Pedobiologia **43**, 537–546 (1999) Urban & Fischer Verlag http://www.urbanfischer.de/journals/pedo



# Simulation of growth and flux of carbon and nitrogen through earthworms

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Accepted: 12. April 1999

Summary. Earthworms contribute to carbon and nitrogen cycling directly through the accumulation (consumption), storage (assimilation) and turn over (respiration, excretion, mortality) of nutrients from their tissues. An energetics-based model was designed to describe the flows of C and N through three components: litter, earthworm, and byproducts pools. Litter C and N pools contained insoluble nutrients that were consumed by earthworms. A portion of consumed C and N were assimilated from the earthworm gut and used for growth and maintenance of earthworm tissue. Earthworm byproducts included C and N defecated in earthworm casts as well as C and N released from earthworm tissue through respiration and excretion. The effect of litter quality, soil temperature and soil moisture content on C and N fluxes through earthworms were simulated. Tissue C accumulation was validated using growth data and N fluxes were validated with <sup>15</sup>N-nitrogen consumption, assimilation and excretion data from laboratory studies with Aporrectodea tuberculata (Eisen). Sensitivity analysis indicated most uncertainty in the function describing the effect of soil temperature on litter C and N consumption. C and N storage and turn over from earthworm tissues was greatest when the litter C:N ratio was 10 and declined as the litter C:N ratio increased to 30. Tissue C and N accumulation was affected strongly by soil temperature and moisture, and optimal conditions for earthworm growth were at 15 °C and 30 % (w/w) soil moisture content. Further work involving the addition of a dynamic population structure to the model and validation with data from field studies is underway to determine the contribution of earthworms to ecosystem-level fluxes of C and N.

Key words: Earthworms, dynamic model, growth, energetics, carbon, nitrogen

## Introduction

Earthworms have a significant role in nutrient cycling through the accumulation, storage and turn over of nutrients from their tissues via consumption, assimilation, respiration, excretion and mortality processes (Blair et al. 1995). Earthworms consume an estimated 2–15 Mg of organic matter ha<sup>-1</sup> y<sup>-1</sup> (Hendriksen 1991; James 1991; Lavelle et al. 1989; Shipitalo et al. 1988) and are responsible for 5–30% of total heterotropic soil respiration (Hendrix et al. 1987; Rozen 1994; Satchell 1967). The flux of N through earthworms in agroecosystems has been

0031-4056/99/43/06-537 \$12.00/0

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estimated to range between 10–83 kg N ha<sup>-1</sup> y<sup>-1</sup> (Andersen 1983; Böström 1988; Christensen 1987; Curry et al. 1995; Parmelee & Crossley 1988).

Despite considerable research on the contribution of earthworms to nutrient cycling, there are still wide gaps in our knowledge of the physiological and environmental factors that influence C and N fluxes through earthworms. Feeding habits and life history attributes of different ecological groups (Bouché 1977) as well as the stage of development of individuals can alter C and N fluxes through earthworms (Bolton & Phillipson 1976; Daniel et al. 1996). Nutrient fluxes through earthworms may be regulated by the quantity and quality of organic substrates and environmental factors (e.g. soil temperature and moisture) (Böström 1987; Bohlen et al. 1997; Daniel 1991; Moody et al. 1995; Shipitalo et al. 1988; Whalen & Parmelee 1999b). Mechanistic mathematical models can be used to understand and analyze these complex ecological processes.

Few attempts have been made to model C and N fluxes through earthworms. Marinissen & deRuiter (1993) developed two models to estimate the contribution of earthworms to N cycling in agroecosystems. The first method combined consumption, assimilation and respiration rates with earthworm secondary production and mortality to calculate N flux through earthworms, while the second method calculated N flux based on mortality, urine and mucus production. The large disparity in the N fluxes calculated using the two methods was attributed to uncertainty in many of the parameter estimates. The REAL model of Bouché et al. (1997) used an energetics approach to estimate the flux of N through under field conditions. Annual N flux through an earthworm population with a biomass of 15 g (dry weight) m<sup>-2</sup> was calculated to be 60 kg N ha<sup>-1</sup> y<sup>-1</sup>, which is consistent with N flux measurements reported in the literature. However, the model was not validated with field estimates, and Bouché et al. (1997) recommended further studies on earthworm consumption, assimilation and tissue production. The models developed by Marinissen & deRuiter (1993) and Bouché et al. (1997) are limited in their application since they are 'static' data driven models.

