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Population dynamics and adaptive strategies of *Martiodrilus carimaguensis* (Oligochaeta, Glossoscolecidae), a native species from the well-drained savannas of Colombia

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Abstract

Martiodrilus carimaguensis (Oligochaeta, Glossoscolecidae) is a large, anecic native earthworm species which was found in natural and disturbed savannas in the Oxisols of the Colombian Llanos. Its population dynamics were studied in a native savanna, and in a 17 years old grazed grass-legume pasture where density and biomass were higher. Monthly cast deposition on the soil surface in the improved pasture was 38.4×10^3 fresh casts ha^{-1}, eleven times more than in the native savanna. A strong relationship was found between numbers of *M. carimaguensis* and numbers of fresh surface casts. Different patterns of adaptation to the dry season were observed for adults and juveniles. Adults are active for eight months whereas juveniles enter diapause 3–4 months earlier. The vertical distribution pattern of the earthworm population also shows marked seasonal changes. © 1998 Elsevier Science B.V.

Keywords: Population dynamics; Adaptive strategies; *Martiodrilus carimaguensis*; Oligochaeta; Glossoscolecidae; Savannas

1. Introduction

There is a lack of information on the biology of tropical earthworms (Dash and Patra, 1977; Lavelle, 1978). Of the few species which have been fully studied in both temperate and tropical ecosystems, most have been introduced by man, e.g., *Pontoscolex corethrurus* Müller and *Dichogaster bolaui* (Michaelsen). In most disturbed areas local earthworm communities disappear, being displaced by introduced species (Lavelle and Pashanasi, 1989; Lavelle et al., 1987; Bohlen et al., 1995).

However, less attention has been paid to the role of those native earthworm species that are well-adapted to perturbation of natural ecosystems. In Carimagua, man-made pastures derived from natural savannas retained their original earthworm biodiversity and their biomass increased from 4.8 g fresh weight m^{-2} in the native savanna to 51.1 g fresh weight m^{-2} (Decaëns et al., 1994). One species, *Martiodrilus carimaguensis* (Jiménez et al., in press) has been greatly favoured by this land use, increasing significantly in abundance and biomass (P<0.001).

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M. carimaguensis is a large anecic earthworm species belonging to the family Glossoscolecidae, with an average adult size of 9.3 mm in diameter and 194.3 mm in length and a fresh weight of 11.2 g (in 4% formaldehyde) (n=29). Its body colour is dark-grey on the dorsal side and light-grey on its ventral side (Jiménez et al., in press).

2. Materials and methods

2.1. Study site

The study area is located at the CIAT-CORPOICA (Centro Internacional de Agricultura Tropical and Corporación Colombiana de Investigación Agropecuaria agreement) Carimagua Research Station, in the well-drained isohyperthermic savannas of the Eastern Plains of Colombia (4°37′ N and 71°19′ W and 175 m altitude). Average annual rainfall and temperature are about 2280 mm and 26°C, respectively, with a dry season from December to March. Soils are of two types: predominant low-fertility Oxisols in the upland ('altos') and Ultisols in the low-lying ('bajos') savannas. The former are characterized by their acidity (pH (H_2O) 4.5), a high Al saturation (>90%) and low values of exchangeable Ca, Mg and K. Chemical factors that contribute to acid–soil infertility and subsequent effects on plant growth are complex and include Al toxicity, low content of available P and low rates of N mineralization (Rao et al., 1993).

Two different and contrasting systems were evaluated: a native savanna (NS) without management, in which the predominant plant species were *Andropogon bicornis*, *Gymnopogon* sp., *Panicum* sp., *Trachypogon* sp., *Imperata* sp., and a 17 year old grazed improved pasture (IP) comprising an exotic African grass, *Brachiaria decumbens* cv. Basilisk, and a tropical forage herbaceous legume species, *Pueraria phaseoloides* CIAT 9900 ('kudzu').

