Earthworm communities in Native Savannas and Man-Made Pastures of the Eastern Plains of Colombia

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Number of figures: 6

Number of tables: 8

Key words: Abundance, Biomass, Diversity, Earthworm community, Pasture, Land management, Tropical Savannas.

This paper is also a portion of the Ph. D. thesis submitted by the first author.

ABSTRACT

The structure and seasonal changes of earthworm communities were evaluated in a natural Savanna and in an introduced grass-legume pasture in a Colombian oxisol over a period of eighteen months. One plot of 90x90 m was isolated in each of the systems and each month five samples of $1m^2$ x 0.5 m and 10 of 20x20x20 cm were randomly selected from a stratified block design. Species richness was similar in the two evaluated plots (7 species), whereas diversity H' index (Shannon and Weaver, 1949) was clearly different, 2.89 in natural Savanna and 1.29 in pasture. This is explained by differences in earthworm community structure. Average annual density in Savanna was 49.8, ranging from 10.8 to 135.8 ind. m^{-2}, and biomass was 3.3 g m^{-2} (hand-sorting method), ranging from 0.9 to 11.5 g m^{-2}. In the man-made pasture, density was 80.1 ind m^{-2} on average, ranging from 24 to 215.8 ind m^{-2} and biomass was more than tenfold higher, ranging from 29.2 to 110.4 g m^{-2}. This was especially due to the presence of a large glossoscolecid anecic species, Martiodrilus carimaguensis n. sp. (Jiménez and Moreno, in press), which has been greatly favoured by conversion of savanna to pasture. Endogeic species were dominant in the natural Savanna whereas the anecic species accounted for the 88% of total earthworm biomass in the pasture. Figures of total earthworm density and biomass were significantly different in the two systems studied (t-test). The results indicate a clearly positive response of earthworm communities to improved pastures, a type of land use that is increasingly adopted in moist neotropical savannas.

INTRODUCTION

Tropical savannas form one of the most predominant ecosystems in South America with an overall extension of almost 250 millions ha. By definition, savannas are communities with a dominant grass layer and a discontinuous tree layer, which may make up 10-50% of the total plant cover (Johnson and Tothill, 1985).

Oxisols cover an area of more than 60% in the tropics, with low pH, low nutrient content and limited organic pools (Sánchez & Salinas, 1983). They are the result of long-term pedogenic processes and have led to the establishment of acid tolerant faunas which may be abundant and active (Lavelle et al., 1995). The Eastern Plains of Colombia (locally called “Llanos”) are covered with acid savannas that are used for extensive grazing systems. In the absence of such interventions as sowing of introduced grasses and application of fertilizers, these lands are usually managed in extensive holdings of low productivity (Fisher et al., 1995).

The number of species in a given community is usually lower after replacement of the original system, since those resources that are exploited by a community become uniform and biodiversity may be reduced (Lavelle, 1986). In tropical acid soils, pastures derived from forests or savannas may have high biomasses of soil macroinvertebrates (Lavelle and Pashanasi, 1989; Decaëns et al., 1994). Exotic species tend to colonize these new habitats and eliminate endemic species that are poorly adapted to such disturbances. The high development of exotic populations may be a factor of soil degradation. It has been reported that populations of Pontoscolex corethrurus (Glossoscolecidae), a pantropical endogeic species, compact the soil and eventually create problems (Rose and Wood, 1980; Pashanasi et al., 1992; Barros et al., 1996).

There is an important lack of information concerning the species composition and structure of earthworm communities in tropical savanna sites. Only a few studies have dealt with this matter; Dash and Patra, (1977) and Senapati (1980) made an important contribution to the study of Indian earthworms; Lavelle (1978) and Lavelle et al. (1981) studied the earthworm fauna in the natural savannas of Ivory Coast and Mexico, respectively.

This study aimed to evaluate the effect of improved pastures on the structure and abundance of earthworm communities from the native Savannas. Research was conducted at the CORPOICA-CIAT Carimagua Research Station on the Colombian Eastern Plains. A preliminary survey of soil macrofauna communities in contrasting land use systems had shown a spectacular response of macroinvertebrate populations to perturbations induced by land management (Decaëns et al., 1994). Natural savannas with a highly diverse plant community that produces low quality organic matter are replaced by a much more productive system, that associates two species that produce high quality forage. Earthworm biomass in natural ungrazed savannas was ca. 4.8 g m^{-2}, whereas in grass-legume grazed pastures this value increased up to 50.0 g m^{-2} (Table 1).

A survey of earthworm communities was carried out during eighteen months in order to follow the dynamics of the different earthworm populations.

MATERIALS AND METHODS

Site description

The study area is located at the Centro Nacional de Investigaciones Agropecuarias (CNIA), Carimagua, in the Eastern Plains of Colombia (4° 37' N, 71° 19' W and 175 meters altitude). Respective average annual rainfall and temperature are 2280 mm and 26 °C, with a dry season from December to March (Figure 1). Vegetation is dominated by well-drained isohyperthermic savannas with predominantly infertile Oxisols in the upland (“altos”) and Ultisols in the lowlying (“bajos”) savannas. The former are characterized by their acidity (pH in water = 4.5), a high Al saturation (> 90%) and low contents of exchangeable Ca, Mg and K (Lascano and Estrada, 1989). Chemical factors that contribute to acid soil infertility and subsequent effects on plant growth are complex. They include Al toxicity, low contents of available P and low rates of N mineralization (Rao et al., 1993). Soils at the study site have been defined as fine, kaolinitic, isohyperthermic typic Haplustox (clay loam soil). Predominant plant species are Andropogon bicornis, Gymnopogon sp., Panicum sp., Trachypogon sp. and Axonopus sp.

Two contrasting systems were evaluated, an ungrazed natural Savanna and a 17-yr old grazed pasture that associates an exotic African grass, Brachiaria decumbens cv. Basilisk, and a tropical forage herbaceous legume species, Pueraria phaseoloides CIAT 9900 (“kudzú”), adapted to acid-soil conditions. The pasture, established on a previous Savanna site, was fertilized with (kg ha^{-1}) 44 P, 40 K, 14 Mg and 22 S at establishment and with 10 P, 9 K, 92.5 Ca, 9 Mg and 11.5 S each second year for the next nine years (Lascano and Estrada, 1989). Stocking rates for the improved pasture are 1 cattle ha^{-1} in the dry season and 2 cattle ha^{-1} in the wet season . The main physical and chemical soil properties of both systems are shown in Table 2. No significant differences in relation to soil physical and chemical conditions are apparent between these two sites, located in the same edaphological unit (IGAC, 1974).