This paper outlines an energetics-based model developed to simulate the physiological processes by which C and N are consumed, accumulate and turn over from earthworm tissue. The objectives of the study are (1) to present a mechanistic mathematical interpretation of C and N fluxes through earthworms, based on scientific information in the literature, (2) to validate the model using laboratory data on the accumulation and fluxes of C and N by *A. tuberculata*, and (3) to predict the effects of litter quality, soil temperature and soil moisture content on C and N fluxes through earthworms.

## **Materials and Methods**

### Outline of the model

The model has three main components through which C and N fluxes are calculated, including litter, earthworm and byproduct pools (Figs. 1 and 2). Litter C and N pools contain insoluble nutrients consumed by earthworms. Earthworm C and N pools consist of the earthworm gut, through which ingested litter passes, and earthworm tissue, where assimilated C and N is used for growth (accumulation of structural biomass) and maintenance (respiration and mucus production). Byproducts of earthworm production include C and N defecated in earthworm casts, as well as C and N released from earthworm tissue through respiration, excretion and mortality. However, since the age structure of earthworm populations were not included in the model, C and N released from earthworms through mortality was not considered because survivorship varies depending on the age or stage of development of individuals. In the present model configuration, C and N byproducts accumulate during model simulation and transformation of C and N released from earthworms (e.g. N losses through leaching, denitrification or volatilization) are not considered. For simplicity, effects of earthworms on C and N cycling through fragmentation of litter and interactions with soil microflora were not modelled.

C and N fluxes through earthworms were described using differential equations, and the transfer rates from all pools were functions of first-order rate constants. To validate the model with results from <sup>15</sup>N tracer studies, N dynamics in total N (<sup>14</sup>N-nitrogen plus <sup>15</sup>N-nitrogen) and <sup>15</sup>N-nitrogen pools were modelled. It was assumed that there was no difference in the rate at which <sup>15</sup>N-nitrogen and total N were accumulated and released by earthworms. Symbols, units and interpretation for state and compo-



und variables in the model are given in Tables 1A and 1B. Parameters used to initialize the model are outlined in Table 2, and were derived from literature data for the well-studied lumbricid *Lumbricus terrestris* L. (Binet & Trehen 1992; Bohlen et al. 1995; Bolton & Phillipson 1976; Böström 1988; Curry et al. 1995; Daniel 1991; Dash & Patra 1977; Hameed et al. 1994; Hutchinson & King 1979; Ketterings et al. 1997; Martin et al. 1992; Needham 1957; Parmelee & Crossley 1988; Rozen 1994; Shipitalo et al. 1988).

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Table 1. Symbols, units and interpretations of the (A) state variables and (B) compound variablesin the model(A)

Variable	Unit	Interpretation
$F_{C}$	g	Carbon insoluble compounds, available for earthworms
$F_N$	g	Nitrogen insoluble compounds, available for earthworms
FISN	g	<sup>15</sup> N-nitrogen insoluble compounds, available for earthworms
G	g	Carbon in earthworm gut
$G_N$	g	Nitrogen in earthworm gut
GISN	g	<sup>15</sup> N-nitrogen in earthworm gut
$T_{C}^{ISR}$	g	Carbon in earthworm tissue, store
$T_N$	g	Nitrogen in earthworm tissue, store
TISN	g	<sup>15</sup> N-nitrogen in earthworm tissue, store
$E_{C}$	g	Cumulative carbon excreted from tissue in mucus
$\vec{E_N}$	g	Cumulative nitrogen excreted from tissue in mucus and urine
EISN	g	Cumulative <sup>15</sup> N-nitrogen excreted from tissue in mucus and urine
$D_{C}$	g	Cumulative carbon defecated in casts
$D_N$	g	Cumulative nitrogen defecated in casts
$D_{15N}$	g	Cumulative <sup>15</sup> N-nitrogen defecated in casts
$R_C$	g	Cumulative carbon dioxide respired by earthworms
<b>(B)</b>		