2.2. Earthworm sampling

One 90×90 m plot was selected in each system and divided into 10×10 m regular quadrats. Earthworms were hand-sorted monthly from five 1×1×0.5 m soil monoliths (after Lavelle, 1978) taken at random from within five randomly-chosen quadrats in each plot. The sampling depth was varied seasonally to take into account the vertical migration of this species. The sample was split into 10 cm layers and earthworms collected from each layer were washed in water and fixed in 4% formalin. They were separated in the laboratory into adults (with clitellum and associated glands) and juveniles (lacking clitellum and glands), counted and weighed. Cocoons obtained were also counted and weighed.

2.3. Surface cast deposition

As an anecic species, *M. carimaguensis* has the ability to deposit large tower-like casts, up to 15 cm in height, on the soil surface. In both systems these surface casts, which are easily distinguished from other depositions, were counted in two monthly randomly-chosen 1 m^2 samples and classified into two broad categories, fresh and dry. Casts were oven-dried at 60°C for 72 h and weighed.

3. Results

3.1. Density and biomass

The mean population density of *M. carimaguensis* ranged from 0 in November 94 to 0.6 m^{-2} in September 95 in the natural savanna, and from 11 m^{-2} (September 94) to 23.2 m^{-2} (May 95) in the improved pasture (Fig. 1). The highest densities were recorded at the beginning of the rainy season and the increase in numbers in October 94 was due to the hatching of new juveniles. The average densities in the improved pasture and native savanna, respectively, were 17.9 m^{-2} and 0.2 m^{-2}.

Earthworm biomass ranged from 0.24 g m^{-2} (March 94) to 8.76 g m^{-2} (September 95) in the native savanna, and from 26.5 g m^{-2} (January 95) to 94.8 g m^{-2} (May 94) in the improved pasture (Fig. 1), the mean values being 0.6 g m^{-2} and 52.6 g m^{-2} in the two habitat types. A significant correlation was found between monthly values of biomass and precipitation in the improved pasture (r=0.821; P<0.01), but not in the native savanna. The highest values of biomass appeared at the onset of the wet season when all the population was active.

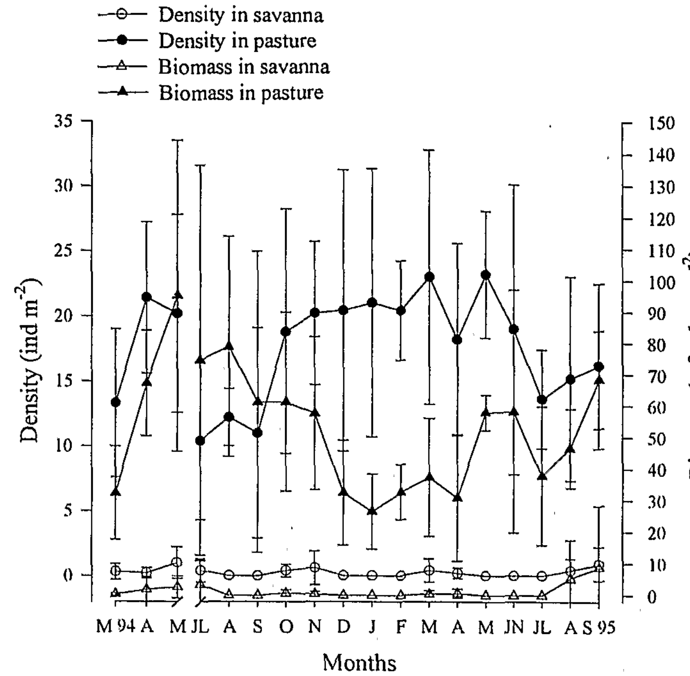

Fig. 1. Abundance and biomass (±S.D.) of *M. carimaguensis* in the native savanna and improved pasture.

In July–August there was a reduction in biomass due to the inactivation of juveniles. At the end of the rainy season values of biomass declined by 50% as adults went deeper into the soil to become inactive after emptying their guts.

