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A SIMULATION MODEL OF VERTICAL MOVEMENTS OF AN EARTHWORM POPULATION (*MILLSONIA ANOMALA* OMODEO, MEGASCOLECIDAE) IN AN AFRICAN SAVANNA (LAMTO, IVORY COAST)

SERGE MARTIN[1] and PATRICK LAVELLE[2]*

[1]Ministère de l'Environnement, 14 boulevard du Général Leclerc, 92524 Neuilly-sur-Seine and
[2]Laboratoire d'Ecologie, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris Cedex 05, France

Summary—The conception and realization of the model DRILOTROP originated from the will to synthesize the knowledge accumulated on dynamics and effects on soil properties of populations of *Millsonia anomala*. Gaps in our knowledge have been identified and new hypotheses regarding the role of earthworms in savannas have been formulated.

Vertical movements of earthworms are determined by abiotic (i.e. soil moisture and temperature) and biotic factors (i.e. individual behaviour); these factors combine their effects to determine movements of the whole population. The relative contribution of these factors to the determinism of vertical movements have been calculated using mathematical optimization techniques. The effects of vertical movements and individual variability on dynamics of a population are discussed.

INTRODUCTION

The purposes of several models were to (1) synthesize the knowledge concerning earthworms and test its coherence, (2) better understand physical and biological processes in soil.

Reichle (1971) modelled carbon flow through an earthworm population in a temperate forest of the U.S.A. Mitchell (1983) simulated population dynamics of *Eisenia fetida* and its effects on waste conversion. Bouché and Kretzschmar (1977) conceived a conceptual model of the role of earthworms in soil. Lavelle and Meyer (1983) constructed the model "Allez-les-Vers" which describes population dynamics of the geophagous tropical earthworm, *Millsonia anomala*, and is based on the instantaneous description of each worm or cocoon.

The model Allez-les-Vers allowed to better understand the determinism of mortality, reproduction and growth of *M. anomala*. However, it has not been possible to use this model to simulate the role of earthworms in soil because of imperfection in the formulation of their vertical movements.

The vertical movements model, which is the object of this paper, is a submodel of the model DRILOTROP (=tropical drilosphere). The later model was derived from the model Allez-les-Vers to simulate the functioning of the drilosphere system in soils. The vertical movements model constitutes one of the major improvements of the model DRILOTROP in comparison with the model Allez-les-Vers.

*Author for correspondence.

THE MODEL DRILOTROP

The model DRILOTROP is based on miscellaneous studies realized in the Lamto savannas (Ivory Coast) and, particularly, on the ones about the earthworm *M. anomala* (Lavelle, 1971, 1978). This species represents 50–75% of the earthworms biomass according to the different facies of savanna.

General characteristics of the model

The model is fundamentally determinist. However, it contains several stochastic processes. Most of the equations are non-linear. The model is written in FORTRAN.

General structure of the model

System states variations are discrete. Iteration interval is of 1 day. Every simulation runs over 1 yr.

Every earthworm constitutes one separate entity. The set of cocoons which were produced by a single worm and during a single reproduction period are also considered as an entity, called "incubation".

Each entity is represented in the computer memory by a set of consecutive words corresponding to the different attributes taken into account.

Soil is considered as horizontally homogenous. Hydric and thermal soil profiles are simulated daily by a model specially designed by Clément (1980). Organic matter profile is constant.

After an initialization period, at the beginning of the simulation, the program calculates, each day, the changes in attributes of every entity (Fig. 1).

After every iteration, entities are counted.