	Unit	Interpretation
$\overline{F_{CN}} = F_C / F_N$	-	C:N ratio of litter
$F_{NN} = F_{ISN}/FN$	-	$\frac{15N}{(14N + 15N)}$ ratio of litter
$p_E = a_I - (a_2 F_{CN})$	-	palatability function for consumption
$t_E = a_3 (a_4 - t_p)^{a5} \exp(-a_6 (a_4 - t_p))$	-	soil temperature modifier of consumption
$w_E = a_7 (-w)^{a/8} \exp(a_9 w)$	-	soil moisture content modifier of consumption
$rew_{CN} = \left( \left( T_C / T_N \right) - ew_{min} \right) / \left( ew_{max} - ew_{min} \right)$	-	C:N ratio of earthworm tissue
$tr_{c} = \exp(q(1/tp_{a} - 1/(tp_{b} + tp)))$	-	soil temperature modifier of basal respiration

# Differential equations for the state variables

The C litter pool,  $F_C$  in the model consists of degradable but insoluble organic C, consumed by earthworms. Litter consumption was assumed to followed Michaelis-Menten kinetics at a maximum specific rate of v relative to the amount of litter C,  $F_C$  and the half saturation constant, k. Litter consumption was also affected by the parameters  $p_E$ ,  $t_E$  and  $w_E$ , where  $p_E$  is litter palatability (influenced by the C:N ratio of the litter), and  $t_E$  and  $w_E$  are soil temperature and moisture modifiers of litter consumption. Consumption of litter C by earthworms is

$$\frac{dF_C}{dt} = v T_C \frac{F_C}{k + F_C} p_E t_E w_E \tag{1}$$

Eq. (2) describes the N litter pool  $F_N$  and is analogous to Eq. (1) except that  $F_C$  is divided by the C:N ratio of the litter pool,  $F_{CN}$ . Eq. (3) describes the <sup>15</sup>N-nitrogen litter pool  $F_{I5N}$  and is analogous to Eq. (2) except that  $F_N$  is multiplied by the <sup>15</sup>N/(<sup>14</sup>N + <sup>15</sup>N) isotopic ratio of litter,  $F_{NN}$ .

$$\frac{dF_N}{dt} = \left(v \ T_C \ \frac{F_C}{k + F_C} \ p_E \ t_E \ w_E\right) F_{CN} \tag{2}$$

$$\frac{dF_{ISN}}{dt} = (v T_C \frac{F_C}{k + F_C} p_E t_E w_E) F_{CN} F_{NN}$$
(3)

After litter C is consumed by earthworms, it moves into the earthworm gut,  $G_C$ , where it is immediately partitioned. A portion of the ingested litter C in the  $G_C$  pool is absorbed across the earthworm intestinal tract and used in active metabolism and growth, and the remaining C in the intestinal tract is

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defecated into the cast C pool. The absorption of C by earthworms occurs at the rate sb relative to the quantity of C,  $Q_C$  that is consumed, where  $Q_C = (dF_C/dt)$ , and is regulated by setting limits on the C:N ratio of earthworm tissue with the parameter  $rew_{CN}$ . The parameter  $rew_{CN}$  regulates the C:N ratio of earthworm tissues between upper  $(ew_{max})$  and lower  $(ew_{min})$  limits as a function of earthworm tissue C,  $T_C$  and earthworm tissue N,  $T_N$ . As litter N becomes less available, the C:N ratio of earthworm tissues will increase towards  $ew_{max}$ . This parameter prevents accumulation of C in earthworm tissues when the supply of N in food is depleted. The portion of earthworm gut C,  $G_C$  which is absorbed by earthworms is given by  $(s_b Q_C rew_{CN})$ , and the unabsorbed portion of gut C which is defecated in casts is given by  $Q_C - (s_b Q_C rew_{CN})$ . Since consumed food is immediately partitioned between assimilated and defecated mass, the gut component of the model is not dynamic but has been included for heuristic purposes.

$$\frac{dG_C}{dt} = Q_C - (s_b Q_C rew_{CN}) - [Q_C - (s_b Q_C rew_{CN})]$$
(4)