In the native savanna, *M. carimaguensis* comprised up the 15.1% of the total earthworm biomass, while in the improved pasture this value rose to 85.1%. The remainder of the biomass was contributed by five other native species, four endogeics and one epigeic.

No relationship was found between average monthly numbers of individuals and soil moisture, but significant correlations were observed between soil moisture and biomass (r=0.651; P<0.01) and the percentage activity of the overall population (r=0.673; P<0.01).

3.2. Surface cast production

On average, fresh cast production in the improved pasture was eleven times greater than in the native savanna (Table 1). The total dry weight of earthworm casts collected during one year in the native savanna

Table 1
Monthly average production of casts by *M. carimaguensis* per m^2 (numbers±S.D.) in the two systems

Condition	Native savanna		Improved pasture	
	Wet season	Study period	Wet season	Study period
Dry casts	7.15±3.5	6.38±3.4	20.38±7.9	17.35±8.9
Recent fresh casts	0.31±0.5	0.23±0.5	3.25±3.8	2.48±3.6
Non recent fresh casts [a]	0.12±0.2	0.09±0.21	1.77±2.1	1.39±2.0
Total	7.58±3.6	6.72±3.6	25.43±10.3	21.21±11.9

[a] Fresh casts dry underneath.

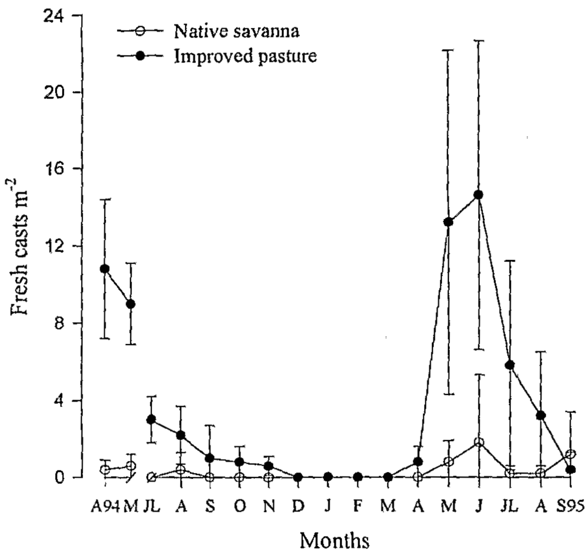

Fig. 2. Monthly average numbers (±S.D.) of fresh *M. carimaguensis* casts per m^2.

was 31.3 Mg ha^{-1}, while in the improved pasture it was 37.7 Mg ha^{-1}.

Both average monthly fresh cast and total cast production were significantly higher ($P<0.01$, t-test) in improved pasture than in native savanna, reflecting the differences in abundance of *M. carimaguensis* (Fig. 2). Fresh cast production declined during July 94 and July 95 when all the juveniles had already descended some tens of cms to enter diapause and only adults remained active. A positive correlation between numbers of fresh casts and the density of individuals in the first 10 cm was observed in the improved pasture ($r=0.907$; $P<0.01$).

3.3. Vertical distribution

M. carimaguensis was too scarce to establish patterns of vertical distribution in the native savanna, and data are only available for the improved pasture (Fig. 3). The population occurred at an average depth of 30.1 cm in the pasture, with a minimum in May (13.5 cm) and a maximum during the summer (47.6 cm). More than 50% of the total population was located in the top 30 cm and in the wet season more than 80% of individuals were close to the surface where the organic matter content is higher. Cocoons were laid at a depth of 20 to 50 cm.

