

## Projecting soil fauna influence on long-term soil carbon balances from faunal exclusion experiments

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### Abstract

In soil ecology, many investigations of faunal influence on, e.g. soil carbon flows have been performed. However, analysis of long-term effects of faunal activity on, e.g. long-term soil carbon pool changes are uncommon.

We analyse possible effects on long-term soil carbon balances of soil fauna activity on humus and litter decomposition rates as well as litter humification ratio (the fraction of litter that eventually becomes humus). Results from published soil fauna experiments (measurements made in presence versus absence of organisms) are re-interpreted as parameter changes for a soil carbon model (ICBM, see <http://www.mv.slu.se/vaxtnaring/olle/ICBM.html>), which is used for projections of soil C pools and fluxes during a 30-year period.

Model outputs indicate that changes in humification ratio and old material (“humus”) decomposition rates have much greater influence than changes in young material (“litter”) decomposition rate on total soil carbon dynamics. We point out the risk of putting too much faith in model projections, and underline the need for long-term research data as a base for long-term model projections. © 2001 Elsevier Science B.V. All rights reserved.

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### 1. Introduction

There has been a gap between soil ecology focused on organisms, and long-term ecosystem processes, such as soil carbon loss or gain (Smith et al., 1998; Andrén et al., 1999). In soil ecology, much effort has been put into investigations of which and how many organisms are present, what they consume and how much they respire, how they interact, etc. These efforts have produced a wealth of information con-

cerning possible effects of the presence or absence of organisms, but only little information on the long-term ecosystem-level effects of an organism or functional group (e.g. Andrén et al., 1990; Brussaard, 1994).

The interest in investigations of long-term balances of soil carbon has grown recently due to the connection between carbon fluxes to and from the soil and atmospheric CO<sub>2</sub> levels (Schimel et al., 1994; Schlesinger, 1997; Lal et al., 1998, 2001), and also in soil ecology/zoology steps have been taken in this direction (Coleman and Hendrix (2000), and papers cited therein).

Simple models describing the dynamics of soil carbon have been fairly successful in describing the

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carbon dynamics as well as providing a good base for predictions of what will happen when land use and/or climate changes. These models usually assume that the soil organisms always are there and do their work, controlled only by substrate quality, soil temperature, moisture and texture (Paustian et al., 1997; Smith et al., 1998). In spite of this, a model of this type can be used for linking results from short- or medium-term faunal exclusion experiments to long-term soil carbon dynamics.

In this paper, we use the introductory carbon balance model (ICBM) (Andrén and Kätterer, 1997) to project the long-term (30-year) effects on soil carbon pools and fluxes of presence/absence of soil organisms or organism groups. The objectives are as follows:

1. to make long-term mathematical extrapolations based on results from animal exclusion experiments;
2. to show how the extrapolations depend on the results of the exclusion experiments, and also that they depend on how we interpret these results.

## 2. Materials and methods

### 2.1. The ICBM model

Soil carbon models are usually based on first-order kinetics; organic soil carbon is mineralised (respired as  $\text{CO}_2$  by soil organisms) at a rate proportional to the pool size, e.g.  $k = 1\%$  per year. This means that a large pool will give a higher  $\text{CO}_2$  output than a small pool, even if the parameter  $k$  is the same in both cases. Consequently, to maintain the larger pool, a larger input is needed, and if the input is too low the pool size will decline until the output balances the input (steady-state conditions, see Andrén and Kätterer, 2001).

The heterogeneity of organic soil carbon is usually managed by using two or more different pools, each with a specific  $k$  value. Alternatively, one pool with a continuously changing average quality can be used (Ågren and Bosatta, 1998). However, for periods up to 100 years, predictions of total soil organic matter (SOM) dynamics are not particularly sensitive to the way soil C is partitioned in pools (Hyvönen et al., 1998); different models yield very similar results.

External, mainly climatic, factors influencing decomposition rates are usually represented as a multiplier to the  $k$  parameter, starting at 1. A deep-frozen soil will thus have a multiplier close to 0, and very little respiration regardless of the value of  $k$ .

ICBM is an analytically solved model with only two pools (young:  $Y$ ; old:  $O$ ) and five parameters ( $i$ ,  $k_Y$ ,  $k_O$ ,  $h$ ,  $r_e$ ), and is based on a few fundamental assumptions.

1. Annual carbon input to the soil from roots and shoots ( $i$ ) is constant during each model run (Fig. 1). The model can also be run as a conventional simulation model with variable  $i$  and  $r_e$ .
2. SOM is divided into two pools, one 'young' ( $Y$ ) and one 'old' ( $O$ ) (Fig. 1).
3. Respiration from these pools is determined by pool size multiplied by the first-order rate constants  $k_Y$  and  $k_O$ , respectively, multiplied by  $r_e$ , a factor summing up all external influences such as temperature, moisture, etc. (Fig. 1).
4. The fraction of the annual outflux from  $Y$  that enters the  $O$  pool is determined by the 'humification coefficient' ( $h$ ), and the remaining fraction ( $1 - h$ ) is respired as  $\text{CO}_2$  (Fig. 1). The value of parameter  $h$  is dependent on litter quality and, e.g. soil clay content.

