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Impact of land management on soil macrofauna in the Oriental Llanos of Colombia

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Abstract

The effect of different types of land management on the soil macrofauna of the savanna has been assesed using the T.S.B.F. method. Macrofauna of the forest and savanna has a high density (4293 and 2830 ind.m^{-2}) and moderate biomass (13.6 and 15.3 g.m^{-2}). Traditional grazing significantly increase earthworm biomass but does not modify biomass (16.8 g.m^{-2}) and density (1971 ind.m^{-2}). Burning the savanna leads to a momentarily but important disruption of the soil fauna. After 6 months, soil macrofauna has regained its initial level. When stocking rate increase, contribution to biomass of different groups is modified. These results are probably due to the modification of the soil microclimate and to the imput of cow dung. Improved pastures have an important earthworm population (22.9 to 51.1 g.m^{-2}) composed of native species, and a high macrofauna diversity (26 to 32 units). This results from the improving of the quality of the organic matter brought to the soil (litter and cow dung). Annual high input cultivations results in a spectacular decrease, both quantitative and qualitative, in the invertebrate populations (3.2 to 4.3 g.m^{-2}, 429 to 592 ind. m^{-2} and 18 units). This phenomenon may be explained by the effect of the tilling of the soil, the fertilization and by the decrease of the soil organic matter.

Keywords: Soil macrofauna, earthworms, biomass, density, taxonomic richness, savanna, gallery forest, Colombia, land management.

Impact de la gestion de la terre sur la macrofaune des sols dans les Llanos Orientaux de Colombie.

Résumé

L'impact de différents types d'utilisation de la terre sur la macrofaune du sol de la savane a été évalué en utilisant la méthode T.S.B.F. La macrofaune de la forêt et de la savane possède une densité élevée (4293 et 2830 ind.m^{-2}) et une biomasse moyenne (13,6 et 15,3 g.m^{-2}). L'utilisation traditionnelle de la savane provoque une augmentation significative de la biomasse des vers de terre mais ne modifie pas la biomasse (16,8 g.m^{-2}) et la densité (1971 ind. m^{-2}). Le passage du feu entraîne une perturbation momentanée mais importante de la faune du sol. Après 6 mois, le sol a retrouvé une faune équivalente à celle qu'il possédait avant le feu. Si l'on augmente la charge animale, la contribution à la biomasse des différents groupes est modifiée. Ces résultats sont probablement liés à la modification du microclimat du sol et à l'apport de bouses de vaches. Les pâturages améliorés abritent une importante population de vers de terre (22,9 à 51,1 g.m^{-2}) composée d'espèces natives et une macrofaune riche en taxons (26 à 32 unités). Ceci est le résultat de l'amélioration de la qualité de la matière organique apportée au sol (litière et bouses de vaches). Les cultures annuelles fortement fertilisées montrent une diminution spectaculaire, quantitative et qualitative, des populations d'invertébrés du sol (3,2 à 4,3 g.m^{-2}, 429 à 592 ind.m^{-2} et 18 unités taxonomiques). Ce phénomène peut être expliqué par l'action du travail du sol, de la fertilisation et par la diminution de la matière organique du sol.

Mots-clés : Macrofaune du sol, vers de terre, biomasse, densité, richesse taxonomique, savane, forêt galerie, Colombie, gestion du sol.

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INTRODUCTION

The Eastern Llanos of Colombia are a broad area of savanna still poorly exploited through traditional cattle ranching. An intensification has recently been attempted in the most accessible areas. Various techniques are tested such as management of natural pastures or improved pastures, rotations of culture and improved pastures, intensive cropping. The sustainability and impact on soil quality of these techniques are still poorly known (Fisher *et al.*, 1992). The effect on soils of e.g., the introduction of african grasses, simplification of the plant community or different levels of stocking rates are totally ignored. The accelerated degradation of large areas of pastures in Amazonia puts ecologists in fear that the systems under study are neither sustainable nor conservative in biodiversity.

Among the numerous factors that determine the quality of soils, biological regulations, operated by soil macroorganisms (living roots and macroinvertebrates) may be determinant (Lavelle *et al.*, 1994). These systems play a key role in the conservation of soil fertility since they affect the physical and chemical properties of the soil, organic matter and nutrient cycling and plant growth (Lavelle *et al.*, 1994; Stork and Eggleton, 1992).

Macroinvertebrates have different effects on the processes that determine soil fertility. They regulate microbial populations responsible for the mineralisation and humification processes and consequently influence organic matter cycling and the release of nutrients assimilable by plants. Through their mechanical action on the soil, they contribute to the formation of stable aggregates which may protect a part of soil organic matter from a fast mineralisation and therefore constitute a nutrient reserve potentially available for plants. Macroinvertebrates can modify texture and physical properties of the soil in the upper horizons that they inhabit (Lavelle *et al.*, 1994). Macrofaunal activities may also favour plant growth (Spain *et al.*, 1992). The diversity and abundance of macroinvertebrate communities and the relative importance of major groups such as termites, earthworms and ants can therefore be used as indicators of soil quality (Stork and Eggleton, 1992).

The present study has been carried out at the research station of Carimagua (CIAT-ICA). Special attention was paid at testing the effect of a large variety of pasture management practices such as burning of the native savanna, introduction of african grasses (*Brachiaria decumbens*), and improvement with legumes (*Pueraria phaseoloides*), and different stocking rates. On the other hand, we tried to test the assumption that pastures create "green deserts" when installed at the expense of native forests or savannas.