Every 10 days, the program gives detailed pictures of the population as well as of the value of the

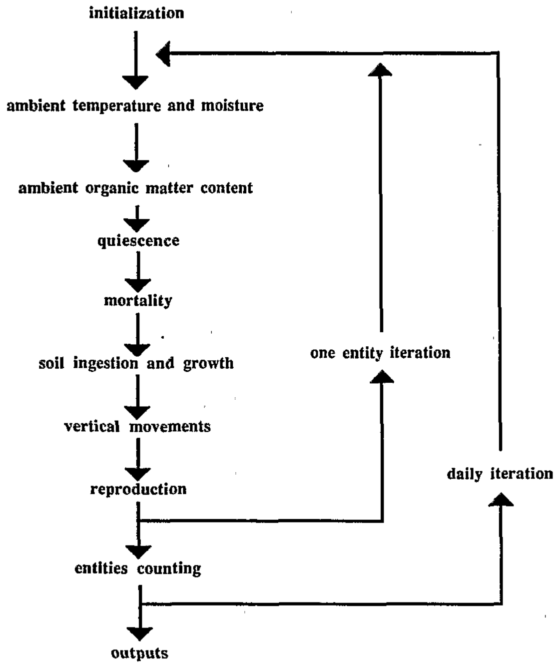

Fig. 1. General structure of the model DRILOTROP.

main parameters of its functioning: density, biomass, structure, tissular production and soil ingestion.

THE VERTICAL MOVEMENTS

A priori, we had considered that everything occured as if *M. anomala* was looking for places where conditions were optimum and was led by the gradients. Further in this paper, we shall explain why, and how, we had to complete this point of view.

Horizontal movements of earthworms were neglected in the model DRILOTROP because (1) field observations show that worms move laterally over very short distances (Lavelle, 1971; Mazaud and Bouché, 1980) and (2), since soil is considered as horizontally homogenous, horizontal movements would not change the environment of the worms.

The environmental factors affecting vertical distribution of M. anomala

The environmental factors which influence earthworms behaviour are (Lee, 1985):

food supplies
moisture
temperature
oxygen and carbon dioxide concentrations for respiratory exchange
light
soil texture
pH and electrolyte concentrations.

Among these factors, we retained the first three ones—food supplies, moisture and temperature—likely to affect vertical distribution of *M. anomala*. We do not have any information about the role of the next two factors. The last two are almost constant in the soil horizons inhabited by worms.

The preferences

The moisture. The moisture preference is the moisture content value under which laboratory determinations indicate that feeding is at a maximum (Lavelle and Meyer, 1977).

The temperature. The temperature preference was determined by the same way as the moisture preference (Lavelle, 1978). These two preferences depend on earthworms weights.

The food supplies. Earthworms are assumed to be seeking the highest organic matter content, in the topsoil.

The mathematical formulation

The search for the optimum. For every worm, the daily search for the optimum is the resultant of three components: (1) and (2) the moisture and temperature gradients produce, each, a vertical movement proportional to the difference between the optimum value and the ambient value, (3) the organic matter content gradient results in a constant vertical movement towards the surface. These movements are daily means.

When the optima of an earthworm are not located at the same depth, the earthworm is placed in a conflict of motivations (Cabanac, 1984, 1989). The resulting vertical movement of the earthworm is its behavioral response in this process.

The individual factor. Until now, we have considered that all the worms of the same weight behaved the same way in given conditions and that their movements were just led by their common optimum. It is obvious that such a situation does not actually occur. Field observations indicate that worms of different weights may be found at the same place, even if, on an average, large worms are found deeper than small ones. Moreover, laboratory experiments (Lavelle, pers. commun.) showed wide incursions of worms into zones with a very low organic matter content when temperature and moisture were optimum everywhere.

We did not find any accurate experimental data about the determinism of individual migratory behaviour of earthworms. We introduced a fourth component, which may be called random component, for their vertical movements. This component produces a daily movement, upwards or downwards, for every worm. The amplitude of this movement is comprised between zero and a maximum which is proportional to the amount of soil ingestion by the worm during the day. By this way, we expressed that the amplitude of individual movements of earthworms depends on the amount of ingested soil but that its direction is random.

