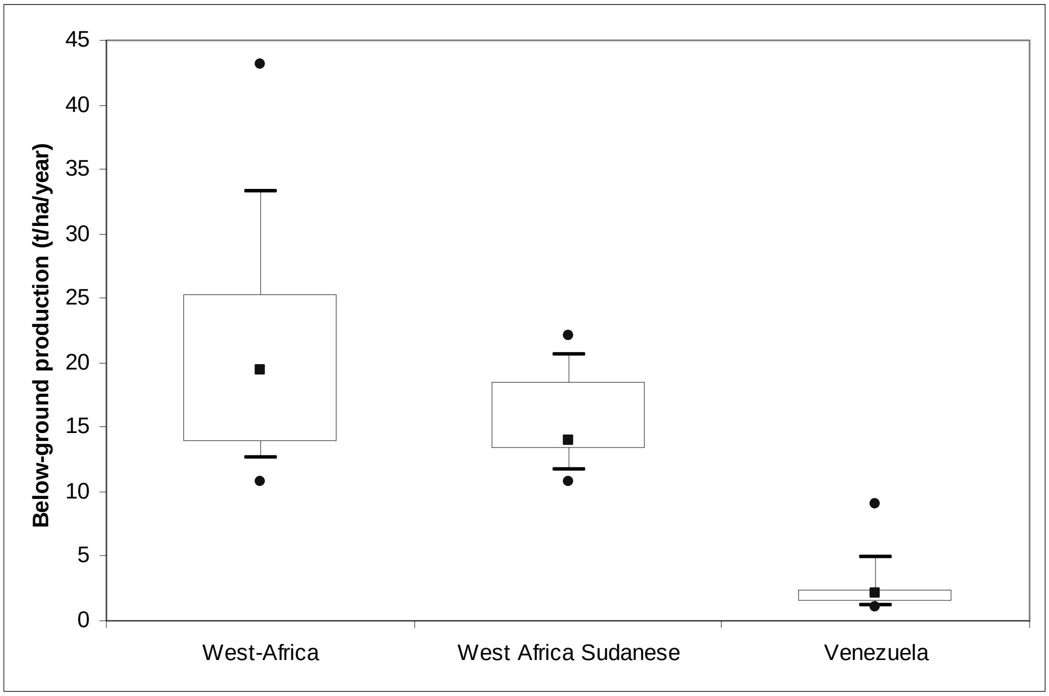

Figure 3. Below-ground primary production of the grass layer in 14 Venezuelan, 12 West African and 5 West African Sudanese vegetation stands.

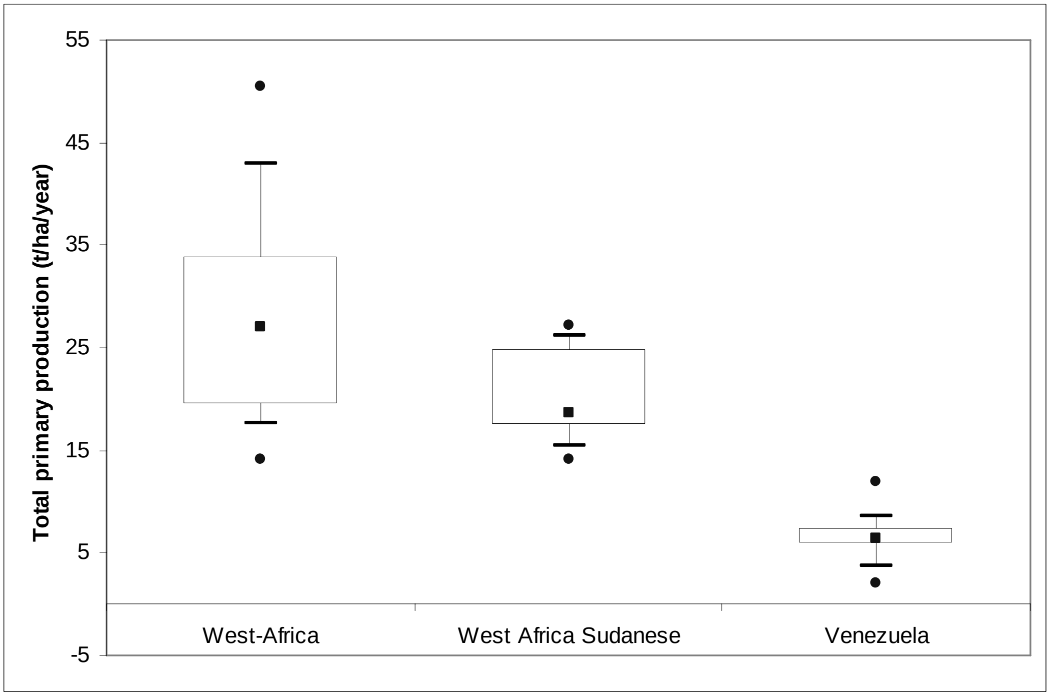

Figure 4. Total primary production of the grass layer in 12 West African (1), 14 Venezuelan (2), and 5 West African Sudanese (3) vegetation stands.

Overall, the total primary production (TPP) in the studied savannas ranges from less than 3.36 to over 50 t ha^{-1} yr^{-1}, distributed in less than 1 to almost 10 for the APP and just more than 1 to above 43 for the BPP (Table 5), these values are consistent with those presented by Grace et al. [4] for different savannas around the world (14.4 t ha^{-1} yr^{-1}). Total primary production in Venezuelan savannas was lower than in West Africa and also than in Sudanese West African savannas (Fig. 4).

The shoot/root ratios of primary production (A/B) were not much different in the West African savannas (Burkina Faso and Ivory Coast), ranging from 0.17 to 0.56, whereas in the Venezuelan savannas the values were more heterogeneous with a range from 0.32 to 5.29 (Table 5 and Fig. 6). Tested with a Mann-Whitney test, the value differed between Venezuela and West Africa (Ua = 157, z = -3.73, P one tailed = 0.0001, P two tailed = 0.0002) and between Venezuela and Sudanese West Africa (Ua = 67, z = -2.92, P one tailed = 0.0018, P two tailed = 0.0035, and Fig. 5).