MATERIALS AND METHODS

Characteristics of the study area

The research station of Carimagua (4°30′N, 7°30′W) is located in the phytogeographic unit of the "Altillanura Plana". In this area, vegetation comprises well drained savannas in the upland areas ("altos" and "planos") and gallery forests in the lowlying areas ("bajos").

The climate is subhumid tropical with an annual mean temperature of 26°C and precipitations of 2300 mm (CIAT's data, means of the years 1972-1992). Two seasons can be observed *i.e.*, a dry season with average monthly precipitations of less than 100 mm, from December to March, and a wet season with average monthly precipitations greater than 100 mm, from April to November.

Two types of soil can be found in the area of Carimagua *i.e.*, Oxisols (Tropeptic Haplustox Isohyperthermic) in the "altos" and "planos" and Ultisols (Ultic Aeric Plintaquox) in the "bajos". They have good physical properties (porosity, water retention) but present a great chemical poverty (CEC$<$5 mEq/100 g), acidity (pH$<$5), and a high level of aluminic saturation ($>$80%).

Choice of the sites

Sampling has been carried out on clay-silt oxisols during the rainy season, from May to August 1993.

Three different management options have been considered for the soil macrofauna, *i.e.*, traditional extensive cattle raising on natural pastures (sites III, IV, V, VI, VII), intensive breeding systems on improved pastures (VIII, IX) and high input cropping systems (X, XI). Sampling has been carried out in plots with natural vegetation and in other grazed or cultivated plots:

I. Gallery forest.

II. Savanna protected against fire and grazing for more than four years.

III, IV, V. Savanna burned and grazed with a low stocking rate (0.25 an./ha), sampled respectively 15 days (III), 6 months (IV) and one year (V) after the fire.

VI, VII. Savanna burned and grazed with moderate (VI) and high (VII) stocking rates (0.5 and 0.75 an./ha), 16 months after the fire.

VIII. 15 year-old *Brachiaria decumbens* pasture (1.67 an./ha) established on natural savanna.

IX. 15 year-old *B. decumbens* + Kudzu (*Pueraria phaseoloides*) pasture (1.67 an./ha) established on natural savanna.

X. 2 month high imput rice, first crop on a natural savanna.

XI. 8 month high imput cassava, in a 20 year-old plantation, implanted on a natural savanna.

Sampling method and data processing

Sampling has been done using the method recommended by the Tropical Soil Biology and Fertility programme (Lavelle and Pashanasi, 1989; Anderson and Ingram, 1993).

At each site, 10 samples of 25 cm × 25 cm × 30 cm were taken at regular 5 m intervals, along a line whose origin and direction had been chosen at random. A metallic frame was used to isolate soil monoliths which were dug out with a spade and divided into 4 successive strata (*i.e.*, litter, 0-10, 10-20, 20-30 cm). Each stratum was then carefully hand-sorted in a large 40 × 60 cm tray and macroinvertebrates were collected, killed and kept in 75% alcohol, except for the earthworms which were previously fixed in 4% formalin during 2 or 3 days.

Invertebrates were then identified among 57 broad taxonomic units (Orders or Families), counted and further grouped in 7 larger units, *i.e.*, earthworms, termites, ants, Coleoptera, Arachnida, Myriapoda and “other invertebrates”. Density and biomass of each of these 7 major groups has been determined. Biomass was further corrected because all invertebrates lose weight as a result of fixation in alcohol (19% for earthworms and termites, 9% for ants, 11% for Coleoptera, 6% for Arachnida and Myriapoda and 13% for the “other invertebrates”.

A principal component analysis (PCA) was performed with GraphMu and MacMul programs (Thioulouse, 1989; 1990) to compare invertebrates communities among the various types of land use, and to try to identify their determinant. Thirty nine variables have been used that describe macrofauna, physical and chemical soil properties, stocking rates and herbaceous vegetation characteristics. Sites X and XI were not considered in this analysis because information on soil characteristics was not available. Results between treatments have been compared with a Student test in order to point out significant differences.

All the results are a compilation of the 10 individual samples, except for site XI where only 4 samples had been taken.

RESULTS

Two factors accounting for 66,4% of the total variance have been extracted by the PCA (*fig.* 1, *table* 1).

Factor I explains 42.0% of variance. It may be defined as **the overall effect of vegetation.** Gallery forests are clearly separated from grassland, especially sites with minimum cover like savanna, 15 days after the fire or with high stocking rates. This factor characterizes soils with high silt content (63%), good porosity (60%), high aluminic saturation (88%) and high Mg (0.2 mEq/100 g) and K (0.1 mEq/100 g) contents. In these soils, macrofauna has a high population density and high taxonomic richness (*i.e.* number of taxa recorded). Myriapoda and others arthropods (especially Cicadidae larva, Blattodea and Isopoda) have a high biomass and earthworms, ants, termites and Myriapoda are present at a high densities.