This two-pool five-parameter model is analytically solved, i.e. simulation techniques are not necessary and solutions can be directly calculated for any given time. Parameters for ICBM have been estimated using data from a Swedish long-term agricultural experiment with various organic amendments and N fertiliser dosage (Andrén and Kätterer, 1997; Persson and Kirchmann, 1994; Hyvönen et al., 1996). The model has also successfully been applied to soil

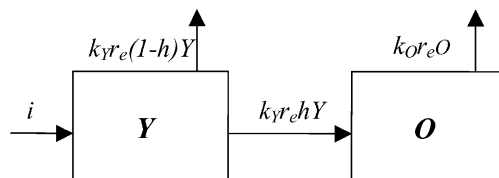


Fig. 1. Soil carbon pools, fluxes and parameters used in the ICBM model.  $Y$  and  $O$  denote 'young' and 'old' pools, respectively ( $i$ : annual input;  $k_Y$ : decomposition rate constant for  $Y$ ;  $k_O$ : decomposition rate constant for  $O$ ;  $h$ : humification ratio;  $r_e$ : external rate multiplier).

carbon data from 99 treatments in north European long-term agricultural field experiments (Kätterer and Andrén, 1999), and has been extended to also include soil nitrogen, microbial biomass, etc. (Kätterer and Andrén, 2001).

The steady-state equation for carbon in the  $Y$  pool is

$$Y_{ss} = \frac{i}{r_e k_Y}. \quad (1)$$

For carbon in the  $O$  pool, the corresponding equation is (when  $Y$  is in steady state)

$$O_{ss} = \frac{hi}{r_e k_O}. \quad (2)$$

The total soil C at steady state,  $T_{ss}$ , can thus be expressed as

$$T_{ss} = \frac{i}{r_e} \left( \frac{1}{k_Y} + \frac{h}{k_O} \right). \quad (3)$$

In a typical ICBM application,  $k_Y \gg k_O$ , since young plant material ‘litter’ decomposes at a much higher rate than old organic matter ‘humus’. Therefore, when conditions are not too far from steady state, most of the soil carbon is in the  $O$  pool (cf. Eqs. (1) and (2), division by  $k_Y$  and  $k_O$ , respectively).

In the present application, the measured effects of presence/absence of organisms on soil carbon balances were taken from the literature and expressed as changes in parameters in ICBM according to the following rules (see Fig. 1 for parameters and fluxes).

1. If litter mass loss or  $\text{CO}_2$  evolution rate is affected,  $k_Y$  is changed (but alternative approaches involving  $r_e$  and  $h$  are shown in the following).
2. If humus (assumed to be equivalent to the  $O$  pool) quality and thus decomposition rate is affected,  $k_O$  is changed.
3. Similarly, the humification quotient,  $h$ , is changed if the fraction of the total outflux from  $Y$  that enters  $O$  is affected.
4. If the general conditions for primary production (or more precisely soil carbon input) changes,  $i$  is changed.
5. Finally, if the general conditions (temperature, moisture, soil cultivation, etc.) for SOM decomposition change,  $r_e$  is changed.

In the following, we shortly review results obtained in organism exclusion experiments, indicate how we

transformed these to parameter and/or pool changes in ICBM, and present the model projections.

## 2.2. The experiments

### 2.2.1. A soil microcosm with and without bacterial grazing

Coleman et al. (1978) measured respiration in soil microcosms with bacteria (*Pseudomonas* spp.) only, and with bacterial-feeding amoebae (*Acanthamoeba* spp.) and nematodes (*Mesodiplogaster* spp.) separately and in combination (see Anderson et al., 1978). Glucose was added to half of the microcosms to mimic rhizosphere (plant) carbon inputs. The experiment lasted for 24 days and the presence of microbial grazers significantly increased  $\text{CO}_2$  evolution. Glucose addition both increased overall respiration and the increase caused by addition of grazers. The decrease when amoebae and nematodes both were excluded was 24% without glucose addition and 40% with glucose addition.

We assumed that these changes affected parameter  $k_Y$  and used the model to predict what would happen to soil carbon if these effects were consistent over a 30-year period. In this case, we used the default parameter set producing steady-state conditions in a field in central Sweden (Table 1 and Fig. 2) and only changed  $i$  and  $k_Y$ , thus applying the laboratory results to a field situation. We simulated three cases.