The capacity of tropical grasses to accumulate below-ground carbon has been always well emphasized [66,72,73], the A/B ratio, in turn, is affected by factors associated to root development such as soil fertility, soil texture and structure and water availability. In the case of *Trachypogon* savannas, the

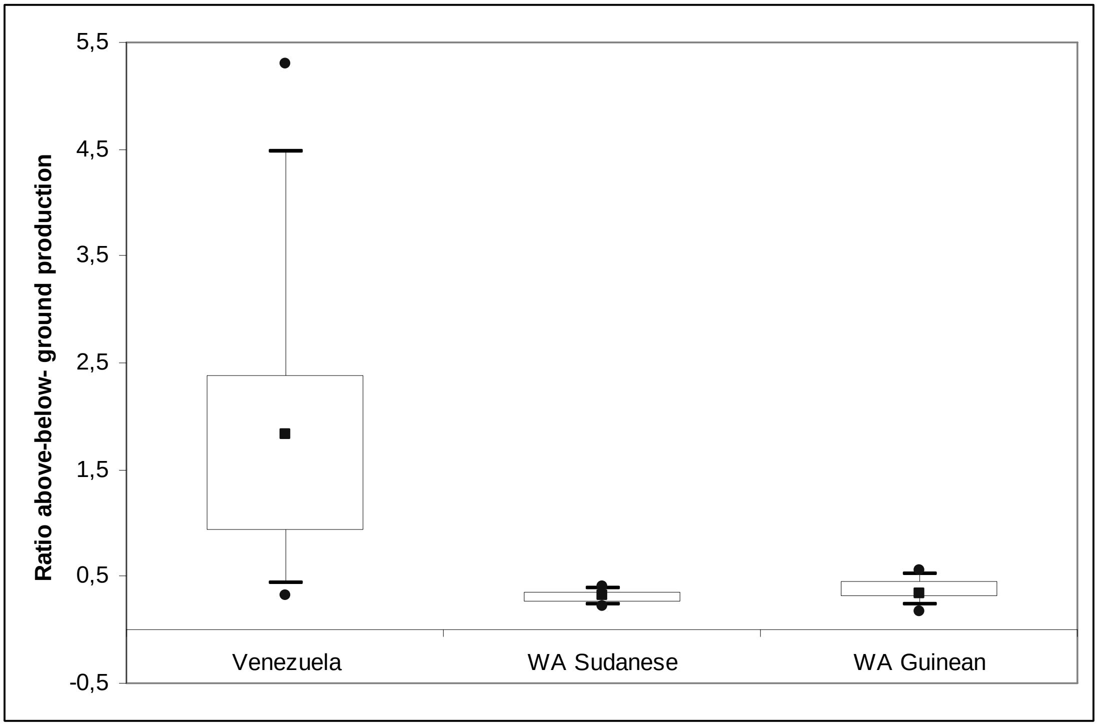

Figure 5. Above/below production ratio of in 14 Venezuelan, 12 West African vegetation and 5 West African Sudanese vegetation stands.

relatively high ratios (Fig. 5) of assimilate partitioning between shoots and roots (A/B) does not correspond to the nutrient stress-tolerant strategy proposed by Chapin [74] for wild plants growing in unfertile soils. On the other hand, in the more fertile soils of Lamto, on the contrary, underground biomass primary production was higher (Table 5). So, this trait may be better explained in terms of an adaptation or African grass species to both violent and recurrent vegetation fires and herbivory. Although, fires are more violent in Guinean savannas they do not differ from Sudanese ones regarding A/B ratio (Mann-Whitney test: Ua = 22, z = -0.65, P one tailed = 0.2578, P two tailed = 0.5157).

Nitrogen cycling in well drained savannas

The main soil characteristics of the studied sites at Lamto and La Iguana are presented in Table 6.

Main nitrogen inputs and outputs in the studied savannas

Atmospheric depositions (wet and dry deposition)

Anthropogenic activities (e.g. industrial, agricultural, etc) and natural biochemical processes (e.g. denitrification, reduction, oxidation, etc) are the main source of organic and inorganic compounds that are emitted to the atmosphere. In savannas, both these sources of N are important, and ash produced by fires *in situ* or in nearby areas can be deposited as dry deposition or washed out from the atmosphere and dissolved in the rain. In this way, precipitation can return nutrients lost by fires and other volatilization processes to the soil. Inorganic inputs of N from bulk precipitation are relatively low in savannas, unless the savanna is located near an industrial or polluted area. Mineral nitrogen inputs by precipitation in Venezuelan savannas ranged from 2.2 Kg N ha^{-1} yr^{-1} in savannas of Calabozo to 6.2 Kg N ha^{-1} yr^{-1} in a place more distant from urban activities at Estación Experimental, La Iguana (Table 7) [40,75]. This precipitation input in N is very similar to the value presented for savannas of *Loudetia* located at comparable geographical latitude (Fig. 1) at Lamto, Ivory Coast, Africa (1.3-2.3 Kg NO_3 ha^{-1} yr^{-1} and 3.0 Kg NH_4 ha^{-1} yr^{-1}) according to Villecourt and Roose [41]. Information on organic N-sources in Trachypogon savannas located in Central, Venezuela is almost non-existent, whereas for Lamto savannas these have been reported to be as much as 14.5 Kg ha^{-1} yr^{-1} [41,42]. In general typical mineral N inputs in Africa are reported to be very low [76].

Table 6. Main soil characteristics of the studied sites at La Iguana (Venezuela) and Lamto (Ivory Coast).

Station	Depth, cm	pH	C g kg^{-1}	N g kg^{-1}	C/N	Silt-clay g kg^{-1}
La Iguana*	0-20	5.65	10.0	0.17	58.8	67
	20-50	5.80	5.7	0.20	28.5	63
Lamto**						
Savanna of *Loudetia*	0-10	5.1-6.7	7.5-9.0	0.55-0.66	13.6	257***
	10-30	5.1-6.3	5.3-6.1	0.47-0.57	11.3-10.7	190***
	30-50	5.1-6.3	3.4-4.8	0.42-0.55	8.1-8.7	140***
Savanna of *Andropogon*	0-10	5.1-6.7	7.5-9.0	0.55-0.66	13.6	265***
	10-30	5.1-6.3	5.3-6.1	0.47-0.57	10.7-11.3	265***
Savanna Protected from fire	0-10	5.1-6.7	10.1-12.1	0.62-0.97	12.5-16.3	-
	10-30	5.1-6.4	7.1-8.8	0.55-0.89	9.9-12.9	-
	30-50	5.1-6.55	7.0-7.2	0.56-0.85	8.5-12.5	-

* Modified from Chacón, 1988[40]; ** Modified from Abbadie, 1983[37]; ***Mean values from Bonvallot et al. [77].