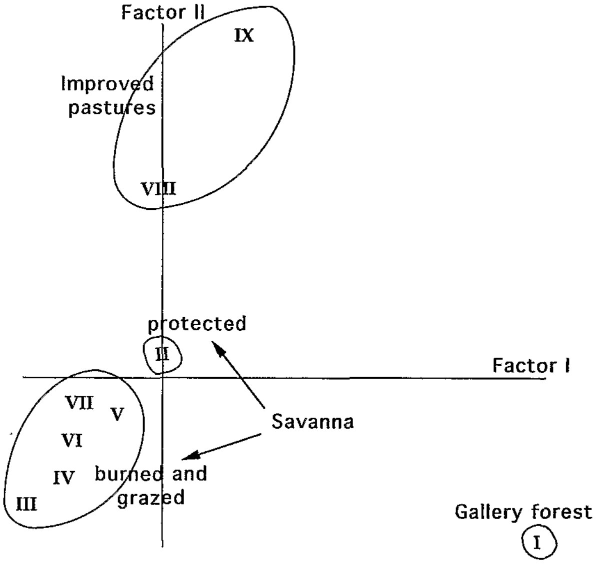

Figure 1. – Localization of the different sites studied in relation with the first two factors extracted from the P.C.A.

Table 1. – Major correlations between variables in the first two factors extracted in the PCA.

Factor I: 41.96% of the total variance			
Earthworm density	0.74	Density % in litter	0.58
Termites density	0.80	Mg content	0.75
Ants density	0.68	K content	0.86
Myriapoda density	0.98	% aluminic saturation	0.91
Macrofauna density	0.90	% clay	–0.91
Myriapoda biomass	0.83	Water infiltration	0.97
“Others” biomass	0.83	Soil density	–0.86
N of taxa	0.81	% porosity	0.99
Factor II: 24.4% of the total variance			
Ants density	0.85	pH	0.83
"Others" density	0.68	Ca content	0.90
Earthworms biomass	0.91	Resistance to penetration	–0.77
Coleoptera biomass	0.60	% of legumes	0.84
Macrofauna biomass	0.92	Stocking rate	0.88

Factor II accounts for 24,4% of variance and represents **the effect of the soil fertility**. This factor clearly separates the gallery forest and savannas from the improved pastures. It characterizes soils with a low penetration resistance (12-14 g.cm^{-2}) and high Ca content (0.53 mEq/100 g), supporting a vegetation with a high proportion of legumes (48%) which have the highest stocking rates (1.67 an./ha). Biomass of macroinvertebrates is high due to the large contribution of earthworms. Ants are little represented contrary to Coleoptera which have a high density and biomass.

Five main situations may thus be distinguished: gallery forest, savanna protected from fire, natural pastures, improved pastures and crops (*fig.* 1).

The **gallery forest** had the highest taxonomic richness and population density and a medium biomass (*table* 2.A, 2.B). Invertebrates mostly inhabited the first 10 cm of the soil (84%) and only 4% were found in the litter layer (*fig.* 4). Earthworms, termites, ants, Myriapoda and other arthropods presented the highest density observed (*table* 2.B, *fig.* 3). Earthworms were the major component of biomass (35%), followed by termites (18%) and Myriapoda (11%). Other arthropods, principally Gryllotalpinae, Cicadidae, Blattodea and Isopoda, represented 19% of the biomass (*table* 2.A, *figs.* 2, 5).

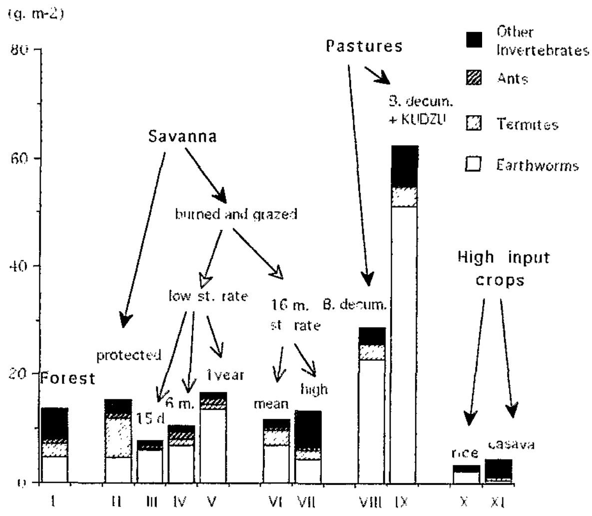

Figure 2. – Distribution of macrofauna biomass among the 11 sites studied (d = days; m = months; st. rate = stocking rate).

The **protected savanna** also had a high population density and taxonomic diversity and a medium biomass. The soil was densely colonized down to 20 cm but only 1% of the invertebrates inhabited the litter. Termites (47%) and earthworms (31%) were the major components of biomass (*fig.* 6).

In the **burned and grazed savanna** with a moderate stocking rate (0.25 an./ha), one year after the fire (site V), macrofauna had a rather similar biomass and density to that in the protected plot, with a lower taxonomic richness. Populations were concentrated in the upper part of the soil, with 5% in the litter layer and 78% in the 0-10 cm layer. Biomass was largely dominated by earthworms (82%) and termites (4%) were unimportant.

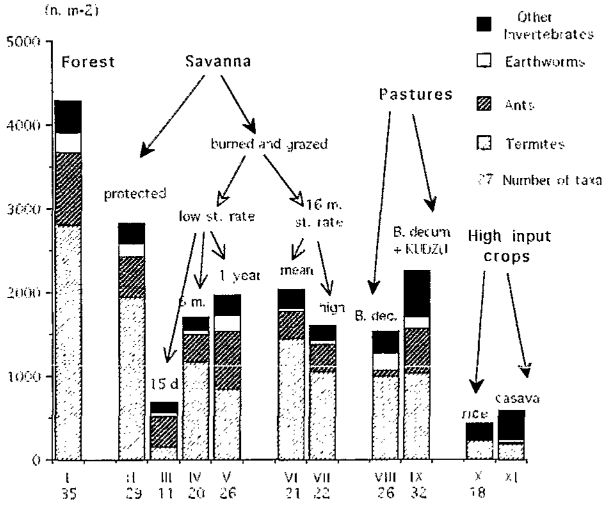

Figure 3. – Distribution of macrofauna density among the 11 sites studied (abbreviations as in *figure* 2).