The resulting movement. The previous consideration may be synthesized in the following equation:

$$(\text{daily vert.}^1\ \text{mov.}^t) = \frac{f_{1(\text{moist. grad.})} \times |(\text{ambient moist.}) - (\text{optimum moist.})|}{K_1}$$
$$+ \frac{f_{2(\text{temp. grad.})} \times |(\text{ambient temp.}) - (\text{optimum temp.})|}{K_2}$$
$$+ f_{3(\text{OM content grad.})} \times K_3$$
$$+ f_{4(\text{worm, day})} \times (\text{daily soil ingestion}) \times K_4.$$

The functions f_1, f_2 and f_3 take the values -1, 0 or $+1$ according to the directions of moisture, temperature and organic matter content gradients.

Each day and for every worm, the function f_4 takes a random value which is uniformly distributed between -1 and $+1$.

The values of the parameters K_1, K_2, K_3 and K_4 measure the respective importances of the four components we distinguished for the vertical movements. No experimental data allowed us to directly determine these parameters. Consequently, we evaluated them by calibration of the model DRILOTROP. We attempted to minimize the differences between the weight structures of simulated populations and the ones of observed populations.

Obviously, this problem does not have any algebraic solution. We used an iterative optimization technique, the SIMPLEX technique (Daniels, 1978).

We found the following values for the four parameters:

$$K_1 = 11\ \text{cm}^{-1}$$
$$K_2 = 9.7°\text{C cm}^{-1}$$
$$K_3 = 0.66\ \text{cm}$$
$$K_4 = 0.185\ \text{cm g}^{-1}.$$

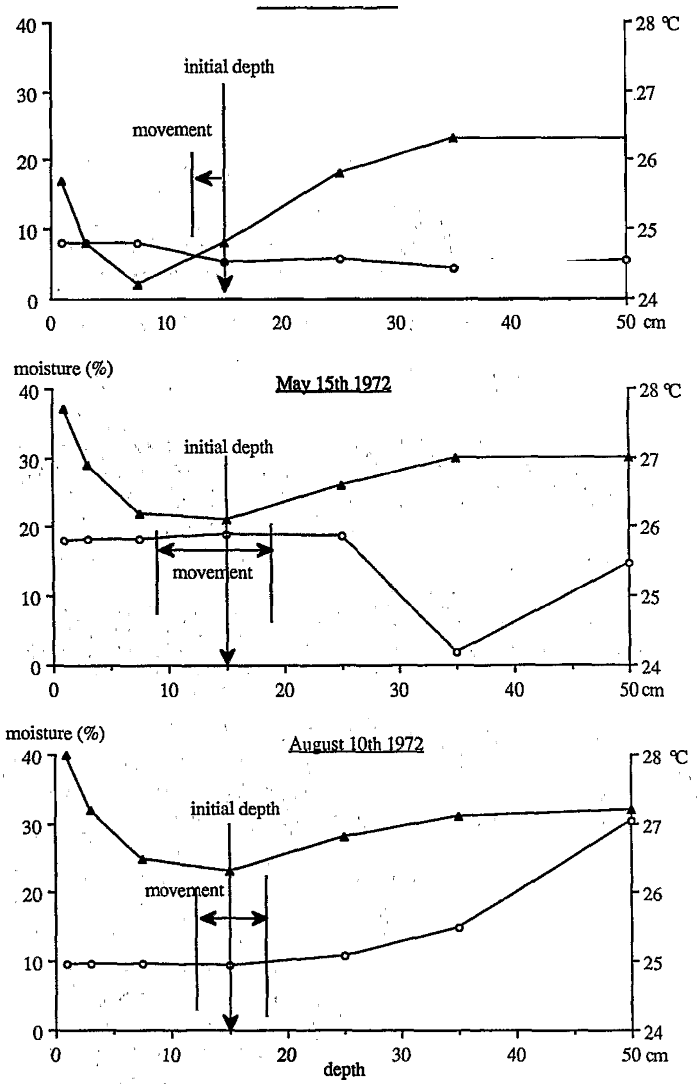

Fig. 2. Three examples of daily vertical movements. (○) Soil moisture; (▲) soil temperature.