Biological nitrogen fixation

In savannas yearly fires volatilize up to 19-30 % of the N required for the net primary production of savanna herbaceous vegetation [8,28]. N volatilized by fires and nitrogen losses due to leaching and erosion are not compensated for by the scarce inorganic N inputs from precipitation, mentioned above [8]. This situation could cause a progressive reduction in the potential productive capacity of savannas in the absence of additional mechanisms of N input, apart from precipitation [27,37,40,78]. Consequently, N budgets must be balanced by biological N fixation. In general, N fixation can occur in savannas from three different sources: (1) rhizobium-legume symbiosis [79]; (2) organisms located in the rhizosphere, rhizoplane and endorhizosphere of grasses [80]; and (3) microbial crusts on the soil surface formed by cyanobacteria [81].

N fixation by rhizobium symbiosis

African and South American savannas are characterized by their great diversity of herbaceous and woody leguminous species and the proportion of leguminous tends to increase under moderate and over grazing. Previous studies indicated that, although most of the native leguminous species formed nodules, they seemed inactive or with reduced N fixation compared to cultivated legumes due to the soil acidity and poor base contents [78,82]. Furthermore, rhizobium-legume associations are of little importance in the plant canopy because of the small proportion of legumes [8]. At Lamto the effect of leguminous species on N cycling is also difficult to evaluate, the leguminous/total biomass ratio rarely exceeding 1 % [37,42]. It seems that tropical species show a low specificity to rhizobium strains compared with that of temperate species, resulting in a less efficient system. Therefore, this mechanism of N fixation seems to be less crucial for the nitrogen economy of savannas than the other N-fixing mechanisms mentioned above.

N-fixation by organisms located in the rhizosphere, rhizoplane and endorhizosphere of savanna grasses

Nitrogen fixation by organisms associated with the rhizosphere, rhizoplane and endorhizosphere could be an important source of available N in nutrient-poor soils of savannas. Estimates of nitrogen fixation by the acetylene reduction method (nitrogenase activity, NA) in the soil-plant system were 13.7 and 7.8 kg ha^{-1} yr^{-1} for burned and protected plots [28], respectively in savannas of *Trachypogon plumosus* and *Paspalum carinatum* located at Estación Experimental La Iguana, Central Venezuela (Table 7). Apart from *Trachypogon*, other plant species were found in very small numbers, such as the legumes *Phaseolus linearis* and *Cassia hispidula*, both with small nodules (less than 5 mm), pink in the inside and testing positive for NA.

Balandreau and Villemin [43] and Balandreau [44], using the same experimental method, obtained similar values of NA in *Loudetia* and *Andropogon* savannas (12 kg ha^{-1} yr^{-1} and 9 kg ha^{-1} yr^{-1}, respectively) in the Ivory Coast (Africa) (Table 7).

These reports make clear that N_2 fixation mediated by leguminous symbionts is relatively low as compared to the activity of free-living organisms associated with the grass roots. During the dry season, the low water availability in savannas could be a major limiting factor for microbial and NA activity. In burned plots NA activity is positively correlated with rainfall and soil moisture, whereas the same correlation was poorer and barely significant for the protected plots [28]. At La Iguana NA was always higher in the burned plot than in the protected plot, although the differences are slightly smaller. In the Venezuelan protected plot; the increase in NA in the dry season indicates the effect of rhizosphere conditions (moisture content, exudates, pH) on associated organisms.

N-fixation by microbial crust system

Taking into account the microbial crust cover and NA measurements, N_2 fixation by microbial crusts can be estimated to be 2.4 and 4.0 kg $ha^{-1}yr^{-1}$ in burned and protected *Trachypogon* savannas respectively (Table 7) [28]. However, the calculated contribution of N_2-fixing organisms in these crusts to N-cycling could differ from the earlier estimates due to the close relationship between the NA and the micro-environmental conditions at the moment of sampling. In any case, fixation should be less than 13.5 kg $ha^{-1}yr^{-1}$, a value which would be met if the maximum NA recorded was maintained during the 214 days that cyanobacteria remained active. Balandreau [44] for *Loudetia* savannas at Lamto have estimated a nitrogenase activity of 21 g ha^{-1} d^{-1} corresponding about 2 kg $ha^{-1}yr^{-1}$ during the period that crusts remained active (Table 7).

Moisture content in the microbial crusts strongly influences NA activity, which is limited to the rainy season. Furthermore, sampling was done on the surface soil where N-fixing bacteria are most active. During the dry season no NA was recorded in *Trachypogon* savannas, even after 24 hours of crust re-wetting. This could indicate that cyanobacteria are very active and responsible for N fixation during the wet season, whereas between rainy seasons they are dormant due to the severe drying of the soil. It appears that the soil system needs a long period of continuous rehydration to restart N_2-fixation activity.

Nitrogen outputs

Losses by fires

As previously noted, burning of vegetation during the dry season is the rule in savannas [83,84]. This factor is supposed to have been pivotal for the origin and maintenance of savannas and since behaves like a selective force which maintains the dominance of fire-tolerant species. As regards nutrient cycling, fires cause rapid mineralization and loss of nutrients. In the case of gaseous elements, like N and S, losses occur by volatilization and the spread of ashes, whereas in the case of sedimentary elements, like P and bases, losses by fire are due simply to the spread of ashes [9,27].