An increase in the stocking rates did not have any significant effect on biomass and density but taxonomic diversity decreased down to 22 taxa. The relative contribution of earthworms to biomass decreased from 82% (low stocking rate) to 61% (moderate stocking rate) and 34% (high stocking rate), while other groups became more important such as termites (13% of the biomass), Coleoptera (24%), Arachnida (20 %) and Myriapoda (5%) (*figs.* 5, 6). Vertical distribution did not change and invertebrates were still concentrated in the 0-10 cm layer (68 to 78% of individuals).

Fire had a spectacular short-term effect on macrofauna. Fifteen days after savanna had been burnt, the invertebrate communities presented a very low population density, biomass and taxonomic richness. The vertical stratification was modified with a large proportion of individuals accumulated in the 10-20 cm (24%) and 20-30 cm (40%) strata (*fig.* 4). Earthworms were still dominant (more than 70% of the biomass), since termites and "others" were highly affected (*figs.* 5, 6).

After 6 months, soil fauna had been regenerated: biomass and density were not significantly different from value recorded in the initial savanna and taxonomic richness increased to 20 taxonomic units. The 0-10 cm layer also had been recolonized and comprised 80% of the population.

Macroinvertebrate communities of **improved pastures** were characterized by a high biomass and taxonomic richness and a medium population density. Earthworms largely dominate as they comprised 80% of the overall biomass (*fig.* 2.) and two native savanna species, *i.e.* the anecic (*Martiodrilus sp.*, Glossoscolecidae) and the mesohumic endogeic (*Andiodrilus sp.*, Glossoscolecidae), were dominant. Pastures sown to *Brachiaria rachiaria decumbens* and *Pueraria phaseoloides* (Kudzu) had the highest

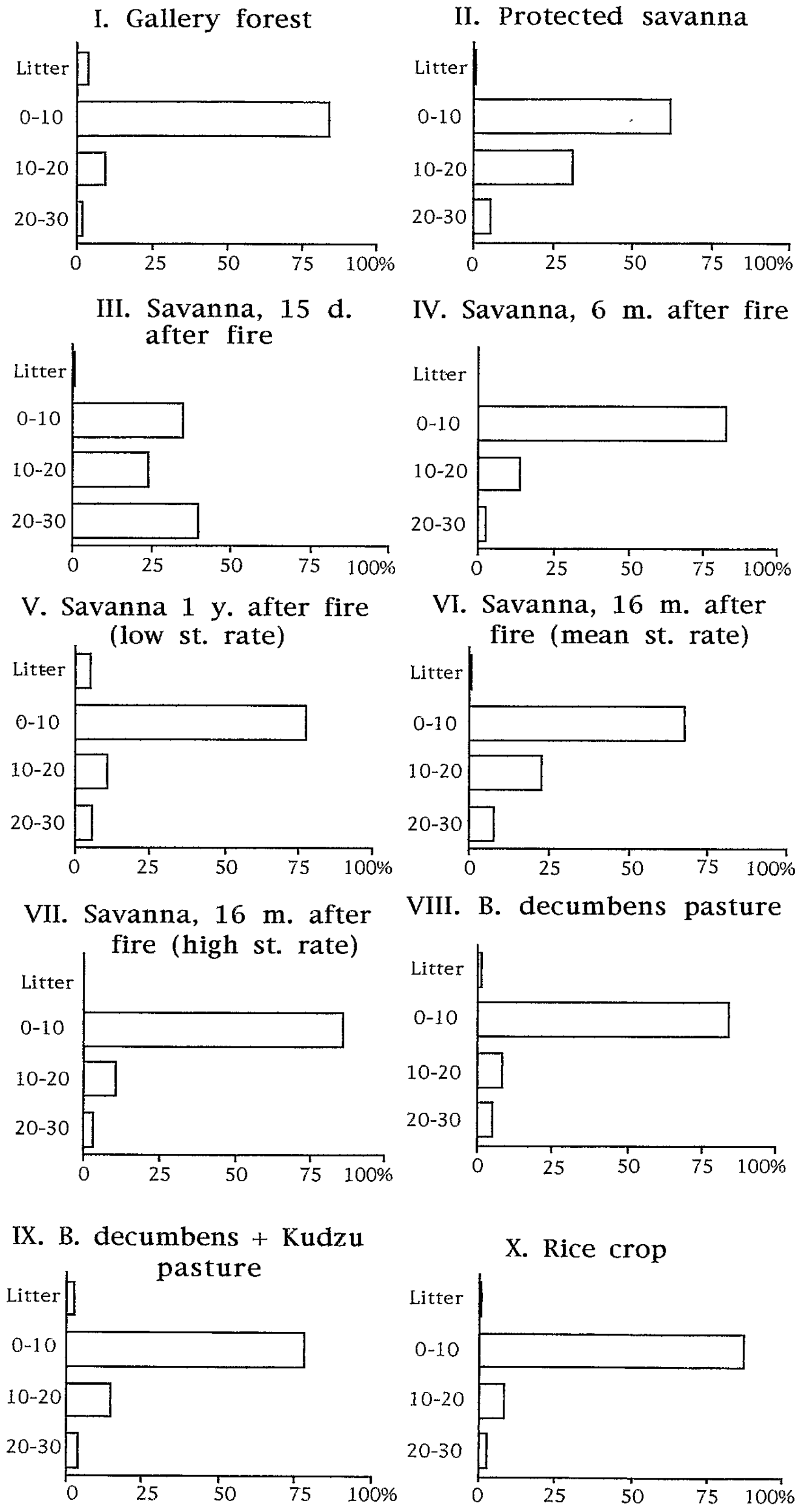

Figure 4. – Vertical distribution of macrofauna density in the 11 sites studied.