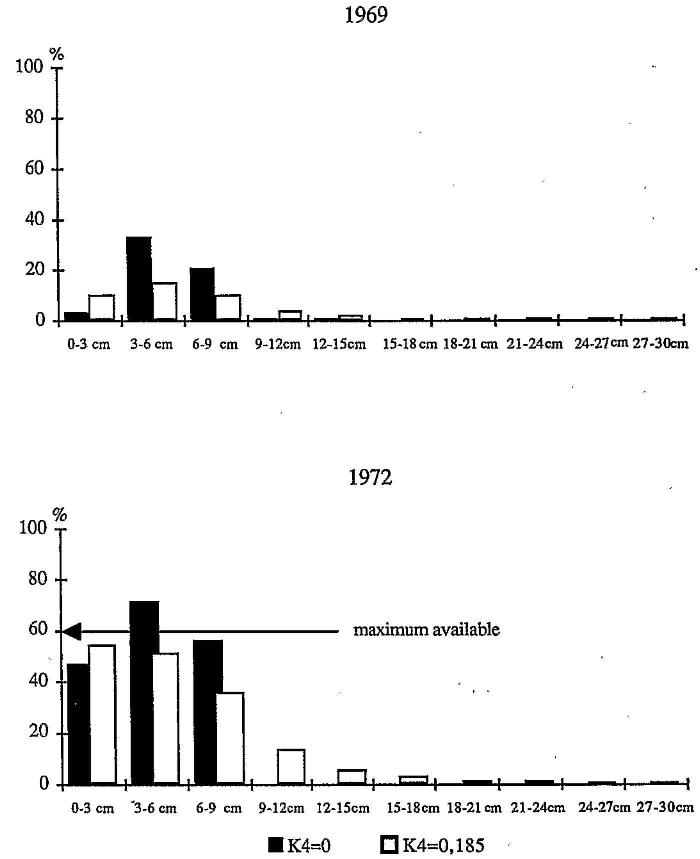

Fig. 3. Vertical distribution of annual soil ingestion (expressed in percent of the amount of colonized soil), with and without random individual movement.

RESULTS OF THE SIMULATIONS

Three examples of daily vertical movements (Fig. 2)

On 15 January 1972, during the dry season, consider an earthworm weighing 2.5 g and 15 cm deep in the soil. According to its weight, its temperature preference is equal to 25°C and its moisture content preference is 19.5%. Ambient temperature is equal to 24.7°C and ambient moisture content to 5.3%. In the topsoil, moisture content reaches 8%. Let us assume that this worm is still active despite the great probability it had entered a state of quiescence. It is almost at its temperature optimum. On the other hand, the low moisture content is very unfavourable and the daily amount of ingested soil is not higher than 2.4 g.

The worm will move upwards 1.3 cm by the effect of moisture content gradient and another 0.7 cm by the effect of organic matter content gradient. On the other hand, temperature will not influence its behaviour. The random individual vertical movement may vary up to 0.5 cm.

Finally, during this day, the earthworm will move upwards over a distance included between 1.5 and 2.5 cm. On this day, earthworms are not very active and they try to reach the topsoil layers that dew makes less dry.

Now, let us consider an earthworm weighing 2.5 g, 15 cm deep in the soil, on 15 May 1972, i.e. in the middle of the first wet season. Ambient temperature is equal to 26.1°C and ambient moisture content to 18.9%. The worm is at its temperature optimum and near its moisture optimum. It will ingest 28 g of soil during the day.

The upward movement due to organic matter content gradient will be equal to 0.7 cm and the random individual vertical movement will be equal to, at most, 5.2 cm.

At the end of the day, this worm will be between 9.1 and 19.5 cm deep. In this situation, climatic conditions do not affect the worm's behaviour and vertical distribution is only related to food search.