After the passage of the fire more than 90-95 % of the herbaceous aerial cover is lost, and most of the organic elements are destroyed in the form of CO, CO_2, NO and NO_2. In Trachypogon savannas losses of 8.2 kg N $ha^{-1}yr^{-1}$ have been measured [78], whereas at the more fertile soils of Lamto Experimental Station losses of 17 and 23 kg N $ha^{-1}yr^{-1}$ have been reported for *Loudetia* and *Andropogon* savannas respectively (Table 7) [37]. The higher N losses from Lamto savannas are in good agreement with their higher above-ground primary production (Table 8).

Nitrogen losses by leaching

Unlike agricultural ecosystems, the loss of nitrogen by internal drainage is relatively small in well-drained savannas, which is understandable since the water-soluble levels of N forms are always scarce, except perhaps at the beginning of the rainy season when substantial organic matter decomposition occurs. The losses of nitrogen in the savannas of Estación Experimental La Iguana in Guarico Central were estimated at 2.1 kg N kg $ha^{-1}yr^{-1}$ [78], whereas for a *Loudetia-Andropogon* savanna at Lamto, Ivory Coast, 5.6 kg N $ha^{-1}yr^{-1}$ was reported to leave the system through internal drainage (Table 7), mostly in organic form [41,42]. In savanna ecosystems information on nutrient losses by leaching is scarce and perhaps related to methodological inconveniences for designing and installing an effective system to catch leachates. As a consequence, more accurate measures are still needed.

Denitrification and emissions of NO and N_2O

As a rule, the NO_3 pools in the soils of the tropical savannas of South America and Central Africa are low, which means that the rates of nitrification are also negligible; nonetheless the levels of the intermediate NH_4 are significant. Therefore, the losses by denitrification in savannas should be insignificant due to the low levels of nitrate and organic matter and the acidic pH of the soils [42]. In a recent review Bustamante et al. [10] presented values of N emissions in savannas (NO and N_2O) which ranged from 0.5 to 4.0 kg ha^{-1}. Even so, soil emissions of NO from tropical savannas are still uncertain [10].

N internal cycling

N uptake by savanna plants

Information about N uptake for primary production in savannas is scarce when compared to production data. Comprehensive studies on N cycles in *Trachypogon* savannas estimated values of 43.6 and 43.0 kg N ha^{-1} yr^{-1} for the N uptake required for NPP in the unburned and burned savannas, respectively (Table 8). Other estimates from the maximum standing crop and average N concentrations in burned savannas of Calabozo, Guarico, Venezuela gave uptake values of 11.8-24.0 kg N ha^{-1} yr^{-1} [85]. In the more productive Lamto savannas, Abbadie [37] reported N uptake values of 74 and 54 kg N ha^{-1} yr^{-1} for the *Loudetia* and *Andropogoneae* savanna respectively (Table 8).

N released by decomposition and mineralization processes

Soil organic matter contents in *Trachypogon* savannas are in general very low (Table 6), in keeping with the low primary production of these savannas (Tables 5). The high temperatures and relatively abundant rainfall in tropical regions result in a substantial rate of OM decomposition, particularly in well-drained savannas. Studies of decomposition rates of organic matter and N mineralization in *Trachypogon* savannas have demonstrated that decomposition rates show a seasonal trend, with the highest rates occurring in the rainy season in accordance with a higher water availability and microbial activity in the soil profile.

N released by decomposition processes

Table 8 presents the rates of disappearance of above-ground organic matter (standing dead and litter) and the amounts of N released during the decomposition processes in burned and unburned *Trachypogon* savannas respectively. At La Iguana Experimental Station, above-ground organic matter decomposition ranged between 2.6 and 2.7 t ha^{-1} yr^{-1} for unburned savannas, and 0.5 and 0.7 t ha^{-1} yr^{-1} for burned savannas [78]. The differences are related to the slow accumulation of dead material due to periodical fires in the burned savannas, that in turn reduce the amount of organic matter that can be decomposed by biophysical factors (temperature, humidity, microorganisms, meso- and microfauna). In the same studies, N released from dead leaves (Table 8) ranged between 5.6 and 5.9 kg ha^{-1} yr^{-1} (unburned savannas) and 1.4 and 1.7 kg ha^{-1} yr^{-1} (burned savannas). These amounts accounted for 6-7% and 13-17% of the N taken up by plants for primary production in burned and unburned savannas respectively. At Lamto, values appeared within the range

Table 7. N inputs, and outputs (kg N ha^{-1} yr^{-1}) in savannas of Lamto and La Iguana.

	La Iguana Unburned	La Iguana Burned	Lamto Protected	Lamto *Loudetia* Burned	Lamto *Andropogon* Burned
N Inputs					
Precipitation	6.2	6.2	19.0*	19.0*	19.0*
N_2 fixation soil-plant system	7.8	13.7	10.0	12.0	9.0
N_2 fixation microbial crusts	4.0	2.4	2.0	2.0	2.0
Σ inputs	**18.0**	**22.3**	**31.0**	**33.0**	**30.0**
N Outputs					
Fire	0	8.2	0	17.0	23.0
Leaching	2.1	2.1	5.6	5.6	5.6
Σ outputs	**2.1**	**10.3**	**5.6**	**22.6**	**28.6**

* Include organic-N

Table 8. Above and below ground primary production, net primary production-N and above OM matter decomposition and N released from decomposition-mineralization processes in savannas of Lamto and La Iguana.

Location	Aboveground biomass (Mg ha^{-1} yr^{-1})	Belowground biomass (Mg ha^{-1} yr^{-1})	Total biomass (Mg ha^{-1} yr^{-1})	Total N uptake (kg ha^{-1} yr^{-1})	Aboveground OM disappearance (Mg ha^{-1} yr^{-1})	N released (decomposition/ mineralization) (kg ha^{-1} yr^{-1})
La Iguana*						
burned	4.00	2.17	6.17	43.0	0.5-0.7	1.4-1.7
Unburned	4.40	1.38	6.08	43.6	2.6-2.7	5.6-5.9
Lamto**						
Andropogoneae burned	12.26	14.42	26.68	74.0	0.68	9.4
Loudetia burned	10.28	14.79	25.07	54.0	1.06	3.4
Loudetia unburned	14.31	18.57	32.88	85.0	18.84	5.3

obtained at La Iguana for both parameters (organic matter disappearance and N release), except in the savanna of *Loudetia* unburned which had long been protected from fire, where the great accumulation of dead material significantly increased the O.M. disappearance by biophysical factors such as humidity, microorganisms and soil fauna (Table 8).