Table 2. – Macrofauna composition in the 11 studied sites (S.R. = stocking rate). **2.A.**: mean biomass; **2.B.**: mean density (S.E. in brackets). Letters represents the significant differences (90%) obtained after Student tests: a = different value from II; b = different value from I; c = different value from V; d = different value from IX; e = different value from VIII; Site XI was not inclued in the analysis.

A. Biomass (g . m^{-2}). Compilation of the 10 individual samples, except for the site XI (4 samples).

	Gallery forest	Savanna						Pastures		Crops	
			burned and grazed								
		protected	low S.R. (after fire)			moderate S.R.	high S.R.	*B. decumbens*	*B. decumbens* and Kudzu	rice	cassava
			15 days	6 months	1 year	16 months	16 months				
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Earthworms	4.72 (1.02) d,e	4.78 (1.96) c,d,e	6.13 (2.00) d,e	7.10 (2.57) d,e	13.77 (5.03) a,d,e	7.08 (3.99) d	4.48 (1.77) d,e	22.95 (9.11) a,b,c,d	51.09 (18.76) a,b,c,e	2.30 (2.11) d,e	0.53 (0.34)
Termites	2.50 (0.71) a	7.14 (5.07) b,c,e	0.20 (0.12) a	1.04 (0.55) a	0.65 (0.20) a	2.70 (1.33) a	1.73 (0.74) a	2.74 (2.01) a	3.64 (2.12)	0.18 (0.19) a	0.59 (0.35)
Ants	0.95 (0.46)	1.00 (0.63)	0.60 (0.40)	1.50 (1.26) e	1.16 (0.58)	0.49 (0.42)	0.63 (0.34)	0.04 (0.02)	0.49 (0.18)	0.00 (0.00)	0.09 (0.0)
Coleoptera	1.22 (0.52) d	0.99 (0.29) d,e	0.77 (0.29) d,e	0.75 (0.34) d,e	1.20 (0.30) d,e	1.04 (0.31) d,e	3.21 (1.26) a,c	2.38 (0.59) a,c	2.49 (0.31) a,b,c	0.43 (0.15) d,e	1.29 (1.18)
Arachnida	0.07 (0.04)	0.83 (0.78)	0.24 (0.13)	0.07 (0.05)	0.05 (0.03)	0.20 (0.15)	2.61 (2.73) b,c,d,e	0.08 (0.09)	0.49 (0.31)	0.03 (0.04)	0.00 (0.00)
Myriapoda	1.53 (0.72) a,c,e	0.24 (0.08) b,c,d	0.03 (0.04) b,d	0.02 (0.02) b,d	0.00 (0.00) a,b,d	0.03 (0.04) b,d	0.66 (0.57) d	0.39 (0.18) b,d	1.46 (0.76) a,c,e	0.27 (0.23) b,d	1.41 (0.83)
Other invertebrates	2.59 (1.67) a,c,e	0.35 (0.15) b,d	0.00 (0.00) d,e	0.02 (0.02) b,d	0.00 (0.00) b,d	0.09 (0.04) b,d	0.07 (0.04) b,d	0.24 (0.10) b,d	2.80 (1.64) a,c,e	0.02 (0.02) b,d	0.57 (0.06)
Total	13.58 (2.29) d	15.33 (5.31) d	7.97 (1.89) a,d,e	10.50 (2.61) d	16.83 (5.03) d	11.64 (5.12) d,e	13.40 (3.33) d	28.82 (10.27) d	62.46 (18.84) a,b,c,e	3.23 (2.25) a,d,e	4.31 (1.19)

Table 2. – B. Density (n . m^{-2}). Compilation of the 10 individual samples, except for the site XI (4 samples).

	Gallery forest	Savanna						Pastures		Crops	
		burned and grazed									
		protected	low S.R. (après le feu)			moderate S.R.	high S.R.	*B. decumbens*	*B. decumbens* and Kudzu		
			15 days	6 months	1 year	16 months	16 months			rice	cassava
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Earthworms	251 (44) a,d	157 (65) b	48 (9) a,b,c,d,e	46 (12) a,b,c,d,e	192 (45)	32 (10) a,b,c,d,e	56 (16) a,b,c,d,e	213 (24) d	139 (25) b,e	18 (6) a,b,c,d,e	27 (12)
Termites	2 806 (895) c,d,e	1 955 (1053)	147 (106) a,b,c	1 181 (762) b	845 (231) b	1 443 (457) b	1 050 (374) b	992 (709) b	1 034 (600) b	222 (214) a,b	195 (105)
Ants	862 (329) d	472 (294)	371 (316)	325 (126) b	685 (351) e	331 (185)	331 (156)	75 (15) b,c	534 (281)	11 (8) b,c	19 (12)
Coleoptera	110 (18) c,d,e	131 (35) c,d	107 (26) c,d,e	104 (33) c	198 (37) a,b	152 (20) d	126 (21) c,d	187 (28) b	240 (31) a,b	99 (16) c,d,e	104 (23)
Arachnida	19 (6) e	18 (7)	21 (4) c,e	6 (3) a,b,d	10 (4) d	10 (4) d	10 (4) d	8 (4) b,d	22 (8) c,e	3 (2) a,b,d	11 (12)
Myriapoda	125 (20) a,c,d,e	34 (8) b,c	3 (2) a,b,d	13 (5) a,b,d	3 (2) a,b,d	11 (5) a,b,d	10 (5) a,b,d	18 (5) b,d	38 (10) b,c,e	14 (10) b,d	91 (18)
Other invertebrates	118 30 a,c,d,e	64 9 b,d	0 0 a,b,c,d	29 8 b,d	38 8 b,d	50 12 b,d	26 5 b,d	48 8 b,d	259 55 a,b,c,e	61 22 b,d	144 21
Total	4 293 (1 077) c,d,e	2 830 (1 059)	698 (333) b,a	1 704 (745) b	1 971 (432) b	2 029 (497) b	1 608 (477) b	1 541 (747) b	2 267 (871) b	429 (230) a,b,d	592 (125)