Earthworm sampling

Sampling was performed monthly from March 1994 to September 1995 in both systems, except in June 1994. A plot 90x90 m was isolated in each system and divided into regular quadrats of 10x10 m to obtain a total number of 81 sampling units. Extraction of earthworms was a combination of hand sorting of $1m^2$ x 0.5 m depth samples and washing-sieving of 20x20cm x 20 cm depth monoliths (Lavelle, 1978). From each plot, five $1m^2$ and 10 washing-sieving monthly samples were randomly taken (except for March 1994, n = 3 and 6, respectively).

Sampling depth varied seasonally to take into account the vertical migration of species like Martiodrilus carimaguensis, that are normally found at 80 cm depth during the dry season (Jiménez et al., in press). A trench was dug around the quadrat to avoid a possible migration of some individuals laterally out of the block and facilitate the separation of strata. The sample was subdivided into layers 10 cm thick. All earthworms were carefully collected, washed in water and fixed in 4% formalin (10% of the commercial dilution). They were separated in the laboratory into species, adults, juveniles and cocoons, counted and weighed separately (fresh weight in formol, 15% lower than their live weight on average).

Estimation of earthworm weight

One of the disadvantages of the hand-sorting method is that a significant proportion of the larger individuals are cut into pieces, making rather difficult the evaluation of individual weights. Relationships have been sought between the weight of one complete specimen and biometric variables that could be measured in the anterior part of the body. The maximum preclitellar diameter was used to estimate the total weight of incomplete individuals. The relationship was either linear or exponential and corrections were made accordingly (Figure 2 a-f).

Soil moisture measurement

Soil samples were taken in each stratum and placed in plastic bags when hand-sorting of $1m^2$ monoliths was performed. They were carried to the laboratory and six subsamples were extracted from each bag, weighed (nearly 100 g wet soil) and oven-dried for at least four days. The water content of the soil was calculated from the expression:

$$[(\text{Wet soil weight} - \text{dry soil weight})/\ \text{dry soil weight}] \times 100$$

Surface cast deposition

In both systems tower-like surface casts belonging to the large anecic species, <u>M. carimaguensis</u> (Glossoscolecidae) were counted to estimate population numbers since they are easily distinguished from other casts. These casts were removed from the selected sampling unit soon before the extraction of the $1m^2$ block and classified as follows: dry, freshly deposited and freshly non-recent deposited (more than one day old). Each month, two quadrats of the total five $1m^2$ samples were randomly selected to pick up all castings, which were oven dried and weighed to evaluate cast production in both systems.

RESULTS

Species richness, diversity and evenness

In the Carimagua region, 21 species of earthworms have been collected. In the two systems studied species richness was very similar, i.e., 8 in the native savanna and 7 in the pasture (Table 3). Andiorrhinus n. sp. 2. is the only savanna species that was not collected in the pasture. In the savanna it seems to be very rare since only one specimen was collected during the survey. No exotic species were collected in the pasture and all the 7 species collected were also present in the native savanna.

The diversity index was computed using annual average values of biomass, as is recommended when these data are available (Ludwig and Reynolds, 1988; Barbault, 1992). The transformed Shannon indexo btained for savanna was 2.89 whereas in the pasture system this index decreased to 1.29. Respective values of evenness, H'/lnS (Pielou, 1975) were 0.51 and 0.27.

The family Glossoscolecidae, endemic in the Neotropics, was the most abundant with 6 species: Andiodrilus n. sp., Andiorrhinus n. sp. 1, Andiorrhinus n. sp. 2, Martiodrilus carimaguensis, Glossodrilus n. sp. and epigeic n. sp. Two species, one belonging to each of the families Octochaetidae and Ocnerodrilidae, were also found.

The earthworm community comprised species of diverse sizes and ecological functions; two species were epigeic, 4 endogeic and 1 anecic. In the deeper strata of soil, where soil organic matter content is low, specimens of the family Ocnerodrilidae were regularly found in casts deposited in the vertical burrows dug by large individuals of M. carimaguensis. They would split these massive casts into finer granular structures.

Density and biomass

Yearly means of both earthworm density and biomass in savanna were 49.8 ind m^{-2} and 3.26 g m^{-2}, whereas in pasture density was 80.1 ind m^{-2} and biomass showed a more than tenfold increase (57.1 g m^{-2}). Differences in density and biomass were significant ($p < 0.002$ and $p < 0.001$), mainly due to a strong stimulation of populations of M. carimaguensis, when the savanna was converted into improved pasture (Figure 3a, b).

Differences between the plots in monthly average soil moisture content were significant (p = 0.028, t-Test). The natural savanna was wetter than the improved pasture (Table 4) and values of density and biomass were highly correlated, at 1% level, with average soil moisture (except biomass figures in NS, at 5%). On the contrary, an ANOVA analysis showed that differences in soil moisture along strata between the two systems were not significant at 5%.

Monthly values of density and biomass were closely linked to soil moisture and the occurrence of a four-month dry season led to a severe decrease in density. In savanna, density was minimum in February 95 (10.8 ind m^{-2}) and maximum in July 94 (135.8). The minimum value of density in pasture was also observed in February 95 (24 ind m^{-2}) and maximum in May 94 (215.8). Biomass in savanna was minimum in March 94 (0.74 g m^{-2}) and maximum in September 95 (11.5). In the pasture plot biomass was minimum in January 95 (29.2 g m^{-2}) and maximum in May 94 (110.4). A delay in resumption of earthworm activity was observed in the second year of the study as the onset of the wet season occurred one month later than normal. In September sampling depth was extended to follow vertical migrations of populations of M. carimaguensis that start from July on; values of density and biomass in August 1994 are probably underevaluated since part of the population had probably started into migrate to deeper horizons.