3.4. Adaptation to the dry season

M. carimaguensis showed interesting behaviour, with a true diapause, although different patterns were found between adults and juveniles. The latter were only active for four months, from April to July, so they entered diapause much earlier than adults which remained active until December (for 8 months). Inactivation occurred after the individuals went down to 60–110 cm. Each individual built an aestivating chamber at the end of its semi-permanent burrow in which it coiled itself up, after emptying its gut, and ceased activity until the onset of the wet season. The end of the burrow was usually sealed with several septae to avoid loss of tegumental moisture, which is vital to support a minimal rate of respiration. The degree of activity during the whole study period is shown in Fig. 4. In the second year of study there seemed to be a delay in resumption of activity as the rainfall in April 95 (155.7 mm) was very similar to that in March 94 and only ca. 60% of the population was active. By May 95 the entire population was active again.

3.5. Reproductive strategy

In August, after juveniles became inactive, adults started the reproductive period and one month later the first cocoons were deposited at a depth of 20–50 cm. Cocoons collected in the field, nearly always from pasture sites, and incubated under laboratory conditions were found to have a maximum incubation period of 48 days. The incubation time was long compared to other tropical earthworms since they are exposed to minimal environmental fluctuations at that depth.

The cocoons were yellowish, becoming slightly brown just before hatching, oval in shape (25×15 mm) and weighing on average 1804 mg. Two individuals (1.91±0.3 S.D., $n=46$), with an average weight of 760 mg, hatched out from each cocoon and rapidly burrowed down to enter diapause.

The fecundity (number of cocoons per adult per year) was somewhat low (ca. 0.49) though the cocoon weight: adult weight ratio was 0.19, the highest ever recorded in temperate or tropical ecosystems. A single cocoon peak was observed in August 94, just after juveniles descended into the deeper soil layers and adults started the reproductive period (Fig. 5).