densities of Coleoptera, Arachnida and "others invertebrates" and a high biomass of earthworms, Myriapoda and "others invertebrates" (*fig.* 5). The vertical distribution was similar to the one found in the traditional pasture (site V) since invertebrates were mostly concentrated in the 0-10 cm layer (78 to 84%).

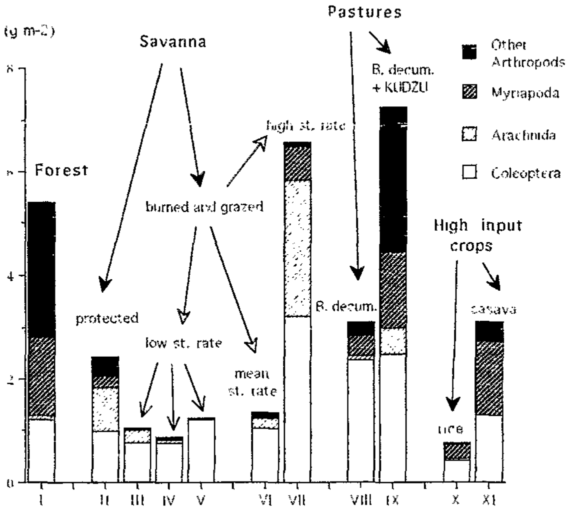

Figure 5. – Distribution of macrofauna biomass among the larger units of invertebrates (other than earthworms, termites and ants) in the 11 sites studied (abbreviations as in *figure* 2).

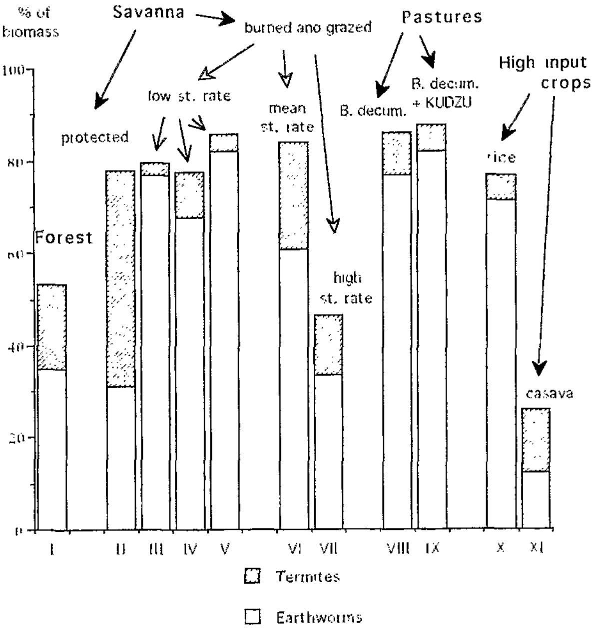

Figure 6. – Relative contribution of eartworms and termites to biomass in the 11 sites studied (abbreviations as in *figure* 2).

Annual high input croping systems (rice and cassava) had the lowest biomass and density and a low taxonomic richness. In the rice plot, earthworms were the major component of biomass (48%) while termites only represented 37% (*fig.* 6). Macrofauna was clearly concentrated in the 0-10 cm layer (87%).

DISCUSSION

Land management at Carimagua results in spectacular modifications of the macroinvertebrate communities of the soil. Biomass, in most of the sites, is dominated by earthworms, especially by a large anecic species (*Martiodrilus sp.*, Glossoscolecidae) and, in some cases, by another large endogeic mesohumic species (*Andiodrilus sp.*, Glossoscolecidae). Density is generally dominated by termites.

Gallery forest have a rather diverse and abundant fauna. Population density is lower than in Côte d'Ivoire, comparable to that of peruvian Amazonia and temperate beechwood, and superior to that of other tropical forests in Mexico, Nigeria and Sarawak. Invertebrate populations have a biomass similar to that of temperate beechwood and of mexican and nigerian tropical forest, 2 to 6 times superior than in Sarawak, but largely inferior to the values recorded in Peru and in Côte d'Ivoire (*table* 3). This is due to the very low earthworm biomass, 3 times lower than the average value (12.9 $g.m^{-2}$) calculated by Fragoso and Lavelle (1992) from 12 forests in Central and South America, Africa and Asia. Myriapoda represents 11% of biomass like in Peru and Mexico (Lavelle and Kohlman, 1984; Lavelle and Pashanasi, 1989) and other groups such as Gryllotalpinae, Cicadidae, Isopoda or Blattodea are of some importance (*fig.* 5).