Differences in the species structure of communities were also observed. In the natural savanna system the most abundant species, in terms of biomass, was Glossodrilus n. sp., a thin medium-sized endogeic species living at an average depth of 7 cm, and endogeic species accounted for more than 80% of total earthworm biomass. In the man-made pasture Martiodrilus carimaguensis was the major component, accounting for 88% of total earthworm biomass, and endogeic species only contributed 12% of total earthworm biomass (Figure 4). In the pasture system only three species had increased populations significantly greater than in the natural system, i. e., Andiodrilus n. sp., Andiorrhinus n. sp. 1 and Martiodrilus carimaguensis (Table 5).

Surface cast deposition

M. carimaguensis deposits big tower-like casts, up to 10 cm in height and 5 cm in diameter, at the soil surface. These earthworms are large (9.3 mm in diameter and

194 mm length on average for adults) and they inhabit semi-permanent vertical burrows.

Production of these casts differed greatly in the savanna and pasture with the soil surface in the pasture system almost totally covered by these casts. Fresh casts indicated the presence of an active individual. A very significant relationship ($p < 0.01$) was observed between the number of fresh casts and the number of individuals collected in the upper 10 cm of soil during the rainy season (Figure 5). The r coefficient was very close to 1 indicating that every active individual produces one cast.

Cast production also showed marked seasonal fluctuations, with maximum production at the beginning of the rainy season and no activity in the dry season (Figure 6). The number of fresh casts was eleven times greater in the pasture than in the savanna (Table 6). However, in one year, from October 1994 to September 1995, the total weight of casts collected, fresh and dry, was 31.3 tonnes ha^{-1} in the native savanna, whereas in the improved pasture these figures rose up to 37.7 tonnes ha^{-1}.

Seasonal variations of activity

Tropical savannas are defined by a marked seasonality of environmental conditions. Soil moisture fell to values ranging from 12.6 to16.5% (pF 4.2 = 15.4%) in the upper 10 cm (dry soil basis) during the dry season at Carimagua. The minimum value obtained in the pasture in the dry season was 13.5%. During the rainy season the highest value obtained in both savanna and pasture systems was respectively 34.7 and 34.6%, with an average value of 26.1 and 24.7%. In natural and disturbed savannas, differences in earthworm activities were observed, depending on the species considered. All earthworms were inactive during the dry season, from December to March. The soil water content also varied with depth, explaining the differences in the seasonal cycles of the different species.

Two endogeic species, Andiodrilus n. sp. and Andiorrhinus n. sp. 1, did not seem to exhibit any strategy or resistant form during the dry season. They simply descended some tens of cm in the soil (in the 30-50 cm stratum) and entered a quiescent state. Many earthworms died and survivors initiated reproduction early in the wet season to rapidly increase their populations. A large number of earthworms were found dead with their tegument completely dry.

Glossodrilus n. sp. combined two strategies: quiescence of individuals coiled up inside a cavity plastered with mucus and resistant cocoons produced at the end of the wet season, in November. At the beginning of the rainy season all the quiescent individuals became active and surviving cocoons hatched.

Martiodrilus carimaguensis exhibited the most interesting behaviour, with a true diapause and different patterns for adults and juveniles respectively. Juveniles were active during only four months, from April to July, whereas adults remained active until December (i. e., 8 months). Inactivation occurred after the individuals had gone down to 60-100 cm depth (30.1 cm is the average living depth) and built an aestivating chamber in which they coiled themselves up, after emptying their guts. They then remained quiescent until the next rainy season. In controlled conditions there was no response when aestivating earthworms were introduced into soil with water content near field capacity indicating that a true diapause, physiologically induced, was occurring. Another outstanding feature was that the aestivating earthworm usually closed up the end of the gallery with several septa, built with cast material, to avoid a loss of integumental moisture, vital to support a minimal respiration rate. The combination of these forms of behaviour allows this species to reduce the otherwise high risk of mortality during the unfavourable conditions of the dry season.

Cocoons of this anecic species, ovoid in shape and light brown coloured with an average size of 25x15 mm, were deposited at 20 to 50 cm depth in contrast to adults and juveniles at greater depth. Two individuals, weighing 760 mg each on average (n = 33), emerged from one cocoon but soon moved deeper into the soil during the period August-December where they became inactive (Jiménez et al., in press). The ratio cocoon weight/adult weight is the highest ever recorded in any study of earthworm communities (Table 7).

The small oligohumic earthworm species of the family Ocnerodrilidae (20-30 mm in length), burrowed deep into the soil and was inactive during the whole dry season. During the rainy season they were found feeding on casts of M. carimaguensis and splitting them into much smaller aggregates. They also fed on other organic matter pools, i.e., some Scarabeinae nests.

DISCUSSION

The objectives of this study were to make a contribution to the study of South American savanna earthworms and to investigate the effects of the establishment of tropical forage pasture on the earthworm community in supposedly low-fertility Savanna soils, especially when plant species of high below-ground production were used, resulting in increased availability of litter residues and soil organic matter (Sombroek et al., 1993; Thomas et al., 1995).

Some studies on the ecology of earthworms in tropical ecosystems have dealt with the role of endemic species (Lavelle, 1978; Senapati, 1980; Nemeth, 1981; Lavelle and Pashanasi, 1989; Fragoso, 1993) and their adaptation when natural systems are replaced. The situation at Carimagua greatly differed from many tropical American pastures that have been established in place of primary rain forest, where earthworm communities are overdominated by only one exotic, mesohumic endogeic neotropical glossoscolecid species, Pontoscolex corethrurus Müller, 1857, as in Yurimaguas, Peru (Lavelle and Pashanasi, 1989), Florencia, Colombia, (Jiménez, pers. obs.), Manaus, Brazil, Mexico and Costa Rica (Fragoso and Lavelle, 1992) and Ecuador (Lavelle, pers. comm.).

Pastures are functionally similar to savannas (Lavelle et al., 1994). When they are established in forest areas with high annual rainfall mainly peregrine species with pantropical distributions are present, i.e., P. corethrurus Müller, 1857 and Polypheretima elongata (Perrier, 1872). Pastures, alone or associated with legumes, derived from natural savannas are more likely to conserve the native earthworm community than those established on original rain forest sites.