Soil N: NO_3 and NH_4 forms. Release of N by mineralization

The total N concentrations of savanna soils can be very variable, from less than 100 mg N kg^{-1} soil in sandy soils to values above 2000 mg N kg^{-1} soil in more clayey and silty soils [85]. The concentrations are related to the local abundance of leguminous species and frequency of fire [28,40]. In general, water-soluble (readily available) or mineral N forms in well-drained *Trachypogon* savannas may reach around 30 to 40 mg N kg^{-1} soil, and within the mineral forms, ammonium (NH_4) is more abundant than nitrate (NO_3). N mineralization was found to be insignificant for a Venezuelan Inceptisol of IES after 21 days of laboratory incubation [86], whereas in a savanna on Ultisols in Central Guarico, equal mineralization rates were found in macro and micro-aggregates in the rainy season (12.7-13.2 mg N kg^{-1} soil $month^{-1}$, [87]).

At Lamto, on *Loudetia-Andropogon* seasonal savannas, only a small fraction (5 kg ha^{-1} yr^{-1}) of the nitrogen content of the gramineous component for an annually burned savanna enters through mineralization of the soil organic matter [45,88]. Since fire destroys almost all the epigeous component, most of the nitrogen cycled comes from the N stored in dead roots (40 kg N ha^{-1} yr^{-1}).

N associated with soil fauna activities

In *Trachypogon* savannas and using a conservative estimate of earthworm population density, it has been estimated that 3 and 34 kg ha^{-1} yr^{-1} of inorganic N in the savanna and introduced pasture respectively may be released in fresh casts [89]. If underground and above ground cast production are taken into consideration e.g. 14 and 114 Mg ha^{-1} for the natural and the introduced-pasture savanna respectively, then a significant contribution to the N budget (internal recycling) in those ecosystems derives from deposition of casts.

Termites are recognized as the most important decomposers in tropical forest and savannas, strongly affecting soil organic matter and nutrient dynamics. The role of termite activity in the nitrogen economy in savannas is more difficult to assess; in general an increase in N content has been reported in mounds (that act as hotspots) compared with the associated soils [86,90]. The presence of hotspots of nutrients may affect ecosystem processes on certain spatial and temporal scales [91]. Also associated to *Nasutitermes* in South American savannas has been reported the existence of N-fixing bacteria in termite guts [92,93].

Microbial forms of N

The microbial biomass (MB) mediates the transformation (mineralization-immobilization) of biogenic nutrients (C, N, P, S) between the inorganic and organic forms; therefore it plays an important role in nutrient cycling. It also acts as an important sink for plant nutrient conservation and utilization in tropical savannas. In the soils of the Orinoco savannas, in general, the contents of soil biomass carbon (C-MB) are low (100- 200 mg kg^{-1}) which is in agreement with the low soil organic matter content of the soils [85]. In Venezuelan savannas the microbial biomass nitrogen (N-MB) followed a similar pattern to the C-MB, e.g. low values (around 10-30 mg kg^{-1}) associated with the low levels of organic matter. C-MB values presented for Brazilian Cerrado soils are much higher (250-850 mg kg^{-1}) with a peak for microbial activity occurring at the beginning of the rainy season [94]. Little information has been published for microbial biomass in Lamto savannas, however Vanlauwe et al., [95], working with 13 soils from moist West African savannas, reported values of microbial carbon ranging from 22 to 210 mg C kg^{-1} and from 3.4 to 46.2 for N-MB, while Jouquet et al., [96] analyzing the effects of fungus-growing termites on soil microbial communities, reported values of soil microbial biomass nitrogen of 12-20 mg kg^{-1}.

Nitrogen budgets

As previously stated, complete nutrient budgets for world savannas are almost non-existent. Technical difficulties and the need for long-term studies are the main hurdles to overcome. With the information presented above on the main N inputs and outputs, a comparative preliminary report on N budgets in well-drained savanna at Lamto, Ivory Coast and La Iguana, Venezuela is presented (Table 7). Particular emphasis was given to biological inputs through symbiotic association; we are aware that an accurate budget is difficult to assess, particularly, if it rests on assumptions of insufficient understanding, or in processes difficult to accurately be measured such as: N inputs via N fixation, N-leaching and N losses via trace gases (especially NO).

In our study at La Iguana the N budget was positive even for burned savannas, since losses, including N volatilization through fire and leaching (10.3 kg ha^{-1} yr^{-1}) were balanced by the inputs in rainfall and biological fixation, if we include the maximum values of N emission (NO+ N_2O) presented by Bustamante et al. [10] for the llanos region (4.0 kg ha^{-1} yr^{-1}), the budget is still positive. Forty per cent of the total N incorporated into the system by total net primary production comes from internal recycling; the rest is extracted by roots from the soil store, that, in turn, has originated from mineralization-decomposition processes of aerial and subterranean biomass, biological activities and finally from precipitation. The amount of N required for net primary production reached 43.6 and 43.0 kg $ha^{-1}yr^{-1}$ in the protected and burned plot, respectively (Table 8) in *Trachypogon* savannas, whereas in the African savannas values were double, i.e. 85.0 and 74.0 for protected and burned savanna, respectively (Table 8). According to their primary production levels, the lower fixation values for microbial crusts represent 6 % of the N needed for annual plant primary production in the burned *Trachypogon* savanna and 9 % in the protected savanna. In African savannas the contribution of the microbial crust was much lower. N fixation mediated by free-living organisms associated with grass roots can account for a very large proportion of the N input in the protected, and in the burned savanna. Overall, out of the total amount of N required for the net primary plant primary production in the Venezuelan burned savanna, free-living organisms could be contributing 37 %, compared with 27 % for protected savanna. In burned *Trachypogon* savanna dinitrogen fixation (16.1 kg ha^{-1} yr^{-1}) exceeds the volatilization loss (6.2 kg ha^{-1} yr^{-1}) and budgets are positive even if including the maximum values of N emission (NO+ N_2O). In the African savanna analyzed, symbiosis and the input in precipitation exceeded the losses due to leaching in protected savanna, whereas in burned savanna deposition inputs compensate for the fire loss. Therefore, and addressing the question presented in the introduction: The estimated amounts of dinitrogen fixation and deposition inputs seem to be enough to maintain plant primary production under periodical fires in both African and South American savannas here analyzed.