In **savanna protected from fire**, macrofaunal density and biomass are significantly lower than those measured in african savanna of Côte d'Ivoire. Earthworms biomass is 3 to 10 times lower than in the african savannas (*table* 3) and only represent 31.2% of biomass whereas termites are the major component (46.6%) of biomass.

The **traditional management practice** does not affect biomass nor density of macrofauna but slightly reduces taxonomic richness. Biomass is much lower than in traditional pastures in Perou, whereas density is rather similar (*table* 3). Termites are highly affected and their importance decreases from 46.6% of biomass in the protected savanna to 3.9% . Inversely, earthworms are favoured, since their biomass is three fold increased and then represents 82% of total biomass (*fig.* 6). These results confirmed observation made in the USA and in Côte d'Ivoire (Lavelle, 1983b.; James, 1988) that grazing increases earthworm populations.

Burning the savanna seems to directly destroy a large part of the soil macrofauna. Population density, biomass and taxonomic richness clearly decreased and termites seemed to be the most sensitive group (*fig.* 6). Fire also affected the distribution in depth

Table 3. – Density ($n.m^{-2}$) and biomass ($g.m^{-2}$) of soil macrofauna and earthworms in various studied sites.

		Macrofauna		Earthworms		
Locality	Vegetation type	Biomass	Density	Biomass	Density	Reference
Colombia	Gallery forest	13.6	4 294	4.7	251	This study
Côte d'Ivoire	Tropical forest	74.2	5 747	52.3	171.2	Gilot *et al.*, in press
Nigeria	Tropical forest	16.4	3 119	10.2	34	Madge, 1969
Mexico	Tropical forest	16.4-18.9	888-3 011	9.8-10.7	8-132	Lavelle and Kohlmann, 1984 Lavelle *et al.*, 1981
Peru	Tropical forest	24.1-53.9	4 099-4 303	11.9-28.2	85-120	Lavelle and Pashanasi, 1989
Sarawak	Tropical forest	2.4-6.8	663-2 579	0.4-1	24-42	Collins, 1980
Germany	Temperate beechwood	12.7	4 035	10.7	205	Schaefer, 1990
Colombia	Savanna	15.3	1 830	4.8	157	This study
Côte d'Ivoire	Savanna	29.7-84.8	2 015-10 905	17-48.6	188-400	Lavelle, 1983 Lavelle *et al.*, 1992
Colombia	Traditional pasture	8-16.8	698-2 029	4.5-13.8	32-192	This study
Peru	Traditional pasture	82.3-121.2	1 768-2 347	78-116.4	474-573	Lavelle and Pashanasi, 1989
Colombia	Improved pasture	28.8-62.5	1 541-2 267	22.9-51.1	139-213	This study
Peru	Improved pasture	110.9-159.2	922-1 546	103.2-153	546-740	Lavelle and Pashanasi, 1989
Mexico	Improved pasture	–	–	35.8-55.5	620-948	Lavelle *et al.*, 1981
India	Improved pasture	–	–	30.2-56	17.4-800	Dash and Patra, 1977 Sepanati, 1980
Colombia	High input crops	3.2-4.3	429-592	0.5-2.3	18-27	This study
Peru	High input crops	3.1	730	1.5	14	Lavelle and Pashanasi, 1989

of the community since 15 days after burning, the 0-10 cm layer only comprised 35% of the invertebrates (*fig.* 4). Macrofauna quickly regenerated and, after 6 months, had recovered its initial biomass, density and taxonomic diversity while the 0-10 cm layer has been recolonized. These observations are in contradiction with the results of Athias *et al.* (1975) in Côte d'Ivoire, that indicate a delayed effect of burning whereas no immediate effect has been observed. The difference between both situations may result from the timing of burning. Fires studied in Côte d'Ivoire had been set during the dry season when large part of fauna is already adapted to the stress linked to drought, and termites are not affected by burning since they live either deep in the soil or in surface mounds with thick walls (Josens, 1972). At Carimagua, no preadaptation to the stress brought about by fire seems to exist.

Overgrazing does not affect biomass and population density but reduces taxonomic richness. The increase of the stocking rate reduces the relative importance of earthworms (only 33.4% of biomass in the most highly grazed plot) (*fig.* 6). This can be due to a modification of soil microclimate induced by the reduction of the herbaceous vegetation. Coleoptera are abundant in the most highly grazed plots (*fig.* 5) (7.1% of biomass in the medium and 24% in the high stocking rate) but remains less important than in Mexican pastures (25 to 48 $g.m^{-2}$) (Villabos and Lavelle, 1990). The increased inputs of cow-dung to the soil probably explain this change.

Macrofauna communities in **improved pastures** have a medium population density, and a high biomass and taxonomic richness, although biomass remains inferior to that measured in other tropical pastures. Native earthworms of the savanna are the major component of biomass (80%) with absolute values of 22.9 to 51.1 $g.m^{-2}$, equivalent to other improved pastures in Mexico or India but still inferior to Peruvian pastures (*table* 3). This increase of biomass is certainly due to the improvement of the quality of the litter brought to the soil in the form of cow-dung and legume leaf and root litter. Addition of legumine leaves rich in nitrogen, in the case of *B. decumbens* + Kudzu pasture, maintains taxonomic richness and increases biomass to values 4 times higher that in the protected savanna.