1. No plants present, but bacterial grazers present. This is the non-glucose treatment with nematodes and bacteria present. Here we set the input,  $i = 0$ . In this way, we predict what would happen to the soil if no plant input occurred, e.g. if we incubated a soil sample in the laboratory for 30 years at field (central Sweden) temperature and moisture conditions.
2. No plants present as in 1, but here we assumed that no bacterial grazers were present by reducing  $k_Y$  with 24% (see above), i.e.  $k_Y = 0.61$ .
3. We can instead assume that plants were present (glucose added) giving an annual input enough to maintain steady state, and then remove the bacterial grazers. Starting from the steady-state conditions, we reduced  $k_Y$  by 40% according to the observations by Coleman et al. (1978), i.e.  $k_Y = 0.48 (=0.6 \times 0.8)$ .

Table 1

Parameters and pools used in ICBM<sup>a</sup>

<i>i</i>	$Y_0$	$O_0$	$k_Y$	$r_e$	$h$	$\Delta Y$	$\Delta O$	$T_{ss}$	Comment	Source
0.2	0.25	4.16	0.8	1	0.125	0	0	4.41	All, default setting	Andrén and Kätterer (1997)
0	0.25	4.16	0.8	1	0.125	−0.25	−0.91	0	No glucose, entire fauna	Coleman et al. (1978)
0	0.25	4.16	0.61	1	0.125	−0.25	−0.91	0	No glucose, no bacterivores	Setälä et al. (1988)
0.2	0.25	4.16	0.48	1	0.125	+0.17	−0.02	4.58	Glucose, no bacterivores	
0 <sup>b</sup>	3.0	0.0	0.20	2.68	0.30	−3.0	+0.57	0	With fauna	
0 <sup>b</sup>	3.0	0.0	0.20	1.91	0.30	−3.0	+0.66	0	No fauna, assumed $r_e$ change	
0 <sup>b</sup>	3.0	0.0	0.20	2.68	0.49	−3.0	+0.93	0	No fauna, assumed $h$ change	Clements et al. (1991)
0 <sup>b</sup>	3.0	0.0	0.14	2.68	0.30	−3.0	+0.58	0	No fauna, assumed $k_Y$ change	
0.491	0.41	6.82	0.8	1.5	0.125	0 <sup>c</sup>	0 <sup>c</sup>	7.22	With worms, litter + soil	
0.478	0	0	0.8	1.5	0.125	+0.40	+1.05	7.04	Litter layer buildup during 20 worm-free years	
0.013	0.408	6.77	0.8	1.5	0.125	−0.40	−1.05	0.19	No worms, soil below litter	
0.491	0.80	6.67	0.8	1.5	0.125	−0.39	+0.06	7.17	Soil after ploughing of worm-free plot	

<sup>a</sup> An example of a parameter combination resulting in steady-state conditions, followed by changes according to exclusion experiments, the net change in  $Y$  and  $O$  soil carbon pools after 30 years due to the parameter changes, and the calculated steady-state values for total organic soil carbon ( $T_{ss}$ );  $i$  ( $\text{kg m}^{-2}$  per year) = annual C input;  $Y_0$  = initial amount of young C;  $O_0$  = initial amount of old C ( $\text{kg m}^{-2}$ );  $k_Y$  (per year) = decomposition constant for young C;  $k_O$  (per year) = the decomposition constant for old C is kept constant at 0.006 in these examples;  $r_e$  (dimensionless) = factor for external influence on C decomposition;  $h$  (dimensionless) = ‘humification coefficient’.

<sup>b</sup> In these experiments, soil C is given in grams per microcosm.

<sup>c</sup> In these experiments, the changes are calculated on a 20-year basis.

### 2.2.2. A microcosm experiment with faunal community addition

Setälä et al. (1988) investigated the effects of the addition of a diverse soil fauna (Collembola, Acari, Enchytraeidae, Nematoda) in defaunated birch leaf litter. The presence of soil animals increased cumulative  $\text{CO}_2$  evolution for 20 weeks by 32%, or alternatively faunal absence decreased  $\text{CO}_2$  evolution by 24%.

The initial mass of litter was 3.00 g, and final mass after 20 weeks was 2.71 g without fauna, and 2.605 g with fauna present. Thus, exclusion of fauna reduced the mass loss by about 27%, which matches well with the 24% reported decrease in  $\text{CO}_2$  evolution. The 20-week period was recalculated to 0.385 year (20/52 weeks).