At Carimagua, even though the installation of a pasture system is clearly a disturbance, the original species richness of earthworms in the savanna was conserved in pure or legume-based improved pastures. However, the pasture was less diverse than the savanna when the Shannon index H’ (Shannon and Weaver, 1949) was computed and not all the species were favoured by adoption of this system.

The drilosphere, one of the four major components of the biological systems of regulation in the soil (Lavelle et al., 1993) has been proved to have an important role in grasslands, where very active drilosphere systems are well-developed. Lee (1985) and Syers and Springett (1984) point out the high values of earthworm population and biomass supported in grasslands. Kouassi (1987) studied the endogeic macrofauna of savannas and pastures in Ivory Coast and found that earthworms were the main component of total macrofauna biomass, with differences between savannas and pastures: earthworm biomass ranged from 6.5 g m^{-2}, in the dry season, to 70.9 g m^{-2} in the wet season in pastures. Similar values for savannas ranged from 3.0 to 26.3 g m^{-2}.

The number of earthworms found in the natural savanna at Carimagua is low compared to other tropical savanna sites (Table 8) and biomass values in the pasture system are high compared with other tropical sites, though comparisons must be made with caution since different extraction methods were used . In Table 9 values of earthworm density and biomass at Carimagua and their relative contribution to both earthworm abundance and biomass are compared to other humid tropical sites.

Barois et al. (1988) and Lavelle and Pashanasi (1989) have reported live earthworm biomass in improved pastures as high as 1000 to 3000 kg ha^{-1}. Both communities were overdominated by single species populations of exotic endogeic earthworms which accounted for 80 to 100% of biomass. At Carimagua, however, live earthworm biomass was 620 kg ha^{-1} and one anecic species comprised 88% of total earthworm biomass.

The casting activity of M. carimaguensis was limited to the wet season, as was also reported by Gates (1961) and Madge (1969) for tropical species of earthworms. According to Edwards and Bohlen (1996) counting soil surface casts gives an idea of the activity of earthworms, but it is by no means a valid assessment of the actual abundance and overall activity of earthworm populations. In this study we have demonstrated a very close relationship between the number of fresh casts deposited by M. carimaguensis at the soil surface and the number of individuals in the first 10 cm of soil. Population density can therefore be estimated from the number of fresh casts. Evans and Guild (1947) also observed a strong relationship for two lumbricid earthworms, A. longa and A. caliginosa. On the other hand, Lavelle (1978) indicates that respectively 1.7 and 3.5% of total soil ingested by M. anomala (Megascolecidae) and small polyhumic Eudrilidae is deposited as surface casts.

Despite the large differences between production of fresh casts of M. carimaguensis when both systems are compared, the total accumulation of weighed casts was not so different; maybe in the improved pasture there is a reingestion of their faeces after microbial incubation has occurred, defined by Swift et al. (1979) as an external rumen, or in savanna this species may be more active and so produce a larger amount of casts per biomass unit. Lavelle et al., (1989) showed that earthworms ingest a larger amount of soil when they are fed on poor soils.

There is a need to investigate why in most farm pastures in the Neotropics there is evidence of progressive degradation in contrast with Carimagua where there is no evidence of degradation up to date. The question of why this is so remains unanswered and very little is known about the processes that contribute to sustainability or to degradation of pastures in the tropics (Fisher et al., 1995). Furthermore, the possible contribution of endemic earthworm species adapted to the changes that accompany pasture establishment must be considered in order to design agricultural practices with, at least, minimum harmful impact.

Acknowledgements

This study was included within a collaborative research framework between the STD-3 Macrofauna Project, an international programme supported by the European Community focused on the biology, ecology and possibilities of management of earthworm species present in natural and disturbed ecosystens in the tropics, and the Tropical Lowlands Program at the International Center for Tropical Agriculture, CIAT (Cali, Colombia). This study was supported in part by a research grant within the MACROFAUNA programme. We want to thank CIAT (International Centre for Tropical Agriculture), especialy all at Tropical Lowlands Program for scientific, technical and human support. The invaluable help provided by field workers at Carimagua in this back-breaking work is undoubtedly greatly appreciated. Finally, the first author wishes to thank the helpful comments of two anonymous referees on the previous manuscript.

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FIGURE CAPTIONS

Figure 1. Average monthly temperature and precipitation at Carimagua over 22 years (1973-1995).

Source: CIAT database

Figure 2. Estimation of earthworms fresh weight for some studied species from Carimagua (all regressions were signifficant, $p < 0.01$)

Figure 3. Monthly average changes in density (a) and biomass (b) of earthworms at Carimagua (numbers m^{-2} ± standard deviation)

(Hand-sorting method)

Figure 4. Annual relative contribution of the different ecological categories to total earthworm biomass.

(The size of the circles is proportional to biomass values)

Figure 5. Correlation between the number of fresh casts and the abundance of M. carimaguensis in the improved pasture system ($P < 0.01$).

(Data obtained during the rainy season, from April to December 1994)

Figure 6. Monthly average number of fresh casts of M. carimaguensis in both systems.

TABLE CAPTIONS

Table 1. Total earthworm (EW) and macrofauna (MC) biomasses in different ecosystems at Carimagua using the TSBF method (Decaëns et al., 1994)

Table 2. Main physical and chemical soil properties of the systems studied (CIAT analysis).

Table 3. List of species found in two systems at Carimagua.

Table 4. Monthly soil moisture (% dry soil basis) in savannah and pasture plots for the whole study period.

Table 5. Diffences in yearly average density and biomass (in italics) per metre square of earthworm species in both systems studied

Table 6. Number of casts of M. carimaguensis per m^2 by month in two systems at Carimagua (mean ± standard deviation).

Table 7. Quantitative characteristics of the reproduction for some temperate and tropical anecic species.

Table 8. Abundance and biomass of earthworms in several tropical savanna study sites.