Contrary to pastures established on a forest precedent, native macrofauna communities seem to be favoured by the improvement of trophic conditions and there is no proliferation of exotic species of earthworms like in many tropical pastures (Lavelle *et al.*, 1981; Lavelle and Pashanasi, 1989). Other groups of some importance are Isopoda, indicators of a humid soil microclimate, and Coleoptera, certainly favoured by the input of cow-dung and increased root biomass (*fig.* 5).

High input cropping results in a dramatic decrease of taxonomic richness, population density and biomass. These results confirm other observations made in Peru (*table* 3) and can be explained by the negative action of soil tillage, fertilisation (especially when it induces an acidification of the soil), modification of the soil microclimate, non-target effects of pesticides and decrease of the reserves of carbon available in the soil as a result of the destruction of the perenial vegetation (House and Parmelee, 1985; Reddy and Goud, 1987).

CONCLUSION

In general, macroinvertebrate populations clearly respond to perturbations induced by soil management.

The traditional exploitation of the savanna as natural pastures has little influence on soil fauna and recolonisation of soil after fire is fast. Earthworms are favoured by grazing and fire but their importance decreases with overgrazing. Termites respond in clearly opposite manners and the ratio of earthworms/termites may be considered as a sensitive indicator of the state of the environment.

Sowing improved fodder plants and increasing animal production in improved pastures has a very important impact on soil macrofauna, especially on earthworm populations which increase their biomass from 4.8 to up to 51.1 $g.m^{-2}$. The association of *B. decumbens* + Kudzu seems to be of high value regarding the conservation of soil quality and biodiversity since it also maintains savanna taxonomic richness. The improvement of leaf litter quality and the great quantity of cow-dung brought to the soil can explain these results. Establishing improved pastures on a natural savanna does not transform the medium into a "green desert" but, to the contrary, increases the activity of local macrofauna communities.

Annuals crops have a dramatic effect on earthworms and arthropod populations, with a spectacular decrease of biomass, population density and taxonomic richness. The factors responsible for this phenomenon can be found in agricultural practices such as tillage, fertilisation or application of pesticides, in the reduction of root production and the modification of the soil microclimate occuring after the clearing the natural vegetation.

Macrofauna of tropical soils seems to be a very sensitive factor, but further research is needed to understand the dynamics of populations experiencing major disturbances and processes of recolonisation by macrofauna in regenerating environments. This will allow to design practices which allow a better conservation or the development of macrofauna and indicates ways to stimulate the activities of existing fauna soils or introduce better adapted species to restore soil fertility.

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APPENDIX

List of the taxonomic units collected in the soil during the sampling period

Taxonomic units	**Sites**
EARTHWORMS	
Glossoscolecidae	I, II, III, IV, V, VI, VII, VIII, IX, X
Megascolecoidea (Acanthodrilidae and/or Ocnerodrilidae)	I, II, V, VI, VII

ISOPTERA	
Rhinothermitidae	I, II, III, IV, V, VI, VII, VIII, IX, X
Termitidae	I, VII
Kalotermitidae	I
HYMENOPTERA	
Formicidae	I, II, III, IV, V, VI, VII, VIII, IX, X
Others	I, II, V, VI, VIII
COLEOPTERA	
Carabidae	I, II, III, IV, V, VI, VII, VIII, IX, X
Elateridae	I, II, III, IV, V, VI, VII, VIII, IX, X
Scarabaeidae	I, II, III, IV, V, VI, VII, VIII, IX, X
Chrysomelidae	I, II, III, IV, V, VI, VII, VIII, IX, X
Staphylinidae	I, II, IV, V, VII, VIII, IX, X
Curculionidae	I, II, IV, V, VI, VII, IX, X
Tenebrionidae	I, II, IV, V, VI, IX, X
Lampyridae	VI, VIII, IX
Others	I, II, VI, X
Alleculidae	III, IV
Scaphidiidae	V, VII
Pselaphidae	V, IX
Cicindelidae	IV
Eucteridae	VII
Clavigeridae	IX
Sylphidae	IX
Leiodidae	IX
Passalidae	V
Byrrhidae	X
Coccinelidae	I
ARACHNIDA	
Araneida	I, II, III, IV, V, VI, VII, VIII, IX, X
Acarina	I, II, V, VIII
Phalangida	II, VIII
Chelonethida	I, II
MYRIAPODA	
Geophilomorpha	I, II, III, IV, V, VI, VII, VIII
Opisthospermophora	I, III, V, VII, VIII, IX, X
Scolopendromorpha	I, II, IV, V, VI, VIII, IX
Others	V, VI, VIII, IX, X
Polydesmida	I, II, VIII, IX
NEMATODA	I, II, IV, V, VI, VII, VIII, IX, X
HOMOPTERA	
Cercopidae	VII, VIII, IX
Cicadidae	I, IV, V, X
Cicadellidae	II, IX
HEMIPTERA	
Others	I, II, IV, V, VI, VII
Corimelaenidae	VI, VII
Reduvidae	I, II, IX
Cydnidae	II.
ORTHOPTERA	
Blattidae	I, II, V, VIII, IX
Gryllotalpinae	IV, VII
Gryllinae	IX
Mantidae	IX
LEPIDOPTERA	I, IV, VII, IX
EMBIOPTERA	I, V
CRUSTACEA	
Isopoda	I, II, VIII, IX
THYSANURA	
Lepismatidae	II
DIPTERA	I, II, VI, VIII, IX, X
DERMAPTERA	I
MOLLUSCA	
Helicidae	I, VIII, IX
Limacidae	IX
DIPLURA	I