ROLE OF EARTHWORMS IN THE N CYCLE: A FALSIFIABLE ASSESSMENT

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Summary—Due to the great difficulty in measuring N transfers in the field, most N-cycle representations are made from laboratory data extrapolated to field earthworm populations. Nevertheless, since 1975 advances have been made and a general model has been proposed based on field transfer measures, which is applicable to various (anecic) earthworm populations. The advances were, chronologically, as follows: (1) the choice of a conceptual model with measurable compartments and possibly transfers; (2) the use of non-toxic dye for labelling earthworms; (3) the use of additional ^{15}N labelling in field; (4) the improvement of a mathematical model with efficient fitting to field data; (5) the adjusting of a technique to measure the earthworm gut transit in the field; (6) the field validation of predicted results; (7) the description of driving factors (photoperiod, soil temperature and moisture) of the earthworm N activity; and (8) the full description of the knowledge used in the interpretation in an Explained Knowledge Dispenser as an informatics server. This process is presented in the paper and leads to an estimate of 1.75 kg ingested N, 1.15 kg defecated N and 0.6 kg assimilated plus excreted (metabolized) N kg^{-1} of live anecic earthworms y^{-1} in a temperate climate. These results are falsifiable, thanks to new predictions of the model and new field observations. © 1997 Elsevier Science Ltd

INTRODUCTION

The earthworm's role in the N cycle is multiform. This generic concept includes many roles dealing with (1) the fluxes of N compounds (each transfer between two identified ecosystem compartments), and (2) the state changes of identified compartments describing total N content or peculiar N compounds.

Many calculations of N budgets and effects of earthworms on N processes have been published. Until recently, many aspects of the N cycle involving earthworms (earthworm N roles) could not be measured or verified in the field. Thus, hypotheses (valuations and models to obtain values) could not be tested on true systems and potentially rejected in a rigorous fashion. Hypotheses of this kind are not ecologically appropriate, as far as ecology is a science (Bouché, 1990). We do not review these hypotheses here, attempting only to present in a concise manner various conceptual and technical tools which allow feasible assessments that are falsifiable on true systems by predictions and validations. In order to be brief, we focus on short statements relating to N flux calculation issues, and avoid the sub-processes. This paper deals with a synthesis of 20 y of team work; more details about techniques or precise concepts are available in the references, particularly in Bouché and Al-Addan (1996). Table 1 pre-sents the main symbols, compartments, fluxes and concepts (see Bouché, 1990) described here and marked with an asterisk (*).

The conceptual model

Satchell (1963) first tried to estimate the earthworm's role* in the N cycle. His attempt was based on (1) the size of a population (*L*), (2) the biomass turnover (elaboration*; *T*), and (3) the excretion* (*X*), for one single species. The earthworm N role on soil by the gut transit, observed by Stöckli (1928), was not taken into account and was only formalized later in the REAL model (Bouché and Kretzschmar, 1977; Bouché, 1980). Barois and Lavelle (1986) demonstrated the importance of gut excretion* (*Xe*) and reassimilation (*Ax*) between the earthworm's metabolon* (*L*) and its endentere* (*E*) (digestive tract content). Compartments and transfers are shown in Fig. 1.

The microcosms Physical models, such as laboratory or field buried devices, have been intensively used. Among the early usage were Satchell's estimates (1963) using a Needham (1957) excretion* study of earthworms in an aquarium, or a growth curve obtained from a buried *Lumbricus terrestris* L. culture. Microcosms were also used by Lavelle (1971) in a destructed soil technique to estimate gut transit.

Table 1. Main concepts, symbols and means of estimation, with notes briefly defining them