1. We parameterised the model for the following conditions, no input, total initial C mass = 3 g per microcosm.  $O_0$  was set to 0 (no ‘humus’) and  $Y_0$  set to 3.0 g, since only litter was added. For simplicity, we assumed that the 15°C laboratory

conditions had non-limiting moisture conditions, and we have earlier calculated  $r_e = 5.36$  for 25°C and non-limiting moisture (Andrén and Kätterer, 1997). Thus, assuming a reduction in activity of 50% at 10°C temperature reduction ( $Q_{10} = 2$ ), we obtained  $r_e = 2.68$ . The humification coefficient for the birch leaves was set to 0.30, and  $k_Y$  was optimised by fitting the model (as an Excel spreadsheet) to obtain 2.605 g total mass remaining after 0.385 year, which was the value measured with fauna present.

2. Since the exclusion of fauna resulted in 2.71 g remaining after 0.385 year, we could fit any given model parameter to this observation to predict long-term effects of fauna presence/absence. One can argue that the activities of the soil fauna (comminution, mixing, etc.) increases the general conditions for decomposition and thus that  $r_e$  would be reduced by faunal absence. Thus we fitted  $r_e$  to the data to obtain 2.71 g as final mass.
3. One can instead assume that the animals only affect the humification ratio, e.g. the comminution and

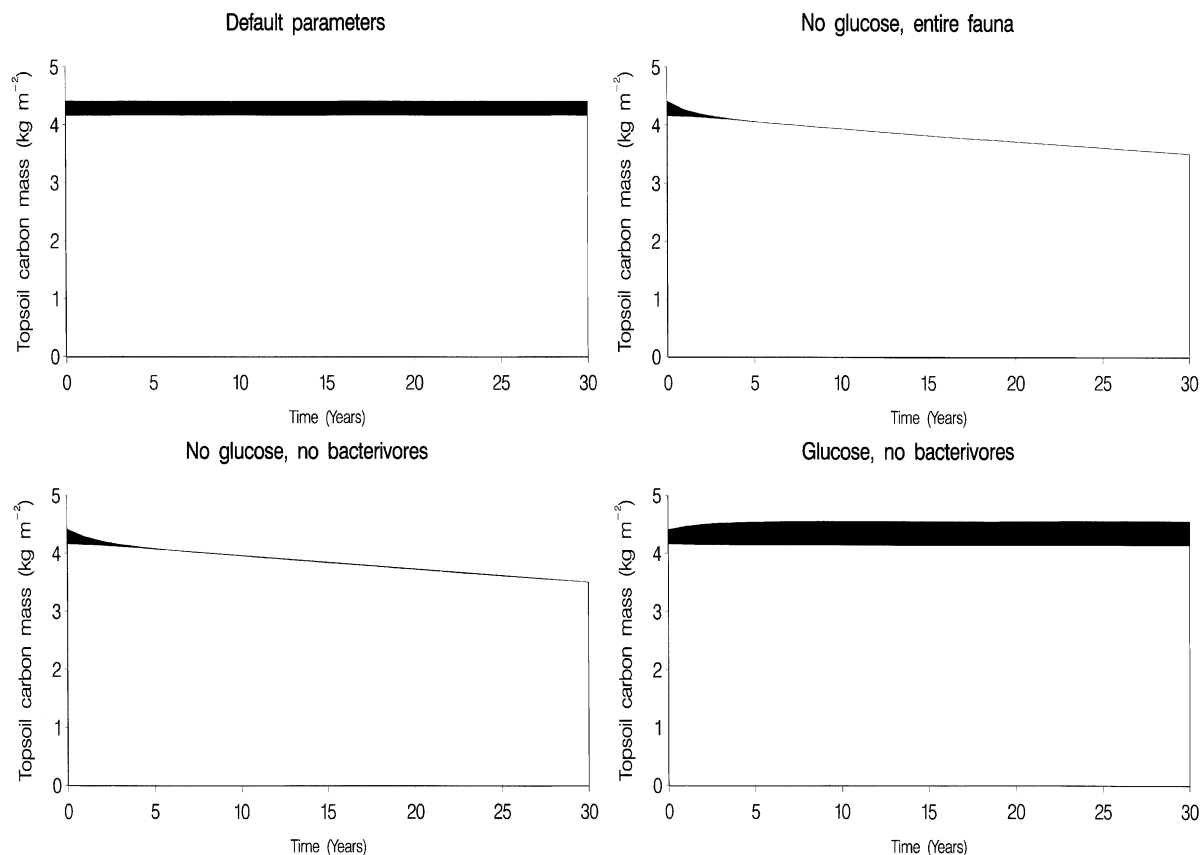


Fig. 2. Carbon dynamics over 30 years, projected using the ICBM model. Default parameter setting and settings derived from results from a microcosm experiment (Coleman et al., 1978) (Y: black area; O: white area).

consumption of litter increases the chances of litter carbon being directly respired instead of humified.

4. Although not very likely, we also assumed that the mesofaunal community only affects the early parts of decomposition, i.e. affects only  $k_Y$  (Fig. 3).