Table 9. Species richness, abundance, biomass and proportion of epigeic, endogeic and anecic earthworms at Carimagua and in other tropical sites

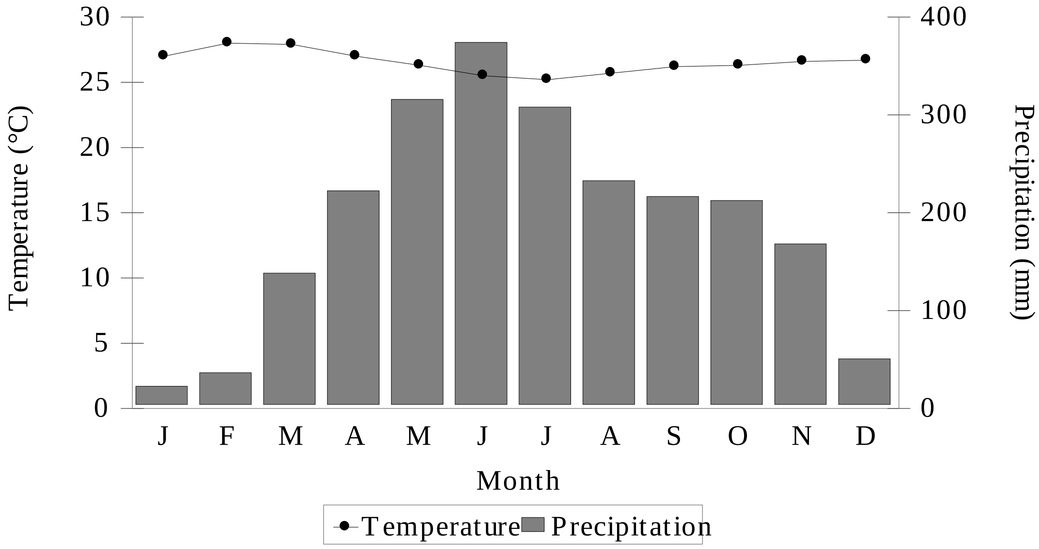
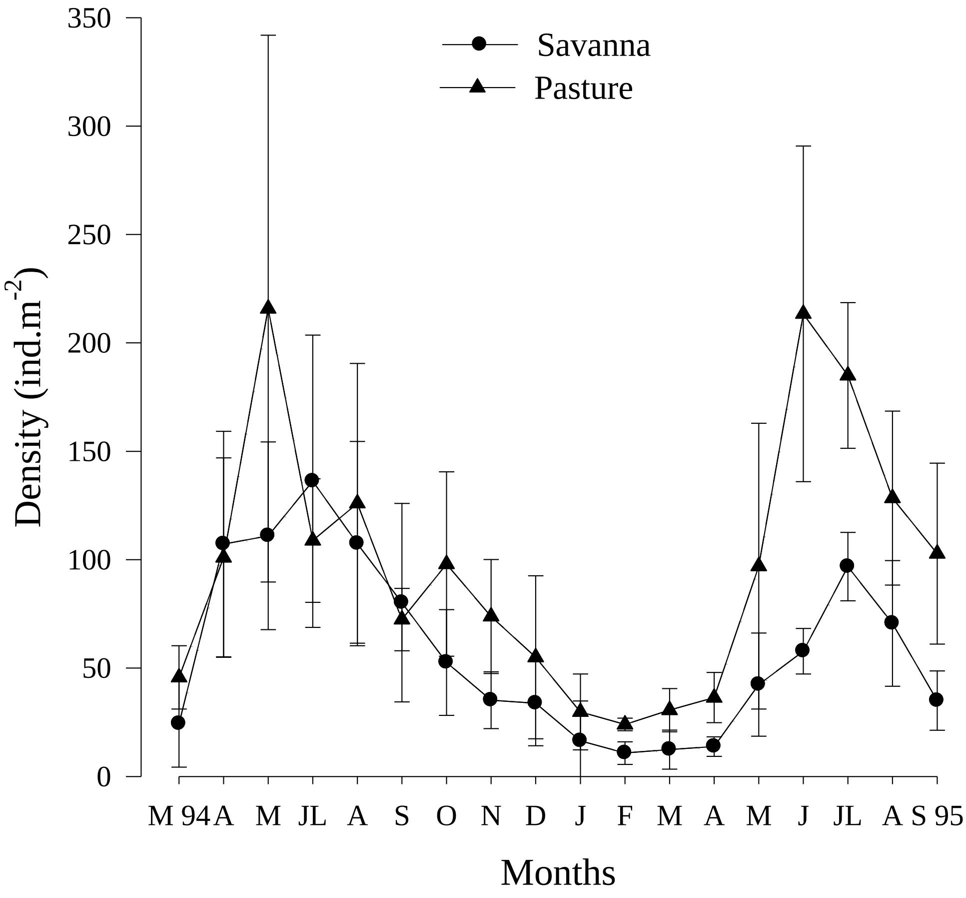
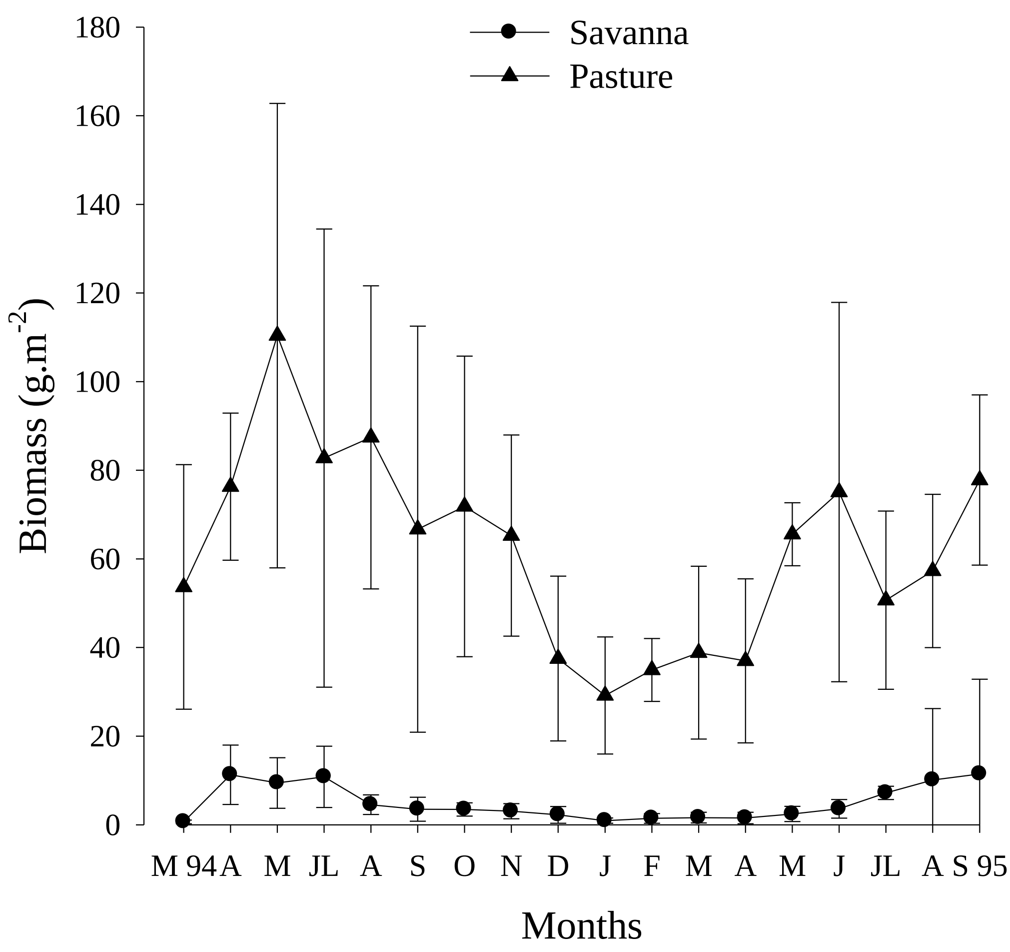