Symbols	Names	Estimation	Notes
A	assimilation	calculated	flux: from E to L
Ai	direct A from I	observed	flux from E to L
Ap	parietal assimilation	no	hypothetical flux from S to L
D	defecation	direct in field	flux: E to S
E	endentere	direct from field	compartment: content of the digestive tract flux: emanation of organism's dead tissues T (see Petrusewicz and McFadyen, 1970)
E	elaboration	assumed as T	aptitude to use time, space and composition heterogeneities (see Bouché and Al-Addan (1995)
–	heterochresty	–	
I	ingestion	calculated	flux of S to E
L	earthworm biomass	direct from field	compartment: sum of a given class of earthworm metabolon[*] compartment of an organism strictly limited by its genome control without spatial discontinuity (see Bouché. 1990)
–	metabolon	direct from field	Mib is calculated as a function of temperature, moisture and photoperiod (Bouché, 1975). It measures the level of the activity compartment: external to L and E
Mib	mobility index	calculated	
–	role		any function related to steady-state change and flux control
S	surrounding	not measured	flux of E to L of Xe flux of L to S as tissues (organs, dead zygotes, amputated parts, etc.)
T	"lost" earthworm tissue	assumed	flux from L to E (= Xe) and to S (= Xp) as fluid molecules
X	excretion	measured as Xs	flux from E to L of Xe
Xa	Xe reassimilated	not measured	flux from E to $S = Xe - Xa$
Xd	defecated excretion	$Xd = Xe - Xa$	flux from L to E
Xe	excretion in E	not measured	flux from L to S
Xp	parietal excretion in S	$Xp = X - Xd$	$Xs = Xd + Xp$
Xs	observed excretion	direct in field	

Most microcosms are devoted to measuring earthworm flux roles.

The mathematical models

Satchell also introduced the three mathematical parameters needed to estimate earthworm roles: (1) biomass size (state variables), (2) driving factors (e.g. temperature, moisture) regulating earthworm activity, and (3) the flux constant (for example, N excretion[*]) in standardized biomass and driving factor conditions. The extrapolation was made using mathematical functions (vs temperature) for seasonal changes. These mathematical models also extrapolate individual observations to sets [e.g. Satchell (1963) on one population; Bouché (1971) on one ecological category and by steps to an earthworm community; G. Ferrière (unpubl. PhD thesis, University of Lyon 1, 1986)]. However, all these extrapolations (translocation in space, evolution in time and set composition in referred functional components) are predictions allowing model validations. All these mathematical extrapolations (including interpolations) allow the use of the REAL submodel described in Fig. 1 in any field - in grassland, a culture or a forest. Only local population biomasses and seasonal values of driving factors are needed: REAL allows information translocations for data sources and predictions (Bouché, 1980).

The challenge: the validation

For each estimate we need: (1) a clear integrated conceptual model on earthworm N role[*], such as the REAL model (Fig. 1); (2) good community structure and size estimates; (3) the measure of earthworm roles[*], often in microcosms; (4) the expression of
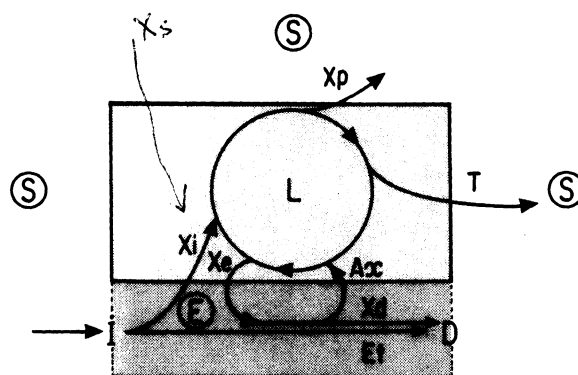

Fig. 1. Conceptual submodel of the compartment $L + E$ of REAL. L, E and S are, respectively, the compartments: earthworms, endentere (digestive tract content) and the surrounding. The food ingested (i) is assimilated (A) or transferred directly (Et) to the defecation (D). The excretion (X) occurs mostly through the external body wall (Xp) and also to the endentere (Xe); it is then partly reassimilated (Ax) or defecated (Xd).

roles[*] vs driving factors; (5) the mathematical tool to extrapolate in time, space and composition (e.g. other individuals, stages, populations, communities). The extrapolation allows the results to be predicted and these predictions **must be validated in the field**. This is only possible if our conceptual, microcosm and mathematical models are falsifiable, i.e. they provide predictions which can be field-checked. Until recently, we have had no means with which to measure ingestion, assimilation, excretion and defecation of N in the field. Here, we summarize these field validations.

<center>MATERIAL AND METHODS</center>

Community estimates

The sampling of an earthworm community is a common drawback of any earthworm role[*] estimate. This is the reason that the first estimates by Satchell (1963) were restricted to *L. terrestris* L., one of the few species well estimated by the formalin technique he used. This question has been discussed elsewhere with regard to the ethophysic technique (Bouché and Gardner, 1984) which gave two pieces of information: the biomass estimates and the mobility index (Mib), measuring the metabolic control by driving factors (see time interpolations below).