Similar to Eq. (4), litter N and litter <sup>15</sup>N-nitrogen which move into the earthworm gut pools  $G_N$  and  $G_{15N}$  are assumed to immediately flow into earthworm tissue at a rate,  $ka_N$  relative to the quantity of N,  $Q_N$  or  $Q_{15N}$  that is consumed where  $Q_N = (dF_N/dt)$  and  $Q_{15N} = (dF_{15N}/dt)$ . The portion of the gut N pool,  $G_N$  that is assimilated into earthworm tissue N,  $T_N$  is  $(ka_N Q_N)$ . Non-assimilated N from the gut N pool is defecated in casts using the function  $[Q_N - (ka_N Q_N)]$ 

$$\frac{dG_N}{dt} = Q_N - (ka_N Q_N) - [Q_N - (ka_N Q_N)]$$
(5)

$$\frac{dG_{15N}}{dt} = Q_{15N} - (ka_N Q_{15N}) - [Q_{15N} - (ka_N Q_{15N})]$$
(6)

Gut C,  $G_C$  that is absorbed across the intestinal tract of earthworms is partitioned into two C pools: C respired in anabolic processes (e.g. energy used for the production of new earthworm tissues, see Eq. (16)), and C that is incorporated into new earthworm tissue. The incorporation of assimilated C into the earthworm tissue C pool,  $T_C$  is a constant function  $ka_C$ , and the function which describes this process is  $[ka_C (s_b Q_C rew_{CN})]$ . C is lost from the tissue C pool,  $T_C$  through basal metabolism (e.g. maintenance of respiration), which is influenced by a soil temperature function for basal respiration,  $tr_C$  and the quantity of earthworm tissue C,  $T_C$ . C loss from the earthworm tissue C pool,  $T_C$  via basal metabolic processes is expressed as  $(rb_C tr_C T_C^b)$ .

C is also lost from earthworm tissue C,  $T_C$  through the excretion of C-containing mucopolysaccharides (mucus), which is secreted by earthworms to lubricate their body surface and facilitate respiration and movement through the soil. Mucus production is expressed in terms of the loss of N from the tissue N pool,  $T_N$  and adjusted by the C:N ratio of mucus,  $m_{CN}$  using the function ( $m_m b_m T_N rew_{CN} m_{CN}$ ). The excretion of mucus by earthworms is regulated by the C:N ratio of earthworm tissue using the parameter  $rew_{CN}$  (see Eq. (8)).

$$\frac{dI_C}{dt} = ka_C \left( s_b \, Q_C \, rew_{CN} \right) - \left( rb_C \, tr_C \, T_C^b \right) - \left( m_m \, b_m \, T_N \, rew_{CN} \, m_{CN} \right) \tag{7}$$

The uptake of N and <sup>15</sup>N-nitrogen from the earthworm gut into earthworm tissue N pools  $T_N$  and  $T_{1SN}$ is influenced by the rate at which N is assimilated into earthworm tissues,  $ka_N$  from consumed N,  $Q_N$ using the function  $(ka_N F_N)$ . The loss of N from earthworm tissue N,  $T_N$  occurs through the excretion of metabolic byproducts (urine and urea) and mucus, where  $u_m$  is the proportion of N excreted as urine and urea,  $m_m$  is the proportion of N excreted in mucus, and  $b_m$  is the rate of N excretion from earthworm tissue N,  $T_N$ . N loss from earthworm tissue through excretion is regulated by the parameter  $rew_{CN}$  which allows for the conservation of N in earthworm tissues when litter N,  $F_N$  is limiting and less N is assimilated into earthworm tissues, or the excretion of excess N when litter N is high. N excretion from the tissue N pool,  $T_N$  is expressed as  $[(u_m \ bm \ T_N + m_m \ b_m \ T_N) \ rew_{CN}]$ .

$$\frac{dT_N}{dt} = ka_N Q_N - [(u_m b_m T_N + m_m b_m T_N) rew_{CN}]$$
(8)

$$\frac{dT_{ISN}}{dt} = ka_N Q_{ISN} - [(u_m b_m T_{ISN} + m_m b_m T_{ISN}) rew_{CN}]$$
(9)

In the model, C and N excreted from earthworm tissue C,  $T_c$  and tissue N,  $T_N$  pools through the production of mucus and metabolic byproducts (urine/urea) accumulate in the excretion C and N pools,  $E_c$ ,  $E_N$ , and  $E_{ISN}$  according to Eqs. (10) – (12).