30
25
20
15
10
5
0
Temperature (°C)
400
300
200
100
0
Precipitation (mm)
J F M A M J J A S O N D
Month
Temperature
Precipitation

Figure 1



Savanna
Pasture
Density (ind.m^{-2})
350
300
250
200
150
100
50
0
M 94 A M JL A S O N D J F M A M J JL A S 95
Months

Figure 3 a)



Savanna
Pasture
Biomass (g.m-2)
180
160
140
120
100
80
60
40
20
0
M 94 A M JL A S O N D J F M A M J JL A S 95
Months

Figure 3 b)

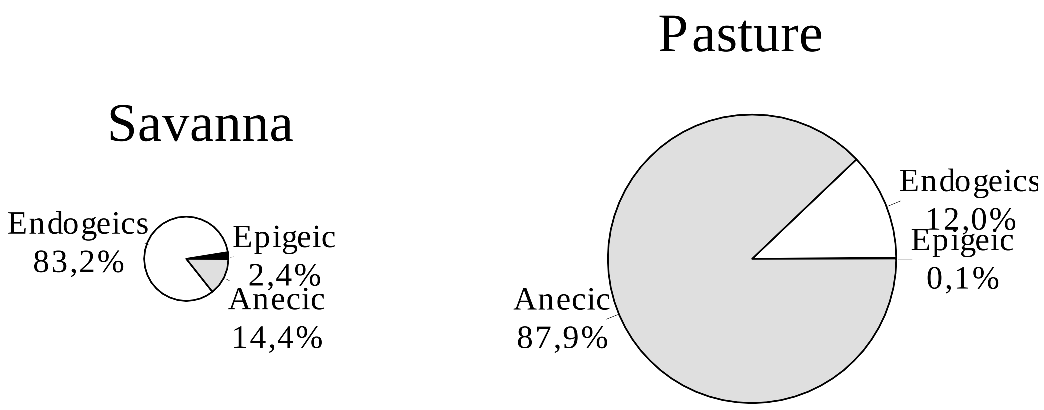
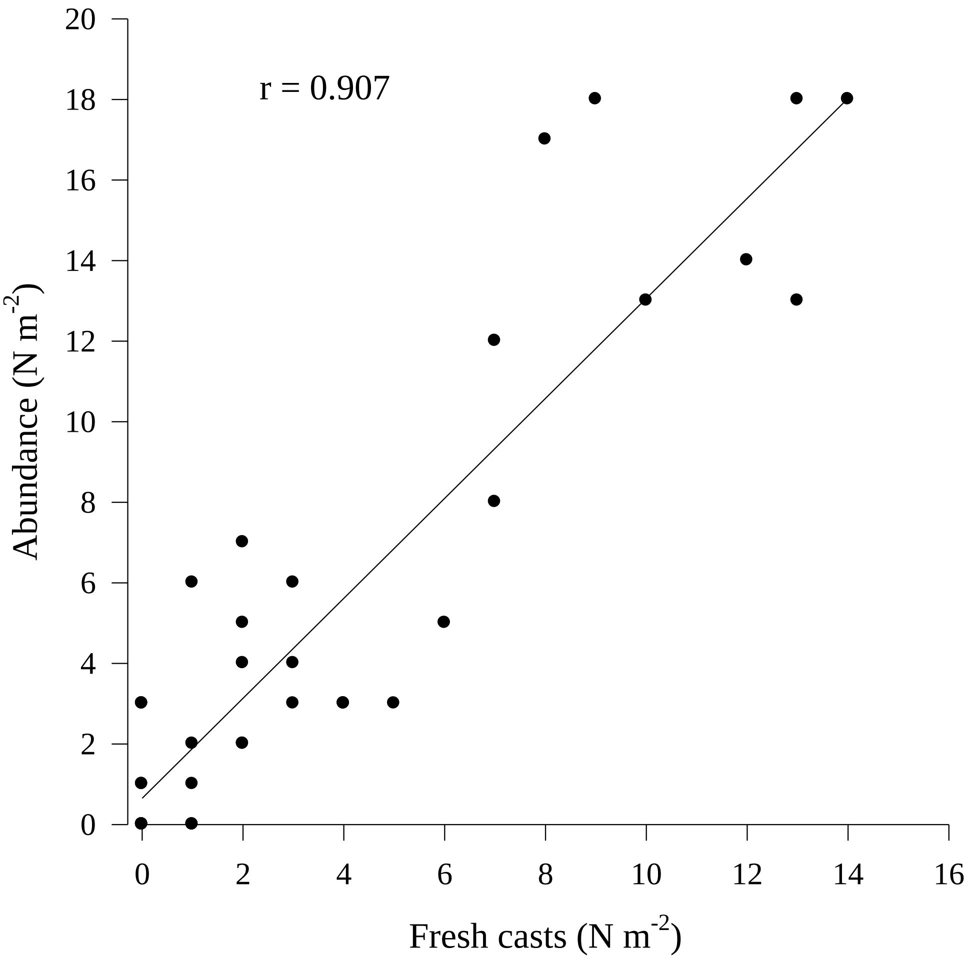
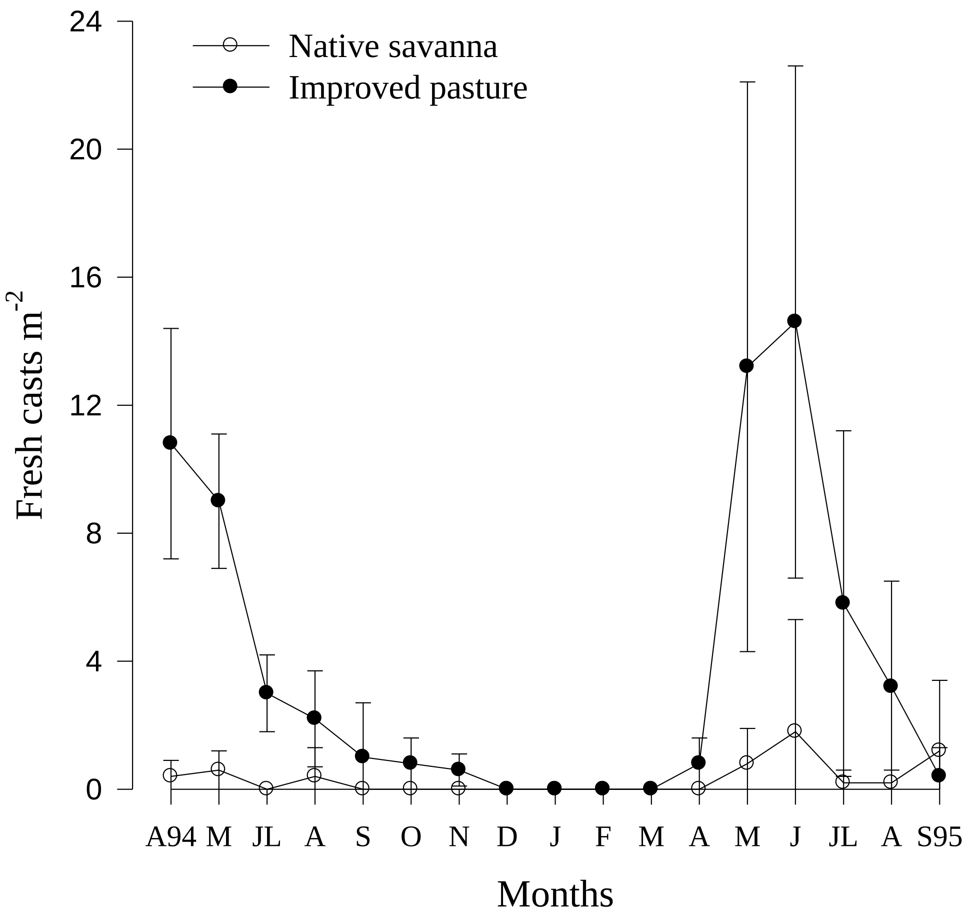