Final conclusions

Above ground primary production (APP) is very variable in savannas, in the three regions studied figures range from 0.56 (Cabruta site, Venezuela) to 10.36 t ha^{-1}yr^{-1} (Lamto 3 site, Ivory Coast). The higher production was observed in Ivory Coast savannas with values that doubled those of Burkina Faso and Venezuela. The higher production in Ivory Coast as compared to Venezuelan savannas cannot be explained by precipitation since it that does not differ greatly between them. Therefore, it is more likely related to soil fertility that is higher in Ivory Coast sites (Table 6) respect Venezuelan savannas. However, the lower precipitation in Burkina Faso can account for the biomass differences between Sudanese (Burkina Faso) and Guinean (Ivory Coast) savannas.

The above ground primary production of savannas in Venezuela did not significantly differ from that in Burkina Faso, which suggests a major role of other factors, apart from precipitation. As a rule, the drier the climate, the closer the relationship between precipitation and net primary production, however, the link is a complex one, involving the total amount of rain, the seasonal distribution, the influence of the precipitation of the preceding year on the water content of the topsoil, and an additional effect of the ligneous cover density.

Similarly, the below-ground primary production (BPP) shows a large range from 1.12 t ha^{-1}yr^{-1} in Calabozo (Venezuela) to 43.18 t ha^{-1} yr^{-1} in Lamto 1 (Ivory Coast). The highest values were found again in Ivory Coast savannas, with twice the values of the drier Burkina Faso sites and five fold the values of the Venezuelan sites. In the case of the underground primary production, there were differences between the Venezuelan and Burkina Faso sites with a much higher primary production in the latter. Overall, the total mean primary production (TPP) in the studied savannas reached a value of 14.80 distributed in 5.06 Mg ha^{-1} yr^{-1} for the APP and 9.74 Mg ha^{-1} yr^{-1} for the BPP.

Therefore, addressing the questions presented in the introduction:

There is a strong difference in production (aerial and subterranean) between Ivory Coast and Venezuelan savannas that corresponds to the dominance of *Andropogon sp.* instead of *Trachypogon sp.* This information confirms previous results addressing *Trachypogon* savannas as one of the lowest productive in the world.

With the information presented on the main N inputs and outputs, a comparative preliminary report on N budgets in well-drained savanna at Lamto, Ivory Coast and La Iguana, Venezuela is presented. The N budget was positive even for burned savannas, since losses, including N volatilization through fire and leaching were balanced by the inputs in rainfall and biological fixation. N fixation mediated by free-living organisms associated with grass roots and microbial crusts can account for a very large proportion of the N input in the protected, and in the burned savanna. In response to the question posed in the introduction: The estimated amounts of dinitrogen fixation and deposition inputs seem to be enough to maintain plant production under periodical fires in both African and South American savannas analyzed here. Consequently, data support the idea that the vegetation in the natural savanna has needed to evolve under this constraint which imply a positive or near to steady-state nitrogen budget.

Acknowledgements

The first author (Danilo López-Hernández) wishes to thank IRD (Institut de Recherche pour le Développement) for the financial support and possibility of bibliographic researching during stays as academic visitor. This study was supported with grants from Consejo de Desarrollo Científico y Humanístico (CDCH) and Consejo Nacional de Ciencia y Tecnología (CONICIT).

In memoriam of Professor Maxime Lamotte, pioneer of tropical ecological studies, and an enthusiastic promoter of: African and South American ecological comparisons.

References

1. Hétier, J.M., and López, R. 2005, Tierras llaneras de Venezuela. Editorial Venezolana, Mérida, Venezuela.
2. Nix, H.A. 1983, Bourliere, F (Ed), Ecosystems of the World, Tropical Savannas, Elsevier Scientific Publishing, Amsterdam, pp 37-61.
3. Grace,J., San José, J.J., Meir, P., Miranda, H., and Montes, R. 2006, J. Biogeogr., 33, 387.
4. Sarmiento, G., and Monasterio, M. 1975, Tropical Ecological Systems, Golley, F.B., and Medina, E., (Eds), Ecological Studies 11, Springer Verlag, 223.
5. Sankaran, M., Hanan, N. and others 2005, Nature, 438, 846.
6. San Jose, J.J., Montes, R., and Rocha, C. 2003, Forest Ecol Manag 184, 17.
7. Beerling, D., and Osborne, C. 2006, Global Change Biology, 12, 2023.