$$\frac{dE_C}{dt} = m_m b_m T_N rew_{CN} m_{CN}$$
(10)

$$\frac{dE_N}{dt} = (u_m b_m T_N + m_m b_m T_N) rew_{CN}$$
(11)

$$\frac{dE_{ISN}}{dt} = (u_m b_m T_{ISN} + m_m b_m T_{ISN}) rew_{CN}$$
(12)

The defecation of C and N from the earthworm gut pools,  $G_C$  and  $G_N$  accumulate in cast C and N pools,  $D_C$ ,  $D_N$ ,  $D_{15N}$  are accounted for in Eqs. (13) – (15).

$$\frac{dD_C}{dt} = Q_C - (s_b Q_C rew_{CN})$$
(13)

$$\frac{dD_N}{dt} = Q_N - (ka_N Q_N) \tag{14}$$

$$\frac{dD_{I5N}}{dt} = Q_{I5N} - (ka_N Q_{I5N})$$
(15)

The sink of C,  $R_c$  generated from the respiration of C by earthworms through active and basal metabolic processes is accounted for in Eq. (16). Anabolic metabolism is the portion of gut C,  $G_c$  which is absorbed through the intestinal wall and used for the production of earthworm tissue C,  $T_c$  at the rate  $kr_c$  according to the function  $[kr_c (s_b Q_c rew_{CN})]$ . C respiration through basal metabolism is expressed as  $(rb_c tr_c T_c^b)$ .

$$\frac{dR_C}{dt} = kr_C \left( s_b F_C rew_{CN} \right) + \left( rb_C tr_C T_C^b \right)$$
(16)

In the differential equations described above, it was assumed that earthworms fed only on the organic matter provided in the  $F_C$ ,  $F_N$  and  $F_{ISN}$  pools. C and N in earthworm cast pools were considered to remain separate from litter pools since coprophagy is not common in most earthworm species (Edwards & Bohlen 1996).

### Computer simulations

The model was coded in Time-Zero Version 3.0 (Quaternary Software 1995), and numerical integration of the differential equations was conducted with the Runge-Kutta method of the fourth order. The model was designed for simulating short-term changes in C and N fluxes through earthworms and therefore daily time steps were used for rate integration. Preliminary runs to determine whether litter and earthworm compartments were in equilibrium used initial parameter values given in Table 2.

Sensitivity analysis was conducted using a Monte Carlo sampling design with simple random sampling to evaluate the effects of various parameters on model results. Carbon fluxes through earthworms in the model were validated with *A. tuberculata* growth data under different conditions of soil temperature (10 °C and 18 °C) and moisture (20 %, 25 % and 30 % (w/w) soil moisture content) (Whalen & Parmelee 1999a) using the Hooke and Jeeves algorithm for parameter estimation. Parameter estimation for N fluxes through earthworms was validated short term (48 h) measurements of <sup>15</sup>N excretion (R. W. Parmelee et al. unpublished), <sup>15</sup>N consumption and <sup>15</sup>N assimilation (Whalen & Parmelee 1999b) data for *A. tuberculata* determined at 10 °C and 18 °C under laboratory conditions.

The effect of litter quality on the functioning of the compartments in the model, simulations were performed with litter C:N ratios of 10, 20 and 30. The effects of soil temperature and soil moisture content on the accumulation, storage and turn over of nutrients in the model were examined using three

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	Value	Unit	Interpretation
v	0.2	g C g <sup>-1</sup> TC d <sup>-1</sup>	Maximum consumption rate of litter by earthworms
k	50	gC	half-saturation constant for consumption of litter
$a_1$	1.6	-	Parameter of palatability function of consumption
$a_2$	0.04	-	Parameter of palatability function of consumption
tp	15	°C	soil temperature
$a_3$	0.515	°C <sup>-1</sup>	Parameter of temperature function of consumption
$a_4$	28	°C	Parameter of temperature function of consumption
$a_5$	1.84	-	Parameter of temperature function of consumption
$a_6$	0.297	°C-1	Parameter of temperature function of consumption
w	15	kPa	soil moisture content
$a_7$	0.549	kPa-1	Parameter of soil water function of consumption
$a_8$	0.793	-	Parameter of soil water function of consumption
$a_9$	0.113	kPa-1	Parameter of soil water function of consumption
Sb	0.15	$d^{-1}$	Absorption rate of C by earthworms
ewmin	8	-	Minimum C: N ratio of earthworm tissue
ewmax	12	-	Maximum C: N ratio of earthworm tissue
ka <sub>N</sub>	0.3	d-1	Assimilation rate of N by earthworms
$ka_C$	0.66	d-1	Assimilation rate of C by earthworms
$rb_{C}$	0.0146	d-I	Respiration rate of C in basal metabolism
q	5555.56	°C <sup>-1</sup>	Parameter of basal metabolism temp. function
$tp_a$	292	°C	Parameter of basal metabolism temp. function
$tp_b$	273	°C	Parameter of basal metabolism temp. function
b	-0.29	-	Respired fraction of C from earthworms
$m_m$	0.5	-	Proportion of N excretion from mucus
$b_m$	0.2	$d^{-1}$	Excretion rate of N from earthworms
$m_{CN}$	4	-	C: N ratio of mucus
$u_m$	0.5	-	Proportion of N excretion from urine
$kr_{C}$	0.34	d-1	Respiration rate of C in anabolic metabolism