Savanna
Endogeics
83,2%
Epigeic
2,4%
Anecic
14,4%
Pasture
Endogeics
12,0%
Epigeic
0,1%
Anecic
87,9%

Figure 4



r = 0.907
Abundance (N m-2)
Fresh casts (N m-2)
0
2
4
6
8
10
12
14
16
18
20
0
2
4
6
8
10
12
14
16

Figure 5



24
20
16
12
8
4
0
Native savanna
Improved pasture
Fresh casts m-2
A94
M
JL
A
S
O
N
D
J
F
M
A
M
J
JL
A
S95
Months

Figure 6

Table 1

Ecosystem	EW biomass[1]	MC biomass	% EW biomass
Improved Pasture	51.1	62.5	82
Native Savanna	4.8	15.3	31
Gallery Forest	4.7	13.6	35
High-input annual crop	2.3	3.2	71

[1]g fresh weight m^{-2}

Table 2

	Native Savanna	Improved Pasture
Carbon (%)[†]	3.44 ± 1.67	3.41 ± 1.46
P (ppm) (Bray II)	1.26 ± 0.38	2.91 ± 2.22
P (ppm)*	3.85 ± 0.85	4.82 ± 2.04
pH	3.97 ± 1.55	4.97 ± 0.07
Al[1]	2.42 ± 0.12	1.90 ± 0.19
Ca[1]	0.36 ± 0.26	0.89 ± 0.20
Mg[1]	1.22 ± 2.43	0.33 ± 0.27
K[1]	0.32 ± 0.68	0.71 ± 1.37
H[1]	2.01 ± 2.17	1.44 ± 2.44
N total[2]	1538.87 ± 250.77	1670.37 ± 116.03
P total[3]	184.75 ± 8.74	226.75 ± 12.83
Texture	Clay	Clay

[†]Walkey-Black modified (with heat)
* Bray II modified
[1] milliequivalent x 100 g $soil^{-1}$
[2] p.p.m.
[3] μg g $soil^{-1}$
Average values from 8 samples ± standard deviation
CIAT analysis (D. K. Friesen and M. Rivera).
Date: September 1993

Table 3

Species	Family	Site[†]	Ecological category[‡]	Adult weight (g)[þ] Maximum	Average
Andiodrilus nov. sp.	Glossoscolecidae	NS, IP	Endogeic	2.50	1.3
Andiorrhinus nov. sp.	Glossoscolecidae	NS, IP	Endo-anecic	10.7	7.1
Andiorrhinus nov. sp. 2	Glossoscolecidae	NS	Endo-anecic	4.9*	-
Dichogaster nov. sp.	Octochaetidae	NS, IP	Epigeic	0.03	0.02
Epigeic nov. sp.	Glossoscolecidae	NS, IP	Epigeic	0.10	0.06
Glossodrilus nov. sp.	Glossoscolecidae	NS, IP	Endogeic	0.20	0.09
Martiodrilus carimaguensis nov. sp.	Glossoscolecidae	NS, IP	Anecic	25	11.2
Ocnerodrilidae nov. sp.	Ocnerodrilidae	NS, IP	Endogeic	0.013	0.006

[†] NS: native savanna, IP : improved pasture.