#### 2.2.3. A long-term field experiment with earthworm exclusion

Clements et al. (1991) studied the effects of 20 years of absence of earthworms in a field experiment under perennial ryegrass (*Lolium perenne*). At the end of the experiment, they measured the amounts of leaf litter, soil C, SOM and a number of other soil physical and chemical properties, and compared the earthworm-free plots with control plots. The earthworm-free plots had

a thicker litter layer, lower SOM concentration, lower gravimetric soil water content, but higher bulk density and the same yields of grass as the controls.

We used data from plots with/without earthworms receiving 188 kg N ha<sup>-1</sup> per year as fertiliser. Final carbon mass in the topsoil (excluding the litter layer) was calculated from C concentration, bulk density and topsoil thickness, and became 7.18 and 5.62 kg m<sup>-2</sup> for plots with or without earthworms, respectively. Assuming 45% C in the litter, the litter layer contained 0.039 and 1.449 kg, respectively. Summing up topsoil and litter carbon, we obtain 7.22 and 7.07 kg m<sup>-2</sup> for plots with or without earthworms, respectively. Thus, earthworm presence mainly redistributed the carbon within the profile, but did not much affect the total amount. The measured crop yield was also similar in

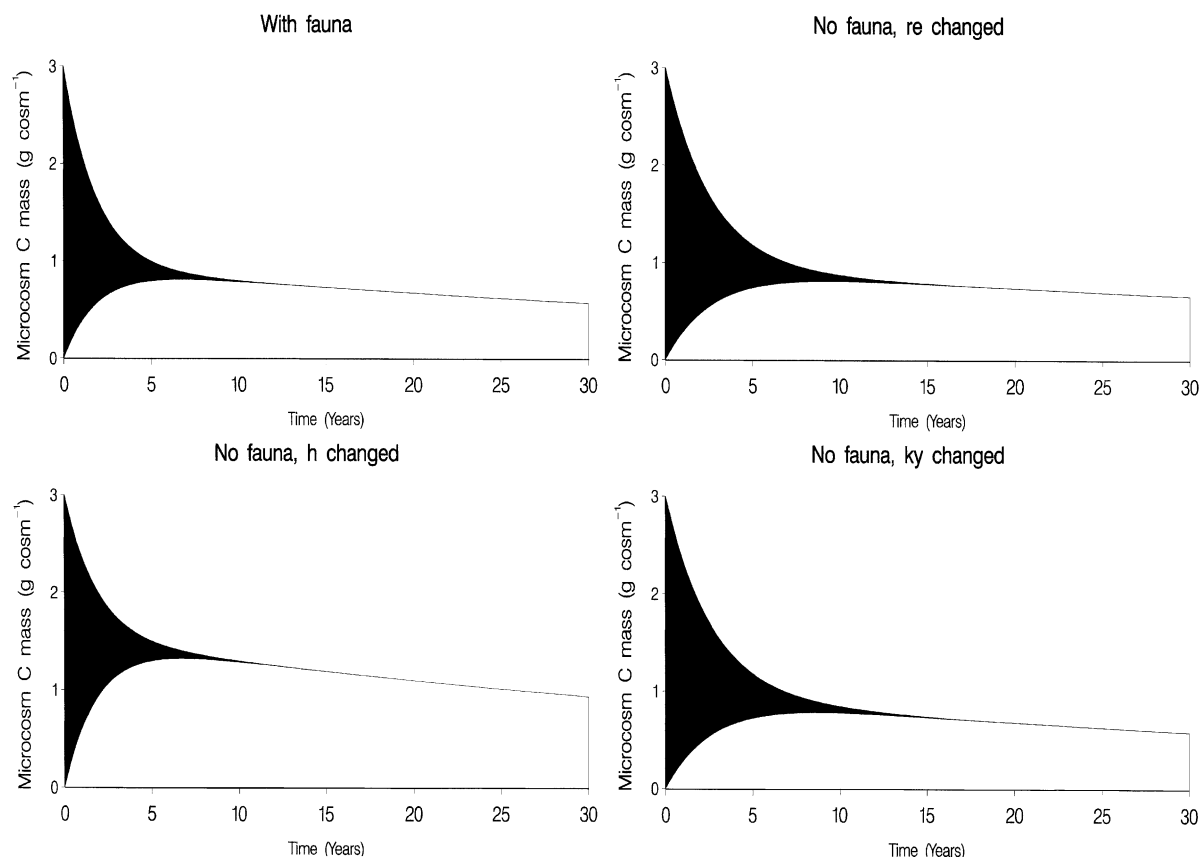


Fig. 3. Carbon dynamics over 30 years, projected using the ICBM model. Parameter settings derived from results from a microcosm experiment (Setälä et al., 1988) with birch litter (Y: black area; O: white area).

treatments with and without earthworms, and therefore probably  $i$  was similar with and without worms.