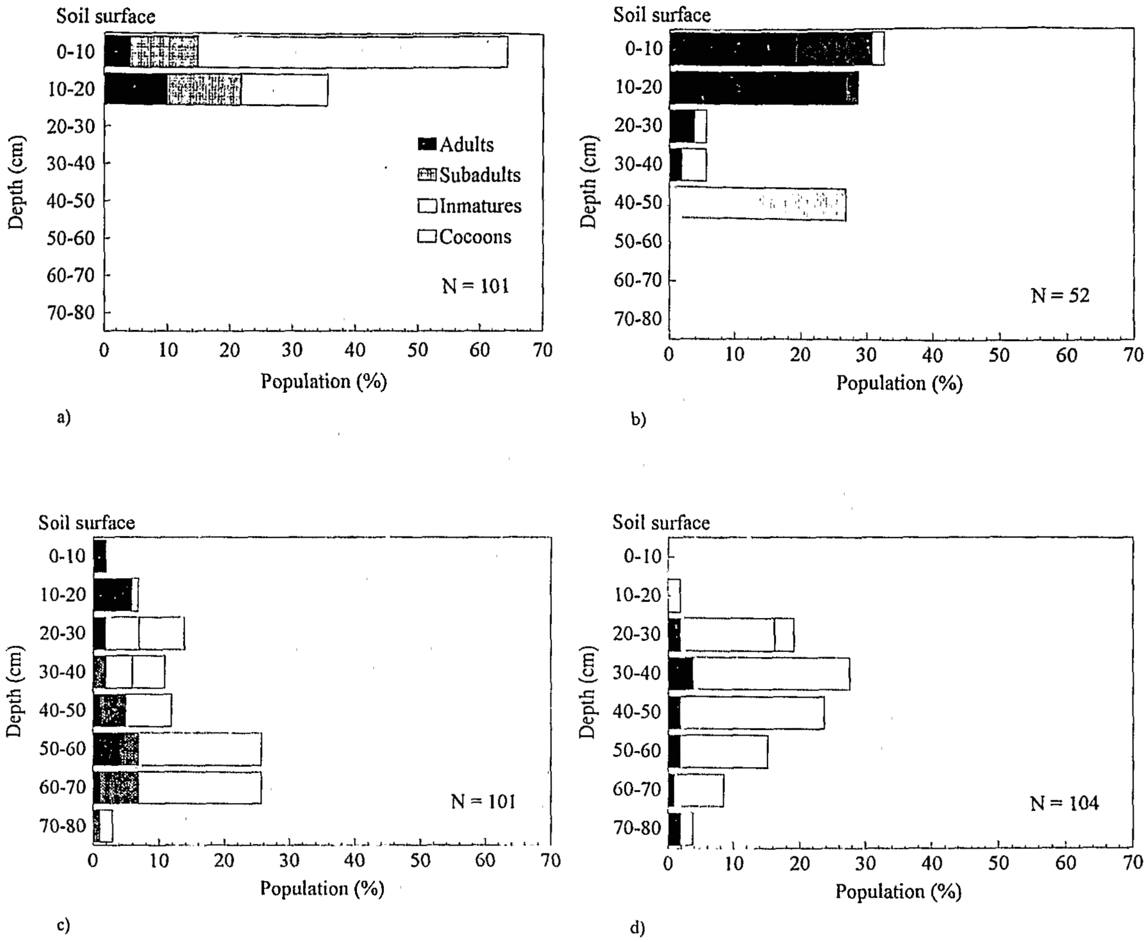

Fig. 3. Vertical distribution of *M. carimaguensis* in improved pasture in May 1994 (a), July 1994 (b), November 1994 (c) and January 1995 (d).

4. Discussion

There is little information on the population dynamics of anecic species in other comparable sites. The anecic species *Millsonia lamtoiana* (Omodeo and Vaillaud, 1967) ranged in density from 0.02 to 1.43 ind. m^{-2}, and in biomass from 0.01 to 8.43 g fresh weight m^{-2} in the savannas of Lamto, Ivory Coast (Lavelle, 1978), very similar values to those obtained in the present study. Soil moisture is the most important of all environmental variables for earthworms in tropical soils (Lavelle, 1983). Garnsey (1994) also reported a correlation between earthworm biomass and soil moisture in the Midlands of Tasmania.

M. carimaguensis has a patchy distribution pattern with high density spots alternating with low density areas (Jiménez, unpublished). There is strong evidence for vertical migration of this species during unfavourable conditions, with the population as a whole reaching 80 cm depth before the onset of the summer. The ability to aestivate before the onset of summer and to construct deep semi-permanent burrows explains why the population is less affected by drought and is able to maintain its density during the dry season. Earthworm aestivation has been observed throughout temperate regions (Evans and Guild, 1948; Nordström, 1975; Anderson, 1980), in Africa (Madge, 1969) and in Australia (Garnsey, 1994), but this is the

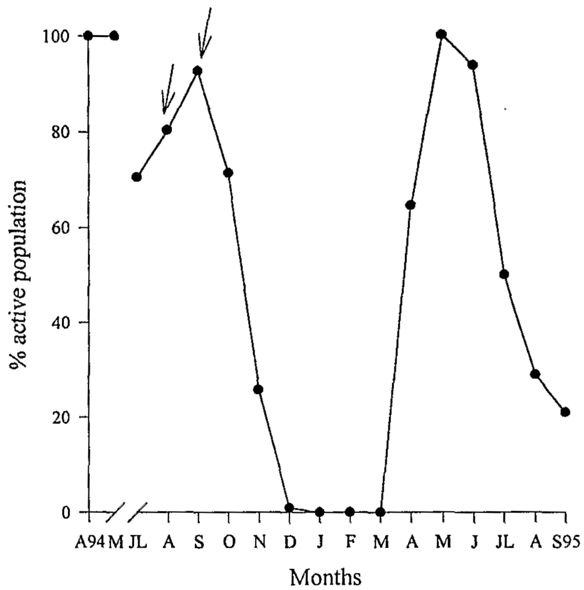

Fig. 4. Activity of the total population of *M. carimaguensis* in improved pasture (arrows indicate months with underestimated values).