[‡] Anecic, live in the soil but feed on the soil surface; Epigeic, live and feed on the soil surface; Endogeic, live and feed in the soil. (After Bouché, 1972 and Lavelle, 1981, 1983)

[þ] in formalin

* Only one specimen

Table 4

	Native savanna	Improved pasture
March 1994	20.3 ± 1.4	22.7 ± 0.8
April	23.7 ± 0.8	24.6 ± 0.5
May	25.0 ± 1.0	24.5 ± 0.7
July	25.8 ± 1.3	25.1 ± 0.5
August	26.1 ± 1.1	25.3 ± 0.6
September	25.5 ± 1.0	24.5 ± 0.9
October	23.5 ± 1.0	23.5 ± 0.7
November	26.2 ± 1.4	24.7 ± 1.1
December	23.3 ± 1.0	22.7 ± 0.5
January 1995	17.8 ± 0.8	18.0 ± 1.0
February	16.5 ± 0.8	16.2 ± 0.5
March	20.7 ± 1.3	18.0 ± 0.6
April	21.7 ± 0.6	19.0 ± 0.7
May	24.6 ± 1.2	23.9 ± 1.0
June	26.4 ± 0.9	26.4 ± 0.8
July	25.6 ± 1.0	25.7 ± 1.7
August	25.2 ± 1.0	23.3 ± 0.5
September	24.9 ± 1.1	22.8 ± 0.2

[1] Average value and standard deviation

Table 5

Species	Savanna	Pasture
Andiodrilus n. sp.	2.3	5.0
	0.82	*2.39**
Andiorrhinus n. sp.	0	0.6*
	0	*1.78**
Epigeic n. sp.	13.1	6.6
	0.25	*0.15*
Glossodrilus n. sp.	50.1	51.2
	3.04	*4.43*
M. carimaguensis	0.2	18.2**
	0.47	*50.74***
Ocnerodrilidae n. sp.	14.9	22.6
	0.08	*0.13*

* $p < 0.05$
** $p < 0.001$

Table 6

Condition	Native savanna		Improved pasture	
	Wet season	Study period	Wet season	Study period
Dry	7.2 ± 3.5	6.4 ± 3.4	20.4 ± 7.9	17.4 ± 8.9
Fresh recent	0.3 ± 0.5	0.2 ± 0.5	3.2 ± 3.8	2.5 ± 3.6
Fresh non recent	0.1 ± 0.2	0.1 ± 0.21	1.8 ± 2.1	1.4 ± 2.0
Total	7.6 ± 3.6	6.7 ± 3.6	25.4 ± 10.3	21.2 ± 11.9

Table 7

Species	Ecological type	Adult weight (mg)	Cocoon weight (mg)	Fecundity	Cocoon weight /Adult weight	Reference
Millsonia lamtoiana	Epianecic	32000	320	3.1	0.01	Lavelle, 1978
Lampito mauritii	Epianecic?	1220	26	9.3	0.02	Senapati, 1980
Allolobophora longa	Anecic	2150	60	8	0.03	Evans and Guild, 1948
Lumbricus terrestris	Epianecic	5230	57.1	-	-	Evans and Guild, 1948
Martiodrilus carimaguensis	Anecic	9580	1804	0.49	0.19	This study

Table 8

Locality	Savanna category	Rainfall (mm)	Duration of study (months)	Surface sampled (m^2)[1]	Depth (cm)[2]	Extraction method[3]	Numbers (ind. m^{-2})	Biomass (g. wet wt. m^{-2})	Reference
Berhampur, Orissa (India)	*Cynodon dactylon* and *Hygrorhiza* sp. grasslands	1250	18	11.3	20	HS	64-800	30.2	Dash and Patra (1977)
Sambalpur, Orissa (India)	grazed irrigated pasture	1343	13	4.1	40	WS	17.4	41.0	Senapati (1980)
	ungrazed irrigated pasture	1343	19	5.9	40	WS	24.7	56.0	Senapati (1980)
Lamto (Ivory Coast)	grass savanna	1183	24	288 + 23.04	60	HS, WS	188	38.0	Lavelle (1978)
	shrub savanna	1183	24	288 + 23.04	60	HS, WS	287	48.6	Lavelle (1978)
	unburnt shrub savanna	1276	12	288 + 23.04	60	HS, WS	400	35.9	Lavelle (1978)
Carimagua (Colombia)	*Andropogon* spp. savanna	2280	18	88 + 7.04	50	HS, WS	58.0	5.0	This study
	grazed pasture	2280	18	88 + 7.04	50	HS, WS	96.9	62.1	This study

[1] When two different extraction methods have been used on two different soil samples, the second number indicates surface layer extracted by the washing method.
[2] At Carimagua the soil depth varied across time to a maximum of 90 cm in the dry season.
[3] Hand-sorting (HS) or washing-sieving (WS) techniques.

1

Table 9

	Ecosystem	Density N m^{-2}	Biomass g m^{-2}	Nº of spp.	Epigeics % D	Epigeics % B	Endogeics % D	Endogeics % B	Anecics % D	Anecics % B
Carimagua	Pasture	96.4 (24-215.8)	62.2 (29.2-110.4)	7	1.9	0.1	79.8	12.0	18.3	87.9
	Savanna	57.8 (10.8-135.8)	5.0 (0.7-11.5)	8	6.8	2.5	92.8	83.2	0.4	14.3
Humid tropics[1]	Pasture	310 (93-740)	59.7 (0.6-153)	6.5 (2-9)	0.75	1.75	99.25	98.25	0	0
	Savanna	236 (187-286)	44.1 (38-50.1)	8 (8)	3.5	6.5	96.5	93.5	0	0

[1] Source: Fragoso (1992)