Community-level estimates must be based on biomass and not on the number of individuals, due to the large variability of earthworm individual biomass. In fact, each individual weight must be measured and its data characteristics later aggregated into a convenient set (by life stages, species, ecological categories, communities, etc.) (Bouché, 1990; Soto and Bouché, 1993).

Nitrogen compartments and fluxes measures

The REAL submodel (Fig. 1) comprises three compartments: earthworm biomass (L), endentere[*] (E) and the surroundings (S) of E + L compartments (Table 1). The E and L compartments are very easy to estimate from community measures and by partitioning the two compartments by dissection (with a marginal mixing), by gut washing or by filter paper cleaning, which both have limitations (Bouché, 1966; M.B. Chaudonneret, *pers. commun.*). The REAL model also describes interchanges between earthworm and endentere[*], with soil and plants. We do not analyse these fluxes here, instead reducing them to the exchanges with the compartment surrounding (S).

The main difficulties occur in true measurements of fluxes (i.e. exchanges between compartments).

Extrapolation, prediction and validation

Both to expand the use of our knowledge and to falsify our interpretations, we must extrapolate or interpolate our data observed in true systems or in microcosms. This is done in various steps.

Compositional and spatial extrapolations. Interpolations between individuals were made with an increasing risk of error. Firstly, from observed individuals to individuals of the same species and same life stage; then, in a second step, to all stages of the same species; and then to all individuals of the same ecological category and sometimes, due to lack of knowledge, to all earthworms. This allows the extrapolation of results in the same local earthworm community or between spatially distributed populations or communities.

Time interpolations. These were made between dates using the **level of activity** determined by the Mib[*] index. This Mib[*] index has been calculated as a function of three driving factors—soil profile temperatures, soil profile moistures and day length (Heidet and Bouché, 1991; Heidet, 1996)—and validated by Al-Addan (1992) on the seasonal rhythm of surface cast production.

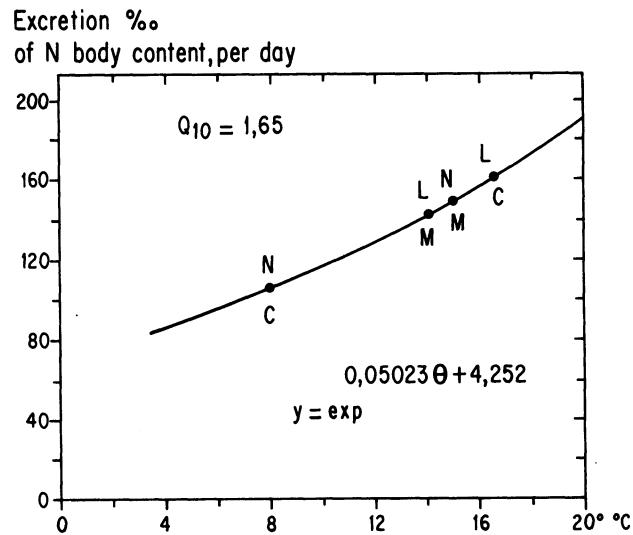|	
Defecation[*]:	A recent development, the LAB technique, which measures defecation (D) (flux from E to S), is described in Bouché and Al-Addan (1996) and gives estimates with a limited uncertainty (+10%).
Excretion[*]:	Excretion (X) is measured by double-tagging earthworms captured in the field: (1) by dyeing to recognize N-labelled individuals in the field (Meinhardt, 1976; D. Mazaud, unpub. PhD thesis, National Institute of Agriculture, Paris-Grigaon, 1979); (2) fully labelling with ^{15}N (Ferrière, *loc. cit.*); (3) releasing into the field; and (4) recapturing at different time intervals to measure ^{15}N excretion[*] in the milieu by parietal excretion[*] (Xp) or endentere (Xe) (techniques and mathematics of fitting are described in Ferrière, *loc. cit.*;Ferrière and Bouché, 1985). The faeces ^{15}N indicates the fraction (Xd) of the total N excretion (X) in the defecation flux (D). As pointed out above in the introduction, this fraction does not represent the Xe flux because a large proportion of N-Xe is probably reassimilated as N-Ax.
Assimilation[*]:	At steady state (assuming no net biomass changes applicable only to adults and cocoons), the ^{14}N assimilation (A) compensates ^{15}N excretion (X). If not, the change in biomass must be calculated as a complementary variable. Consequently the technique used is the same as for X.
Elaboration[*]:	This is the emanation of N as earthworm tissues (T) (amputated parts, cocoon envelopes, dead animals). The lack of a demographic falsifiable estimate (with one non-generalizable exception), (Lavelle, 1971) always requires assumptions to be made here. We use Satchell's assumption: T is three times the biomass y^{-1}.
Ingestion*:	Because of the heterochresty[*] of the earthworm, it is impossible to calculate the ingested N directly from gut transit observed in D (earthworms choose their tiniest food and we ignore their choices). We can calculate the ingestion[*] by $I = D + Xp + T$.