1. Assuming that the plots with earthworms were in steady state, and that the climate factor  $r_e$  was 1.5 (set higher for Rothamsted, England, than the default value of 1 in central Sweden; see Kätterer and Andrén, 1999), we can calculate  $i$  ( $=0.491$  kg) and the pools, using Eqs. (1)–(3) and the models' default parameters (Table 1 and Fig. 4).
2. We can separately model the accumulation of the litter layer in the earthworm-free plots during 20 years. Assuming no surface litter layer when the grassland was sown, we can calculate the annual input (0.478 kg) necessary to build up a litter layer containing 1.449 kg C after 20 years of earthworm-free conditions (Table 1 and Fig. 4).

3. To examine the long-term effects of only 13 g per year reaching the soil below litter when earthworms were excluded, we can use the parameter values described in 1, but reduce  $i$  to 13 g (0.491 – 0.478).
4. A major advantage of modelling is the ability to make 'what-if' experiments. We plough the earthworm-free topsoil, including the litter layer that has accumulated during 20 years. We assume that after the ploughing, the grass is rapidly re-established, earthworms return and  $i$  returns to its initial 'steady-state' value.

We have to calculate the initial values, i.e.  $Y_0$  and  $O_0$  immediately after ploughing. The soil then contains  $Y_0 = 0.40$  and  $O_0 = 1.05$  kg from the ploughed litter layer (see (2) above and Table 1). We can assume that the standing crop of roots and stubble at ploughing is

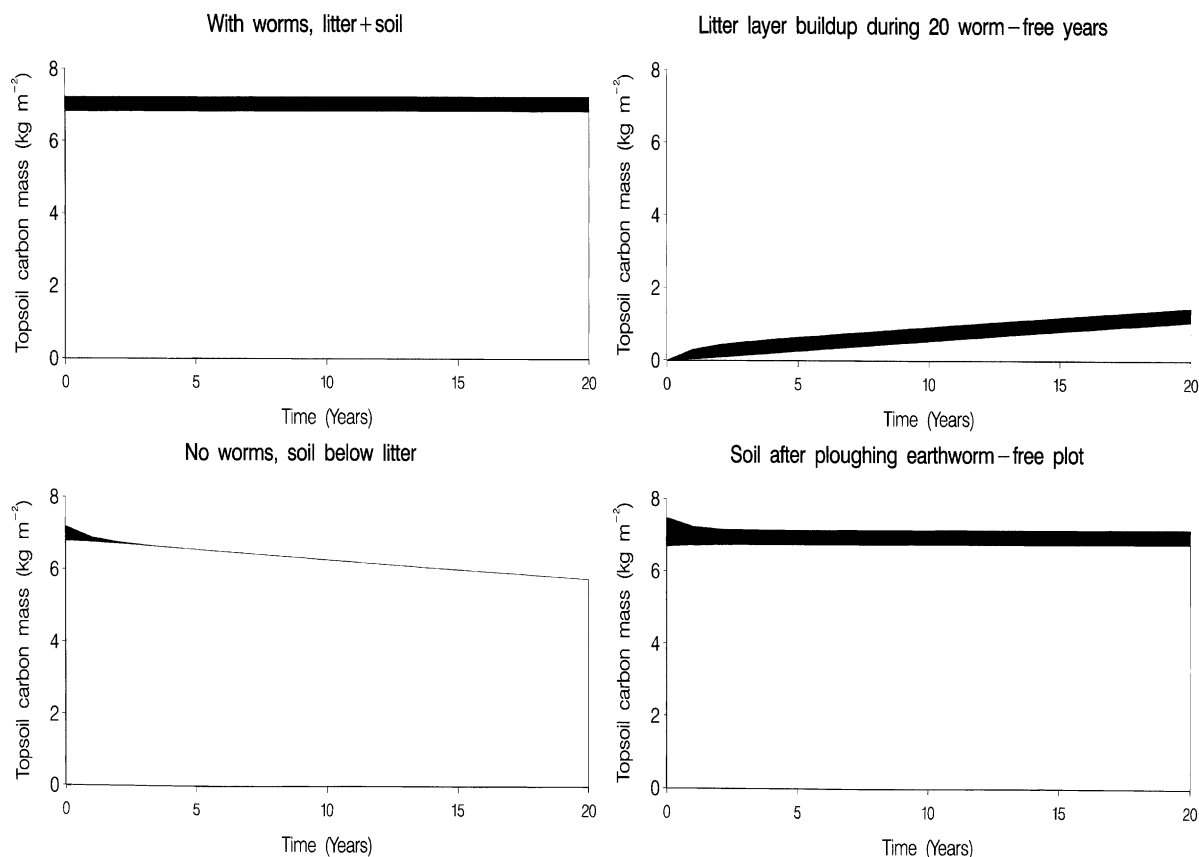


Fig. 4. Carbon dynamics over 20 years, projected using the ICBM model. Parameter settings derived from results from a 20-year-long field experiment with exclusion of earthworms (Clements et al., 1991) (Y: black area; O: white area).