8. Chacón, P., Lamotte, M., and López-Hernández, D. 1992, Comptes Rendus de l'Academie des Sciences, Paris, t. 315, série III, 209.
9. Hernández-Valencia, I., and López-Hernández, D. 2002, Revista de Biología Tropical 50, 1013.
10. Bustamante, M.M.C., Medina, E., Asner, G.P., Nardoto, G.B., and García-Montiel, D.C. 2006, Biogeochem. 79, 209.
11. Rippstein, G., Amezquita, E., Escobar, G., and Grollier, C. 2001, Agroecología y Biodiversidad de las Sabanas en los Llanos Orientales de Colombia. G. Rippstein, G. Escobar and, F. Motta (Eds) CIAT, Colombia, 1.
12. Fournier, A. 1991, Phénologie, croissance et production végétales dans quelques savanes d´Afrique de l´Ouest. Editions de l´ORSTOM. Collection Etudes et Thèses. Paris. p 312.
13. Van Chi Bonnardel R. 1973, Grand atlas du continent africain. Jeune Afrique, Paris, 335 p.
14. Berrio, J.C., Hooghiemstra, H., Behling, H., Botero, P. and van der Borg, K. 2002, The Holocene 12: 35.
15. López-Hernández, D. 1995, Global land use change: A perspective from the Columbian Encounter. Turner, B., Gómez-Sal, A., González Bernáldez, F. and Di Castri, F. (Eds). Consejo Supremo de Investigaciones Científicas (CSIC). 405.
16. Brossard, M., and López-Hernández, D. 2005, Natures Sciences et Sociétés 13, 266.
17. Perles, C., 1977. Préhistoire du feu. Masson, Paris, New York, Barcelone. p 180
18. Sarmiento, G., 1984. The ecology of neotropical savannas. Harvard Univ. Press. Cambridge.
19. San José, J.J., and Fariñas, M. 1983, Ecol., 64, 447.
20. Devineau J.L., Lecordier C., Vuattoux R, 1984, Candollea, 39, 103.
21. Sawadogo, L., Tiveau, D., and Nygård, R. 2005, Agric Ecosystems Environ 105, 335.
22. López-Hernández, D., Hernández-Hernández, R.M., and Brossard, M. 2005, Interciencia, 30, 623.
23. López-Hernández, D., Hernández-Valencia, I., and Güerere, I. 2008, Bioagro, 20, 151.
24. Williams, D.G., and Baruch, Z. 2000, Biological Invasions., 2, 123.
25. Rondón, M.A., Acevedo, D., Hernández, R.M., Rubiano, Y., Rivera, M., Amézquita, E., Romero, M., Sarmiento, L., Ayarza, M., Barrios, E., and Rao, I. 2006, Carbon sequestration in soils of Latin America. Lal R, Cerri C, Bernoux M, Etchevers J, Pellegrino C (Eds.) Haworth Press Inc. New York. pp 213.
26. Frost, P.G.H., and Robertson, F. 1985, Determinants of tropical savannas. IVBS # 3. Walker B.H. (Ed)., IRL Press. pp 93.
27. Cook, G.D. 1994, Austral Ecology 19, 359.
28. López-Hernández, D., Santaella, S., and Chacón, P. 2006, European J Soil Biol 42, 43.
29. Cobo, J.G., Dercon, G., and Cadisch, G. 2009, Agric. Ecosyst. Environ. (2009), doi:10.1016/j.agee.2009.11.006
30. Baruch, Z. 2005, Interciencia, 30, 488.

31. López-Gutiérrez, J.C., Toro, M., and López-Hernández, D. 2004, Soil Biol Biochem., 36, 1675.
32. López-Gutiérrez, J.C., Toro, M., and López-Hernández, D. 2004, Agriculture & Environment 103, 405.
33. Kwa, C. 1987, Soc. Stud. Sci., 17, 413.
34. Lachenal, G. 2005, La Revue pour l'histoire du CNRS, 13, 1.
35. Milner, C., and Hughes, E. 1968, Methods for the measurement of primary production of grasslands, London, Blackwell Scientific Publications, IPB, Handbook No 6, 70p.
36. Singh, J.S., and Yadava, P.S. 1974, Ecol Monogr 44, 351.
37. Abbadie, L. 1983, Contribution à l´étude de la production primaire et du cycle de l´azote dans les savanes de Lamto (Côte d´Ivoire). Programme MAB savanes. Travaux des chercheurs de la Station de Lamto (Côte d´Ivoire). p 136
38. Long, S.P., García Moya, E., Imbamba, S., Kamnalrut, A., Piedade, M. Scurlock, J., Shen, Y., and Hall, D. 1989, Plant and Soil, 115, 155.
39. Marín, D., De Martino, G., Guenni, O., and Guedez, Y. 2001, Fourrages, 165, 89.
40. Chacón, P. 1988, Dynamique de la matière organique et de l´azote dans une savane à *Trachypogon* du Venezuela. PhD thesis. University of Paris VI.
41. Villecourt, P., and Roose, E., 1978. Ecol. Biol. Sol 16, 9.
42. Abbadie, L. 2006, Lamto Structure, Functioning, and Dynamics of a Savanna Ecosystem, Abbadie, L., Gignoux, J. Le Roux, J., Lepage, M., (Eds.), 255.
43. Balandreau, J., and Villemin, G. 1973, Rev. Ecol. Biol. Sol 10, 25.
44. Balandreau, J. 1975, Activité nitrogénasique dans la rhizosphère de quelques graminées. Thèse de doctorat es sciences naturelles, Université de Nancy I, p 159
45. De Rham, P. 1973, Rev, Ecol, Biol. Sol 10, 169.
46. Burkina Faso Atlas. 1998, Les Editions J.A. Paris, 62 p.
47. Gonzalez de Juana, C., Iturrales, J., and Picand, X. 1980, Geología de Venezuela y sus cuencas petrolíferas. Edic. Foninves, Caracas, Venezuela, 407p.
48. Schargel, R., and Gónzalez, R.A. 1973, Estudio Agrológico Preliminar. Ministerio de Obras Públicas. Caracas, Venezuela.
49. Fournier, A., Floret, Ch., Gnahoua, G.M. 2001, Végétation des jachères et succession post-culturale en Afrique tropicale. in FLORET Ch., PONTANIER R. (eds) La jachère en Afrique tropicale. Vol. II De la jachère naturelle à la jachère améliorée. J. Libbey Eurotext, 123.
50. San José, J.J., and Montes, R. 2001, Forest. Ecol. Manag., 150, 293.
51. López-Hernández, D., García, M. and, Niño, M. 1994, Journal Appl Ecol., 31, 303.
52. Brossard, M., López-Hernández, D., Lepage, M., and Leprun, J.C. 2007, Biol. Fertil. Soils 43, 437.
53. Josens, G. 1972, Études biologiques et écologiques des termites (Isoptera) de la savane de Lamto Pakobo (Côte d´Ivoire). PhD thesis. Free University of Brussels (ULB), Brussels.
54. López-Hernández D., Brossard, M., Fardeau, J.C., and Lepage, M. 2006, Biol Fert Soils 42, 207.