Table 2. Initial parameters used in the model

levels of soil temperature (10 °C, 15 °C, and 20 °C), and three levels of soil moisture (20%, 25% and 30% (w/w)). Finally, the storage and loss of C and N from earthworm tissues was simulated under optimal environmental conditions.

## Results

The growth of newly-hatched A. *tuberculata* to maturity under laboratory conditions (Whalen & Parmelee 1999a) was compared with model simulations. The model accurately predicted earthworm growth under various combinations of soil temperature (10 °C and 18 °C) and moisture conditions (20, 25, and 30 % (w/w) soil moisture content). Actual and simulated growth for A. *tuberculata* in soil moistened to 25 % (w/w) soil water content at 10 °C is given in Fig. 3.

The effect of litter quality on earthworm growth was determined by varying the litter C:N ratio between 10 and 30 under constant soil temperature and moisture conditions. The quantity of litter available for consumption and earthworm growth was not limited during the simulation. Earthworm weight gain was greatest when the litter C:N ratio was 10, and declined as the litter C:N ratio increased. After 100 d, the model predicted that the consumption of litter with a C:N ratio of 10 would result in 74 % and 86 % greater earthworm mass, respectively, than consumption of litter with a C:N ratio of 20 or 30.

The effect of soil temperature on earthworm growth was determined at 10 °C, 15 °C and 20 °C. After 100 d simulation, earthworm mass was greatest at 15 °C and lowest at 20 °C. There was a greater than 90% reduction in earthworm mass as the temperature increased

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Fig. 3. Model simulation of *A. tuberculata* growth. Measured values were from Whalen & Parmelee 1999a for *A. tuberculata* juveniles maintained at 10 °C and 25 % (w/w) soil moissture content

from 15 °C to 20 °C, and a 70 % reduction in earthworm mass as the soil temperature declined from 15 °C to 10 °C. Sensitivity analysis suggested that much of the uncertainty in the functioning of the model was associated with this parameter. The consumption of litter by earthworms was strongly influenced by the soil temperature, which in turn affected the accumulation of biomass through earthworm growth. Changes in the soil moisture content had a much less dramatic effect on earthworm weight gain during a 100 d simulation. Earthworm mass increased over 50 % as the soil moisture content increased from 20 % to 30 % (w/w).

The storage and loss of C and N from the tissue C and tissue N pools were examined using the model. When litter quality and environmental conditions were optimized (litter C: N = 10, soil temperature =  $15 \,^{\circ}$ C, soil moisture =  $30 \,\%$ ), the C accumulation in earthworm tissue was 0.361 g C during a 100 d simulation. C loss from mucus secretion was  $34 \,\%$  of the tissue C content, while C losses from anabolic and basal metabolism were only  $7 \,\%$  of the tissue C content. The loss of N through mucus and urine excretion was  $10 \,\%$  of the tissue N content under these conditions.

#### Discussion

Model simulations have shown that the physiological fluxes of C and N through earthworms depend critically on the environmental conditions that govern the processes by which earthworms accumulate, store and turn over nutrients. The accumulation and loss of C and N from earthworm tissues was influenced strongly by litter quality (litter C:N ratio) and soil temperature, and to a lesser extent, by soil moisture content. The model predicts that as the C:N ratio of litter increases, earthworm growth declines because less litter C and N is consumed and assimilated into earthworm tissues. Further studies are required to determine whether this prediction is valid for earthworm populations under field conditions.