0.40 kg C (cf. Pettersson, 1993), which adds to  $Y_0$  at ploughing. For the soil below the litter layer, we have the measured value of 5.62 kg C, which approximately can be classified as only  $O_0$ , since the low input during 20 worm-free years will reduce  $Y$  to almost 0, as calculated in (3) above. Thus, for the total topsoil at ploughing,  $Y_0$  becomes  $0.40 + 0.40 = 0.80$  kg and  $O_0$  becomes  $1.05 + 5.62 = 6.67$  kg (Table 1 and Fig. 4).

### 3. Results and discussion

#### 3.1. A soil microcosm with and without bacterial grazing

1. Without plant input, the 'young' or litter fraction would disappear within a few years, but only 16%

of the humus would disappear during the 30-year period (Fig. 2). Note that since we have no input, the final steady-state values for both pools is 0, but it will take a very long time to approach that for the humus fraction, since a  $k_O$  of 0.006 per year (Table 1) gives a half-life for humus of 115 years.

2. Clearly, removing the bacterial grazers did not have a major influence in this case, but initially there were some differences, e.g. after 2 years, there was a slightly higher  $Y$  mass and a slightly lower  $O$  mass. This is explained by the fact that reduced  $k_Y$  both reduces  $Y$  loss rate and influx to  $O$  (Fig. 1).
3. With plants present and bacterial grazers removed, the  $Y$  mass increases fairly rapidly by 67%, and  $Y$  mass is then maintained at this new steady-state level (Fig. 2, cf. Eq. (1)). As in the previous example, initially there is a very small decline in  $O$

mass, but after  $Y$  has approached its steady-state value,  $O_{ss}$  is not affected (cf. Eq. (2)). The total soil carbon steady-state value increased from 4.41 to 4.58 kg C m<sup>-2</sup> by removing the bacterial grazers (Table 1).

### 3.2. A microcosm experiment with faunal community addition

1. When we optimised  $k_Y$  to match the observed total mass after 20 weeks, it became 0.20 per year, considerably lower than that used as ICBM default (0.8). However, given the differences in litter quality (birch leaf litter versus cereal straw), this difference is not unrealistic. The model projected that after 3 years, only 0.59 g of  $Y$  remained; most remaining litter was in the  $O$  fraction (0.70 g). After 30 years, 0.57 g or 19% of the initial mass would remain, all in the  $O$  fraction (Table 1 and Fig. 3).
2. Assuming that the fauna affected only  $r_e$ , the  $r_e$  obtained by fitting to 2.71 g remaining after 1 year becomes 1.91 instead of 2.68, and this has consequences for the long-term predictions. After 30 years without fauna, 0.66 g would remain instead of 0.57 g, i.e. 22% of the initial mass corresponding to a 16% increase in final mass due to fauna exclusion (Table 1 and Fig. 3).
3. Assuming that the fauna affected only  $h$  would result in an  $h$  without fauna of 0.49 instead of 0.30, and after 30 years without fauna as much as 0.93 g would remain instead of 0.57 g, i.e. 31% of the initial mass corresponding to a 63% increase in final mass due to fauna exclusion (Table 1 and Fig. 3).
4. If we assume that the mesofauna only affects  $k_Y$ , faunal absence reduces  $k_Y$  to 0.14, but the remaining mass after 30 years is not much affected by faunal absence, 0.58 instead of 0.57 g remaining after 30 years. However, as can be seen by comparing the black areas in Fig. 3, the  $Y$  fraction remains for a longer period than with the other parameter settings; after 3 years, 0.94 g of  $Y$  remained, compared with only 0.59 g in the parameter setting including fauna. Thus, if we accept that faunal presence increases  $k_Y$ , we have a population-stabilising negative feedback not only related to food but also to habitat. An abundant

fauna increases 'young' litter disappearance, and this litter is the habitat for the fauna. Conversely, a low abundance would increase the habitat and the opportunities for a population increase (cf. Zheng et al., 1999). Note that usually in nature and in most ICBM applications, there is a continuous or at least annual input of litter to the soil. Therefore, a reduced  $k_Y$  will increase the steady-state value for  $Y$  (Eq. (1)), and thus the  $Y$  fraction present at any given time (see Section 3 in Coleman et al. (1978) example).