Excretion ‰
of N body content, per day

Fig. 2. Validation of microcosm studies (M) by field studies (C) and extrapolation procedures in space (N = C̆teaux near Dijon; L = Lavérune near Montpellier), time (N = April, May 83; L = Sept., Oct. 1988) and composition (N = *Nicodrilus longus*, Ude; L = *Lumbricus terrestris* L.). Estimation of the temperature effect when moisture and photoperiod are not limiting factors. (Four estimates based on 81 N isotope ratio.)

Extrapolation allows validations. The possibility of predicting the future earthworm N-cycle functions in another space or time or composition (taxon) condition allows validation of predicted values, i.e. creates falsiability. Some validations are given below (excretion*, Fig. 2)

RESULTS

Compartments estimates

$L + E$ mean earthworm biomass (live weight, full gut) is 100 g m^{-2} ($n = 52$) in France and Belgium. The endentere (E) varies widely, depending of species, food ingested, physiological conditions, etc. We adopt here an L compartment of 100 g m^{-2} live earthworm as the mean annual biomass. A live weight of 100 g is similar to 15 g dry weight or 1.5 g body N (M.B Chaudonneret, *pers. commun.*). We do not need E and S estimates. As indicated above, earthworm roles are proportional to biomass.

Excretion estimates

The excretion* field estimate is close to a 10% N body content d^{-1} at 8°C. (Ferrière, *loc. cit.*; Ferrière and Bouché, 1985). This increases with temperature and depends on a temperature Q_{10} value of 1.65. From the first estimates, predictions were made using a mathematical model (M Samih, unpubl. PhD thesis, Montpellier University, 1988) and compared to new field observations by R. Hameed (unpubl. PhD thesis, Montpellier University, 1989).

Microcosm studies made by Ferrière (*loc. cit.*) and Cortez *et al.* (1989) were validated in the field (Fig. 2) (Hameed *et al.*, 1994). The interpolation of results

using the Mib* index gives a mean value of Xs =58.3 g N y^{-1} for 100 g live worms. Where Xs is the observed excretion balance, $Xs = Xd + Xp$.

Ferrière (*loc. cit.*) observed a defecated excretion* (Xd) of 1.7% of the observed N excretion* (Xs) for *Nicodnilus longus* (Ude), while Hameed (*loc. cit.*) estimated an Xd of 6.9% of Xs for *L. terrestris* L. On this poor basis, we adopt Xd as 4.3% of Xs. Now, Xp is 55 g N y^{-1} and Xd is 2.5 g N y^{-1}, for 100 g live worms.

Barois and Lavelle (1986) demonstrated in microcosm conditions that the excretion* to endentere* (Xe) was at least partly "compensated" for by a reassimilation (Ax) of N in Xe. We have no field estimate of this important interchange but we can measure directly the balance $Xe - Ax = Xd$. The true excretion* ($X = Xe + Xp = Xd + Ax + Xp$) is greater than the observed exrcetion* ($Xs = Xd + Xp$).

Assimilation estimates

Currently, a field falsifiable assessment is only possible for the N assimilation* (N flux from Endentere to the earthworm L) from ingested material (Ai). The assimilation (A) also includes the reassimilation (Ax) of the excretion* to endentere* (Xe), which escapes our ability to measure it. $Ai = Xd + Xp = Xs$ at body steady state. A steady state is when L biomass does not change ($\delta L = 0$) and there is no elaboration (T) of dead tissues.

In full, $Ai = Xs + \delta L + T$. In steady-state conditions for individual adult earthworms (i.e. excluding mortality and cocoon production), $Ai = Xs$ is directly observed in field, as described above where ^{15}N release is replaced by ^{14}N from ingested natural soil.