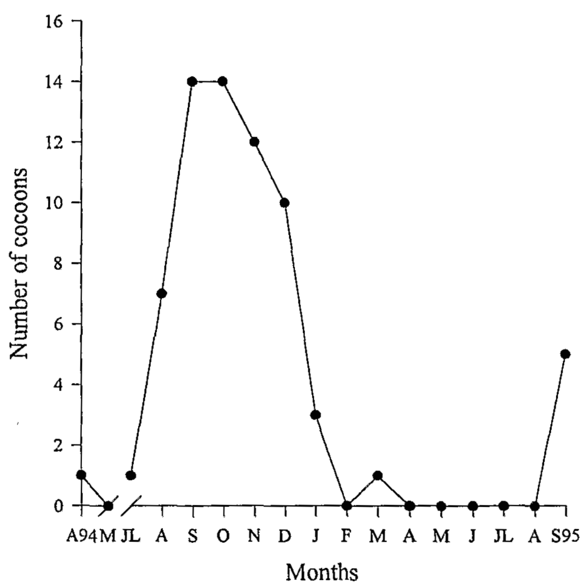

Fig. 5. Numbers of cocoons obtained monthly in five 1 m^2 samples from improved pasture.

first time it has been studied in South American glossoscolecid earthworms.

Soil surface casting activities have been reported by Madge (1969) and Lavelle (1978), although there are few reports dealing with cast production by earthworms in agroecosystems (Bhadauria and Ramakrishnan, 1989). Watanabe and Ruaysoongnern (1984) reported 24.5 Mg ha^{-1} $year^{-1}$ of cast material, less than obtained here in both systems, and 15.7–40 Mg ha^{-1} $year^{-1}$ in five and 15 year old fallows, respectively (Bhadauria and Ramakrishnan, 1989).

When the N content of soil is high the C/N ratio is reduced, and in soils with low C/N ratios earthworm densities may decline (Kale and Krishnamoorthy, 1981). But pastures at Carimagua are also introducing C into the soil (Fisher et al., 1994) so the C/N ratio becomes higher and this may, subsequently, be related to an earthworm increase. The C/N ratio in the savannas is 25, and the C/N ratios for tropical pastures with and without legumes are 30 and 35, respectively (Fisher, pers. comm.).

Grasslands are known to support high earthworm populations and biomass (Lee, 1985; Syers and Springett, 1983). Litter composition is the primary factor determining these high values (Cuendet, 1984; Mishra and Ramakrishnan, 1988). Differences in the litter quality, and large inputs of cattle dung which is rapidly incorporated into the soil by this species and dung beetles, may also be factors responsible for the enhancement of *M. carimaguensis* activity in improved pastures.

The anecic behaviour of *M. carimaguensis* is likely to be of great importance in regard to the cycling of carbon and nutrients in grass–legume pastures which need the nitrogen input provided by the legume. It has also been observed that grass and legume roots colonize the casts that are in the burrows, and that a small ocnerodrilid oligohumic earthworm feeds upon these casts (Jiménez et al., 1994). The interrelations among earthworms, casts in burrows and roots located very close to these casts in the soil profile, and the role of earthworms in carbon and nutrient cycling in grass–legume pastures generally, merit further study.

Despite the low density of this species and the low number of fresh casts in the native savanna, the weight of total casts collected during one year does not differ much from that in improved pasture. Perhaps in the latter system the high activity of earthworms leads to a reingestion of their own casts, after a microbial incubation has occurred (Swift et al., 1979).

Finally, improved pastures have greatly enhanced soil micro- and macrobiological activity which in turn improves chemical and physical properties, i.e., soil quality parameters. Recent studies at Carimagua are considering the possibilities of management in agricultural plots where zones of great earthworm activity, i.e. improved pastures, are placed adjacent to annual crops in order to facilitate the spread of populations and colonization of those systems. Since Lavelle et al. (1994) have provided a better understanding of local soil faunal activities and the potential use of native species in tropical agroecosystems, we suggest that further studies should take into account the influence of such activities on both physical and chemical soil properties.

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