### 3.3. A long-term field experiment with earthworm exclusion

1. Assuming that the earthworm plots were in steady state, the steady-state value for the  $Y$  fraction became 0.41 kg and for the  $O$  fraction 6.82 kg, and the necessary annual input was 0.491 kg per year (Table 1 and Fig. 4).
2. Optimisation of the input results in an  $i$  to litter of 0.478 kg per year (Table 1 and Fig. 4), which would indicate that only  $0.491 - 0.478 = 0.013$  kg m<sup>-2</sup> would remain as annual input to the soil below the litter (see (1) above and (3) below). The steady-state value for the litter carbon becomes 7.04 kg m<sup>-2</sup>.
3. The lack of earthworm activity results in 5.73 kg m<sup>-2</sup> soil carbon mass after 20 years, in good agreement with the 5.62 kg reported by Clements et al. (1991). However, this would result in a steady-state value for the soil carbon of less than 0.2 kg, which hardly is realistic (Table 1 and Fig. 4). This could be due to the fact that the ICBM model is not designed to handle the long periods of time needed to approach this calculated steady state (after 100 years ICBM predicts that 2.9 kg would still remain), but one can easily exclude a more or less inert soil C pool, only model  $Y$  and  $O$  and add the inert pool as a baseline. Alternatively, one can make the quite realistic assumption that  $r_e$  in the litter is considerably lower than in the whole profile (e.g. the litter dries out frequently). Reducing  $r_e$ , e.g. to 1 in the litter input calculation above (2) would give an annual input to the soil below the litter of  $491 - 418 = 73$  g m<sup>-2</sup>. Thus, it is not difficult to improve the assumptions as well



as the results, but without actual measurements this is perhaps too easy; we need long-term data for valid long-term projections.

4. Ploughing the earthworm-free plots results in a fairly rapid loss of about half the *Y* fraction, and a slight increase in the *O* fraction (Fig. 4). After 20 years, the total amount of carbon ( $7.14 \text{ kg m}^{-2}$ ) has not quite reached the pre-experiment steady-state mass of soil carbon ( $7.18 \text{ kg}$ ). This asymmetry is typical due to the non-linearity of the processes involved, 20 years of treatment and 20 years of restoration do not usually result in a return to the initial values.

#### 4. Concluding remarks

The most important insight of this analysis is that an effect of soil fauna on soil C, measured as mass loss or respiration rate, observed in short-term studies can result in quite different soil C dynamics in the long-term, depending on where in the decomposition cascade the soil fauna is assumed to have an influence. If soil fauna is assumed to mainly affect the fresh litter of comparatively high quality (i.e. *Y* pool through  $k_Y$ ), the long-term influence on soil C is much lower than when the fauna is assumed to mainly affect the soil C fractions of low decomposability (*O* pool through  $r_e$ ,  $h$ , or  $k_O$ ). This difference is due to the larger pool size of *O* than *Y* and higher sensitivity in long-term predictions of the parameters regulating the *O* pool than the *Y* pool. However, this is not merely a consequence of the parameterisation of this particular model; it is both logical and widely accepted that the more decomposable fractions will be depleted earlier, and old material will on average be less decomposable.

To improve the long-term predictions on effects of soil fauna on soil C dynamics, we thus need long-term experiments to generate values of parameters  $r_e$ ,  $h$  and  $k_O$ , regulating the size of *O* pool. Even better would be if we could find a method to rapidly estimate  $r_e$ ,  $h$  and  $k_O$  (for ICBM, other models will have similar but not identical demands), and then put our trust in the models. Similar conclusions have been reached using a one-component soil carbon model with changing average quality (Hyvönen et al., 1998).

There are a number of possible faunal features and effects on soil carbon balances not discussed here,

e.g. succession, improving soil conditions creating increased plant input, acting as pests or pest competitors, etc. However, we cannot think of any possible faunal effect that could not at least tentatively be described by the model by modifying a parameter or two.

The approach used here, to use a simple model for testing consequences of assumptions by changing parameters in a spreadsheet, does not require advanced modelling skills, only a PC with an electronic spreadsheet and a few equations. We see the model as an instrument for examining the logical consequences of certain assumptions. Linear extrapolations and interpolations made without a mathematical model often lead to incorrect conclusions, in spite of the apparent simplicity of the calculations, and we strongly recommend the use of models of the kind described here as logical support tools.

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In the original version of the ICBM model (Andrén and Kätterer, 1997), parameters  $k_Y$ ,  $k_O$  and  $r_e$  were called  $k_1$ ,  $k_2$  and  $r$ , but they are otherwise identical to those used here. Model equations and ready-to-run programs (Excel, SAS) for parameter optimisations and projections are available at <http://www.mv.slu.se/vaxtnaring/olle/ICBM.html>. The development of the ICBM model was supported by grants from the Swedish Environmental Protection Agency. This work contributes to the GCTE Core Research Programme, which is a part of the IGBP.

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