Defecation estimates

This measurement is directly possible by bran-labelling food directly in the field (Bouché, 1981), or by the LAB technique (Bouché and Al-Addan, 1996). This field measure must be interpolated using the sub-model of activity (SMA) of the REAL model (Bouché, 1980) for seasonal variation and using ecological categories between species and milieu in space-time interpolations. Various field estimates vary between 2.2 kg dw of soil faeces produced y^{-1} 100 g^{-1} live anecic earthworms (Bouché, 1981), and 2.94 ± 0.3 kg dw (Al-Addan, 1992); we adopt 2.7 kg ± 0.3.

The defecated N is from two fractions: an ingested fraction making a transit in endentere (*Et*), often as stable organic compounds; and a tiny fraction (*Xd*) of excreted *Xe* not reassimilated as *Ax* (i.e. $Xd + Et = D$). Nitrogen in *D* could be directly field-assessed by total N measured in faeces, and *Xd* by the ^{15}N fraction from labelled earthworms.

Tissue elaboration

Elaboration[*] is the flux from an organism of solid (tissue) material (Petrusewicz and MacFadyen, 1970). This was the focus of most International Biological Programme "production" estimates and was assumed to be as higher as the 2/3 of total N fluxes in Satchell's first assumption. This is currently the weakest knowledge we have. We have no validated field demographic models. We have only assumptions about the output from compartment *L* of cadavers, amputated parts and cocoon envelopes. In the absence of falsifiable measurements, the best course is to follow Satchell and to assume that *T* flux is 3 times the earthworm biomass, i.e.

$$T = 1.5 \times 3 = 4.5 \text{ g N m}^{-2} \text{ y}^{-1}$$

(with a biomass of 100 g m^{-2}).
This is probably the smallest earthworm N flux.

Ingestion

At present, ingestion* cannot be directly measured in the field nor deduced from microcosm studies, due to the heterochrestic[*] earthworm behaviour. Ingestion can be calculated as $1 = D + Xp + T$, where the two main components are field-measured and calculated from falsifiable models:

$$D = 174.2 \pm 17.4 \text{ and } Xp = 55.8$$

$$I = 174.2 + 55.8 + 4.5 = 234.5 \text{ g N m}^{-2} \text{ y}^{-1}$$

(with a biomass of 100 g m^{-2}).

DISCUSSION

Improvements in field measurements and in the design of falsifiable models, since the first estimates of the role of the earthworm in N dynamics were made by Satchell (1963), now allow predictions which can be verified in true systems (i.e. fields). The design of models giving priority to falsifiability led to improvement of a series of techniques: earthworm dyeing and labelling; field-microcosms: field body-temperature readings; close mathematical fittings and lab microsm design and limitations.

Today, these improvements have resulted in falsifiable predictions and also improved experimental designs (Samih, *loc. cit.*). These predictions have led to validation of models and control of previous results (Hameed, *loc. cit*). In the earthworm's N-cycle role, most bulk valuations on compartments (*L, E*) and fluxes (*I, A, X, D*) can be assessed, with a "simplified" general model. This assessment can be expanded to soil and plant exchange by the use of ^{15}N as a tracer (Ferrière, *loc. cit.*; Bouché and Ferrière, 1986) but depends on milieu driving factors controlling the activity of soil and plant compartments. Thus, modelling can be focused on more precise processes. For example, the potentially important processes of *Xe* and *Ax* are at present not measurable in true systems, i.e. assessments are not falsifiable. Other functions can be neglected, such as whether assimilation is really limited to two fluxes (*Ai* and *Ax*), and whether there is an *Ap* flux (assimilation from *S* to *L* through the body skin).

These days, we need, in the main, more control, more repetition, more validation of **falsifiable** models and results and their related techniques. Basically, we know the N-cycle contribution of the earthworm, and we know this contribution is not negligible, contrary to most texts on the N-cycle.

These text books adopt the McIntosh (1985) point of view that "ecology was not, and is not, a predictive science", while all exact science must be falsifiable, as ecology was originally defined (Bouché, 1990). This paper contributes to this restored ecology. The present improvements need good appraisal of concepts, techniques and methods which are dispatched in various publications. This rigorous fashion could be hardly improved by this means of communication. An Explained Knowledge Dispenser, ROLUMBRIC, will soon give full access to facts and interpretations in the computer server ECORDRE.

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