Lastly, let there be an earthworm, still weighing 2.5 g and 15 cm deep but on the 10 August 1972, during the little dry season. The topsoil is dry but the deeper layers remain wet. Ambient moisture content is equal to 9.3% and ambient temperature to 26.3°C. Temperature fits the worm but moisture content is too low. Daily soil ingestion will be equal to 17.4 g.

The vertical movement of this worm will be the resultant of (1) a downward component due to moisture content gradient, equal to 0.9 cm, (2) an upward component due to organic matter content, equal to 0.7 cm and (3) the random individual component at most equal to 3.2 cm.

Table 1. Annual values of demographic parameters in function of K_4 values (means on 10 simulations)

	1969		1972			
	$K_4=0$	$K_4=0.185$	$K_4=0$	$K_4=0.185$	$K_4=0.24$	$K_4=0.3$
Soil ingestion (T/ha/yr)	205	159	709	666	632	494
Mean annual biomass (Kg/ha)	88	65	309	256	240	192
Mean annual population size (worms/10 m^2)	80	65	255	233	178	142
Annual mortality (worms/10 m^2/yr)	137	149	385	272	267	283
Annual reproduction (worms/10 m^2/yr)	197	104	422	298	192	70

At the end of the day, the worm will be between 12 and 18.4 cm deep.

In these miscellaneous examples, vertical movements due to environment are small in comparison with the random individual component. Their role rather seems to allow worms to escape very unfavourable conditions than to make them follow the fast vertical fluctuations of their preferences.

Interpretation of the parameter K_4 (random individual component of vertical movements)

In order to better understand the significance and the effects of the random individual component of vertical movements, we gave several values to the parameter K_4, including zero value. Then we tried to interpret the outputs of the model DRILOTROP. Results, which are means calculated on ten simulations, are presented in Table 1.

Initially, we thought that the random individual component might constitute a factor of stability for the whole population by sharing the hazards in case of fast climatic changes.

However, a comparison between results obtained with $K_4=0$ and $K_4=0.185$ does not bring any element to strengthen this hypothesis.