55. San José, J.J., Montes, R., Stansly, P.A., and Bentley, B.L. 1989, Biotropica 21, 353.
56. López-Hernández, D., Niño, M., Nannipieri, P., and Fardeau, J.C. 1989, Biol. Fert. Soils 7, 134.
57. Netuzhilin, Y., Chacón, P., Cerda, H., López-Hernández, D., Torres, F., and Paoletti, M. 1999, *Management of tropical agroecosystems and benefical soil biota*. Reddy, M.V. (Ed), Science Publishers Inc.: Enfield, NH, USA, pp. 291.
58. Lavelle, P. 1978, Les vers de terre de la savane de Lamto (Côte d´Ivoire): peuplements, populations, et fonction dans l´écosystème. PhD thesis. University of Paris VI.
59. Dash, M., and Patra, U.C. 1977, Rev. Ecol. Biol. Sol 14, 461.
60. Lavelle, P., Dangerfield, M., Fragoso., C., Eschenbrenner, V., López-Hernández, D., Pashanashi,B., and Brussard, L. 1994, The Biology Management of Tropical Soil Fertility. Woomer, O.L., Swift M.J. (Eds). TSBF: Wiley-Sayce. pp 137.
61. Jimenez, J.J., Moreno, A.G., Decaëns, T., Lavelle, P., Fisher, M.J., and Thomas, R.J. 1998, Biol. Fert. Soils 28, 101.
62. Araujo, Y., and López-Hernández, D. 1999, Biol. Fertil. Soils 29, 413.
63. Furley, P. 2006, Progress in Physical Geography, 30, 1.
64. Cesar, J. 1971, Etude quantitative de la strate herbacée de la savane de Lamto (Moyenne Côte d´Ivoire). Thèse de 3° Cycle, Botanique tropicale, Faculté de Sciences, Paris, 95 p.
65. Blydenstein,J. 1962, Bol. Soc. Venez. Cienc. Nat., 23, 139.
66. Hernández-Valencia, I. 1996. Dinámica del fósforo en una sabana de Trachypogon de los Llanos Altos Centrales. Ph.D. Thesis. Universidad Central de Venezuela. 183 p.
67. San José, J.J., and Medina, E. 1976, Bol. Soc. Venez. Cienc. Nat., 33, 75.
68. San José, J.J., and Medina, E. 1977, Trop. Ecol., 17, 113.
69. Guinand, L., and Sánchez, P. 1979, Productividad primaria, fenología y composición florística de un tipo de sabana situado en el Territorio Federal Amazonas. Venezuela.Trabajo Especial de Grado. Fac. Ciencias, Univ. Central Venezuela, Caracas, 172p.
70. Lourido, J., 1983. Diferencias en la partición de biomasa, nutrientes, diversidad y otras características de la vegetación entre seis sabanas del Estado Guarico. Trabajo Especial de Grado. Fac. Ciencias, Univ. Central Venezuela, Caracas.
71. Susach, F. 1984, Caracterización ecológica de las sabanas de un sector de los Llanos Centrales Bajos de Venezuela. Ph.D. Thesis. Universidad Central de Venezuela.
72. Scurlock, J.M., and Hall, D.O. 1998, Global Change Biol., 4, 229.
73. Fournier, A., 1987. Bull Ecol 18 (4), 409.
74. Chapin, F.S. III. 1980, Ann. Rev. Ecol. Syst. 11, 233.
75. Montes, R., and San José, J.J. 1989, Biogeochem, 7, 241.
76. Giller, K.E., Cadish, G., Ehaliotis, C., Adams, E., Sakala, W., and Mafongoya, P. 1997, Replenishing Soil Fertility in Africa. SSSA Special Publication no 51. pp 151.

77. Bonvallot, J., Dugerdil, M., and Duviard, D. 1970, La Terre et la Vie : Revue d'Ecologie Appliquée, 1970, (1), p. 3.
78. Chacón, P., López-Hernández, D., and Lamotte, M. 1991, Revue Écol. Biol. Sol 28, 67.
79. Izaguirre-Mayoral, M.L., Carballo, O., Flores, S., Mallorca, M.S., and Oropeza, T. 1992, Symbiosis 12, 293.
80. Medina, E., and Izaguirre, M.L. 2004, Trop. Ecol. 45, 87.
81. Isichei, A.O. 1981, Nitrogen cycling in West African ecosystem, Roswall, T. (Ed) Royal Swedish Academy of Sciences, pp 191.
82. Medina, E., and Bilbao, B. 1991, Modern Ecology: Basic and applied aspects. Esser, G., Overdieck D (Eds). pp 295. Elsevier Science Publishing. Amsterdam.
83. Vareschi, V. 1962, Bol. Soc. Venez. Cienc. Nat., 23, 9.
84. Vuattoux, R. 1976, Deuxième note. Ann. Univ. Abidjan, série C, tome XII, 35.
85. López-Hernández, D., and Hernández-Valencia, I. 2008, *International Commission on Tropical Biology and Natural Resources*, [Eds. Kleber Del Claro et al.]. *Encyclopedia of Life Support Systems* (EOLSS), Developed under the Auspices of the UNESCO, Eolss Publishers, Oxford ,UK.
86. López-Hernández, D. 2001, Soil Biol. Biochem. 33, 747.
87. Hernández-Hernández, R.M., and López-Hernández, D. 2002, Soil Biol. Biochem. 34, 1563.
88. Abbadie, L., Mariotti, A., and Menaut, J.C. 1992, Ecology 73: 608-613.
89. Decaëns, T., Rangel, A.F., Asakawa, N.,.and Thomas, R.J. 1999, Biol. Fertil. Soils 30, 20.
90. Lee, K.E. and Wood, T.G. 197, Pedobiologia 11, 376.
91. Jimenez, J.J., Decaëns, T., and Lavelle, P. 2006, Soil Biol. Biochem. 38, 1132.
92. Sylvester-Bradley, R., de Oliveira. L.A., and Gomez Bandeira, A. 1982, Social Insects in the Tropics. Jaisson P. (Ed) Villatanause, France, Université Paris XIII. 2, 236.
93. Bentley, B.L. 1984, J Insect Physiol. 30, 653.
94. Nardoto, G.B., and Bustamante, M.M.C. 2003, Pesquisa Agropecuaria Brasileira 38, 955.
95. Vanlauwe, B., Nwoke, O.C., Sanginga, N., and Merckx, R. 1999, Soil Biol. Biochem. 31, 1071.
96. Jouquet, P., Ranjard, L., Lepage, M., and Lata, J.C. 2005, Soil Biol. Biochem. 37, 1852.