Changes in soil temperature had a profound effect on the C and N flux through earthworms. The model simulated accurately earthworm weight gain compared to the growth of *A. tuberculata* at 10 °C and 18 °C under laboratory conditions and predicted that weight gain would be greatest at 15 °C. Further work will be required to determine whether the soil temperature function in the model provides a good basis for predicting earthworm growth and C and N fluxes through earthworms under field conditions. One improvement to the model would be to change the way in which soil moisture is expressed. A function describing soil water potential rather than soil moisture content would be of greater utility for field studies.

The direct flux of C and N through earthworms involves the turn over of nutrients from earthworm tissues through respiration, excretion and mortality. The model predicts that the greatest flux of C and N from earthworm tissues during a 100 day simulation occurred through the excretion of C and N. A relatively small quantity of C was released from earthworm tissues through respiration. The model could provide a basis for simulating ecosystemlevel fluxes of C and N through earthworms. However, more work would be required to develop this physiological-based model into an ecosystem-level model. The structure of the model is, of course, a simplification of the real situation. An obvious improvement to the



#### Acknowledgements

Funding for this study was provided by a grant from the US Department of Agriculture.

#### References

- Andersen, N. C. (1983) Nitrogen turn over by earthworms in arable plots treated with farmyard manure and slurry. In: Satchell, J. E. (ed) Earthworm ecology: from Darwin to vermiculture. Chapman and Hall, London, pp. 139–150.
- Binet, F., Trehen, P. (1992) Experimental microcosm study of the role of Lumbricus terrestris (Oligochaeta: Lumbricidae) on nitrogen dynamics in cultivated soils. Soil Biology and Biochemistry 24, 1501–1506.
- Blair, J. M., Parmelee, R. W., Lavelle, P. (1995) Influences of earthworms on biogeochemistry. In: Hendrix, P.F. (ed) Earthworm ecology and biogeography in North America. Lewis Publishers, Boca Raton, FL, pp. 127–158.
- Bohlen, P. J., Parmelee, R. W., McCartney, D. A., Edwards, C. A. (1997) Earthworm effects on carbon and nitrogen dynamics of surface litter in corn agroecosystems. Ecological Applications 7, 1341-1349.
- Bohlen, P. J., Edwards, C. A. (1995) Earthworm effects on nitrogen dynamics and soil respiration in microcosms receiving organic and inorganic nutrients. Soil Biology and Biochemistry 27, 341–348.
- Bolton, P. J., Phillipson, J. (1976) Burrowing, feeding, egestion and energy budgets of Allolobophora rosea (Savigny) (Lumbricidae). Oecologia 23, 225-245.
- Böström, U. (1987) Growth of earthworms (*Allolobophora caliginosa*) in soil mixed with either barley, lucerne or meadow fescue at various stages of decomposition. Pedobiologia 30, 311–321.
- Böström, U. (1988) Ecology of earthworms in arable land. Population dynamics and activity in four cropping systems. PhD thesis, Rep 34, Swed Univ Agric Sci, Uppsala.
- Bouché, M. B. (1977) Stratégies lombiciennes. In Lohm, U., Persson, T. (eds) Soil organisms as components of ecosystems. Ecological Bulletins (Stockholm) 25, 122–132.
- Bouché, M. B., Al-Addan, F., Cortez, J., Hameed, R., Heidet, J.-C., Ferriere, G., Mazaud, D., Samih, M. (1997) The earthworm role in the nitrogen cycle: a falsifiable assessment. Soil Biology and Biochemistry 29, 375–380.
- Christensen, O. (1987) The effect of earthworms on nitrogen cycling in arable soil. Proceedings of the 9th International Colloquium on Soil Zoology, Nauka, Moscow, pp. 106–118.
- Curry J. P., Byrne D., Boyle K. E. (1995) The earthworm population of a winter cereal field and its effects on soil and nitrogen turn over. Biology and Fertility of Soils 19, 166-172.
- Daniel, O. (1991) Leaf-litter consumption and assimilation by juveniles of *Lumbricus terrestris* L. (Oligochaeta, Lumbricidae) under different environmental conditions. Biology and Fertility of Soils 12, 202–208.
- Daniel, O., Kohli, L., Bieri, M. (1996) Weight gain and weight loss of the earthworm Lumbricus terrestris L. at different temperatures and body weights. Soil Biology and Biochemistry 28, 1235–1240.
- Dash, M. C., Patra, U. C. (1977) Density, biomass and energy budget of a tropical earthworm population from a grassland site in Orissa, India. Revue d'Ecologie et de Biologie du Sol 14, 461–471.
- Hameed, R., Cortez, J., Bouché, M. B. (1994) Biostimulation de la croissance de Lolium perenne L. par l'azote excrete par Lumbricus terrestris L. – mesure au laboratoire de ce debit. Soil Biology and Biochemistry 26, 483–493.
- Hendriksen, N. B. (1991) Gut load and food-retention time in the earthworm Lumbricus festivus and L. castaneus: a field study. Biology and Fertility of Soils 11, 170–173.
- Hendrix, P. F., Mueller, B. R., Bruce, R. R., Langdale, G. W., Parmelee, R. W. (1992) Abundance and distribution of earthworms in relation to landscape factors on the Georgia Piedmont, USA. Soil Biology and Biochemistry 24, 1357–1361.