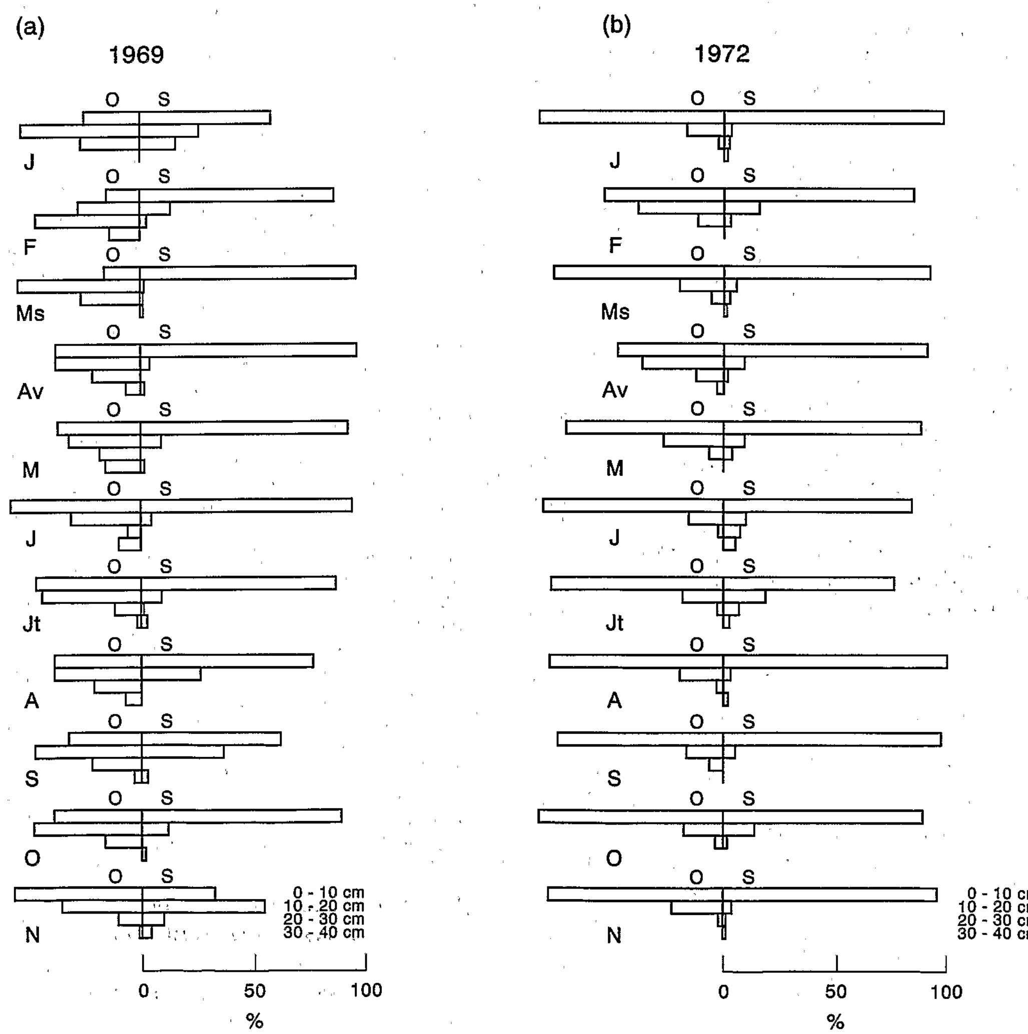

Fig. 4. Monthly vertical distributions of *M. anomala* for the years 1969 and 1972 (observed and simulated).

On the contrary, mean annual population size and mean annual biomass are highest with $K_4 = 0$, as well for the year 1972 as for the year 1969.

When the value of K_4 is increased, as in 1972, mean population size, mean biomass, reproduction and ingested soil amount decrease. Mortality remains the same in absolute value.

So, the significance of the parameter K_4 does not distinctly appear through the demography of simulated worms populations.

The answer rather seems to be within vertical distribution of soil ingestion. Figure 3 shows that vertical distribution of soil ingestion repartition is clearly different with and without random individual vertical movement.

These simulations show that, during the year 1972, without random individual vertical movements, worms would have exclusively ingested soil in the 0–12 cm soil layer, with a maximum of 73% of the soil in the 3–6 cm soil layer.

The results of Blanchart (1990) indicate that *M. anomala* cannot eat more than 60% per year of the soil that it colonizes because it does not re-ingest soil which is still structured in casts.

Thus, the random individual vertical movements, that we introduced into the model DRILOTROP, seem to express a delayed density effect and to allow the worms to better exploit the soil.

Comparisons between observed and simulated vertical earthworms distributions (Fig. 4)

Lavelle observed the vertical distributions of *M. anomala* during the year 1969 (Lavelle, 1971) and the year 1972 (unpublished data).

It is not easy to compare observed and simulated vertical distributions because depth field measurements are not very accurate.

Nevertheless, there is no essential discrepancy for the year 1972.

For the year 1969 which was particularly dry, field measurements indicate that simulated distributions are not deep enough, especially in March. This extreme case emphasizes the limits of the model DRILOTROP. We assume that our hypothesis which based earthworms behaviour upon mean daily climatic conditions might be wrong when maximum values for temperature and drought are very severe for earthworms.

CONCLUSION

The model allowed us to explore the determinism of vertical movements of earthworms which constitute one of the major aspects of their behaviour. The results verify that *M. anomala* which has to burrow to move forwards, is unable to follow the fast fluctuations of its moisture and temperature preferences. At most, it can escape very unfavourable conditions. Only extreme climatic conditions significantly affect the vertical distributions of earthworms. On the other hand, a delayed density effect may prevent the whole population from staying at the same time in the top soil, where organic matter content is maximum.

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