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- Huchinson, K. J., King, K. L. (1979) Consumers. In: Coupland, R. (ed) Grassland systems of the world: analysis of grasslands and their uses. Cambridge University Press, Cambridge, pp. 259–265.
- James, S. W. (1991) Soil, N, phosphorus, and organic matter processing by earthworms in a tallgrass prairie. Ecology 72, 2101–2109.
- Ketterings, Q. M., Blair, J. M., Marinissen, J. C. Y. (1997) The effects of earthworms on soil aggregate stability and carbon and nitrogen storage in a legume cover crop agroecosystem. Soil Biology and Biochemistry 29, 401–409.
- Lavelle, P., Schaefer, R., Zaidi, Z. (1989) Soil ingestion and growth in *Millsomia anomala*, a tropical earthworm, as influenced by the quality of the organic matter ingested. Pedobiologia 33, 379–388.
- Marinissen, J. C. Y., deRuiter, P. C. (1993) Contribution of earthworms to carbon and nitrogen cycling in agroecosystems. Agriculture, Ecosystems and Environment 47, 59-74.
- Martin, A., Mariotti, A., Balesdent, J., Lavelle, P. (1992) Soil organic matter assimilation by a geophagous tropical earthworm based on  $\delta^{13}$ C measurements. Ecology 73, 118–128
- Moody, S. A., Briones, M. J., Piearce, T. G., Dighton, J. (1995) Selective consumption of decomposing wheat straw by earthworms. Soil Biology and Biochemistry 27, 1209–1213.
- Needham, A. E. (1957) Components of nitrogenous excreta in the earthworm *L. terrestris* and *E. foe-tida*. Journal of Experimental Biology 34, 425-446.
- Parmelee, R. W., Crossley, D. A. Jr. (1988) Earthworm production and role in the nitrogen cycle of a notillage agroecosystem on the Georgia Piedmont. Pedobiologia 32, 353–361.
- Rozen, A. (1994) The annual cycle in populations of earthworms (Lumbricidae, Oligochaeta) in three types of oak-hornbeam of the Niepolomicka Forest. III. Energy flow through earthworm populations. Pedobiologia 38, 28–35.
- Satchell, J. E. (1967) Lumbricidae. In: Burges, A., Raw, F. (eds) Soil biology. Academic Press, New York, pp. 259-322.
- Shipitalo, M. J., Protz, R., Tomlin, A. D. (1988) Effect of diet on the feeding and casting activity of Lumbricus terrestris and L. rubellus in laboratory culture. Soil Biology and Biochemistry 20, 233–237.
- Whalen, J. K., Parmelee, R. W. (1999a) Growth of Aporrectodea tuberculata (Eisen) and Lumbricus terrestris L. under laboratory and field conditions. Pedobiologia 43,1-10.
- Whalen, J. K., Parmelee, R. W. (1999b) Quantification of N assimilation efficiencies and their use to estimate organic matter consumption by the earthworms *Aporrectodea tuberculata* (Eisen) and *Lumbricus terrestris* L. Applied Soil Ecology (in press).